Editorial

New Phytologist interactions

'To manage a system effectively, you might focus on the **interactions** *of the parts rather than their behavior taken separately' (Russell Ackoff, born 1919)*

Interaction is the key term that drives the organisation and service that *New Phytologist* offers to authors and indeed the plant science community as a whole. It is also a key term that describes the changing nature of the research we publish. In the current issue, about 40% of the papers are concerned with the interactions of different factors in determining plant responses. Ten years ago, only about 18% of the papers were directly concerned with interactions. This reflects the increasingly complex view and knowledge of the fundamental processes underpinning plant behaviour. No longer is it sufficiently accurate to consider the response of a plant to a single variable; in the field, such a response can be swamped by unexpected responses to other variables. Papers in the first *New Phytologist* volume of 2006 tackle the unexpected by explicitly considering interactions. Old favourites for reconsideration are leaf respiration (Wright *et al.*, in press), CO_2 fertilisation (Edwards *et al.*, this issue, pp. 157–167), salinity (Carter *et al.*, this issue, pp. 123–133) and responses to irradiance (Hovenden & Vander Schoor, in press). In our expanding Evolution section, a paper by Biere & Honders (in press), which will appear in a forthcoming feature on pollinator mutualisms, describes the complex interactions among different kingdoms of plants, animals and fungi, in order to understand the complexities of pollination.

Recognition of the trend towards complexity and interaction has led us to expand our editorial team and we are delighted to welcome on board Henk Schat and Andrea Polle. Henk's research exemplifies the interactive approach to studying heavy metals, applying both genetic and physiological methods to investigate the mechanisms of heavy metal hyperaccumulation in plants (Assunção *et al.*, 2003a; Zha *et al.*, 2004) and tolerance of different species to heavy metals (Assunção *et al.*, 2003b). Andrea brings expertise in applying molecular and physiological techniques to identify the responses of model plant species to global change; in particular, the interaction of *Arabidopsis* and *Populus* with many components, from fungi through heavy metals to nitrogen (Kruse *et al.*, 2003). These appointments reflect our commitment to encourage both new and established areas of the journal, continuing our support for heavy metal and plant research (e.g. *New Phytologist* Vol. 159, No. 2, August 2003) and more recently for functional genomics of poplar (e.g. *New Phytologist* Vol. 167, No. 1, July 2005).

Interactions between Editors, the Central Office, authors and reviewers are taken very seriously by the journal. The approach appears to work well, given the many positive communications we receive from authors. This reflects the high standards that we set our selves and that have been developed by Jonathan Ingram and his Central Office team. Jonathan, our Editorial and Development Manager, has now made a career change and has left *New Phytologist*. He was, in considerable part, instrumental in developing and implementing the new look and efficiency of the journal over the past seven years. We are grateful for his insight and for implementing many significant developments such as the move to Manuscript Central, our online submission process, and for guiding *New Phytologist* to an attractive and well-cited journal. A measure of his success is the rise in the ISI impact factor of *New Phytologist* from 1.719 in 1998 to 3.355 in 2004. We wish him well in his new career.

As one door closes, another opens, and we are delighted to welcome Holly Slater, formerly the Deputy Editorial and Development Manager, as the new Managing Editor of the journal. Holly's scientific grounding is in plant pathology, with specific expertise in the area of molecular genetics of bacteria that cause disease in plants, which she researched both during her PhD and then as a postdoc in the Sainsbury Laboratory at the John Innes Centre in Norwich, UK, and subsequently in the Biochemistry Department of the University of Cambridge. Holly has been with *New Phytologist* for almost three years and this experience has enabled her to move seamlessly into heading the Central Office from April 2005 and getting to grips with a continuous supply of editorial issues that accompany journal life in the 21st century. At a time when both the quantity and quality of research are continuing to increase, *New Phytologist* has worked hard to maintain our service to the community despite a significant rise in submissions. In particular, this is reflected by our rapid handling times, which remain at 30 days, on average, from manuscript submission to first decision. This was complemented by a faster production schedule for 2005, where on average authors could expect their articles to

be published *OnlineEarly* within 30 days from receipt of the accepted manuscript by the publisher. Further to this, to keep the print publication times in step with the flow of manuscripts, we have increased the journal size by 12% for 2006 and combined this with a move away from monthly publication to 16 issues spaced regularly throughout the year. With a larger journal and more frequent publication of issues, authors can be assured that their work will be rapidly disseminated.

Other changes this year include explorations into the changing nature of the publishing market and how best to communicate scientific research in an age where the internet has provided new opportunities for an old tradition. In response to this, *New Phytologist* has joined the Blackwell Publishing *Online Open* trial that enables authors to pay for their articles to be available free to all online. We welcome feedback on this initiative. This is in addition to the existing free content, of Tansley reviews and regular features, funded by the *New Phytologist* Trust.

The Trust's interactions extend beyond publishing the journal to include the International series of *New Phytologist* Symposia. This month, we will be holding two symposia in London, UK; the first will focus on new directions in plant ecological development (23–24 January, Royal Society) and the second on networks in plant biology (26–27 January, Linnean Society). We are also supporting a third meeting this year on the impact of genomics on fungal biology (18–20 September, Nancy, France) and would very much like to see readers and authors of *New Phytologist* at one or more of these events – complete details can be found on our web site (http://www.newphytologist.org). The success of the journal and the additional activities of the Trust comes down to the interaction of authors, reviewers, Advisors and Editors and we would like to take this opportunity to thank you all for choosing *New Phytologist* and to invite your continued support.

Ian Woodward

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Managing Editor

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Key words: eco-devo, Editorial board, genomics, ISI impact factor, networks, open access, *Populus*.

Commentary

Is facilitation in arid environments the result of direct or complex interactions?

For several decades, species competition has dominated in ecological theory. However, since the beginning of the 1990s, facilitation has been recognized as a major driving force of species coexistence in plant communities, particularly in harsh environments. A number of authors (e.g. Bertness & Callaway, 1994; Brooker *et al.*, 2005) have proposed that facilitation should become more important when the environmental stress increases; evidence for these models has been provided, in particular from alpine and arctic tundras (e.g. Callaway *et al.*, 2002). However, most recently, other studies conducted in arid environments have obtained contrasting results, which have caused significant controversy among plant ecologists (Lortie & Callaway, 2005; Maestre *et al.*, 2005), and are in some ways reminiscent of the Grime–Tilman debate of the late 1980s and early 1990s (Thompson, 1987; Tilman, 1987). A paper by Cavieres *et al.* published in this issue of *New Phytologist* (pp. 59–69) is up to date on this debate because they studied changes in biotic interactions with water stress along an altitudinal gradient in the high Andes.

'The method used to quantify biotic interactions may strongly affect the outcome of experiments in arid environments.'

Patterns of variation in positive associations and facilitation with elevation in alpine communities

Cavieres *et al.* used both observational and experimental approaches to test the hypothesis that facilitation should decrease with elevation in Mediterranean mountains because of the prevalence of water stress over temperature stress in dry mountain ranges, as compared with mesic mountain ranges. The authors based their study in the central Andes of Chile (33° S latitude) where the climate is of the Mediterranean type. They selected two positions along the elevation gradient, a dry site at 2800 m and a mesic site at 3200 m, and reported that the cover of the dominant cushion plant *Laretia acaulis* increased from 22 to 30% with elevation. The authors then went on to assess facilitation in terms of the individual factors that vary along the gradient.

Cavieres *et al.* first analysed variation, along the elevation gradient, in spatial associations with the cushion plant *L. acaulis* for a total of 46 species, by comparing vegetation composition within the cushions vs the open areas between cushions. They found that 40% of the whole community was significantly associated with *L. acaulis* at the low site vs only 7% of the species at the high site. Moreover, four species were restricted to the cushions at the low site, whereas no species were found solely within cushions at the high site. They also monitored seedling survival at both elevations for two species planted within the cushions and in the open areas. Survival was higher within the cushions than in the open for the two species, and these differences in survival were higher at low elevation than at high elevation. Abiotic measurements showed that soil water availability was higher during the growing season within cushions than in the open areas only at low elevation, whereas temperatures registered on the bare ground were higher than those of the cushions, in particular at low elevation. Cavieres *et al.* concluded that the facilitation observed with decreasing elevation was mainly explained by the provision of water by *L. acaulis*.

To our knowledge, this is the first study showing that alpine gradients may produce contrasted patterns of variation in positive associations and facilitation with elevation, depending on the climatic context. This result is also consistent with the global study on alpine and tundra communities of Callaway *et al.* (2002), who found no increase in facilitation with elevation for only one site among their 11 mountain ranges; this site was located in the Sierra Nevada of Spain and hence also has a Mediterranean climate, whereas all other sites were located in temperate, boreal or arctic climates. Choler *et al.* (2001) also found for the alpine communities of the French Alps that facilitation was more intense in dry exposed sites located on convex slopes than down slope in mesic sheltered sites. However, they concluded that these changes in facilitation with topography were not necessarily driven by higher provision of water by nurse plants in convex slopes vs concave slopes, because other factors may influence the performances of target species along the topographic gradient, and in particular the level of disturbance, which increases with convexity.

Furthermore, using gradient analyses, they related the intensity of competitive and facilitative interactions measured in their experiment with the position of the site within the niche of the target species. They showed that when neighbors were removed from around target species at experimental sites that were higher in elevation than the distributional mean of the target species, biomass decreased, whereas this result was not observed when the experimental site was drier (up slope along the topographic gradient) than the distributional mean of the target species. In other words, they showed that facilitation allowed species to move up along the elevation gradient but not along the topographic gradient. This means that neighbors may alleviate a thermic stress but are not likely to alleviate a water stress.

Changes in species interactions along water gradients in arid environments

The way species interactions may change along water gradients is becoming a much-debated issue in plant ecology. Most experimental studies have shown that facilitation increases with aridity (e.g. Greenlee & Callaway, 1996; Pugnaire & Luque, 2001; Bertness & Ewanchuk, 2002; Maestre *et al.*, 2003; Liancourt *et al.*, 2005), but others have observed conversely that competition increases with aridity (Tielbörger & Kadmon, 2000; Bellot *et al.*, 2004; Maestre & Cortina, 2004). Gomez-Aparicio *et al.* (2004) analysed the results of multiexperiments conducted in the Sierra Nevada of Spain on 18 000 seedlings of 11 woody species planted with or without 16 different nurse shrubs. They showed that facilitation increases with aridity, both spatially and temporally, as proposed by the Bertness & Callaway model. In contrast, Maestre *et al.* (2005) showed in another meta-analysis that facilitation does not increase with stress in arid environment. However, a detailed statistical reanalysis of this data by Lortie & Callaway (2005) has shown that more rigorous data selection criteria, in particular changing gradients lengths between studies, do not support the original conclusions. Although we agree with Lortie & Callaway (2005) that the study of Maestre *et al.* (2005) included some bias and that therefore the overall conclusions must be treated carefully, some results may shed light on the mechanisms of facilitation in arid environments. In particular, they found that in the case of growth performances, the outcome of experimental studies were opposite for observational and experimental studies. Facilitative interactions were generally observed when the authors (such as Cavieres *et al.*) only compared the performance of target species beneath nurse species vs in adjacent open areas (Pugnaire & Luque, 2001; Bertness & Ewanchuk, 2002; Maestre *et al.*, 2003; Castro *et al.*, 2004; Gomez-Aparicio *et al.*, 2004). In contrast, most of the experiments showing competitive interactions between dominants and subordinated species used removal procedures

(Burger & Louda, 1995; Davis *et al.*, 1998; Pugnaire & Luque, 2001; Maestre *et al.*, 2003), although competitive interactions were also observed in comparisons with open areas (Flores-Martinez *et al.*, 1998; Tielbörger & Kadmon, 2000; Bellot *et al.*, 2004; Maestre & Cortina, 2004).

Direct or complex facilitation in arid environments?

The method used to quantify biotic interactions may strongly affect the outcome of experiments in arid environments; this is because the high levels of natural or anthropogenically induced disturbances produce strong variation in soil depth related to the occurrence of dominants (Aguiar & Sala, 1999). This may explain the contrasting results observed in the recent literature (Fig. 1). In the arid ecosystems of south-east Spain, Maestre *et al.* (2003) have shown that the direct water provision due to shading by the nurse plant *Stipa tenacissima* was outweighed by its own water uptake, leading to direct competition with the subordinated shrub *Pistacia lentiscus*, when measured with removal procedures (right-hand side of Fig. 1). Furthermore, Pugnaire & Luque (2001) and Davis *et al.* (1998) have shown that this competition for water increases with aridity (see Fig. 1). Additionally, Maestre *et al.* (2003) found that water availability and the performance of *Pistacia lentiscus* were the lowest in open areas between the tussocks. They concluded that the net effect of *Stipa tenacissima* was positive and increased with aridity (left-hand side of Fig. 1), but that this effect was complex and driven by differences in physical soil properties and water infiltration rate. Pugnaire & Luque (2001) also found that facilitation increased with aridity in a similar comparison of species performances in the open vs beneath the shrub canopies. Following the results of Pugnaire & Luque (2001), the increase in facilitation, as measured by a comparison with the open areas, overrides the increase in direct competition, as measured with removal procedures (Fig. 1). The facilitation observed by Cavieres *et al.* in the dry central Andes may not be caused by a decrease in evapotranspiration. This complex interaction may involve differences in soil depth and properties between open areas and the cushions, which are likely to increase with aridity because of increasing disturbances. These effects may have produced a higher facilitation when increasing aridity. Other studies, including both removal procedures and comparisons with open areas, are needed to understand better the relative parts of direct and complex interactions in arid ecosystems. However, even if facilitation is not a direct interaction occurring at the patch scale in arid environments, as suggested by an increasing amount of experimental evidence, the complex positive effect demonstrated by Cavieres *et al.* and others at the community scale may be considered as an insurance for biodiversity conservation and ecosystem functioning in arid landscapes.

OPEN   CONTROL   REMOVAL

High elevation

Low stress

Net direct interactions: **competition**

Net complex interactions: **facilitation**

Low elevation

High stress

Fig. 1 Predicted changes in direct (right-hand side) and complex (left-hand side) interactions between a dominant species (in gray) and a subordinated species (in black) under decreasing stress with elevation in an arid mountain range. Direct interactions are quantified by comparing the performances of the subordinated species with and without the dominant species, using removal procedures, whereas complex interactions are quantified by comparing the performances of the subordinated species within the canopy of the dominant species and in naturally occurring open areas.
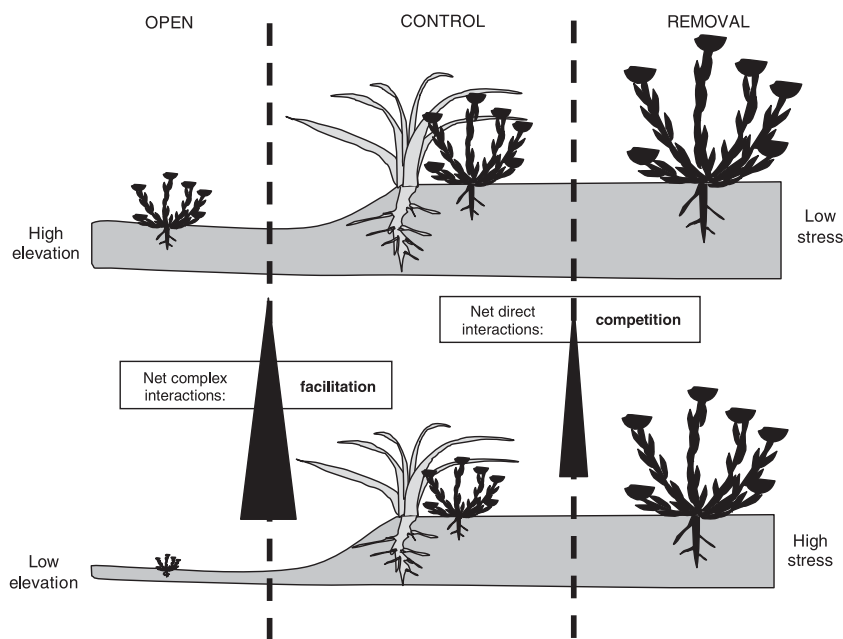
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Key words: alpine communities, arid environments, competition, disturbance, facilitation, removal experiments, spatial associations, water stress.

Common mycelial networks: life-lines and radical addictions

Shared or common mycelial networks (CMNs; Fig. 1) linking the root systems of different plant individuals and species constitute a much studied and debated phenomenon. Although there seems little doubt that there is considerable potential for their existence, the general significance of these networks in plant and fungal ecology remains unknown. There is clear evidence that mycoheterotrophic plants and other plants that lack chlorophyll at early developmental stages (many orchids and Pteridophytes) depend on mycorrhizal fungi for carbon (C) and nutrients (Leake *et al.*, 2004 and references therein). In autotrophic plants communities, the evidence is more equivocal. In a recent review on CMNs, Simard & Durall (2004) state that the strongest support for CMN effects is provided by the improved establishment, survival and growth of ectomycorrhizal (ECM) seedlings around existing ECM plants (Simard & Durall, 2004). However, the results from field studies on seedling establishment in such situations are often confounded by the *de novo* formation of mycorrhizas from spores. In this issue (pp. 169–178), Kazuhide Nara effectively circumvents this complication by capitalising on the harsh environment of the volcanic desert on the south-east slope of Mount Fuji, where spore inoculum is minimal (see Nara *et al.*, 2003). In an elegant experiment, Nara transplanted laboratory generated nurse plant/seedling systems, inoculated with one of 11 ECM species, to the field site and examined colonisation, growth, and N and P uptake by the seedlings after 4 months. The study is notable because it demonstrates that, in general, colonisation by the fungi increased the size and N and P contents of the seedlings. In addition, Nara used ecologically relevant fungi, in other words the dominant local ECM species, many of which are considered intractable in such studies.

'One unanswered question, which has significant consequences for these research areas, is whether increasing diversity in fungal communities results in increased specialisation towards a single host'

Benefits of CMNs to establishing seedlings

Improved establishment of seedlings of ECM plants in close proximity to existing plants of the same (Matsuda & Hijii, 2004) and different (Horton *et al.*, 1999) species is a commonly observed phenomenon. Studies that have compared the ECM communities on the root systems of seedlings and nearby plants have found a considerable overlap in species composition, particularly of ECM species that produce mycorrhizas of the long-distance exploration type (*sensu* Agerer, 2001). This group of fungi are considered to have high C maintenance costs that cannot be readily met by seedlings (Gibson & Deacon, 1990). The presence of these 'high cost' ECM fungi enhances the species richness of ECM communities on seedlings connected to CMNs compared with seedlings establishing in the same environment but without contact to neighbouring plants (Simard *et al.*, 1997b). The increased abundance of these species on seedlings connected to CMNs has been interpreted as an indication that the costs to the seedling of supporting ECM fungi are offset by the larger nurse plant (Simard & Durall, 2004). This compensation could involve utilisation of nurse-plant-derived C by the mycorrhizal fungi during nutrient acquisition for the seedling or the transfer of C from the nurse plant to the seedling via the CMN (Simard *et al.*, 1997a). The ecological significance of C transferred by the latter mechanism under field situations remains contentious (Fitter *et al.*, 1999). In addition to the potential C benefits, the nutrient pool contained within and taken up by the existing ECM mycelia would also be available to the seedling, leading to improved growth.

However, establishing connections to a CMN is not always beneficial to seedlings, at least in the short term. Nara (this issue) and others (e.g. Kytoviita *et al.*, 2003) have found that some fungi do not favour the growth of seedlings, but instead seem to supply the larger plant with nutrients preferentially. This has been interpreted as the fungus investing most resources in C acquisition from the largest C supplier. A parallel situation was observed in mature forests, where the ectomycorrhizal fungi gained most of their C from the largest overstorey trees (Högberg *et al.*, 1999). However, it may be unnecessary to invoke preferential allocation of nutrients to
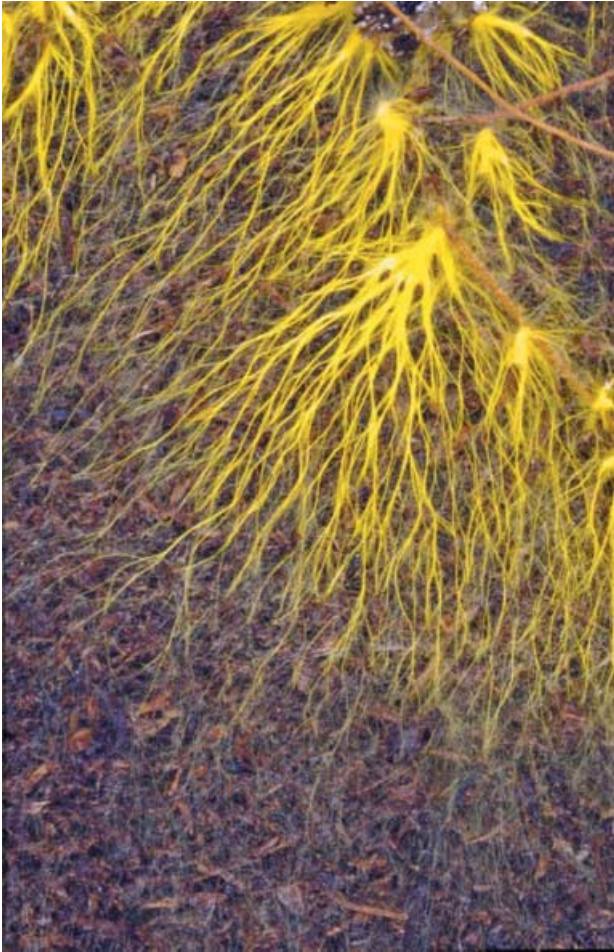
Fig. 1 An extensive mycelial network formed by the ectomycorrhizal fungus *Piloderma fallax* on Scots pine (*Pinus sylvestris*).

the larger nurse plant in order to explain the negative impact of *Laccaria amethystina* on seedling growth observed by Nara. In both laboratory and field studies, where seedlings have been inoculated with *Laccaria* spp., positive, neutral and negative growth responses have been recorded (Kropp & Mueller, 1999). The outcome of any plant–fungus combination appears to be very context-dependent, particularly in relation to substrate nutrient content. The lack of a growth response by the seedlings inoculated with *L. amethystina* in the short term should not detract from the potential benefits of being colonised by ECM fungi in the long run.

… and the effects of mycorrhizal colonisation per se?

The study by Nara, like a number of other studies on the benefits to seedlings of CMNs, utilised nonmycorrhizal nurse plants and seedlings as control plants. It may therefore be difficult to differentiate between the influence of the

network connection and that of ECM colonisation per se. This could be achieved by having seedlings colonised by the same ECM fungi as the nurse plant but having no mycelial connections with the nurse plant. Differences between seedlings connected to the CMN and those not connected would then indicate the influence of the network. Simard & Durall (2004) actually state that, despite numerous studies on seedling establishment, no transfer of nutrients or C from nurse plants to seedlings has been demonstrated and that 'there is more evidence that the benefits arise simply from increased mycorrhization, which may or may not require CMN formation'. However, it is clear that, in the harsh conditions of the field site used by Nara, the establishment of mycorrhizal seedlings outside the influence of a CMN is an extremely rare occurrence.

Common mycelial networks and diversity and function relationships

The study of CMNs in species-rich plant and mycorrhizal fungal communities is very relevant to the examination of relationships between diversity and function in the same communities (van der Heijden *et al.*, 1998; Jonsson *et al.*, 2001). The formation of CMNs and the transfer of nutrients and C coupled with differential effects of plant–fungus combinations could provide a pathway and mechanisms by which increased fungal diversity supports greater plant diversity (Read, 1998). However, one unanswered question, which has significant consequences for both research areas, is whether increasing diversity in fungal communities results in increased specialisation towards a single host. This could, on the one hand, result in decreased potential for the formation of CMNs and, on the other, increase competition between hosts.

Stability, integrity and longevity of common mycelial networks

Fitter *et al.* (1999) noted that the great majority of the work on CMNs has focused on the benefits and consequences for the above-ground plant community. In the intervening period, the situation has not changed. Many aspects of the ecology of mycorrhizal fungal have largely been ignored when considering the significance of CMNs. Many studies refer to CMNs as though they are stable, long-term structures, yet we know that the extraradical mycelia of mycorrhizas are highly dynamic structures, which may turn over rapidly (Staddon *et al.*, 2003; Leake *et al.*, 2004). Considerable significance is also placed upon the size and continuity of ECM fungal genets in contributing to the potential for large CMNs. However, a comparison between saprotrophic forest floor fungi and ECM fungi may be illuminating in this respect. Many saprotrophic fungi form conspicuous fairy rings, in which fruit bodies are arranged in a circle often many metres in diameter. Where these rings

are not related to zones of enhanced litter fall (Frankland, 1998), they represent the radial growth of a mycelium from a central point of origin. The fungi grow out as a mycelia front with the mycelium decaying behind the advancing front. The position of the front is indicated by the position of the fruit bodies. Similar structures are not uncommonly produced by ECM fungi and there is no a priori reason to assume that the integrity of the mycelium is any greater than that of the saprotrophic fungi. Genet size determined by fruit body appearance may therefore give a better indication of how much forest floor a mycelium has grown through, rather than the actual size of the genet. Finally, little attention has been given to the role of fungivory in disrupting the integrity of CMNs. Because fungi form the basis for many soil food webs, it is likely that grazing is a major factor determining the continuity of CMNs. Evidence for the effects of fungivory was recently found by Johnson *et al.* (2005), who demonstrated that the presence of Collembola disrupted the flow of C through the mycelia of arbuscular mycorrhizal fungi in unimproved grassland.

Life-lines and radical addictions

Seedlings establishing in the vicinity of plants supporting an appropriate mycorrhizal mycelium may become colonised and flourish as a consequence. One may ask the question: what benefits accrued to the fungi in colonising a small, struggling host? At least in the short term, benefits may be limited. However, a more relevant question might be: do mycorrhizal fungi have any option but to colonise susceptible roots?

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