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Forum

A. Fitter and D. Robinson

Theory guides, experiment decides: a reply to Wilkinson

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Wilkinson (1999) criticized Fitter *et al.* (1998) for generalizing about the importance to plants of carbon (C) transfer via common mycorrhizal networks. He suggested specifically that our interpretation was inconsistent with the data of Grime *et al.* (1987) and Simard *et al.* (1997). Bergelson & Crawley (1988) questioned Grime *et al.*'s evidence for C transfer, and we will not repeat their criticisms here. Fitter *et al.* (1998) made no reference to the study by Simard *et al.* (1997) on ectomycorrhizal (ECM) species; our paper concerned networks of arbuscular mycorrhizas (AM), the most common form of mycorrhiza among plant species, and was, in any case, written before Simard *et al.* (1997) was published. We showed subsequently how our data related to those of Simard *et al.* and argued that theirs did not unequivocally demonstrate C transfer via mycorrhizal links (Robinson & Fitter 1999). Here, we wish to explain the basis of our scepticism for the idea that mycorrhizal transfer of carbon between plants may be important in understanding plant competition (Wilkinson 1999).

To be functionally important to plants, transferred C must leave the fungus and enter plant cells or, at least, relieve the 'receiver' plant of some of the C cost of supporting the symbiosis from its own photosynthate. There is no unequivocal evidence that either occurs in AM networks. Autoradiographs in Read *et al.* (1985) show that ¹⁴C, originally administered as ¹⁴CO₂ to leaves of a 'donor' plant, was present only in the roots of a receiver, where it was probably in fungal structures (Fitter *et al.* 1998). Physiological studies have yet to find any transfer process that might move C from an AM fungus to a plant (Smith & Smith 1996), although such movement can occur in special cases, notably achlorophyllous plants (Leake 1994). Ectomycorrhizal networks are very different, however; ECM fungi can acquire nitrogen (N) from organic sources in soil and transfer that N to plants (Martin & Botton 1993). The transfer mechanism is unknown, but probably involves organic N, coincidentally providing a transfer mechanism for C. It is therefore likely that some C can move from plant to plant in ECM networks.

Fitter *et al.* (1998) and Robinson & Fitter (1999) examined the available data, and concluded that evidence for the theory that plants share C via common AM networks was equivocal. We agree with Wilkinson (1999) that a 'plurality of mechanisms' might explain the observations, but some mechanisms are more plausible than others. Rather than give equal weight to each mechanism until definitive evidence appears, we prefer the simplest sufficient theory. Existing data suggest that AM networks operate as dispersed C trafficking systems that simultaneously colonize the roots of different plants. This myco-centric interpretation may appeal less to plant ecologists than to mycologists, but we believe it to be more consistent with the evidence than alternative theories.

Theories that cannot be verified by experiment or observation are discarded. If, despite the evidence, they are retained, there is a risk of creating a pseudo-phenomenon, the 'study' of which may stifle genuine progress. We know of no experimental evidence suggesting that interplant C transfer by AM networks is ecologically significant for plants. Speculations on the ecological and evolutionary implications of this process are therefore premature, as is the idea of resource sharing among mycorrhizally connected individuals, as Newman (1988) noted. In contrast, the idea that the AM mycelium operates a C economy based on C transfers among the various mycorrhizas it has created is a powerful and instructive concept for the study of this important symbiosis.

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