

Mycorrhizal networks are best explained by a plurality of mechanisms. A comment on Fitter *et al.*, 1998

'I darsay that you will agree with me that it is very rare to find oneself agreeing pretty closely with any theoretical paper; for it is lamentable how each man draws his own different conclusions from the very same fact' Charles Darwin in a letter to Alfred Russel Wallace. 1 May 1857. (Burkhardt 1996).

In a recent series of experiments described in this journal Fitter *et al.* (1998) studied carbon transfer between the grass *Cynodon dactylon* and the herb *Plantago lanceolata*. They showed large amounts of carbon was transferred between plants linked by arbuscular mycorrhizae and that this carbon remained in fungal structures in the plant root. They proposed 'a mycocentric view of the phenomenon of interplant C transfer, in which the fungal colonies within roots are seen as part of an extended mycelium between which the fungus moves resources depending on the dynamic of its own growth. We do not believe that the transfer has an impact on plant C budgets or fitness, but that it may be a major element in the understanding of fungal C budgets.' (Fitter *et al.* 1998). The impression that they gave in their discussion is that these conclusions apply not only to the particular experimental system they studied but also to mycorrhizal networks in general. It is this generalization I wish to challenge in this paper.

The idea that mycorrhizal transfer of carbon (and other chemicals) between plants may be important in understanding plant competition has slowly been gaining ground (Read 1997). For example, a well-known microcosm experiment by Grime *et al.* (1987) was interpreted by its authors as showing an increase in diversity of the grassland microcosm owing to mycorrhizal-mediated transfer of carbon from canopy dominant plant species to understorey species (see Newman *et al.* 1992 for a more critical discussion). Recently Simard *et al.* (1997) showed a net transfer of carbon between *Betula papyrifera* and *Pseudotsuga menziesii* growing in the field. In a commentary on this work Read (1997) suggested 'that we should place less emphasis on competition between plants and more on the distribution of resources within the community.'. These conclusions appear to conflict with those of Fitter *et al.* (1998); how can this be explained?

I agree with Fitter *et al.* (1998) that it is important to take a mycocentric view as well as asking what, if anything, the plants get out of the relationship. Developing this mycocentric approach; if a fungus has more resources (carbon) than it immediately needs then it has two main options (Wilkinson 1998).

Either store carbon for future use (e.g. Fitter *et al.* 1998) or invest in new plant (in both the botanical and industrial chemical sense) for producing future carbon supplies (e.g. Simard *et al.* 1997). Which option it follows could depend upon conditions at the time. This point is best understood by analogy. Imagine that you have a large amount of money available for investing in works of art (an unlikely situation for most academic ecologists!). You could invest in large sculptures (e.g. works by Henry Moore) or in small porcelain figurines. Which you choose as an investment may not matter but if you live in a politically volatile state you may chose the porcelain as it is easiest to move in a hurry (cf. Chatwin 1988). The conditions you are living under can affect your investment strategy. A mycorrhizal fungus investing in new plant is making a more long-term investment than one investing in vesicle storage which can easily be remobilized.

Lawton (1996) has pointed out that in ecology 'for many phenomena, there are likely to be several contributory mechanisms, and the question is not so much about which mechanism is correct, but about the relative contributions of a plurality of mechanisms.'. Newsham, Fitter & Watkinson (1995) have appreciated this idea, providing a simple graphical model of the relative importance of arbuscular mycorrhizae for phosphate uptake *and* pathogen protection in plants. A similar type of model is probably needed for mycorrhizal networks, rather than just one explanation for the function of all mycorrhizal networks under all conditions. If my art collection analogy is realistic then the expected life span of the plants may be important (e.g. politically stable *vs* politically unstable states). The type of mycorrhizal fungi could also be important; of the studies discussed above, Fitter *et al.* (1998) worked on arbuscular mycorrhizae as did Grime *et al.* (1987), while Simard *et al.* (1997) studied ectomycorrhizae. As certain types of plants tend to have a particular type of mycorrhizal fungus (Allen 1991) these are not independent variables. As a further complication it appears that at least for ectomycorrhizae the association evolved at least twice (Fitter & Moyersoen 1996). This raises the question, should we expect all ectomycorrhizal networks to behave in the same way?

The key point is that mycorrhizal networks are likely to be doing different things under different conditions and a single explanation is unlikely to be correct. As Lawton (1996) stressed 'my explanation is right, yours is wrong may get papers published (and even grants funded) but for many of the ecological phenomena I am familiar with such a polarisation is unwise and unhelpful.'. Fitter *et al.* (1998) have probably described one particular extreme explanation

for the functioning of mycorrhizal networks and are unwise to generalize to all such networks. Plant ecologists probably still need to think about the effects of such networks on plant competition, but should be asking, in which vegetation types will it be of greatest importance?

References

- Allen, M.F. (1991) *The Ecology of Mycorrhizae*. Cambridge University Press, Cambridge.
- Burkhardt, F. (1996) *Charles Darwin's Letters: a Selection*. Cambridge University Press, Cambridge.
- Chatwin, B. (1988) *Utz*. Jonathan Cape, London.
- Fitter, A.H. & Moyersoen, B. (1996) Evolutionary trends in root-microbe symbioses. *Philosophical Transactions of the Royal Society London B* **351**, 1367–1375.
- Fitter, A.H., Graves, J.D., Watkins, N.K., Robinson, D. & Scrimgeour, C. (1998) Carbon transfer between plants and its control in networks of arbuscular mycorrhizas. *Functional Ecology* **12**, 406–412.
- Grime, J.P., Mackey, J.M.L., Hiller, S.H. & Read, D.J. (1987) Floristic diversity in a model system using experimental microcosms. *Nature* **328**, 420–422.
- Lawton, J.H. (1996) Patterns in ecology. *Oikos* **75**, 145–147.
- Newman, E.I., Eason, W.R., Eissenstat, D.M. & Ramos, M.I.R.F. (1992) Interactions between plants; the role of mycorrhizae. *Mycorrhiza* **1**, 47–53.
- Newsham, K.K., Fitter, A.H. & Watkinson, A.R. (1995) Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends in Ecology and Evolution* **10**, 407–411.
- Read, D. (1997) The ties that bind. *Nature* **388**, 517–518.
- Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M. & Molina, R. (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* **388**, 579–582.
- Wilkinson, D.M. (1998) The evolutionary ecology of mycorrhizal networks. *Oikos* **82**, 407–410.

D. M. WILKINSON
Biology and Earth Sciences
Liverpool John Moores University
Byrom Street
Liverpool L3 3AF, UK