Commentary

The surprising diversity of ascomycetous mycorrhizas

Aside from a few well-characterized types such as *Cenococcum geophilum*, most ascomycetous mycorrhizas, with their typically thin mantles and sparse emanating hyphae, have received less attention than their more robust basidiomycetous counterparts. As a result, we know much less about the taxonomy and ecology of these fungi, and we have undoubtedly underestimated their importance in mycorrhizal systems. The paper by Tedersoo *et al.* (pp. 581–596) in this issue confirms many suspected, and describes several new, ascomycetous mycorrhizas in the Pezizales based upon morphotyping and sequencing of ectomycorrhizal root tips from forests in Estonia and Denmark. As well as providing detailed morphological descriptions and photomicrographs, they have inferred phylogenetic affinities based upon DNA sequences from roots and fruiting bodies, and described ecological characteristics. These ascomycetous mycorrhizas were a significant component of the ectomycorrhizal community, comprising 33 species and colonizing between 4.5 and 6.1% of the root tips, further confirming the high diversity of pezizalean mycorrhizas in northern forests.

'*Clearly, looking only through the basidiomycetous lens greatly restricts our appreciation of the physiological and ecological diversity of ectomycorrhizal fungi.*'

The mutualistic paradigm: is bigger better?

It is somewhat ironic that the first rigorous study of ectotrophic mycorrhizas, by none other than A. B. Frank, was stimulated by an interest in truffle cultivation. It was Frank who proposed the term mycorrhiza, and who championed the concept that these fungi were beneficial to their hosts. After Frank's pioneering work and the acceptance of the mutualistic nature of mycorrhizas, although truffles remained a research priority because of their economic value, the focus quickly shifted to the study of basidiomycetous ectomycorrhizas.

The paradigm of mutualism that developed from the time of Frank until the 1980s was that mutualisms evolve to 'benefit the association' (Law, 1985) rather than the individual interests of each partner. An implicit assumption stemming from this paradigm was that bigger and more robust mycorrhizas must be providing bigger and better benefits to their hosts. With their prominent mantles and conspicuous extramatrical mycelium and mycelial strands, basidiomycetes seemed the most likely representatives of highly evolved mutualistic associations, providing maximum benefits to their hosts in the search for nutrients. If bigger is better, then mycorrhiza researchers can be excused for assuming that the thin-mantled and sparse ascomycetous forms were less important and therefore not a priority for study.

By the turn of this century, the concept of mutualism had changed. Models that predict that mutualistic partners necessarily evolve to benefit the partnership are now seen as simplistic. As evidence of 'cheating' and 'exploitation' in mutualistic associations has accumulated (Bronstein, 2001), along with recognition that cost and benefits fluctuate according to biotic and environmental factors (Bronstein, 1994), the mutualistic paradigm has shifted to one of balanced reciprocal parasitism (see Egger & Hibbett, 2004), prone to conflicts of interest that destabilize the partnership (Hibbett *et al.*, 2000). According to this paradigm, mycorrhizas that represent a large carbon drain to their host (i.e. robust forms with large and abundant fruiting bodies) may represent less than optimal associations that could be on the path to dissolution (Egger & Hibbett, 2004). Perhaps it is time to reassess those less robust ascomycetous mycorrhizas.

The unusual characteristics of pezizalean mycorrhizas

If less robust ectomycorrhizas offer a more optimal cost:benefit ratio for plants, then we should examine these mycorrhizas to see if they do potentially offer unique benefits to their hosts. Hutchison (1991) speculated on diagnostic characters to identify ectomycorrhizal fungi. In his dichotomous key, colonies were automatically assumed to be nonectomycorrhizal if they exhibited any one of the following: cellulose or lignin degradation, strong pectinase activity, production of conidia, or rapid growth rates (exceeding 90 mm in 2 wk). Many pezizalean mycorrhizas, particularly those colonizing seedlings after fires, break all the rules. *Wilcoxina mikolae*, *Sphaerosporella brunnea*, and *Geopyxis carbonaria* all form ectomycorrhizas (Danielson, 1984; Yang & Wilcox, 1984; Vrålstad *et al.*, 1998). Yet, they have rapid growth rates (up to 12 mm d^{-1} for *S. brunnea*), *S. brunnea* and *G. carbonaria* effectively degrade cellulose, produce phenol oxidases, and degrade lignin (Danielson, 1984; Egger, 1986), and all have true conidial stages or complex chlamydospores. The wide diversity of new

ectomycorrhizal Pezizales described by Tedersoo *et al.* would be expected to reveal even more diversity within this group.

Pezizalean ectomycorrhizas exhibit features that are considered uncharacteristic of ectomycorrhizal fungi and are more typical of saprotrophs. However, if mycorrhizal mutualisms originate from saprotrophs, as suggested by Hibbett *et al.* (2000), then we should not be surprised to find saprotrophic characteristics in recently evolved mycorrhizal mutualisms. If these are recently evolved associations, before exploitatitive fungal genotypes that drain more carbon and provide fewer resources have had a chance to gain ground, then these 'atypical' ascomycetous forms could be exceptionally important for plant nutrition and fitness. Clearly, looking only through the basidiomycetous lens greatly restricts our appreciation of the physiological and ecological diversity of ectomycorrhizal fungi.

Beyond the Pezizales

The traditional view of ectomycorrhizal dominance by basidiomycetous fungi has been challenged recently on other fronts. *Rhizoscyphus* (syn *Hymenoscyphus*) *ericae*, the archetypal ericoid mycorrhizal fungus, has recently been shown to form ectomycorrhizas on conifers (Vrålstad *et al.*, 2000). *Hymenoscyphus ericae* too demonstrates an unusual ability to degrade complex organic materials and access organic nitrogen (N) and phosphorus (P) sources (Read *et al.*, 2004). Recently, Villarreal-Ruiz *et al.* (2004) demonstrated that a single isolate of *Cadophora* (syn *Phialophora*) *finlandia*, which is part of the *H. ericae* aggregate (Vrålstad *et al.*, 2002), can form both ectomycorrhizas and ericoid mycorrhizas. In a recent *New Phytologist* Commentary, Vrålstad (2004) speculated that perhaps ericoid and ectomycorrhizal fungi should be considered part of a common guild, a proposal that is gaining acceptance as commonalities between ectomycorrhizal and ericoid systems are revealed.

Why stop there? *Cadophora finlandia* was originally considered one of the many dark-septate endophytes (DSEs) that most mycorrhizasts considered to represent nonmycorrhizal and probably parasitic associations. However, a few scientists have argued that DSE fungi do provide benefits, including facilitation of nutrient uptake and stimulation of the mycorrhizosphere community to thwart root diseases (Jumpponen, 2001; Mandyam & Jumpponen, 2005; Summerbell, 2005). Given that endophytic associations appear to be as widespread and abundant as mycorrhizal associations (Mandyam & Jumpponen, 2005), perhaps we should be looking to this group as well to expand our scope of what constitutes mutualistic root associations.

The symbiotic continuum

Several recent papers have called for a re-invigoration of the symbiotic continuum concept (Johnson *et al.*, 1997; Egger & Hibbett, 2004; Mandyam & Jumpponen, 2005; Schulz &

Boyle, 2005), with mutualism occupying a balanced middle-ground between parasitism by the fungus and parasitism by the plant. By limiting our perspectives to one view of what is 'typical', we may blind ourselves to exploring associations that shift between parasitism and mutualism depending upon conditional factors. Just as Tedersoo *et al.* have shown that many more Pezizales need to be incorporated into the definition of the typical ectomycorrhiza, so the work of Vrålstad and others (previously discussed) has shown that the boundaries between ectomycorrhizas and ericoid mycorrhizas are tenuous, and that of Jumpponen and others (previously discussed) that the functional distinctions between mycorrhizal and endophytic fungi are not as clear as we would like. In nature, fungus–root associations are determined by the selective advantage they provide to the fitness of each partner over lifetimes and generations. It is likely that mycorrhizal associations evolve through a series of stages, from establishment to a state of balanced reciprocal parasitism, and finally break down into nonreciprocal parasitism or dissolution, as selection shapes the response of each partner to biotic and environmental constraints. It should come as no surprise that natural systems have evolved such a diversity of root associations; perhaps it is time to more fully recognize this continuum of associations and develop new paradigms to understand the complex interactions that take place between plants and their root-associated fungi.

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Herbivory tolerance and coevolution: an alternative to the arms race?

Herbivores are important in most terrestrial ecosystems and can reach outbreak proportions, causing spectacular levels of damage to many plant species. It is thus widely believed that herbivory is important in plant population dynamics and evolution. Furthermore, plants have a wide array of defenses against herbivores. Plant defense systems are broadly comprised of two components: resistance and tolerance. Resistance traits reduce damage levels either by lowering the probability of herbivore attack or by decreasing the amount of tissue removed. Because resistance factors can affect herbivore fitness, an evolutionary increase in resistance is expected to select for herbivore counter-measures. Tolerance traits, the second type of defense, minimize the adverse effects of damage by enabling the plant to survive, regrow and reproduce after an attack occurs. While it was previously assumed that an evolutionary increase in tolerance has no effect on herbivore fitness (Stowe *et al.*, 2000; Tiffin, 2000), it has been suggested that tolerance traits may impose selection on herbivores (Stinchcombe, 2002). In this issue, Espinosa & Fornoni (pp. 609–614) present the first experimental test of this hypothesis. They found that increasing tolerance levels in the annual plant *Datura stramonium* (Solanaceae) has no detectable effect on fitness components of its defoliating enemy, the leaf beetle *Lema trilineata* (Coleoptera: Chrysomelidae). This finding lends credence to the conventional wisdom that tolerance does not result in an evolutionary 'arms race', and also supports the notion that tolerance is a more evolutionarily stable form of defense than resistance.

'Tolerance can thus modify the plant–herbivore arms race, but can tolerance directly influence the evolution of herbivores?'

The arms race metaphor

Evolutionary ecology has made much progress over the past four decades in understanding resistance, but the study of tolerance gained momentum only in the mid-1990s (Stowe *et al.*, 2000). Perhaps this is because evolutionary ecologists have been fond of the arms race metaphor for the evolution of plant defense and herbivore counter-defense. If a mutation reduces herbivore attack, that mutation should spread (provided any adverse effects of the mutation are small relative to the benefit of reduced damage). Consequently, the herbivore's food source is diminished. However, a subsequent mutation in the herbivore could allow it to counter plant resistance. This new herbivore allele would then spread, increase herbivore load, and thus favor new plant resistance mutations. And so plant and enemy advance up a coevolutionary spiral.

The arms race metaphor became popular with the publication of Ehrlich & Raven's (1964) paper on the