Mycorrhiza (1992) 1:123–125

Mycorrhiza

The role of mycorrhiza in plant populations and communities

Hypha-hypha interactions of vesicular arbuscular mycorrhizal fungi and the consequences for population biology

I. C. Tommerup

CSIRO Division of Forestry, Perth, Private Bag, Wembley 6014, Western Australia

Summary. There is a large body of literature concerning the value of mycorrhiza to plant growth. Recent emphasis on the potential benefits of the fungi to natural ecosystems conservation and productive agriculture has focused attention on the roles and underlying mechanisms of the association. In parallel, recognition that isolates/species of vesicular arbuscular mycorrhizal fungi have variable life-history traits has resulted in investigations focused on the symbiotic fungi rather than the host, a perspective which may reflect the fungal evolutionary strategies. This paper discusses progress in understanding interactions amongst hyphae, which in one form or another are a major component of mycorrhiza and each phase of the life-history.

Key words: Propagules – Competition – Aggressiveness

Introduction

Mycorrhizal fungi are a major microbiological component of plant and soil ecology. They underpin plant function in most natural habitats and may have a similar role in many agricultural and land rehabilitation sites. Any interactions among hyphae of vesicular arbuscular mycorrhizal (VAM) fungi will influence their functional relationships with roots, the soil-root interface and the wider soil matrix. While the value of mycorrhizal fungi may be considered by plant ecologists and agriculturists to be the benefits to plant survival and growth and by soil scientists to be their contribution to the microbiology, organic matter and certain structural aspects of soil, the prime strategy for these fungi, as for any other organism, is to persist.

To survive, these biotrophic fungi must form an association with a host plant which enables them to produce propagules perennating throughout periods when living roots are absent (Tommerup 1988). The life styles of individual VAM fungi associated with susceptible hosts are influenced by three major facets of their environment, namely, the incidence of competitors, stress and disturbance (Tommerup 1985). In the absence of a susceptible host, the nature and importance of stress factors are increased. The fungi have a wide host range, an isolate forming associations with taxonomically diverse hosts (Gerdemann 1975). As a consequence of this, their polycyclic habit and their characteristic of growing through soil to colonise other roots, the fungi may develop an extensive network linking colonies within and among root systems (Francis et al. 1986). Fungal isolates probably have the same host range as the species, although the degree of compatibility between fungal isolates and host lines (sub-species genetic categories) may vary (Tommerup 1988). For plants which are highly resistant to VAM fungi, such as the Brassicaceae and *Lupinus*, there may be more easily recognised differences among isolates in their interaction phenotypes, which indicate fungus strain-host cultivar specificity. Although some crop plants may be resistant, in natural ecosystems where resistant and susceptible plants are interspersed, differentials in susceptibility to the fungi may prejudice the outcome of competitive interactions amongst them.

Many VAM fungi can simultaneously colonise a root segment (Wilson 1984a, b; Francis et al. 1986; Tommerup 1988). Hence, hypha-hypha interactions within a root, at the root surface or in soil may be between hyphae of the same isolate, the same species or different species. Distinguishing the hyphae relies on visual techniques for recognising anatomically distinct hyphae (Abbott 1982), immunological or enzymological (Rosendahl et al. 1989) or restriction fragment length-polymerase chain reaction methods. Developing the specific techniques for the latter is the subject of current research. Competitive interactions in roots/mycorrhiza or at root/mycorrhiza surfaces are discussed below.

Interactions within and among individuals

The question arises as to what is an individual VAM fungus? The form of an individual varies with the stage in the life-history and it may not be a constant genetic entity. Spores have a population of nuclei which may be genetically diverse (Tommerup 1988). Mycelium arising from a spore may or may not have all the diversity of the spore, and a mycelium may have greater diversity due to hyphal fusion with another, probably related, individual and consequent genetic transfer. A key factor for an individual is to maintain or expand its genetic potential and to propagate that to the next generation. That versatility allows the fungus to adopt different strategies under different situations and at different times during its life-history (Tommerup 1992).

Interactions occur between arbuscules and other hyphae and among intra-/extraradicle hyphae in cooperative and competitive frameworks for nutritional aspects such as carbon and phosphorus flow and mycelium survival. Differences within an isolate in survival between arbuscules and other intraradicle hyphae, and thin- and thick-walled hyphae have been quantified to some extent (Mosse 1973; Tommerup 1992; Wilson and Tommerup 1992). Such differences have not been quantified among isolates within a species or among species. Carbon/phosphorus movement occurs within colonies (Cox and Tinker 1976; Cooper and Tinker 1978; Francis et al. 1986; Jakobsen 1991). However, at the level of interactions amongst individual hyphae, the mechanisms of cooperation and competition are yet to be established. The possible role of the host-fungus compatibility phenotype in influencing quantitative aspects is also not understood. These factors are recognised as being important for elucidating key aspects of mycorrhiza function, and current research in several laboratories may provide functional hypotheses in the near future.

Interactions and sexual and asexual reproduction

The capacity for compatible anastomosis amongst vegetative hyphae has been used as a character to distinguish putative genetic similarity/dissimilarity amongst mycelia arising from morphologically similar spores (Tommerup 1988). Within one species, mating type compatibility can overcome vegetative incompatibility (Tommerup and Sivasithamparam 1990). Strands comprised of aggregated vegetative hyphae appear to be rarely formed by VAM fungi, although hyphae may extend radially more than 11 cm from a root (Rhodes and Gerdemann 1975; Jakobsen et al. 1990). However, sporocarps are comprised of loose aggregates of many hyphae which arise as branches from a few hyphae (Abbott and Robson 1979).

Interactions and competition

The ability to obtain energy must be a major factor in interactions among hyphae. Both the mechanisms for acquiring energy and whether or not species/isolates differ in their capacities to do so are at present unknown. Observations indicate that in susceptible portions of roots prior occupation does not eliminate a competitor and many species can have overlapping colonies in a root (Wilson and Trinick 1983; Wilson 1984a; Rosendahl et al. 1989). Fungi vary in their abilities to cohabit. Comparisons among pairs of fungi showed that those which were most aggressive and most likely to reduce colonisation by another were least likely to be found as dual occupants (Wilson and Trinick 1983; Wilson 1984b). Prior occupation of a root may bestow a nutritional advantage to that isolate whether or not nutrient flow is preferentially directed due to colonisation. If the first coloniser of a root region has a nutritional advantage, then geometry of colonisation may be an important attribute of aggressiveness. The fungi vary in their colonisation patterns due to differences in rates of intraradicle growth, amount of hyphae per entry point, and growth of external mycelium along roots before entry points are formed (Tommerup 1992; Wilson and Tommerup 1992). The size, number and distribution of propagules of individuals will be important factors in initiating colonies. Reproduction in one season will affect competitive ability in the next. In relatively nonstressed, undisturbed environments, persistence of an individual will depend on its competitive and aggressive ability, for which hyphal networks seem to be a particularly important component (Wilson and Tommerup 1992).

Interactions and stress

Environmental stress is imposed by physical or chemical factors which limit the production of fungal biomass and propagules. Species differ in the temperature, moisture and pH extremes for propagule regrowth and biomass production (Tommerup 1992; Wilson and Tommerup 1992). For any one isolate, intra- and extraradicle hyphal growth of mycorrhiza may not necessarily be influenced by particular environmental factors to the same extent as hyphae from non-mycorrhizal propagules. Therefore, in assessing competitive interactions amongst fungi, it is unwise to extrapolate from one life-history phase to another. Furthermore, because at present there is insufficient understanding for any species to confidently extrapolate within a species, for most hyphal characteristics the specific behaviour of an isolate needs to be defined.

Interactions and disturbance

Disturbance can be a destructive environmental change, such as tillage and vegetation clearing, or one which provides new opportunities for colonisation, such as revegetation of fallow soil or mine overburdens. The ecological success of fungi under these conditions will result from their stress tolerance, competitiveness, aggressiveness and ruderal characteristics. Fungi having ruderal characteristics may have both competitive hyphae and many different propagule forms favouring survival (Wilson and Tommerup 1992). Inter- and intraradicle hyphal interactions may also be such that they promote hyphal spread within and among root systems to rapidly produce extensive colonisation (Wilson and

Trinick 1983; Wilson and Tommerup 1992). Density-dependent trade-offs in growth rate and reproduction (Mueller et al. 1991) have not been examined in the context of mycorrhiza.

The future

While much progress has been made in understanding the functioning of mycorrhiza, less is known of the mechanisms governing the interactions among the hyphae. As the level of knowledge of individual isolates and the interactions between pairs of these is increased by following their progress through a variety of regimes, with special allowances made for the processes of polycyclic development, arbuscule formation/senescence and long-short-lived extraradicle hyphae, deterministic and other forms of models will become available. The functional significance of the various differentiated hyphal forms will become clearer now that recent technological advances make it possible to investigate living organisms. Most mycorrhiza studies examine interactions involving plants, fungal symbionts and bacteria/actinomycetes, and the role of the latter in the interactions is being increasingly questioned and examined.

References

Abbott LK (1982) Comparative anatomy of vesicular arbuscular mycorrhizas formed by subterranean clover. Aust J Bot 30:485–490

Abbott LK, Robson AD (1979) A quantitative study of the spores and anatomy of mycorrhizas formed by a species of *Glomus*, with reference to its taxonomy. Aust J Bot 27:363–375

Cooper KM, Tinker PB (1978) Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. II. Uptake and translocation of phosphorus, zinc and sulphur. New Phytol 81:43–52

Cox G, Tinker PB (1976) Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. I. The arbuscule and phosphorus transfer: a quantitative ultrastructural study. New Phytol 77:371–378

Francis R, Finlay RD, Read DJ (1986) Vesicular-arbuscular mycorrhiza in natural vegetation systems. IV. Transfer of nutrients in inter- and intra-specific combinations of host plants. New Phytol 102:103–111

Gerdemann JW (1975) Vesicular-arbuscular mycorrhizae. In: Torrey JG, Clarkson DT (eds) The development and function of roots. Academic Press, London, pp 575–591

Jakobsen I (1991) Phosphorus transport by external hyphae of va mycorrhizas. In: Abstracts of the Third European Symposium on Mycorrhizas. University of Sheffield, Sheffield, p 31

Jakobsen I, Abbott LK, Robson AD (1990) The spread of VA mycorrhizas throughout rootfree soil. In: Allen MF, White SE (eds) Eight North American conference on mycorrhizae. University of Wyoming, Wyoming, p 152

Mosse B (1973) Advances in the study of vesicular-arbuscular mycorrhiza. Annu Rev Phytopathol 11:171–195

Mueller LD, Guo PZ, Ayala FJ (1991) Density-dependent natural selection and trade-offs in life history traits. Science 253:433–435

Rhodes LJ, Gerdemann JW (1975) Phosphate uptake zones of mycorrhizal and nonmycorrhizal onions. New Phytol 75:555–561

Rosendahl S, Sen R, Hepper CM, Azcon-Aguilar C (1989) Quantification of three vesicular-arbuscular mycorrhizal fungi (*Glomus* spp.) in roots of leek (*Allium porrum*) on the basis of diagnostic enzymes after polyacrylamide gel electrophoresis. Soil Biol Biochem 21:519–522

Tommerup IC (1985) Population biology of VA mycorrhizal fungi: propagule behaviour. In: Molina R (ed) Proceedings of the 6th North American Conference on Mycorrhizae. Forest Research Laboratory, Corvallis, p 331

Tommerup IC (1988) The vesicular arbuscular mycorrhizas. In: Sidhu GS (ed) Advances in plant pathology. Academic Press, London, pp 81–92

Tommerup IC (1992) Methods for the study of the population biology of vesicular-arbuscular mycorrhizal fungi. In: Norris JR, Read DJ, Varma AK (eds) Methods in microbiology 2. Academic Press, London, pp 23–51

Tommerup IC, Sivasithamparam K (1990) Zygospores and asexual spores of *Gigaspora decipiens*, an arbuscular mycorrhizal fungus. Mycol Res 94:897–900

Wilson JM (1984a) Comparative development of infection by three vesicular arbuscular-mycorrhizal fungi. New Phytol 97:413–426

Wilson JM (1984b) Competition for infection between vesicular arbuscular-mycorrhizal fungi. New Phytol 97:427–435

Wilson JM, Tommerup IC (1992) Interactions between fungal symbionts: VA mycorrhizae. In: Allen MF (ed) Mycorrhizal functioning. Chapman & Hall, New York (in press)

Wilson JM, Trinick MJ (1983) Infection development and interactions between vesicular arbuscular mycorrhizal fungi. New Phytol 93:543–553