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Occurrence of non-mycorrhizal plant species in south Swedish rocky habitats is related to exchangeable soil phosphate

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Summary

1 Plant species that do not typically form mycorrhiza are most likely to be successful under conditions where mycorrhizal fungi are not important for plant coexistence or where the costs of symbiosis outweigh the benefits. The relative occurrence of non-mycorrhizal species was investigated in relationship to exchangeable soil P in herbaceous vegetation, where arbuscular mycorrhizal (AM) associations are generally common. We investigated a total of 439 sites in rocky habitats with sparse vegetation and 110 meadows with dense vegetation.

2 In both rocky habitats and meadows, soil pH was inversely related to exchangeable P. In rocky habitats plant species richness increased greatly between pH 3 and 5 and was also inversely related to P.

3 Plant communities in rocky habitats contained a relatively larger proportion of non-mycorrhizal species than those in meadows. More non-mycorrhizal species occurred at high soil P in the rocky habitats, but no such relation was found in meadows.

4 Non-mycorrhizal species in rocky habitats were most common at low soil pH (high P availability). Plant species that thrived at extreme soil pH were often non-mycorrhizal.

5 The occurrence of fewer non-mycorrhizal plants in meadows than in rocky habitats supports the hypothesis that AM associations are more important in ecosystems with intense competition among plants. In rocky habitats, where abiotic stress may restrict photosynthesis more than nutrient limitation does, it is adaptive for plant species to utilize strategies other than mycorrhiza, particularly at low pH sites where P availability is likely to be adequate.

Key-words: arbuscular mycorrhiza, pH, phosphorus, plant coexistence, plant strategies, soil acidity, species richness, stress tolerance

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Introduction

Both fossils and molecular studies suggest that arbuscular mycorrhizal (AM) fungi were present in the earliest land plants (Simon *et al*. 1993; Remy *et al*. 1994; Redecker *et al*. 2000), and have been important throughout the evolution of most plant families (Pirozynski & Malloch 1975). AM associations favour modern-day plants because they may improve the uptake of immobile nutrients and confer pathogen resistance (Newsham *et al*. 1995). These symbioses are of particular importance to plants under P limiting conditions (Read 1991).

Not all plant species benefit from mycorrhizal associations to the same degree. There is a continuum ranging from obligate mycotrophs, which always form mycorrhizal associations, to non-mycorrhizal plants that never form mutualistic symbioses with mycorrhizal fungi (Johnson *et al*. 1997). Growth of non-mycorrhizal plants may be inhibited by the presence of AM fungal mycelium (Francis & Read 1995; Johnson 1998). Variation in mycorrhizal dependency has been linked with root morphology, phenology, photosynthetic physiology and life-history strategies of plants. Strongly mycotrophic plants generally have coarser roots than weakly mycotrophic or non-mycorrhizal plants (Baylis 1975; Hetrick 1991). Warm season plants with C4 photosynthesis are generally more highly mycotrophic than cool season plants that utilize C3 photosynthesis (Hetrick *et al*. 1988). Ruderal plant species that quickly colonize disturbed areas and rapidly complete their life cycles are commonly non-mycorrhizal, while taxa that dominate late successional

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plant communities tend to be strongly mycotrophic (Janos 1980; Francis & Read 1994).

Non-mycorrhizal plant taxa are not randomly distributed across plant families. Most members of the plant families Brassicaceae, Caryophyllaceae, Crassulaceae, Cyperaceae, Juncaceae, Chenopodiaceae and Polygonaceae rarely or never form mycorrhiza (Harley & Harley 1987; Newman & Reddell 1987; Tester *et al.* 1987). In a commentary article on the list of mycorrhiza in the British flora (Harley & Harley 1987), Moore (1987) pointed out that 'it is the non-mycorrhizal elements in the British flora that are exceptional, rather than the other way around'. Peat & Fitter (1993) showed that among British angiosperms, non-mycorrhizal species were particularly abundant in aquatic, wetland and saline habitats. They also found that non-mycorrhizal species tended to be habitat specialists and have narrower environmental tolerances than mycotrophic plant species.

Variation in plant mycotrophy may be an important determinant of the species composition of plant communities (Grime *et al.* 1987; Van der Heijden *et al.* 1998; Hartnett & Wilson 1999; O'Connor *et al.* 2002). The ability of plants to benefit from the mycorrhizal mycelium network is an important selection pressure in grassland turf (Francis & Read 1994, 1995; Hart *et al.* 2003). Negative feedback between the population growth rates of plants and mycorrhizal fungi can support a high diversity in plant communities (Bever *et al.* 1997; Bever 1999; Klironomos 2002, 2003).

Grime (1974, 1979) considered the evolutionary trade-offs between stress (phenomena that restrict photosynthetic production) and disturbance (phenomena that destroy plant biomass) and proposed three basic plant strategies: competitors, stress-tolerators and ruderals (Table 1). Furthermore, Grime (1979) predicted that mycorrhizal associations should be common among stress-tolerant plant species inhabiting low-nutrient environments where the benefits of enhanced nutrient uptake will outweigh the photosynthetic costs of mycotrophy. Surveying the distribution of non-mycotrophic species in relation to environmental factors will help reveal the costs and benefits of mycotrophy in natural ecosystems and elucidate the importance of mycorrhiza in structuring plant communities. We assume that the proportion of non-mycorrhizal plants reflects the importance of AM fungi to plant coexistence in a particular habitat. As the effect of AM associations depends on the density of the vegetation (Hartnett *et al.* 1993), we predict that they are more important for plant coexistence in meadows, with dense communities of competitive plants, than in rocky habitats containing sparse patches of stress tolerant plants (Table 1). Furthermore, we hypothesize that AM associations are important in stressed habitats when soil P availability is low, but not when the stress limits photosynthesis more than nutrient uptake (Table 1).

Soil pH is of fundamental importance for P solubility. Availability of P for plant uptake is highest at low soil pH (Tyler 1996); consequently, we expect that AM symbioses will be more beneficial at high soil pH than at low soil pH. We tested these hypotheses in two types of ecosystems in southern Sweden: rocky habitats on shallow soils and meadows developed under the influence of grazing or haymaking. All of our study sites were tree-free and well-drained areas that have been analysed for soil chemistry and plant distribution in previous studies (Tyler 1996, 2000). In both these vegetation types it is possible to find contrasting pH, and the P solubility is normally inversely correlated to pH (Tyler 1996, 2000).

Materials and methods

THE STUDY AREA AND SAMPLING

Our research area comprised southern Sweden, including the Baltic islands of Öland and Gotland (see Tyler 1996, 2000 for further details). Siliceous igneous rocks dominate the bedrock of the study area, while quartzitic sandstone only occurs locally. Widespread are various types of dark igneous rocks, including granodiorite, diorite, gabbro, peridotite, hyperite (diabase) and amphibolite. Archean, Ordovician and Silurian limestone are the different types of limestone. Vegetation in southern Sweden has developed since the last glaciation about 10 000 years ago. Natural weathering and vegetation processes on glacial moraines have largely acidified these sites. In recent decades, acid deposition from human activity has further contributed to soil acidification, although it is still possible to find some meadows with high pH. Soils in areas where the bedrock was exposed by glaciation or, later, by isostatic land-upheaval, are still highly influenced by the composition of the underlying material. It is therefore possible to find strongly contrasting soil properties depending on whether soils

Table 1 Predicted favoured plant strategy and importance of AM associations for plant coexistence in non-woody vegetation with different intensity of disturbance and biotic and abiotic stress. Modification of Table 1 in Grime (1979)

Intensity of disturbance	Intensity of stress	
	Low	High
Low	Competitors (AM associations important)	Stress-tolerators (AM associations important if the stress is related to limited P supply)
High	Ruderals (AM associations not important)	No viable strategy

developed on limestone or quartzitic rocks. For example, limestone soils may have a pH of the soil solution as high as 8, while contrasting acid soils may have a pH as low as 3. There are almost no vascular plant species common to both highly acid and calcareous soil of rocky habitats (Tyler 1996). However, two common characteristics of vascular plant species inhabiting all rocky habitats is the ability to survive periods of drought irrespective of soil conditions and a requirement for high light intensity.

A total of 439 sites in rocky habitats were censused during July or August 1993 and 1994. The floristic composition of each site was based upon the quantity of every species estimated by its percentage cover (vertical projection) within 4-m^2 sample plots. All sites were free of trees or bushes. Soil was sampled at five points down to the bedrock (maximum approved soil depth 20 cm) and pooled to form one composite sample per site (Tyler 1996).

A total of 110 meadow sites with a known management history were analysed during 7 June to 10 July 1998. These sites were distributed evenly in south-eastern Sweden (Tyler 2000). They were well and freely drained, developed on horizontal or sloping, W-S-E facing ground. At each site one 25-m^2 sample area (5×5 m) was delimited. Cover of all vascular plant species was estimated as percentage of the vertical projection of their biomass on the ground. A total of 266 vascular plant species were observed across all meadow sites, but only those recorded in more than 20 sites (64 species) were used in the analysis. Soil was sampled at five points using a 385-cm^3 cylinder with 10-cm length to form one composite sample per site.

SOIL ANALYSES

Soil samples were stored at 5 °C until further treatment. All soil analyses were performed on the < 6 mm fraction. pH-KCl was determined electrometrically using 10 g soil and 50 mL 0.2 M KCl. pH was measured in supernatants obtained by 2-hour extraction in a rotator. Exchangeable phosphate was determined using a flow injection analysis application of the stannous chloride–molybdate method following 30 minutes extraction of 10 g soil at field moisture with unbuffered 100 mL 0.05 M Na_2SO_4 + 0.02 M NaF solution.

STATISTICS AND CALCULATIONS

Regression analysis was used to investigate the relation of soil pH and exchangeable P to plant species richness and the incidence of non-mycorrhizal species. The average pH distribution of plants in the rocky habitats, for species recorded at more than five sites, was calculated from their relative cover in each of nine different pH classes into which sites were divided (from < 3.5 to > 7 and in pH intervals of 0.5 between these extremes). The average pH value of the sites in each class was calculated. Thus if a species had an average cover of 5% in the pH class 3.5–4 and 5% in the pH class 4–4.5 and no occurrence in any other pH class, the average pH distribution would be: 0.5 (relative occurrence) × 3.7 (average pH of the class) + 0.5 × 4.2 = 3.95. In this way the differences in number of sites in each pH class did not influence the calculated average pH distribution. Species belonging to the families, Brassicaceae, Caryophyllaceae, Crassulaceae, Cyperaceae, Juncaceae, Chenopodiaceae and Polygonaceae were considered as non-mycorrhizal species (Harley & Harley 1987; Moore 1987; Newman & Reddell 1987; Tester *et al*. 1987).

Results

RELATIONSHIP BETWEEN P, SPECIES RICHNESS AND pH

The pH of the 439 rocky sites ranged from 2.6 to 7.7 and exchangeable soil P ranged from 0.001 to 5.7 µmol g^{-1}. The meadow sites showed less variability, with soil pH ranging from 3.5 to 7.9 and exchangeable P ranging from 0.009 to 0.73 µmol g^{-1}. Exchangeable P decreased with increasing pH in the rocky habitats (Fig. 1a) and in the meadows between pH 3 and 6, with no further decrease above this pH (Fig. 1b). Plant species richness (number of species per plot) increased between pH 3 and 4.5 at the rocky habitats, while at a higher pH there was no further increase in species richness (Fig. 1c). There was a trend in both the rocky habitats and the meadows for species richness to decrease at very high pH values (Fig. 1c,d). *Rumex acetosella* was clearly the most common species in the rocky habitats (Table 2), but this species was absent from sites with exchangeable P less than 0.01 (Fig. 1a). *R. acetosella* was rare in the meadows and had an average cover of only 0.12% compared with 7.5% in the rocky habitats. Two grasses, *Festuca ovina* and *Arrhenaterum pratense* with 9.4 and 6.7 mean cover, respectively, dominated the meadows. Other common species in the meadows were the forbs *Hieracium pilosella*, *Filipendula vulgaris*, *Plantago lanceolata* and *Achillea millefolium*, with 5.4, 4.7, 3.1 and 2.4% mean cover, respectively.

OCCURRENCE OF NON-MYCORRHIZAL SPECIES

We found a significant negative correlation between species richness and exchangeable P (Fig. 2a) in rocky habitats ($P < 0.001$). The proportion of non-mycorrhizal species was 20% or higher in the majority of rocky habitats and there was a positive correlation between exchangeable P and the proportion of non-mycorrhizal species in the rocky habitats (Fig. 2b). There was an even stronger relationship when the proportion of cover of non-mycorrhizal species was analysed (Fig. 2c). The proportion of non-mycorrhizal cover was rarely higher than 20% in the meadows and we found no relationship ($P > 0.05$) between the occurrence of non-mycorrhizal plant cover and exchangeable soil P there (Fig. 2d).

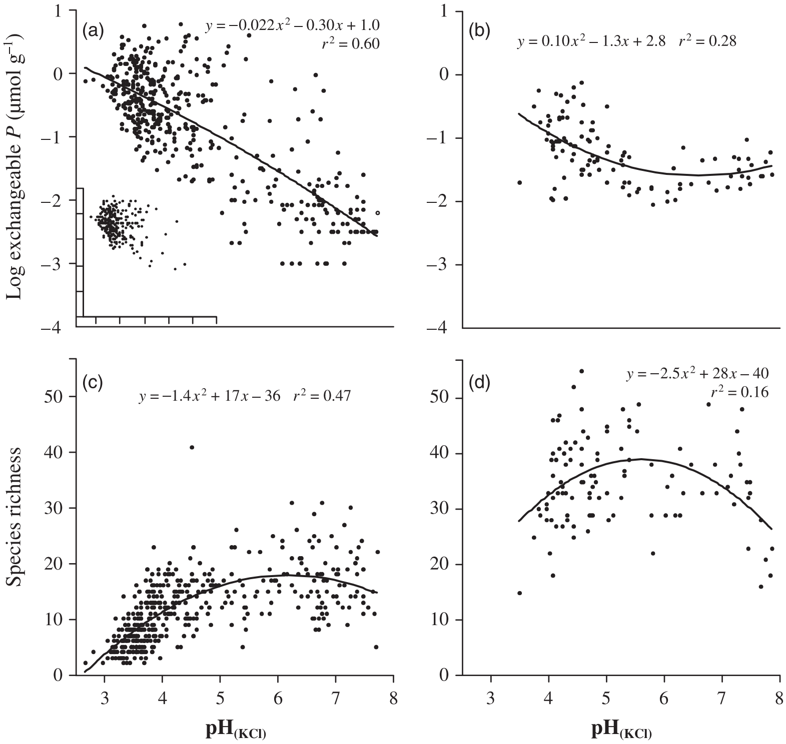

Fig. 1 The relationship (second order polynomial regression) of pH to exchangeable P and plant species richness (number of species per unit sampling area) in rocky habitats (a, c) and meadows (b, d) in southern Sweden. All relationships were significant ($P < 0.001$). Rocky habitats with *R. acetosella* are shown as an inset in (a) with the same axis, but reduced size, as in the large graph. Note that the sampling area used was 4 m^2 in rocky habitats and 25 m^2 in meadow sites.

pH DISTRIBUTION AVERAGE OF PLANTS IN ROCKY HABITATS

The pH distribution average was calculated for the 142 species that occurred in more than five of the rocky sites. A higher proportion of non-mycorrhizal species occurred at a low pH than at a high pH (Fig. 3). The lowest proportion of non-mycorrhizal species occurred at intermediate pH distribution average (5–5.5). The species in this pH class often had a wide pH range (see also Tyler 1996), while the species occurring at either low or high pH can more be regarded as specialized for either acid or high-pH soil (Table 2). Thus the species specialized for extreme pH values were more often non-mycorrhizal than the broad range species. There were four non-mycorrhizal species among the 12 most common species in the rocky habitats, and four non-mycorrhizal species among the 10 most common species in the acid sites. Only one of the 10 most common species in the high-pH rocky sites was non-mycorrhizal. Frequent species in the acid sites were the grasses *Deschampsia flexuosa*, *Aira praecox* and *Agrostis vineale*, in addition to the non-mycorrhizal *R. acetosella* (Table 2).

Discussion

We show that non-mycorrhizal plants in stressed habitats are most successful when soil P availability is not severely limiting. Our results support the hypothesis that a non-mycorrhizal strategy is more successful for stress tolerators than for competitors as there was clearly a higher proportion of non-mycorrhizal species in the high-stress rocky sites than in the more moderate meadow sites. Shallow soil is a stress factor for plants and restricts the distribution of many plant species because it predisposes sites to extreme variation in soil moisture, pH and nutrient availability (Tyler 1996). Non-mycorrhizal plants were most common at extreme soil pH. This is in accordance with the observation that non-mycorrhizal plants usually occur in a narrow range of habitats (Peat & Fitter 1993), which means that they are more specialized or need to be more specialized. In the meadow sites, where interspecific competition is likely to be intense, there was no relationship between either soil pH or exchangeable P and the incidence of non-mycorrhizal species. This corroborates the observation of Read *et al.* (1976), that the occurrence of AM colonization is high both in acid and alkaline grasslands in Britain. Accordingly, AM fungal colonization is important for plant coexistence in grasslands (Grime *et al.* 1987; Van der Heijden *et al.* 1998). In contrast, there seems to be a higher proportion of non-mycorrhizal species both among stress tolerators (this study) and ruderals (Francis & Read 1994) than among the competitive plant species.

The high P solubility at the low pH rocky sites ameliorates one important stress factor for many plants, in contrast to limestone habitats where many plants exhibit

Table 2 The 12 most common species in rocky habitats sorted by frequency in the 439 sites as well as the 10 species with the lowest and the 10 species with the highest average pH distribution. Also the mean cover and average pH distribution is given for each species. *Denotes non-mycorrhizal species

Species	Frequency	Mean cover (%)	Average pH distribution (%)
12 most common			
*Rumex acetosella**	61.5	7.48	3.80
Festuca ovina	53.1	1.32	5.42
Agrostis vinealis	40.8	1.90	3.92
Deschampsia flexuosa	33.9	0.82	3.71
Sedum telephium*	29.4	0.97	4.77
Hieracium pilosella	28.5	0.95	5.60
Calluna vulgaris	28.2	1.43	3.95
*Sedum acre**	27.1	1.18	5.53
Galium verum	26.9	0.75	5.89
Potentilla argentea	24.6	0.53	5.37
*Lychnis viscaria**	23.7	0.69	4.84
Plantago lanceolata	23.2	0.98	5.27
10 most low-pH distributed			
Galium saxatile	1.4	0.02	3.68
*Stellaria graminea**	1.1	0.01	3.70
Deschampsia flexuosa	33.9	0.82	3.71
*Carex pilulifera**	2.5	0.03	3.74
Aira praecox	12.3	0.51	3.75
Hypochoeris radicata	6.4	0.17	3.76
*Silene rupestris**	12.1	0.28	3.79
*Rumex acetosella**	61.5	7.48	3.80
Jasione montana	11.8	0.47	3.92
Agrostis vineale	40.8	1.9	3.92
10 most high-pH distributed			
Globularia vulgaris	1.6	0.05	7.28
Poa alpina	1.6	0.04	7.25
Daucus carota	1.6	0.02	7.18
Ranunculus bulbosus	3.0	0.03	6.99
Vicia cracca	1.1	0.01	6.96
Saxifraga tridentata	4.1	0.04	6.92
Circium acaule	1.6	0.04	6.92
Agrostis stolonifera	2.3	0.03	6.89
*Hornungia petrea**	3.2	0.03	6.83
Medicago lupulina	9.6	0.20	6.74

P limitation (Tyler 1992; Tyler & Olsson 1993). In addition to AM fungi possibly having a less important role in plant nutrition at low soil pH due to the higher P solubility, it may also be that other conditions prevailing in acid soils inhibit AM fungal growth. Indeed some AM fungi are inhibited by low pH (Porter *et al*. 1987; Van Aarle *et al*. 2002) and by aluminium (Vosatka *et al*. 1999). Aluminium toxicity may have importance because Al is released into soil solution at low pH (Tyler 1996). There are, however, usually fungi present that are adapted to most types of conditions and it is therefore more likely that the distribution of non-mycorrhizal species is not due to the lack of AM fungi, but rather due to a less strong selection force for AM symbiosis in certain habitats. It seems clear that extreme conditions can select for other mechanisms of achieving limited nutrients. Several of the plants that cannot grow at high pH, including *R. acetosella*, exhibit P limitation (Tyler 1992; Tyler & Olsson 1993), showing that P availability may be a particularly important limiting factor in limestone soils, in particular for plants lacking either AM colonization or the ability to exude P-releasing organic acids such as oxalic acid (Ström *et al*. 1994). The many studies showing that AM associations are less beneficial for plant growth at high P (Allison & Goldberg 2002) indicate that P is an important factor in our rocky habitats and contributes to plant responsiveness to AM colonization at high pH values (Hayman & Tavares 1985). The results therefore show that P not only reduces AM benefits when supplied artificially, but may also be an important regulator in natural habitats with variation in exchangeable and plant-available P. In other words, the non-mycorrhizal strategy is particularly successful in rocky habitats where P limitation is not a stress factor.

A negative relationship between soil P availability and AM colonization has been reported in many experiments (e.g. Jasper *et al.* 1979; Bååth & Spokes 1989). AM fungal density was also inversely related to extractable soil P during old-field succession (Johnson *et al.* 1991). The intensity of AM colonization is not directly linked to plant benefit, but may instead tell us something about the benefit to the fungi. It is apparently

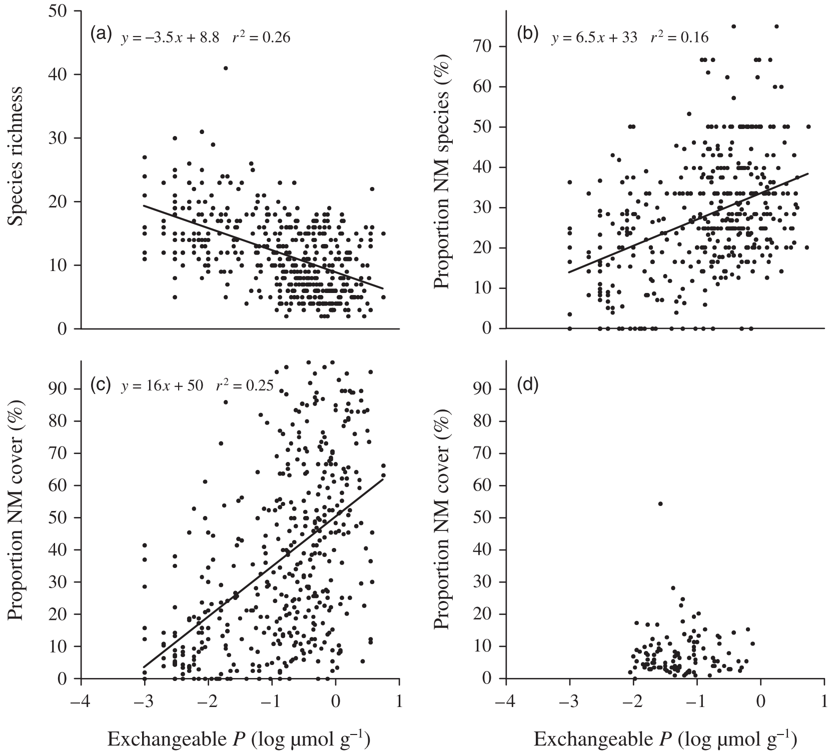

Fig. 2 The relationships of exchangeable P to plant species richness (a) and the relative occurrence of non-mycorrhizal species (NM) in rocky habitats. Non-mycorrhizal occurrence is shown both as the relative number of species (b) and the relative cover for both rocky (c) and meadow sites (d). All linear relationships shown are significant ($P < 0.001$).

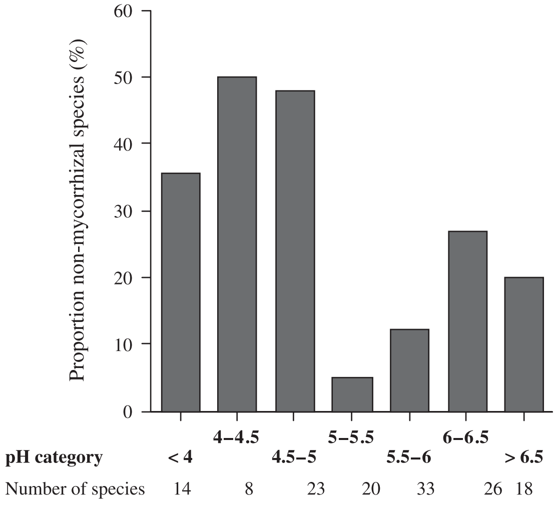

Fig. 3 The proportion of non-mycorrhizal species in different classes of average soil pH distribution for the 142 most common species in the rocky habitats (occurred in more than five of the 429 rocky sites).

not the soil P concentration itself that inhibits AM colonization, but a high P concentration in the roots (Sanders 1975; Menge *et al.* 1978). Fransson *et al.* (2003) showed a negative relation between soil P and AM colonization when acid grassland soils with varying contents of extractable P were used in a glasshouse study. Over a range of exchangeable P of 0.001–2.16 µmol g^{-1}, colonization of *P. lanceolata* by the indigenous AM fungi decreased from 80% at the lowest P levels to below 10% in some of the high P soils. It is therefore also likely that AM plants have less colonization in low pH rocky sites, as found for *P. lanceolata* both in the field and in a glasshouse experiment using limestone and acid soils (Van Aarle *et al.* 2003).

R. acetosella was clearly the most dominant species in acid rocky habitats. This is a non-mycorrhizal species that may be inhibited by the presence of AM fungal mycelium, even when competition from other plants is excluded (Francis & Read 1995). The most likely explanation is that the AM fungal mycelium depleted the P in the calcareous dune sand used, which restricted the growth of the non-mycorrhizal plant seedlings. *R. acetosella* is very dependent on exchangeable P and, in experimental systems, the P concentration in leaves of *R. acetosella* was more closely related to soil P than observed for *P. lanceolata* (Fransson *et al.* 2003). In contrast to *R. acetosella*, *P. lanceolata* is also common in grasslands and can grow over a very wide range of pH values.

Peat & Fitter (1993) found no relation between the occurrence of non-mycorrhizal species and soil fertility. However, P was not specifically considered in the fertility index they used, and it is likely that soil N levels were more important for the habitat classification in their study. N availability is probably less important in regulation of AM colonization as it is much more easily transported in soil solution than P (Marschner 1995). It has, for example, been shown that AM-mediated growth enhancement in

Allium schoenoprasum was reduced by application of P, but not by application of N (Bååth & Spokes 1989).

Plant species richness decreased with increasing exchangeable soil P in rocky habitats formed on acid rocks such as gneiss and granite. We have shown that such habitats support vegetation with a high proportion of non-mycorrhizal plants. Our results indicate that AM associations may be more important as a competitive strategy than as a tolerance strategy, particularly when the stress factor (Grime 1979) is other than a shortage of P. Many studies have pointed out the importance of AM associations for maintaining diversity and as a mediator of plant coexistence (Van der Heijden 2002; Hart *et al*. 2003). The dominance of highly competitive plant species may be reduced in the presence of AM fungi (Grime *et al*. 1987). The importance of AM fungi in mediating plant coexistence could be investigated by studying interactions between non-mycorrhizal and mycotrophic plant species under varying levels of disturbance and abiotic stress. We suggest that non-mycorrhizal plant species will coexist easier with mycotrophic species: (i) if there are no AM fungi present, (ii) under high stress when sufficient P is supplied, and (3) under high levels of disturbance.

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References

Allison, V.J. & Goldberg, D.E. (2002) Species-level versus community-level patterns of mycorrhizal dependence on phosphorus: an example of Simpson's paradox. *Functional Ecology*, **16**, 346–352.

Bååth, E. & Spokes, J. (1989) The effect of added nitrogen and phosphorus on mycorrhizal growth response and infection in *Allium schoenoprasum*. *Canadian Journal of Botany*, **67**, 3227–3232.

Baylis, G.T.S. (1975) The magnolioid mycorrhiza and mycotrophy in root systems derived from it. *Endomycorrhizas* (eds F.E. Sanders, B. Mosse & P.B. Tinker), pp. 373–389. Academic Press, London.

Bever, J.D. (1999) Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecology Letters*, **2**, 52–61.

Bever, J.D., Westover, K.M. & Antonovics, J. (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology*, **85**, 561–573.

Francis, R. & Read, D.J. (1994) The contribution of mycorrhizal fungi to the determination of plant community structure. *Plant and Soil*, **159**, 11–25.

Francis, R. & Read, D.J. (1995) Mutualism and antagonism in the mycorrhizal symbiosis, with special reference to impacts on plant community structure. *Canadian Journal of Botany*, **73** (Suppl. 1), S1301–S1309.

Fransson, A.-M., Van Aarle, I.M., Olsson, P.A. & Tyler, G. (2003) *Plantago lanceolata* L. & *R. acetosella* L. differ in their utilisation of soil phosphorus fractions. *Plant and Soil*, **248**, 285–295.

Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*, **250**, 26–31.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, Chichester.

Grime, J.P., Mackey, J.M.L., Hillier, S.H. & Read, D.J. (1987) Floristic diversity in a model system using experimental microcosms. *Nature*, **328**, 420–422.

Harley, J.L. & Harley, E.L. (1987) A check-list of mycorrhiza in the British flora. *New Phytologist* (Suppl.), **105**, 1–102.

Hart, M.M., Reader, R.J. & Klironomos, J.N. (2003) Plant coexistence mediated by arbuscular mycorrhizal fungi. *Trends in Ecology and Evolution*, **18**, 418–423.

Hartnett, D.C., Hetrick, B.A.D., Wilson, G.W.T. & Gibson, D.J. (1993) Mycorrhizal influence on intra- and inter-specific neighbour interactions among co-occurring prairie grasses. *Journal of Ecology*, **81**, 787–795.

Hartnett, D.C. & Wilson, G.W.T. (1999) Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology*, **80**, 1187–1195.

Hayman, D.S. & Tavares, M. (1985) Plant growth responses to vesicular-arbuscular mycorrhiza. XV. Influence of soil pH on the symbiotic efficiency of different endophytes. *New Phytologist*, **100**, 367–377.

Hetrick, B.A.D. (1991) Mycorrhizas and root architecture. *Experientia*, **47**, 355–362.

Hetrick, B.A.D., Kitt, D.G. & Wilson, G.T. (1988) Mycorrhizal dependence and growth habit of warm-season and cool-season tallgrass prairie plants. *Canadian Journal of Botany*, **66**, 1376–1380.

Janos, D.P. (1980) Vesicular-arbuscular mycorrhizae affect lowland tropical rainforest plant growth. *Ecology*, **61**, 151–162.

Jasper, D.A., Robson, A.D. & Abbott, L.K. (1979) Phosphorus and formation of vesicular-arbuscular mycorrhizas. *Soil Biology and Biochemistry*, **11**, 501–505.

Johnson, N.C. (1998) Responses of *Salsola kali* and *Panicum virgatum* to mycorrhizal fungi, phosphorus and soil organic matter: implications for reclamation. *Journal of Applied Ecology*, **35**, 86–94.

Johnson, N.C., Graham, J.H. & Smith, F.A. (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist*, **135**, 575–585.

Johnson, N.C., Zak, D.R., Tillman, D. & Pfleger, F.L. (1991) Dynamics of vesicular-arbuscular mycorrhizae during old field succession. *Oecologia*, **86**, 349–358.

Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67–70.

Klironomos, J.N. (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology*, **84**, 2292–2301.

Marschner, H. (1995) *Mineral Nutrition of Higher Plants*, 2nd edn. Academic Press, London.

Menge, J.A., Steirle, D., Bagyaraj, D.J., Johnsson, E.L.V. & Leonard, R.T. (1978) Phosphorus concentrations in plants responsible for inhibition of mycorrhizal infection. *New Phytolologist*, **80**, 575–578.

Moore, P.D. (1987) Distribution of mycorrhiza throughout the British flora. *Nature*, **327**, 100.

Newman, E.I. & Reddell, P. (1987) The distribution of mycorrhizas among families of vascular plants. *New Phytologist*, **106**, 745–751.

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.

O'Connor, P.J., Smith, S.E. & Smith, F.A. (2002) Arbuscular mycorrhizas influence plant diversity and community structure in a semiarid herbland. *New Phytologist*, **154**, 209–218.

Peat, H.J. & Fitter, A.H. (1993) The distribution of arbuscular mycorrhizas in the British flora. *New Phytologist*, **125**, 845–854.

Pirozynski, K.A. & Malloch, D.W. (1975) The origin of land plants: a matter of mycotrophism. *Biosystems*, **6**, 153–164.

Porter, W.M., Robson, A.D. & Abbott, L.K. (1987) Factors controlling the distribution of vesicular-arbuscular mycorrhizal fungi in relation to soil pH. *Journal of Applied Ecology*, **24**, 663–672.

Read, D.J. (1991) Mycorrhizas in ecosystem. *Experientia*, **47**, 376.

Read, D.J., Koucheki, H.K. & Hodgson, J. (1976) Vesicular-arbuscular mycorrhiza in natural vegetation systems. I. The occurrence of infection. *New Phytologist*, **77**, 641–653.

Redecker, D., Kodner, R. & Graham, L.E. (2000) Glomalean fungi from the Ordovician. *Science*, **289**, 1920–1921.

Remy, W., Taylor, T.N., Hass, H. & Kerp, H. (1994) Four hundred-million-year-old vesicular arbuscular mycorrhizas. *Proceedings of the National Academy of Sciences USA*, **91**, 11841–11843.

Sanders, F.E. (1975) The effect of foliar-applied phosphate on the mycorrhizal infections of onion roots. *Endomycorrhizas* (eds F.E. Sanders, B. Mosse & P.B. Tinker), pp. 261–276. Academic Press, London.

Simon, L., Bousquet, J., Levesque, R.C. & Lalonde, M. (1993) Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature*, **363**, 67–69.

Ström, L., Olsson, T. & Tyler, G. (1994) Differences between calcifuge and acidifuge plants in root exudation of low-molecular organic acids. *Plant and Soil*, **167**, 239–245.

Tester, M., Smith, S.E. & Smith, F.A. (1987) The phenomenon of 'nonmycorrhizal' plants. *Canadian Journal of Botany*, **65**, 419–431.

Tyler, G. (1992) Inability to solubilize phosphate in limestone soils – key factor controlling calcifuge habit of plants. *Plant and Soil*, **145**, 65–70.

Tyler, G. (1996) Soil chemistry and plant distribution in rock habitats of southern Sweden. *Nordic Journal of Botany*, **16**, 609–635.

Tyler, G. (2000) Integrated analysis of conditions accounting for intersite distribution of grassland plants. *Nordic Journal of Botany*, **20**, 485–500.

Tyler, G. & Olsson, P.A. (1993) The calcifuge behaviour of *Viscaria vulgaris*. *Journal of Vegetation Science*, **4**, 29–36.

Van Aarle, I.M., Olsson, P.A. & Söderström, B. (2002) Arbuscular mycorrhizal fungi respond to the substrate pH of their extraradical mycelium by altered growth and root colonization. *New Phytologist*, **155**, 173–182.

Van Aarle, I.M., Söderström, B. & Olsson, P.A. (2003) Growth and interactions of arbuscular mycorrhizal fungi in soils from limestone and acid rock habitats. *Soil Biology and Biochemistry*, **35**, 1557–1564.

Van der Heijden, M.G.A. (2002) Arbuscular mycorrhizal fungi as a determinant of plant diversity: in search for underlying mechanisms and general principles. *Ecological Studies*, **157**, 243–266.

Van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T. *et al.* (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, **396**, 72–75.

Vosatka, M., Batkhuugyin, E. & Albrechtova, J. (1999) Response of three arbuscular mycorrhizal fungi to stimulated acid rain and aluminium stress. *Biologia Plantarum*, **42**, 289–296.

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