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Editor's note

On the cover of last month's *TREE*, we erroneously announced the presence of the above article in that issue. I apologize to all for the mistake.
Ed.

Multi-functionality and biodiversity in arbuscular mycorrhizas

K.K. Newsham, A.H. Fitter and A.R. Watkinson

Arbuscular mycorrhizas (AM) are formed by over 150 described species of zygomycetous fungi belonging to the order Glomales¹, which colonize the roots of up to two-thirds of all plant species², including most non-woody species and tropical trees³. In addition to other features, AM fungi form specialized structures in plant root cells termed arbuscules, which are the site for the transfer of nutrients between fungus and plant⁴. Nutrients are captured by networks of fungal hyphae radiating into soil around roots and are transported to the plant in exchange for carbon. The nutrient most often implicated in this process is phosphorus (P), a highly immobile element in soil that is therefore frequently limiting to plant growth. Under controlled conditions, it is relatively simple to demonstrate that plants colonized by AM fungi grow better than those that are uncolonized: indeed, there is a wealth of information from laboratory and glasshouse studies to indicate that AM fungi improve plant P-relations. However, results from more realistic field-based studies are less conclusive: in tropical regions, where soils may be strongly P-limiting, AM fungi can be shown to improve plant P-relations^{5–7}, but evidence for a general role of AM fungi in plant P-relations under field conditions in temperate regions is at best conflicting⁸, or at worst absent⁹. This may be because plants growing in soils in temperate ecosystems are less strongly

Plant roots in natural ecosystems are typically colonized by a wide range of fungi. Some of these are pathogenic, others appear to be opportunistic and have no apparent impact, while mycorrhizal fungi are generally regarded as mutualistic. Of the various types of mycorrhizal fungi, the arbuscular mycorrhizal (AM) association is by far the most abundant and widespread. While the most widely accepted model of AM function depends upon plants benefiting from the facilitation of phosphorus uptake, recent data from field-based studies in temperate ecosystems indicate that only plant species with poorly branched root systems benefit from AM fungi in this way: species with highly branched root systems may benefit in other ways, such as by being protected against root pathogenic fungi. These two responses apparently represent extremes along a continuum of AM benefit determined by root system architecture.

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P-limited⁷, and the ubiquity of the association implies that AM fungi may offer other benefits to plant species growing in these regions.

Other common types of mycorrhizas, such as the ectomycorrhizas (which occur on forest trees in temperate and boreal regions³), or the ericoid mycorrhizas (which occur on ericaceous plants mainly in tundra³), are known to be capable of performing a range of functions. For example, members of both types can mobilize and capture organic nitrogen (N) compounds in the soil and transport N to the host plant^{10,11}. Ericoid mycorrhizas also play a significant role in the resistance of plants to toxic metals¹², and the fungal mantle formed around roots by ectomycorrhizas is capable of protecting host plants from pathogens¹³. In neither of these mycorrhizal types is there any indication that P uptake is the sole or even the main function of the mycorrhizal network. Since the selection pressures that have acted upon these other mycorrhizal types will at least to some extent have acted upon the AM fungi, it seems plausible to suggest that the latter will also have

evolved to serve more than one function in plant roots. This, however, is a question that has not been widely addressed. Although AM fungi are known to confer benefits to plants other than improving P acquisition (Box 1), these benefits are normally considered to be subsidiary roles of the AM association.

Box 1. Benefits of AM fungi to plants (other than P facilitation)

- Besides the facilitation of P uptake, AM fungi are known to benefit plants by improving the uptake of other nutrients such as nitrogen¹⁴ and copper¹⁵. The mechanism here appears to be the same as for the enhancement of P uptake, and involves transport through the hyphal network from soil to roots. This can only be effective where transport through soil by diffusion limits the acquisition of ions by root systems. For nitrogen, although the nitrate ion is highly mobile, ammonium ions (often dominant in acid soils) are more strongly adsorbed by soils and diffuse more slowly.
- AM fungi may also benefit plants by limiting the uptake of toxic heavy metals, such as zinc and cadmium, from soil¹⁶. The mechanism here is unknown. Resistance to toxins in plants often involves retention and sequestration in roots, and it may be that the fungal associate offers a larger or more-effective compartment for sequestration.
- Non-nutritional benefits of AM fungi include the improvement of water relations. This has proved to be a controversial area. The cross-sectional area of fungal hyphae connected to a root is typically too small for a significant fraction of the transported flux to pass through hyphae¹⁷, but it is possible that water transport may be significant in delaying wilting at times of extreme water deficit^{18,19}.
- AM fungi have also been shown to improve defence against or to alter interactions with herbivores^{20,21}. This is an area about which little is known, but since mycorrhizal plants often have different leaf chemistries, it would not be surprising if secondary chemistry was also altered.
- AM fungi are known to increase resistance to pathogens, in particular pathogenic root-infecting fungi, such as *Phytophthora parasitica*²² or the cosmopolitan *Fusarium oxysporum*²³. Little is known about the mechanisms behind this increased resistance, although it has been suggested that increased lignification of root cell walls²⁴ or production of phytoalexins by the host in response to AM fungal colonization²⁵ may be responsible.
- Mycorrhizal plant species have a different physiology and ecology to non-mycorrhizal plants, and many other differences from those outlined above probably await discovery. Both ecologists and physiologists need to be aware that the results of experiments on non-mycorrhizal individuals of normally mycorrhizal plant species are most probably artefactual.

AM fungi and P uptake

The critical test of a P-uptake benefit of AM fungi to plants is the demonstration of increased P inflow in the presence of AM colonization. This shows that the host plant has acquired more P per unit of root length in the presence of the association. Values of a few $\text{pmol P m}^{-1} \text{s}^{-1}$ can theoretically be achieved by non-mycorrhizal plants relying on diffusion alone, the exact value depending on the diffusivity of P in soil²⁶. Much higher values than these have been recorded in plants colonized by AM fungi under controlled conditions, where P is more likely to limit growth due to the application of elevated levels of other nutrients²⁷.

There are, however, very few data on P inflows for temperate plant species growing under natural conditions. Inflow data are available for nine species that are consistently colonized by AM fungi in the field^{27,28}, and for seven of these we have estimated their competence to take up P from the soil by measuring the numbers of root tips per milligram of root tissue (i.e. specific root tip number); high values of this variable imply a highly branched root system. The clear positive relationship between specific root tip number and maximum P inflow under natural conditions (Fig. 1) indicates that plant species with more highly branched root systems are more efficient at P uptake from soil. This relationship is not simply a function of AM colonization, as there is no correlation between the mean percentage of root length colonized by AM fungi and maximum P inflow for these seven species (Spearman's rank correlation coefficient = -0.14, $P = 0.758$). Indeed, the plant species with one of the highest levels of AM colonization, the bluebell (*Hyacinthoides non-scripta*), has the lowest P inflow. It is, of course, true that the percentage of root length colonized by AM fungi may not re-

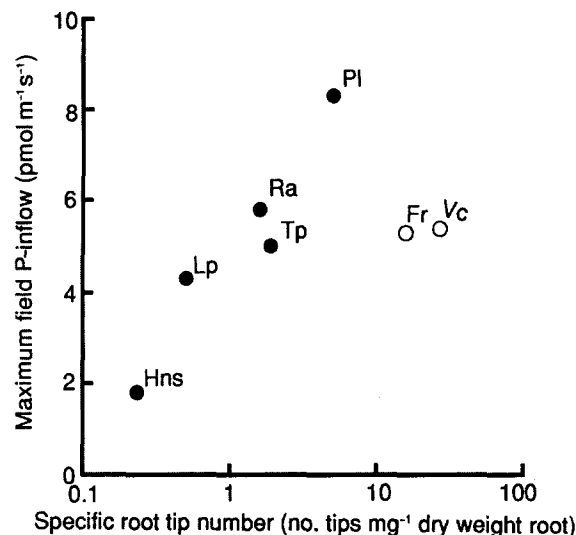


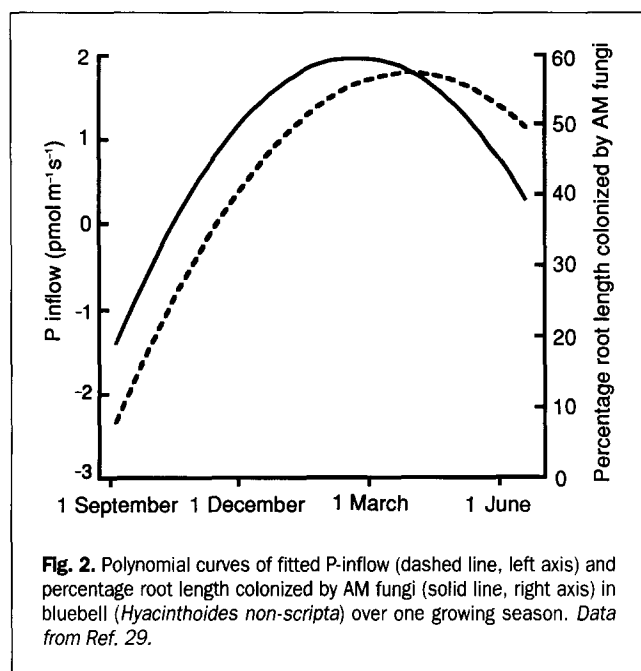
Fig. 1. Maximum field P-inflow as a function of specific root tip number (log scale) for five forbs (filled circles) and two grasses (open circles) that are consistently colonized by AM fungi under natural conditions. Specific root tip number is a measure of root architecture: highly branched root systems will have more meristems per unit of root biomass and thus a high value. Hns, *Hyacinthoides non-scripta*; Lp, *Lathyrus pratensis*; Ra, *Rumex acetosa*; Tp, *Trifolium pratense*; Pl, *Plantago lanceolata*; Fr, *Festuca rubra*; Vc, *Vulpia ciliata* ssp. *ambigua*. Values are means of eight replicates for each species. Spearman's rank correlation coefficient = 0.75, $P = 0.05$. Data from Ref. 27, the experiments described in Ref. 28 and K.K. Newsham, unpublished.

flect the amount of active AM fungus in roots, but at present it is the most robust measure available.

These data suggest that species with highly branched root systems are less likely to benefit from increased P inflow as a result of AM colonization, but since these species have apparently not evolved any resistance to AM fungi, it may be argued that there must be some alternative benefit conferred by the association in these species. Therefore, to indicate the greatest range of potential benefit, here we review the role of AM fungi in the ecology of two temperate plant species with diametrically opposing root system architectures, *H. non-scripta* (Liliaceae) and the annual grass *Vulpia ciliata* ssp. *ambigua* (Poaceae).

AM fungi in the ecology of *Hyacinthoides* and *Vulpia*

AM fungi have an important role in the P nutrition of *Hyacinthoides non-scripta*²⁹. This species is a bulbous perennial in which the annual growth cycle has two main phases, one subterranean from August to February, and one above-ground and photosynthetic after that. Roots newly formed in August become rapidly colonized by AM fungi and undergo a steady increase in AM colonization density to a plateau in March, just after the shoots first emerge above ground and enter a positive C balance. During the subterranean phase of the life cycle, plants lose both C and P and so have negative P inflows, and during the aboveground phase, when colonization density is high, they have positive inflows. The curves for P inflow and AM colonization are closely coincident (Fig. 2). Consequently, when P inflows are plotted as a function of the level of AM colonization, there is a positive relationship between the two parameters: plants with higher levels of AM colonization have higher P inflows under natural conditions²⁹. Confirmation that *Hyacinthoides* is obligately dependent on AM fungi for P uptake comes from a sand-culture experiment in which non-mycorrhizal plants were



unable to take up P added in solution²⁹. In a species with a similar root system and life history, *Ranunculus adoneus*, a comparable relationship between P uptake and AM colonization is found: P uptake corresponds with the development of arbuscules for a brief period in the life cycle of the plant³⁰.

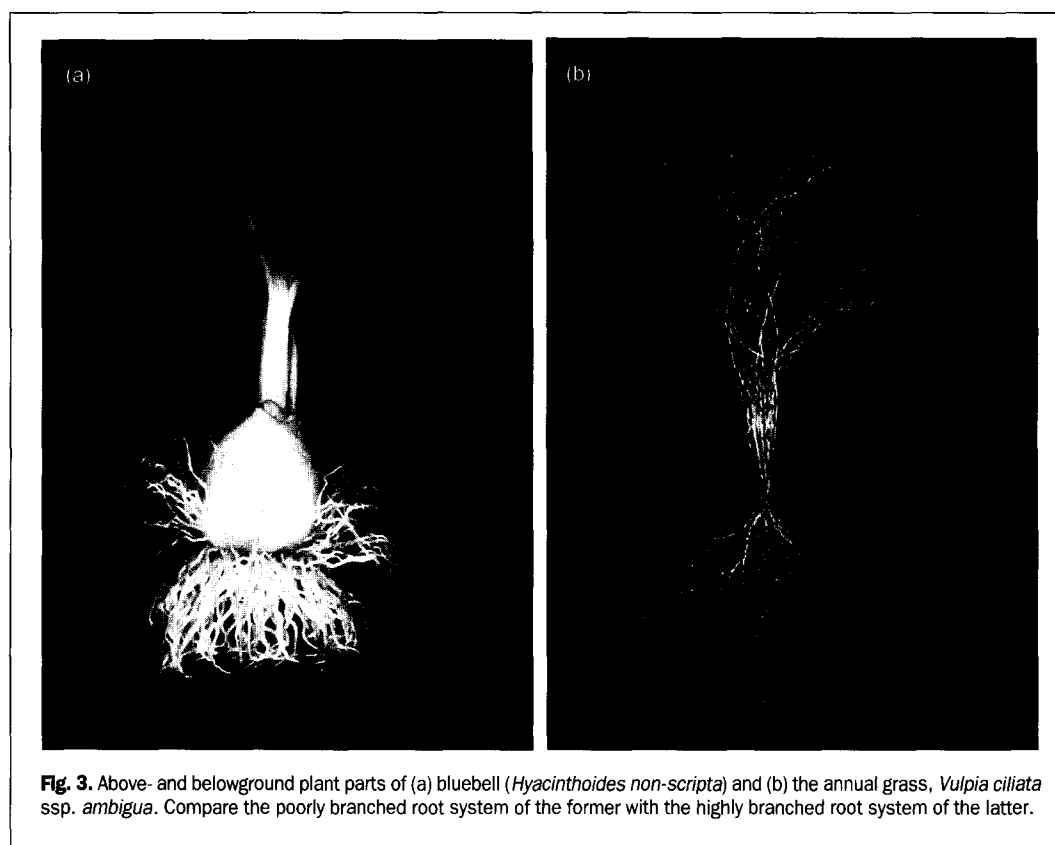
That it is possible to demonstrate a beneficial effect of AM fungi on the P nutrition of *Hyacinthoides* is not surprising, since it possesses a restricted, poorly branched root system (Fig. 3). However, recent results from research into the role of AM fungi in the ecology of *V. ciliata* ssp. *ambigua*, the roots of which are highly branched (Fig. 3), paint an entirely different picture. Experiments using the fungicide benomyl to control AM colonization in natural populations of *Vulpia* have conclusively shown that these fungi play no part in the P nutrition of the grass under natural conditions^{28,31,32}. Irrigation experiments have also demonstrated that AM fungi do not affect the water relations of *Vulpia* in the field³². This therefore raises the question as to why AM fungi continue to persist in the roots of the grass and exactly what benefits they confer in the species.

West *et al.*³² demonstrated that the application of benomyl to natural populations of *Vulpia* reduced AM colonization but did not affect plant performance. They postulated that these null effects of the fungicide on plant performance were because of the simultaneous elimination of beneficial AM fungi and deleterious pathogenic fungi, typically the cosmopolitan

root pathogen *Fusarium oxysporum*. Newsham *et al.*³³ subsequently tested the interaction between the two groups of fungi by the use of a transplant technique. Seedlings of *Vulpia* were grown in the laboratory with a factorial combination of *F. oxysporum* and an AM fungus (a species of *Glomus*) before being planted out in spring 1994 into a natural population of *Vulpia* growing at Mildenhall, UK, from which both fungi had been isolated. The plants were sampled after 62 and 90 days of growth in the field and the data clearly indicated that AM fungi protected the plants from the substantial deleterious effects of *F. oxysporum* on root and shoot growth (Fig. 4). There were no effects of the AM fungus alone on plant growth in the absence of the pathogen, and it also did not improve plant P-nutrition³³. Although the phenomenon of AM fungi protecting plants from pathogenic fungi had been recorded under controlled conditions^{22,23}, this was apparently the first time that AM fungi had been shown to exert a substantial effect upon the performance of a plant species under natural conditions (albeit after transplantation) by protecting it from a widespread root pathogen.

A continuum of AM benefit

The data outlined above indicate that a continuum of AM benefit may exist, which is determined by root system architecture. The concept that the mycorrhizal dependency of a plant species is determined by the type of root system it forms was put forward by Baylis³⁴, whose argument was largely centred on the role of root hairs as P-absorbing organs, which are absent from the roots of plants in the Magnoliales, thereby leading to increased mycotrophy in this order. That root hair length can affect the mycorrhizal dependency of plants has recently been confirmed³⁵. St John³⁶ and Hetrick³⁷ have subsequently expanded on Baylis' ideas to incorporate root system architecture, and Hetrick *et al.*³⁸ have recently identified three groups among 23 tallgrass prairie forbs based upon responsiveness to AM colonization and root system form.



All of these studies have related root form to mycorrhizal dependency in terms of P uptake. However, root form not only influences the dependence of plants on AM fungi for P nutrition, but also influences the susceptibility of plants to root pathogens. For example, root pathogenic fungi enter healthy roots where the developing meristem pushes its way through the outer cortex^{13,39} or through the tips of developing lateral roots⁴⁰. Therefore those plant species (such as *Vulpia*) that are efficient at nutrient uptake because of an abundance of meristems and lateral roots are by that fact also more susceptible to root pathogenic fungi. Conversely, the root architectural characteristics that make *Hyacinthoides* dependent on AM fungi for P uptake also make its roots less susceptible to pathogens, since its root system has so few meristems and laterals. In confirmation of this, pathogenic fungi are very rarely observed in stained root sections of *Hyacinthoides* (J.W. Merryweather, pers. commun.), whereas the roots of *Vulpia* sampled from the field are routinely infected by fungal pathogens⁴¹. *Hyacinthoides* and *Vulpia* therefore apparently represent extremes along a continuum of AM benefit determined by root system architecture. In general, those species with highly branched root systems apparently benefit from AM colonization mostly in terms of protection against pathogens: by contrast, those species with poorly developed root systems apparently benefit from AM fungi in terms of P uptake (Fig. 5). However, other functions of the association, such as protection from herbivory and soil toxins (Box 1), will probably operate on different axes to those defined by root system architecture (Fig. 5).

An evolutionary explanation

Fossil records show that early 'root' systems such as those of *Rhynia*, *Aglaophyton* and *Sawdonia* were poorly developed with few lateral branches^{42,43}. Presumably these plant species would have needed assistance from soil fungi in nutrient capture⁴⁴, as do present-day plant species with poorly developed roots³⁴. This assumption is supported by the presence of arbuscules in the roots of *Aglaophyton*⁴⁵ and by recent estimates based on molecular sequence data that place the origin of AM fungi at 353–462 million years ago, which is broadly coincident with the evolution of terrestrial plants⁴⁶. Both sets of evidence reinforce the suggestion that AM fungi played a vital role in the colonization of the land by plants⁴⁴.

Although knowledge of the evolution of root systems is poor, it seems likely that as plant root systems became more developed, so meristems and laterals became more abundant, resulting in the highly branched systems of, for example, modern grasses^{47,48}. As a consequence of the increased branching of root systems, the needs of plants for AM assistance in nutrient capture would have diminished, but susceptibility to pathogens would also have increased. Therefore, AM fungi may still persist in the roots of many modern-day plant species because of the pathogen protection benefits that they confer, rather than the improvements that they make in plant nutrient-relations.

An explanation of AM fungal biodiversity

The recognition of over 150 different species of Glomalean fungi probably represents what Morton *et al.*⁴⁹ refer to as 'a small fraction of the diversity to be found worldwide'. The AM association is usually assumed not to be host-specific⁵⁰, with a range of taxa being capable of colonizing the roots of a given plant species. Indeed, recent molecular research indicates that several different taxa of AM fungi may colonize the roots of a single plant simultaneously⁵¹. A similar

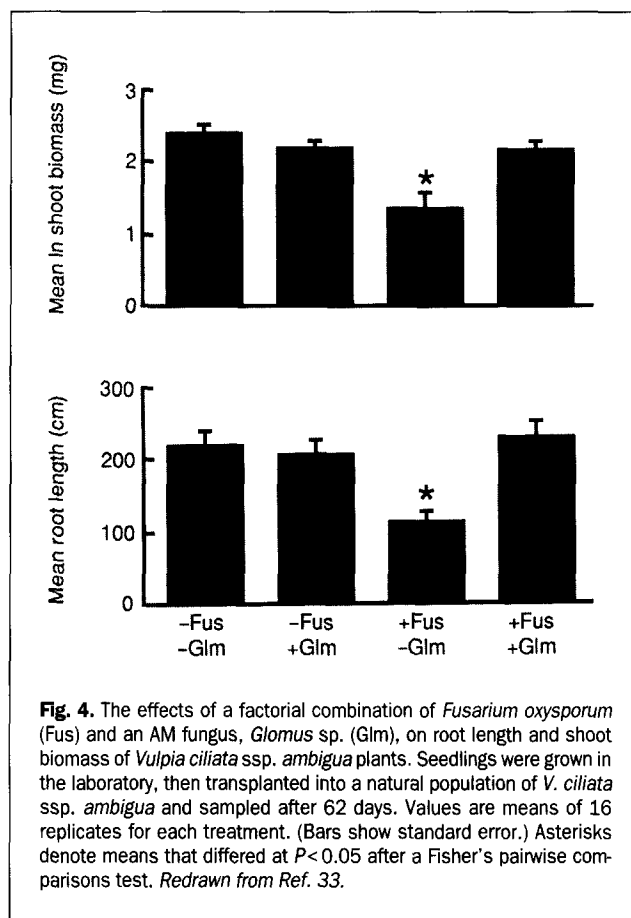


Fig. 4. The effects of a factorial combination of *Fusarium oxysporum* (Fus) and an AM fungus, *Glomus* sp. (Glm), on root length and shoot biomass of *Vulpia ciliata* ssp. *ambigua* plants. Seedlings were grown in the laboratory, then transplanted into a natural population of *V. ciliata* ssp. *ambigua* and sampled after 62 days. Values are means of 16 replicates for each treatment. (Bars show standard error.) Asterisks denote means that differed at $P < 0.05$ after a Fisher's pairwise comparisons test. Redrawn from Ref. 33.

situation has arisen in *Rhizobium* research, where molecular approaches have revealed much greater diversity and specificity than was previously suspected⁵². However, the biodiversity of AM fungal species and the presence of different fungal taxa in the same roots is difficult to explain if the association's only function is assumed to be in P facilitation, since selection on the association should have favoured a few taxa that were the most effective in nutrient capture. This apparent paradox is resolved if the association is viewed as being multifunctional. Furthermore, if most plant species lie somewhere between the extremes of mycorrhizal

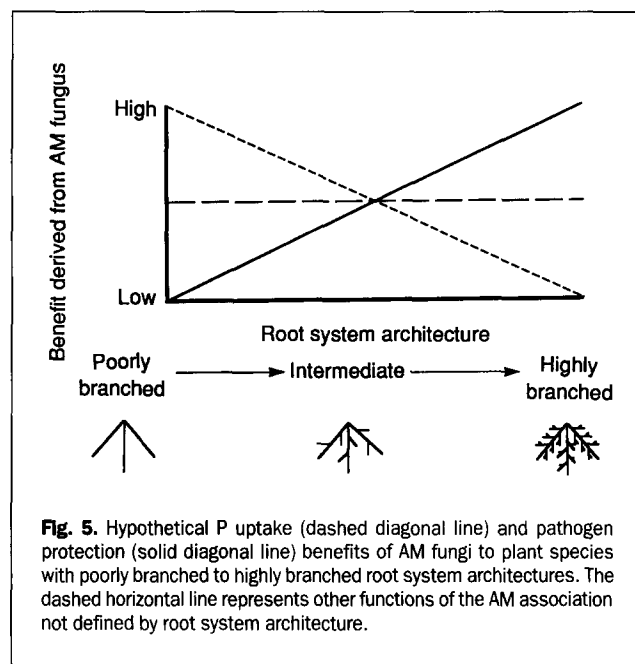


Fig. 5. Hypothetical P uptake (dashed diagonal line) and pathogen protection (solid diagonal line) benefits of AM fungi to plant species with poorly branched to highly branched root system architectures. The dashed horizontal line represents other functions of the AM association not defined by root system architecture.

benefit in the continuum proposed above, the wide diversification of AM fungi becomes more plausible, since more niches would have been available for AM fungi in any one habitat. For example, a well-developed AM mycelial network around the roots is required to ensure effective nutrient facilitation, since fungal hyphae must colonize more soil to be effective P scavengers⁵³. By contrast, AM fungal taxa that are effective against pathogens probably require more internal hyphal development, since roots that are heavily colonized by AM fungi develop fewer subsequent infections by pathogenic fungi³³. It is worth noting that many AM fungal taxa do not promote plant growth⁵⁴ or improve plant P-uptake under controlled conditions⁵⁵. One explanation of their occurrence is that they are 'cheaters'⁵⁶ and that many AM associations are not mutualistic; alternatively, they may play different but positive roles in the association.

Conclusions and future research

Given the ubiquity of AM fungi in plant roots, and the substantial effects that they are known to exert on plant performance, it is apparent that their benefits should be assessed in a wider range of plant species under natural conditions to gain a full idea of their role in plant ecology. As yet, AM function under natural conditions has only been studied in a limited number of plant species, but the data that we have reviewed indicate that pathogen protection benefits of AM fungi might be as significant as nutritional benefits to many plants growing in temperate ecosystems. It is also apparent that a more plausible explanation than that which currently emphasizes P facilitation is required to account for the abundance of AM fungi in the roots of such a wide variety of natural plants. Given the abundance of fungal pathogens in roots³⁹, it is reasonable to assume that AM fungi could protect many plant species from the deleterious effects of root pathogenic fungi, much as they do in *Vulpia*, and that they play a multifunctional role in a wide range of plant species. This is an area of plant ecological research that urgently needs attention, and is one that may help to throw light upon the broader issue of the role of root-colonizing fungi in the population and community ecology of plants.

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