University of Groningen

Nutritional soil heterogeneity and Mycorrhiza as determinants of plant species diversity

Ozinga, WA; van Andel, J; McDonnell-Alexander, Michael P

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

[Link to publication in University of Groningen/UMCG research database](#)

REVIEW

Nutritional soil heterogeneity and mycorrhiza as determinants of plant species diversity

WIM A. OZINGA, JELTE VAN ANDEL and
MICHAEL P. McDONNELL-ALEXANDER

*Laboratory of Plant Ecology, University of Groningen, PO Box 14, 9750 AA Haren,
The Netherlands*

CONTENTS

INTRODUCTION

Patterns in nutrient availability often vary both in space and time (e.g. Pegtel 1987; Stark 1994; Marschner 1995) and small differences can lead to large consequences in the ecophysiological responses and competitive abilities of plant species (Fitter 1982; Wedin & Tilman 1990; Grime 1994). Nevertheless the spatial scale and the degree of spatial heterogeneity and how this might differ among communities are poorly understood. Most plant individuals experience nutrient availability through their fungal partner. Different mycorrhiza types have some important ecological and physiological differences that may have important consequences for the competitive abilities of the associated plants. The impact of mycorrhiza networks relative to other mechanisms on the interaction between plant species remains unclear, but several experiments suggest a considerable influence, at least in some terrestrial ecosystems.

In this review, we will discuss causes and consequences of soil heterogeneity, at spatial scales ranging from individual plants to the level of plant communities, in view of their impact on competition and coexistence. A similar approach will be applied to the issue of effects of mycorrhizal fungi, asking the question whether they intensify interspecific competition or facilitate coexistence.

Nutritional soil heterogeneity

Soil heterogeneity at the spatial scale of individual plants is caused to a large extent by feedback mechanisms between plant and soil (Berendse & Elberse 1990; Wedin & Tilman 1990; Bever 1994; Gross *et al.* 1995). The main mechanisms responsible are interspecific differences in the rate of nutrient uptake and loss, and in the litter chemistry. Due to these feedback mechanisms between plant and soil it remains unclear to what extent soil heterogeneity is a cause or a consequence of heterogeneity in plant species composition. Recently models have been developed which explain species coexistence by resource heterogeneity at a spatial scale below the individual plant

(Huston & DeAngelis 1994). These models allow for the development of nutrient depletion zones around individual plant roots due to nutrient uptake in the roots from the soil solution.

Soil heterogeneity at the spatial scale of plant communities or ecosystems is frequently dealt with in terms of disturbance, as related to species richness. Destruction of vegetation and soil surface creates transient, open areas in which regeneration occurs. Which species from the regional species pool actually colonize an open area depends on the accessibility in space (pattern of surrounding populations, dispersal capacity) and time (longevity of seed banks). However, disturbance can take place at all spatial and temporal levels, but the mechanisms and consequences will differ per scale level (Van Andel & Van den Bergh 1987; Pickett *et al.* 1989). Disturbance at spatial scales below individual plants probably increases soil heterogeneity as experienced by plants, while at higher levels disturbance may level off the experienced soil heterogeneity (e.g. Robertson *et al.* 1993). However, the soil heterogeneity in the community may increase, depending on the kind and frequency of disturbances. The degree of soil heterogeneity is presumably largest at an intermediate level of disturbance, either in space or in time, because then environments from all successional stages will be present (Connell 1978; Grime 1979; Fox 1981; see Rosenzweig & Abramsky 1993 for a discussion).

The role of mycorrhizal partners

In most terrestrial ecosystems mycorrhizal associations between the roots of vascular plants and mycorrhizal fungi are the rule, non-mycorrhizal plants are the exception. Circa 10% of the terrestrial plant species examined do not associate with mycorrhizae (Harley & Smith 1983). In this review we focus on the three most widespread mycorrhizal types: vesicular–arbuscular mycorrhizae (VAM) and the more specialized ectomycorrhizae (ECM) and ericoid mycorrhizas (EM). The ecology of orchids and their mycorrhizal fungi (Dijk *et al.* 1997) will be reviewed in the next issue of this volume.

Most plant species form a relationship with VAM. This is by far the most abundant mycorrhiza type worldwide, but the number of fungal species is relatively low, less than 200 according to Allen *et al.* (1995). ECM occur mainly on woody plants and only occasionally on herbaceous and graminaceous plants (Harley & Harley 1987; Trappe 1987) and involve more than 5400 fungal species (Allen *et al.* 1995). ECM fungi have a higher C demand than VAM fungi, probably due to their more specialized morphology and physiology (Tinker *et al.* 1994). Very few plant species associate with both VAM and ECM, e.g. several species of *Populus*, *Salix*, *Alnus* (Lodge 1989; Lodge & Wentworth 1990; Chatarpaul *et al.* 1989). EM occur mainly in Ericales and are physiologically comparable with ECM. Non-mycorrhizal plants, such as many members of the Cruciferae, Chenopodiaceae, Polygonaceae, Caryophyllaceae (Harley & Harley 1987; Trappe 1987), occur mainly in very wet or saline ecosystems and in ecosystems with a high nutrient availability and/or with recently disturbed soil (Allen 1991; Peat & Fitter 1993).

Arnolds (1991) has pointed to the general decline of ectomycorrhizal fungi in Europe. In vegetation with a high degree of soil disturbance the density and species richness of mycorrhizal fungi is lower (Zak 1992; McLellan *et al.* 1995; Boerner *et al.* 1996; Bundrett *et al.* 1996), and more patchily distributed (Boerner *et al.* 1996). In dune grasslands with a relatively high degree of soil disturbance many facultative VAM plant species form less or no mycorrhizas (Ernst *et al.* 1984; Van Duin *et al.* 1991; Allen 1991).

In ecosystems with a lower degree of soil disruption, the germination and growth of non-mycorrhizal plant species are reduced indirectly through a more efficient nutrient uptake by mycorrhizal plants, but also more directly by the production of mycorrhizal fungi of substances that inhibit root growth of non-mycorrhizal plants (Francis & Read 1994). The favourable effect of disturbance on non-mycorrhizal plants is probably not only caused by changes in the relative availability of light and nutrients, but also by the destruction of mycorrhizal networks. Spatial heterogeneity in the degree of disturbance can create a mosaic of fungal infectivity inside a community dominated by mycorrhizal plants, thereby creating opportunities for establishment of non-mycorrhizal plants.

Mainly due to the narrow diameter of external fungal hyphae (*c.* 3 μm according to Read 1991) in comparison to plant roots, fungi are more precise and more efficient in the uptake of nutrients, especially nutrients with a low mobility (e.g. P and NH_4^+). For these nutrients, mycorrhiza can largely extend the depletion zones around plant roots allowing exploitation of a larger soil volume (Marschner & Dell 1994). The most frequently occurring mycorrhizal types differ largely in the nutrient pools which they can utilize and in the efficiency of nutrient uptake and transport.

The mycelia of mycorrhizal fungi can form networks which physically interlink individuals from different plant species (Francis & Read 1994; Finlay & Read 1986a; Newman 1988; Newman *et al.* 1994; Perry *et al.* 1989a; Eason *et al.* 1991). These networks may either contribute to specific competitive abilities or to coexistence of competing species, thus either counteracting or enhancing the effects of soil heterogeneity.

NUTRITIONAL SOIL HETEROGENEITY

Quantifying soil heterogeneity

Evaluation of the relative influence of soil heterogeneity on the interaction between plant species is complicated partly due to a lack of appropriate tools for quantifying spatial heterogeneity (Robertson & Gross 1994). Application of relatively new geostatistical methods enables a better quantification of spatial patterns in soil heterogeneity (Rossi *et al.* 1992). Spatial patterns can be examined by calculating the degree of autocorrelation between sample points over a range of distance intervals. This method is based on the premise that near neighbours are more likely to experience similar environmental conditions than do far neighbours. The degree of spatial dependence (patchiness) and the spatial scale (patch size) can be depicted graphically, as discussed by Rossi *et al.* (1992), and Robertson & Gross (1994), by means of a semivariogram. The degree of spatially dependent variance at the scale of interest can be indexed by the proportion of the population variance accounted for by structural (spatial dependent) variance (Robertson & Gross 1994).

Spatial dependent variability appears at different scales, as has been demonstrated for soil pH by Robertson & Gross (1994). Such patterns of multiple scaling of variability can be caused by a hierarchy of processes each operating at a different scale (cf. O'Neill *et al.* 1986; Beare *et al.* 1995). It is challenging to couple the patterns at each scale with the underlying processes. Geostatistical analyses revealed that the availability of nutrients in soils can vary greatly at spatial scales relevant to individual plants (Robertson *et al.* 1988; Jackson & Caldwell 1993; Robertson & Gross 1994; Gross *et al.* 1995). Jackson & Caldwell (1993) found in a sagebrush-steppe community over a ninefold average variation in NO_3^- availability and a threefold variation in P availability within a distance of 10 cm.

Soil heterogeneity cannot be measured independent of the vegetation, so it remains unclear to what extent the heterogeneity is a cause or a consequence of variation in species composition. Rosenzweig (1995) strongly suggests that the greater the number of species that coexist at the community level, the larger will be the number of niches they are forced to create. A further complication is the fact that the measured heterogeneity may differ from the heterogeneity as experienced by plants. If, for example, enzymes reach their maximum activity at high nutrient concentrations, data transformation with, e.g. a Michaelis–Menten function, may give a more realistic view of the relevant soil heterogeneity for plants, rather than the plant's response in terms of production (Stark 1994; Jackson & Caldwell 1996).

Individual plants experience soil heterogeneity mainly as heterogeneity in the limiting resource. Soil heterogeneity will in the present review be simplified to the spatial pattern in the availability of these limiting macronutrients, while recognizing that soil heterogeneity is also a relevant issue for micronutrients, toxic elements and soil physical conditions (see e.g. Hairiah 1992). For a more mechanistic understanding we need to know the factors that determine the dynamics of these nutrients at spatial scales relevant to the individual plant.

Nutrient availability and mobility

The availability and mobility of nutrients depend on physical and chemical processes in the soil. Changes in nutrient mobility affect the spatial scale and pattern of soil heterogeneity. The rate of diffusion in the soil strongly depends on the soil water content, as most of the diffusion takes place in the water phase. In dry soils the water phase is limited to the coating of soil particles, which enlarges the travelling distance to a plant root (Stark 1994). Probably, the depletion zones are much smaller in dry soils as compared to moist soils. As a result, plants in chalk grassland communities may experience a relatively high degree of soil heterogeneity at a small scale.

The competition intensity for a limiting resource depends on the degree of overlap between depletion zones of this nutrient for adjacent plant individuals (Robinson 1991). The degree of overlap between depletion zones depends on the length and slope of the concentration gradient (Huston & DeAngelis 1994) and on the morphology and physiology of the root system (Fitter 1994). The length and slope of the concentration gradient is amongst others, determined by the mobility of the nutrient (Stark 1994; Huston & DeAngelis 1994). Various nutrients differ largely in their diffusion coefficient and therefore in their mobility. NO_3^- is relatively mobile in comparison to other nutrients, assuming sufficient soil moisture. So, in soil with a low N availability individual plants may develop wide depletion zones around their roots, thereby strongly decreasing the nutrient availability for neighbouring plants rooting in the same soil volume. The plants will, therefore, experience a relatively high competition intensity. Phosphate in contrast is relatively immobile and the overlap in depletion zones will be much smaller and, consequently, the intensity of competition is probably lower in P limited plant communities. Under such circumstances coexistence between many plant species, limited by the same immobile nutrient, may be possible without competition for this nutrient.

When nutrients are lost from the plant as plant litter, interspecific differences in the chemical composition of plant tissues can influence the mineralization rate of plant litter at a spatial scale of individual plants (Hobbie 1992; Berendse et al. 1992; Berendse 1994; Van Breemen 1995; Van Oorschot 1996). In general the decay rate of organic matter

decreases as the proportion of C (especially lignin) increases relative to the N content (Melillo *et al.* 1982; Aber *et al.* 1990). Plants with a preference for soils with a high N availability often have a relatively high N tissue content (high N turnover: Berendse *et al.* 1992) and by that create positive feedbacks to N availability, often accelerated by herbivores because mineral-rich excretions enhance conditions for grazing by increased plant biomass and nutrient concentrations (Day & Detling 1990; Hobbie 1992; Hobbs 1996).

Root plasticity and nutrient depletion

The root system of plant species can respond to nutrient-rich patches with morpho-logical changes such as root proliferation (Jackson & Caldwell 1989; Campbell *et al.* 1991; Caldwell 1994; Fitter 1994) and physiological changes which enhance nutrient uptake capacity (Jackson *et al.* 1990) or through a response of their mycorrhizal partner (St John *et al.* 1983; Bending & Read 1995; Cui & Caldwell 1996). Morphological plasticity may be most useful to exploit patches, while relatively fast responses such as plasticity in elevated uptake kinetics may be especially important in pulse exploitation (Jackson & Caldwell 1996). The latter authors concluded from modelled nutrient uptake that root proliferation in many cases leads to only a small increase in NO_3^- uptake, but increased uptake kinetics can lead to a large increase in NO_3^- uptake. In contrast, root proliferation leads to a relatively important additional P uptake, while elevated uptake kinetics tended to be less important for P.

Nutrient uptake by plant roots causes a reduction in the nutrient concentration in the soil solution around the roots. For ions with a high mobility (e.g. NO_3^-, K^+) this may also lead to a decrease in the availability of this nutrient for neighbouring plants. A plant species growing in monoculture reduces the concentration of a certain nutrient in the soil solution to an equilibrium value called R^*. At R^* nutrient uptake and nutrient loss are exactly in balance. The species that can reduce the concentration of the limiting nutrient to the lowest value (lowest R^*) is the superior competitor for this nutrient (Tilman 1982, 1985; Wedin & Tilman 1990, 1993). The value of R^* depends on many morphological and physiological plant characters and can be regarded as a summarizing variable of these underlying plant traits. The nutrient uptake rate of an individual plant and the minimum concentration of nutrients to which the roots can deplete the external concentration is also of influence on the size of depletion zones. These differ between plant species and even genotypes within a given species (Marschner 1995).

Robinson (1991) states: 'If the selective influence exerted by competition for resources leads to the evolution in plants of certain phenotypic strategies, the depletion zones are the battlegrounds on which some of those strategies are put to the test. If competition for nutrients and water can shape the structure and dynamics of plant communities, it is clearly important to look at mechanisms by which the depletion zones created by roots come to interact with each other.'

Plants do, however, have opportunities to reduce the degree of overlap between nutrient depletion zones by 'spatial niche segregation' due to differences in root morphology. For example deep rooting plants can utilize nutrients which are not available for plants with a more superficial root system (Berendse 1979, 1982) and by that decrease the relative competition intensity. When inferior competitors have the ability to utilize nutrients from soil areas not exploited by other species, the probability of coexistence with better competitors increases.

The resource ratio model (Tilman 1982, 1985) allows stable coexistence between two plant species if each species is the better competitor for a different resource and if each species consumes relatively more of the resource that more limits its growth. This model thus requires a trade-off between the efficiency of uptake and use of the two resources. Stable coexistence between more species, with each species specialized on different resource ratios, requires spatial heterogeneity in the availability of the limiting resources on a spatial scale equal to or larger than the individual plants. However, the resource ratio hypothesis (Tilman 1985) assumes spatial homogeneity at the scale below individual plants because 'individual organisms can average resource supply rates and physical factors through time and through the region in which they forage' (Tilman & Pacala 1993). For nutrients with a high mobility this seems a reasonable assumption as indicated by field experiments where N was the resource limiting vegetation growth (Wedin & Tilman 1990, 1993; Wilson & Tilman 1993). When the vegetation is limited by less mobile nutrients (e.g. $H_2PO_4^-$ and in acid environments NH_4^+), the assumption of spatial homogeneity seems less realistic. Another important limitation of the resource ratio model is that even under a homogeneous distribution of the limiting nutrient the availability as experienced by individual plants is not the same for all the species, because some of the species have mechanisms for utilizing particular nutrient pools not available for other species. One of the most important mechanisms in this respect is probably the symbiosis with mycorrhiza, as will be discussed later. Finally, the model does not take into account interspecific differences in root morphology which may lead to spatial niche segregation.

The influence of aboveground factors

It is important to bear in mind that there is a strong interaction (or even a trade-off) between competition for nutrients and competition for light in most of the successional seres. The reactions of plants to nutrient-rich patches all consume energy, therefore the effectiveness of root systems in rapidly exploiting enriched patches is probably interrelated with the light consumption of photosynthetic organs (Caldwell 1994). In a field experiment in a shrub steppe community, Cui & Caldwell (1997) found that shading reduced the exploitation of P to a much greater degree in the patchy treatment than in the uniform treatment, whereas the reduction in uptake of the more mobile N varied little with nutrient distribution in both the light, and the shaded treatment. This suggests that a plant species which is a better competitor for light, can cause an indirect decline in the competitive ability for nutrients in neighbouring plants. Shading may be relatively disadvantageous for subordinate species with a high precision in nutrient exploitation.

Reduction of plant biomass inside a plant community (disturbance *sensu* Grime 1979) may be considered enhancing heterogeneity within a plant community, both in space and in time, thus creating opportunities for new species to become established (cf. Grubb 1977). Such small-scale disturbances can interfere directly with plant functioning by the destruction of plant tissue and/or the associated mycorrhizas, and more indirectly by a sudden change in the relative availability of open space, nutrients and light. A lower plant biomass should result in a lower competitive effect on other species, a higher resource availability to surviving plant individuals and hence in a lower competition intensity. A microcosm study by Grime *et al.* (1987) provided evidence that disturbance (in this case mimicking artificial grazing) is an important factor preventing competitive exclusion. From a field experiment, Wilson & Tilman (1993) found that the

total (above- and belowground) relative intensity of competition did not vary with productivity, but was significantly reduced by small-scale disturbance. Spatial heterogeneity in the degree of tissue loss (e.g. herbivory or mortality) has a different effect on the interaction between plant species as compared to more homogeneous tissue losses such as due to mowing (cf. Bakker 1989). Interspecific differences in tissue loss can potentially, like heterogeneity in resource availability, promote a higher species richness.

The regional scale determines which species are potentially capable of colonizing local habitats ('species pool concept', cf. Pärtel et al. 1996). Open space can be regarded as a factor which limits the potentials for germination, establishment and growth of plant species (Grime 1979; Bakker 1989; Tilman 1990, 1994; Bullock et al. 1995). Competition models that include colonization of open places can form a bridge between the spatial scale of individual plants and the regional scale. An attempt to link the spatial scale of individual plants with the regional scale is published by Tilman (1994) who has extended his resource ratio model to spatially subdivided habitats with homogeneous patches as large as adult individual plants. This 'spatial competition model' assumes three-way interspecific trade-offs between competitive ability, colonization capacity and longevity. Gleeson & Tilman (1990) found evidence for a strong trade-off between the N investment to the root system and the allocation to reproductive organs. Plant species with a high N allocation to the roots could reduce the soil concentrations of dissolved NH_4^+ and NO_3^- to significantly lower levels and outcompeted other species (Wedin & Tilman 1990, 1993). The high N allocation to the roots, however, goes at the expense of the colonization capacity. The poorest nitrogen competitors were the quickest colonizers of new areas (Tilman 1990). Coexistence then occurs because species that are inferior competitors have a higher colonization rate and can more rapidly fill an open portion of a habitat and/or have a lower mortality rate. Inferior competitors can survive in this habitat until superior competitors reach the patch and gradually displace the inferior competitor. The creation of new open gaps by local mortality and disturbance is the driving force in this model for survival of these inferior competitors at a regional scale. According to Tilman (1994) species diversity does not require large-scale disturbances, because individual mortality can create enough open gaps. We think, however, that this may lead to an underestimation of the impact of disturbance, because the model concentrates on sexual reproduction. For some species there may be a positive correlation between competitive abilities for nutrients and the ability to colonize neighbouring areas vegetatively by, e.g. stolons. Many clonal plant species are good competitors for nutrients and at the same time quickly colonize surrounding areas (De Kroon & Hutchings 1995). The size of an open area must be considered, because the number of plant individuals colonizing an open place by seed, probably increases with the size of the open patch (cf. Bullock et al. 1995).

Also for consideration is the role of inhibition by plants upon other individuals and species, affecting colonization and growth in neighbouring areas, and so reducing competition. Litter of many plant species, especially trees, is rich in complex polyphenolic substances (e.g. tannins, phenolic acids). These phenolic substances can inhibit the root growth and performance of seedlings already at millimolar concentrations. Plant species differ in their sensitivity to polyphenols. Especially in the early growth stages, grass species are in general less sensitive than dicotyledonous species (Kuiters 1990). The physiological mechanisms behind these growth inhibiting effects are poorly known. The uptake and translocation of some nutrients decrease (Kuiters 1990) causing a decrease in competitive ability for these nutrients (increase in R*). However,

Kuiters (1987) suggests that the growth inhibition at higher concentrations of phenolic acids (1 mM) results mainly from direct interference with metabolic processes. Part of the effect of phenolic substances on plant growth probably takes place indirectly through stimulatory or inhibitory effects on mycorrhizal fungi (Perry & Choquette 1987; Coté & Thibault 1988; Timbal *et al*. 1990; Baar *et al*. 1994). Not only in this respect, but also with regard to plant nutrition, the role of mycorrhiza upon the competition and coexistence of plants is potentially of great importance.

MYCORRHIZA

Mycorrhiza plant interactions

The establishment of mycorrhizal plants in open habitats may be not only limited by the accessibility for the plant species but also by the colonization capacity of mycorrhizal fungi. Many ECM fungal species can form sexual spores in epigeous fruit bodies which are potentially capable of long-distance transport by wind. While in contrast VAM fungi are thought to reproduce exclusively by relatively heavy asexual clamydospores and hyphal fragments and probably have a much lower colonization capacity, most species probably arrive by animal or soil transport (Allen 1991; Malloch & Blackwell 1992). Waalend & Allen (1987) and Boerner *et al*. (1996) found, in a chronosequence after disturbance, no evidence that predisturbance levels of VAM infection intensity would be re-established during the first 25–30 years of succession. In contrast ECM infectiveness and species diversity increase more steadily after soil disturbance (Visser 1995; Boerner *et al*. 1996) or during primary succession (Deacon *et al*. 1983; Last *et al*. 1987; Helm *et al*. 1996). After establishment of an ECM plant, mycorrhiza formation depends on the concentration of nutrient supply (Kamminga-Van Wijk *et al*. 1992). Although the rate of mycorrhiza growth may negatively correlate with the benefit for the plant, the association with host specific ECM fungal species may create a positive feedback. Seedlings from this species get enough C from mature trees to maintain a positive C-balance (Read *et al*. 1985; Yasman 1995) and are in contrast to many other species able to survive under shaded conditions. By an increase in dominance of the ECM plant, the ECM fungi receive more C and can extend their mycelium and spread from living root to living root. Due to the efficient exploitation of a larger soil volume by the fungi the chance of interconnecting on the common mycorrhiza network increases and the mycorrhizas can transport more nutrients to the trees (Perry *et al*. 1989b; Perry *et al*. 1992). The degree of overlap between depletion zones of mycelia from VAM and ECM fungi will, at least in some communities, be reduced by spatial niche segregation. For example, Reddell & Malajczuk (1984) found that *Eucalyptus* roots form ECM in the litter horizon and VAM in the mineral soil below.

Cui & Caldwell (1996) compared the effect of VAM on the nutrient uptake from soils with homogeneous or heterogeneous nutrient availability. VAM increased plant ^{32}P uptake more in nutrient-rich patches than in soils with a uniform P distribution. Even though the increase of local root density in enriched patches was less for mycorrhizal plants than for non-mycorrhizal plants, the effectiveness in P uptake from the soil patches was much higher in mycorrhizal plants. In contrast, the plant $^{15}NO_3^{-}$ acquisition was not affected by either VAM or the N distribution pattern. VAM fungi are presumably especially efficient in the uptake of inorganic P (Gianinazzi-Pearson & Gianinazzi 1989; Marschner & Dell 1994; Cui & Caldwell 1996), while ECM and EM

are more efficient in N limited ecosystems (Read *et al.* 1989; Read 1991). In contrast to VAM fungi, some ECM and EM fungi have abilities to take up N from organic matter and to translocate these nutrients to their host plant (Bajwa *et al.* 1985; Abuzinadah & Read 1986, 1989a,b; Finlay *et al.* 1992; Bending & Read 1995). Enzymatic degradation by ECM and EM fungi has been shown for proteins (Bajwa *et al.* 1985; Abuzinadah & Read 1986, 1989a; Keller 1996), cellulose (Dighton *et al.* 1987), chitin (Leake & Read 1990), lignin (Haselwandter *et al.* 1990; Perotto *et al.* 1997). EM fungi are capable of decomposing even more recalcitrant litter than ECM fungi (Read 1991). Most ECM fungi develop a massive sheath around plant roots which covers a large surface area of the root tips. This sheath has been shown to have important storage capacity for nutrients (Harley & Smith 1983; Högberg *et al.* 1996). This may be a selective advantage in nutrient poor ecosystems with distinct nutrient pulses (e.g. by litter decomposition). It is not clear to what extent compact VAM fungi have storage capacities for nutrients. Through their mycorrhizal partner, ECM and EM plants may be able to utilize an important nutrient pool which is not directly available to non-mycorrhizal and VAM plants, and so have an advantage as regards this nutrient source. Bending & Read (1995) demonstrated that in growth chambers there was a rapid colonization and exploitation by ECM hyphae of introduced patches of organic matter from the fermentation horizon of a pine-forest, which was associated with enhancement of N supply to the ECM plant. Attempts to induce such ECM mycelial proliferation by localized application of NH_4^+ or P were not successful.

Changes in the proportion of nutrients in inorganic or organic form may create changes in the competitive abilities provided by the different mycorrhiza types. For example, an increase in the relative availability of inorganic N will weaken the selective advantages previously obtained by EM and ECM fungi, and lead to more suitable conditions for VAM plant species. This can explain the strong increase of VAM plants such as *Molinia caerulea* and *Deschampsia flexuosa* in many heathland ecosystems experiencing a high deposition of atmospheric nitrogen. The recent increase of *Acer* spp. in many eutrophicated forests in The Netherlands may also be explained at least partly by such a mechanism. The relatively high N content in *Acer* leaves probably favours the decomposition conditions of their litter (Kuiters 1990), thus creating an even more suitable environment for VAM plants (cf. Kuyper 1990; Newman 1991; Read 1991).

Mycorrhizal fungi not only play an important role in plant nutrition; they can also fulfil other functions which may be important for plant survival in the long term. Some species with a compact structure increase resistance against pathogens (Duchesne *et al.* 1988), heavy metals (Dueck *et al.* 1986; Wilkins 1991) and polyphenolic substances (Giltrap 1982). Newsham *et al.* (1995a,b) suggest a trade-off between protecting functions (compact structure) and efficiency of nutrient uptake. There are large interspecific differences in the degree in which various fungal species fulfil the different functions for their plant partner (Bruns 1995). For example, Abuzinadah & Read (1986, 1989a) and Keller (1996) found high interspecific differences in the ability to use various proteins as a nitrogen source, between various ECM fungal species. While ECM plant communities worldwide tend to be low in plant species diversity, the fungal species richness is in general high (Allen *et al.* 1995). During vegetation succession on nutrient poor soils, the proportion of N and P bound in organic form can increase, as with allelopathic substances and pathogen concentrations. Hence, during succession on nutrient poor soils, the benefit for plants of C allocation to the relatively expensive ECM and EM probably increases (Francis & Read 1994).

Interspecific mycorrhizal networks: their role in plant competition and coexistence

Mycorrhizal linkages can transport ^{15}N and ^{32}P within and between plant species (Chiarello *et al.* 1982; Finlay & Read 1986b; Finlay *et al.* 1988). This mainly regards nutrients from dying roots (Newman 1988; Eason *et al.* 1991), thus N and P will be transported through a shorter route to the plant species which are incorporated in the mycorrhizal network. Furthermore Perry *et al.* (1989a, 1992) have demonstrated that a nutrient surplus in certain plant species ('luxury consumption') can be transported to other species by the mycorrhizal fungus. So, mycorrhizal networks may lead to a levelling out of the heterogeneity in nutrient availability as experienced by plants. We are, however, not aware of experiments which quantified the effect of mycorrhizal networks on the degree and scale of nutrient heterogeneity. As the mean diameter of individual fungal mycelia increases during vegetation succession (e.g. Dahlberg 1991, 1995), the spatial scale of heterogeneity in mycorrhizal partners for plants increases. In general ECM fungi have larger mycelia as compared to VAM fungi, which in many species become organized into rhizomorphs, with a large diameter (*c.* 100 μm), making rapid transport of C and nutrients over long distances possible (Marschner 1995). Finlay & Read (1986b) report P transport via ECM mycelial strands over several metres.

The relative plant C allocation to mycorrhizas is probably largest under nutrient poor conditions with a low frequency and intensity of soil disruption (cf. Read 1991; Wallander & Nylund 1992; Tinker *et al.* 1994; Boerner *et al.* 1996), so in these ecosystems mycorrhizas may have a relatively high influence (e.g. VAM in P limited grasslands on calcareous soils and ECM in forest where most N is available in organic form). Differences in the nutrient source utilized by the different mycorrhiza types may create positive feedbacks between plant species, litter quality and mycorrhiza type. For example, shoots of EM plants often contain very large amounts of lignin and complex polyphenolic substances which immobilize much of the nitrogen and inhibit mineralization (Leake *et al.* 1989). Furthermore, the high concentrations of polyphenols inhibit the growth of other plants and fungi (Jalal & Read 1983). In ecosystems with a low availability of inorganic nutrients this may lead to a dominance of EM plants such as *Calluna, Erica, Empetrum* and *Vaccinium* species.

From an experiment with microcosms, Grime *et al.* (1987) found that, in plant communities which were allowed to develop from seeds on nutrient-poor sand, it appeared that through a mycorrhizal network ^{14}C could be translocated from the dominant to subordinate species. This led to an increase in biomass of the inferior competitors, at the expense of the biomass of the dominant and the non-mycorrhizal plant species. Inoculation with VAM caused an increase in plant species diversity in the same order of magnitude as artificial herbivory. When plants receiving carbon become more shaded, they take up more ^{14}C (Read *et al.* 1985; Finlay & Read 1986a). Apparently light-limited plants form a stronger 'sink' for carbohydrates from the common mycorrhizal network. Consequently, the redistribution of C and/or nutrients from dominant plant species to inferior competitors, by interspecific mycorrhiza networks can increase the species richness of the vegetation. In the long term, mycorrhizas can prevent the exclusion of inferior competitors with the ability to 'plug into' common mycorrhiza networks and thereby facilitate coexistence.

ECM are in general more host specific than VAM (Harley & Harley 1987; Trappe 1987). Some ECM fungi form mycorrhiza with only one or a few related plant species

or genera (e.g. some fungal species from the genera *Boletus, Russula, Lactarius, Cortinarius*). Only a very limited number of plant species are capable of interconnecting with such a mycorrhizal network. However, in many cases, especially for ECM plants, an individual plant is associated with a number of different fungal species (Allen 1991) probably forming multiple networks.

In the field, Newman & Reddell (1988) and Gange *et al.* (1993) showed that the presence of VAM can lead to a higher plant species richness. However, due to their higher host specificity, ECM fungi may in general lead to a lower plant species diversity than VAM fungi. Experimental evidence for this 'mycorrhiza hypothesis' is lacking, but Alexander (1989) and Connell & Lowman (1989) found some support for this in tropical forest areas, where both VAM and ECM trees occur. In general, tropical forest dominated by VAM trees has a very high richness of tree species. Low diversity tropical forests, which have one single ECM species dominant with 50–100% of the canopy trees, occur in each of the major world regions of rain forest, as reported by Alexander (1989), and Connell & Lowman (1989). The species richness of these forests comes largely from understorey VAM plant species. This may also offer an alternative explantation for the dominance of only a few ECM tree species in boreal and temperate forests (e.g. *Quercus, Fagus, Betula, Pinus, Picea, Pseudostuga*) but in these regions there are no VAM forest counterparts available for comparison.

In circumstances where relatively few plant species benefit more from VAM association than the co-occurring plant species, the presence of VAM may increase the dominance of these species (Hetrick *et al.* 1989; Hartnett *et al.* 1993, 1994), which even may bring about a reduction in plant species diversity (Bergelson & Crawley 1988). This may be the case in a minority of vegetation types with a high proportion of non-mycorrhizal and facultative VAM plant species. A reduction of plant species diversity may also result from a more host specific ECM fungal species which interconnects only a few of the plant species.

The presence of mycorrhizas has been shown to change the outcome of plant competition experiments in many cases, both for VAM plants (e.g. Allen & Allen 1990; Hartnett *et al.* 1993) and for ECM plants (Perry *et al.* 1989b, 1992). Most studies on the impacts of mycorrhizal fungi on plant competition and coexistence, however, have concentrated on combinations of individuals from two plant species grown in the laboratory and inoculated with only one fungal species. The role of mycorrhizas under field conditions and at the community level is largely unknown. There are very few experiments dealing with plant competition as influenced by different mycorrhiza types. In germination experiments, the presence or absence of mycorrhizas may have an important impact on the outcome. Experimental conditions without mycorrhizas may lead to an underestimation of the performance of mycorrhizal plant species, for conditions in which mycorrhiza networks naturally occur.

CONCLUDING REMARKS

In his almost classical work, Weaver (1958a,b) showed the ecological significance of rooting patterns at the level of plant species adapted to different ecosystems. Apart from variability in root characteristics among ecosystems, within-system environmental heterogeneity came into focus as a factor affecting competition and coexistence in plant communities (e.g. Fitter 1982). Recently, Stuefer (1996) reviewed and evaluated the concept of environmental (or habitat) heterogeneity in view of the responses of clonal

plants. He has shown that habitat heterogeneity encompasses very different phenomena, each offering specific opportunities for plants to respond. He elaborated the concept by distinguishing between scale (dimensions of patches in space or time), contrast (the degree of difference between patches), aggregation (clumped, regular, random), predictability (of scales and frequencies) and spatial covariance (with regard to heterogeneity in availability of different resources). Structural heterogeneity in environmental conditions should be compared with the scales of perception of heterogeneity by plants (the lower and higher limits of which are called 'grain' and 'extent', respectively), to detect functional responses. How can all these aspects be made applicable to our understanding of, for example, the role of competition in structuring plant communities and giving an impetus to vegetation succession (cf. Van Andel et al. 1993).

In the present review, we focused on spatial heterogeneity in soil macronutrients, while also recognizing the importance of heterogeneity in other resources and in abiotic environmental conditions. In the first part we reviewed current insight in causes and consequences of soil heterogeneity, from individual plants to the level of plant communities. In the second part we brought into play the role of mycorrhizal fungi. In this section, we arrive at the meeting point between the two approaches.

For plants without mycorrhiza the perception of spatial heterogeneity in nutrients depends largely on the mobility of the nutrients. Plants can exploit patches of inorganic phosphate by root proliferation and by mycorrhizal uptake. Available nitrate is being exploited by increasing the uptake in a physiological way, in addition to morphological root proliferation. At first glance one may think that the effect of the lower mobility of inorganic phosphate compared to nitrate may be compensated for by VAM fungi. However, VAM appeared to increase P uptake by plants more in nutrient-rich patches than in soils with a more uniform P distribution. These results suggest that heterogeneous availability of inorganic phosphate, as well as nitrate, is possibly advantageous for many plant species.

Quite another problem is whether one plant species is more adapted to environmental heterogeneity than another plant species, and whether competing plants may coexist under such conditions. Several models on resource competition strongly suggest that heterogeneity, both in resources and in conditions, enhances the changes for coexistence, compared to emphasis on competitive exclusion under homogeneous (equilibrium) conditions. Do mycorrhizal associations further contribute to coexistence of plant species by enlarging niche differences or do they counteract the environmental heterogeneity by creating common networks? It is possible to only tentatively start to answer this question. Host specificity, which is relatively rare, may lead to exploration of specific resources, thus increasing the plant's chance to survive and to outcompete cooccurring species. Common networks of VAM, on the other hand, have shown that subordinate species are capable of gaining carbon from dominant species, resulting in an increase of species richness as compared to non-VAM plant cultures. In general, we estimate, mycorrhizal associations can contribute to the species richness of plant communities by counteracting competitive exclusion, thus further enhancing effects of heterogeneous availability of limiting macronutrients. Only in species-poor plant communities, where just a few species benefit from mycorrhizal associations, may non-mycorrhizal species possibly be outcompeted and their abundance decrease.

Further understanding of the mechanisms involved in the fine-tuned balance between competition and coexistence in plant communities depends on further bridging the gap

in knowledge between the levels of the individual plant and the plant community, along with awareness of the potential importance of intermediate levels of plant organization and factors affecting it (cf. Zobel & Moora 1997). The notion of limiting factors, for example, refers to productivity of biomass at the plant community level, whereas it is a condition for species richness. Multiple limitation by nitrogen, phosphorus and potassium, measured at the plant community level, contributes to species richness only if the component plant species are, indeed, differently limited by these nutrients. The ecological relevance of environmental heterogeneity, in this respect, largely depends on the scale of perception of the individual plants. The role of mycorrhizal fungi in upscaling the area of perception is well known for individual plants, but the consequences for perceiving heterogeneity at the level of the plant community can hardly be estimated. It is remarkable that research on within-species variability, at the population level, is almost out of the scope of current interests as far as the response to environmental heterogeneity is concerned, while such a type of research could contribute to a better estimate of, for example, the relevant scale and the evolutionary potential of species.

REFERENCES

Aber, J.D., Melillo, J.M. & McClaugherty, C.A. (1990): Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can. J. Bot.* **68:** 2201–2208.

Abuzinadah, R.A. & Read, D.J. (1986): The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. I. Utilization of peptides and proteins by ectomycorrhizal fungi. *New Phytol.* **103:** 481–493.

Abuzinadah, R.A. & Read, D.J. (1989a): The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. IV. The utilization of peptides by birch (*Betula pendula* L.) infected with different mycorrhizal fungi. *New Phytol.* **111:** 55–60.

Abuzinadah, R.A. & Read, D.J. (1989b): The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. V. Nitrogen transfer in birch (*Betula pendula*) grown in association with mycorrhizal and non-mycorrhizal fungi. *New Phytol.* **112:** 61–68.

Alexander, I.J. (1989): Mycorrhizas in tropical forests. In: Proctor, J. (ed.): *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*, pp. 169–188. Blackwell Scientific Publications, Oxford.

Allen, M.F. (1991): *The Ecology of Mycorrhizae.* Cambridge University Press, Cambridge.

Allen, E.B. & Allen, M.F. (1990): The mediation of competition by mycorrhizae in successional and patchy environments. In: Grace J.B. & Tilman, D. (eds): *Perspectives on Plant Competition.* Academic Press, London.

Allen, E.B., Allen, M.F., Helm, D.J., Trappe, J.M., Molina, R. & Rincon, E. (1995): Patterns and regulation of mycorrhizal plant and fungal diversity. *Plant Soil* **170:** 47–62.

Arnolds, E. (1991): Decline of ectomycorrhizal fungi in Europe. *Agric. Ecosyst. Environm.* **35:** 209–244.

Baar, J., Ozinga, W.A., Sweers, I.L. & Kuyper, Th.W. (1994): Stimulatory and inhibitory effects of needle litter and grass extracts on the growth of some ectomycorrhizal fungi *Soil Biol. Biochem.* **26:** 1073–1079.

Bajwa, R., Abuarghub, S. & Read, D.J. (1985): The biology of mycorrhiza in the Ericaceae. X. The utilization of proteins and the production of proteolytic enzymes by the mycorrhizal endophyte and by mycorrhizal plants. *New Phytol.* **101:** 469–486.

Bakker, J.P. (1989): *Nature Management by Grazing and Cutting.* Kluwer Academic Publishers, Dordrecht.

Beare, M.H., Coleman, D.C., Crossley Jr, D.A., Hendrix, P.F. & Odum, E.P. (1995): A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant Soil* **170:** 5–22.

Bending, G.D. & Read, D.J. (1995): The structure and functioning of the vegetative mycelium of ectomycorrhizal plants. V. Foraging behaviour and translocation of nutrients from exploited litter. *New Phytol.* **130:** 401–409.

Berendse, F. (1979): Competition between plant populations with different rooting depths. I. Theoretical considerations. *Oecologia* **43:** 19–26.

Berendse, F. (1982): Competition between plants with different rooting depths. III. Field experiments. *Oecologia* **53:** 50–55.

Berendse, F. (1994): Litter decomposability—a neglected component of plant fitness. *J. Ecol.* **82:** 187–190.

Berendse, F. & Elberse, W.Th. (1990): Competition and nutrient availability in heathland and grassland ecosystems. In: Grace, J.B. & Tilman, D. (eds): *Perspectives on Plant Competition*, pp. 93–116. Academic Press, London.

Berendse, F., Elberse, W.Th. & Geerts, R.H.M.E. (1992): Competition and nitrogen losses from plants in grassland ecosystems. *Ecology* **73:** 46–53.

Bergelson, J.M. & Crawley, M.J. (1988): Mycorrhizal infection and plant species diversity. *Nature* **334:** 202.

Bever, J.D. (1994): Feedback between plants and their soil communities in an old field community. *Ecology* **75:** 1965–1977.

Boerner, R.E.J., De Mars, B.G. & Leicht, P.N. (1996): Spatial patterns of mycorrhizal infectiveness of soils along a successional chronosequence. *Mycorrhiza* **6:** 79–90.

Bruns, T.D. (1995): Thoughts on the processes that maintain local species diversity of ectomycorrhizal fungi. *Plant Soil* **170:** 63–73.

Bullock, J.M., Clear Hill, B., Silvertown, J. & Sutton, M. (1995): Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos* **72:** 273–282.

Bundrett, M.C., Ashwath, N. & Jasper, D.A. (1996): Mycorrhizas in the Kakadu region of tropical Australia. II. Propagules of mycorrhizal fungi in disturbed habitats. *Plant Soil* **184:** 173–184.

Caldwell, M.M. (1994): Exploiting nutrients in fertile soil microsites. In: Caldwell, M.M. & Pearcy, R.W. (eds): *Exploitation of Environmental Heterogeneity by Plants*, pp. 325–347. Academic Press, London.

Campbell, B.D., Grime, J.P. & Mackey, J.M.L. (1991): A trade-off between scale and precision in resource foraging. *Oecologia* **87:** 532–538.

Chatarpaul, L., Chakravarty, P. & Subramaniam, P. (1989): Studies in tetrapartite symbioses. *Plant Soil* **118:** 145–150.

Chiarello, N., Hickman, J.C. & Mooney, H.A. (1982): Endomycorrhizal role for interspecific transfer of phosphorus in a community of annual plants. *Science* **217:** 941–943.

Connell, J.H. (1978): Diversity in tropical rain forests and coral reefs. *Science* **199:** 1302–1310.

Connell, J.H. & Lowman, M.D. (1989): Low-diversity tropical rain forests: some possible mechanisms for their existence. *Am. Nat.* **134:** 88–119.

Coté, J.-F. & Thibault, J.-R. (1988): Allelopathic potential of raspberry foliar leachates on growth of ectomycorrhizal fungi associated with black spruce. *Am. J. Bot.* **75:** 966–970.

Cui, M. & Caldwell, M.M. (1996): Facilitation of plant phosphate acquisition by arbuscular mycorrhizas from enriched soil patches. I. Roots and hyphae exploiting the same volume of soil. *New Phytol.* **133:** 453–460.

Cui, M. & Caldwell, M.M. (1997): Shading reduces exploitation of soil nitrate and phosphate by *Agropyron desertorum* and *Artemisia tridentata* from soils with patchy and uniform nutrient distributions. *Oecologia* **109:** 177–183.

Dahlberg, A. (1991): *Ectomycorrhiza in coniferous forest: structure and dynamics of populations and communities.* PhD thesis, Uppsala University.

Dahlberg, A. (1995): Spatiotemporal patterns in ectomycorrhizal populations. *Can. J. Bot.* **73:** 1222–1230.

Day, T.A. & Detling, J.K. (1990): Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* **71:** 180–188.

Deacon, J.W., Donaldson, S.J. & Last, F.T. (1983): Sequences and interactions of mycorrhizal fungi on birch. *Plant Soil* **71:** 257–262.

De Kroon, H. & Hutchings, M.J. (1995): Morphological plasticity in clonal plants: the foraging concept reconsidered. *J. Ecol.* **83:** 143–152.

Dighton, J., Thomas, E.D. & Latter, P.M. (1987): Interactions between tree roots, mycorrhizas, a saprotrophic fungus and the decomposition of organic substrates in a microcosm. *Biol. Fert. Soils* **4:** 145–150.

Dijk, E., Willems, J.H. & Van Andel, J. (1997): Nutrient responses as a key factor to the ecology of orchid species. *Acta Bot. Neerl.* **46:** in press.

Dueck, T.A., Visser, P., Ernst, W.H.O. & Schat, H. (1986): Vesicular–arbuscular mycorrhizae decrease zinc-toxicity to grasses growing in zinc-polluted soil. *Soil Biol. Biochem.* **18:** 331–333.

Duchesne, L.C., Peterson, R.L. & Ellis, B.E. (1988): Pine root exudate stimulates the synthesis of antifungal compounds by the ectomycorrhizal fungus *Paxillus involutus*. *New Phytol.* **108:** 471–476.

Eason, W.R., Newman, E.I. & Chuba, P.N. (1991): Specificity of interplant cycling of phosphorus: The role of mycorrhizas. *Plant Soil* **137:** 267–274.

Ernst, W.H.O., Van Duin, W.E. & Oolbekking, G.T. (1984): Vesicular–arbuscular mycorrhiza in dune vegetation. *Acta Bot. Neerl.* **33:** 151–160.

Finlay, R.D. & Read, D.J. (1986a): The structure and function of the vegetative mycelium of ectomycorrhizal plants. I. Translocation of ^{14}C-labelled carbon between plants interconnected by a common mycelium. *New Phytol.* **103:** 143–156.

Finlay, R.D. & Read, D.J. (1986b): The structure and function of the vegetative mycelium of ecto-mycorrhizal plants. II. The uptake and distribution of phosphorus by mycelial strands interconnecting host plants. *New Phytol.* 103: 157–165.

Finlay, R.D., Ek, H., Odham, G. & Söderström, B. (1988): Mycelial uptake, translocation and assimilation of nitrogen from ^{15}N-labelled ammonium by *Pinus sylvestris* plants infected with four different ectomycorrhizal fungi. *New Phytol.* 110: 59–66.

Finlay, R.D., Frostegård, A. & Sonnerfeldt, A.-M. (1992): Utilization of organic and inorganic nitrogen sources by ectomycorrhizal fungi in pure culture and in symbiosis with *Pinus contora* Doug. ex Loud. *New Phytol.* 120: 105–115.

Fitter, A.H. (1982): Influence of soil heterogeneity on the coexistence of grassland species. *J. Ecol.* 70: 139–148.

Fitter, A.H. (1994): Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In: Caldwell, M.M. & Pearcy, R.W. (eds): *Exploitation of Environmental Heterogeneity by Plants*, pp. 305–323. Academic Press, London.

Fox, J.F. (1981): Intermediate levels of disturbance maximize alpine plant diversity. *Nature* 293: 564–565.

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

Gange, A.C., Brown, V.K. & Sinclair, G.S. (1993): Vesicular–arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. *Funct. Ecol.* 7: 616–622.

Gianinazzi-Pearson, V. & Gianinazzi, S. (1989): Phosphorus metabolism in mycorrhizas. In: Boddy, L., Marchant, R. & Read, D.J. (eds): *Nitrogen, Phosphorus and Sulphur Utilization by Fungi*, pp. 227–241. Cambridge University Press, Cambridge.

Giltrap, N.J. (1982): Production of polyphenol oxidases by ectomycorrhizal fungi with special reference to *Lactarius* spp. *Trans. Br. Mycol. Soc.* 78: 75–81.

Gleeson, S.K. & Tilman, D. (1990): Allocation and the transient dynamics of succession on poor soils. *Ecology* 71: 1144–1155.

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

Grime, J.P. (1994): Role of plasticy in exploiting environmental heterogeneity. In: Caldwell, M.M. & Pearcy, R.W. (eds): *Exploitation of Environmental Heterogeneity by Plants*, pp. 1–19. Academic Press, London.

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

Gross, K.L., Pregitzer, K.S. & Burton, A.J. (1995): Spatial variation in nitrogen availability in three successional plant communities. *J. Ecol.* 83: 357–367.

Grubb, P.J. (1977): The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107–145.

Hairiah, K. (1992): *Aluminium tolerance of Mucuna, a tropical leguminous cover crop.* PhD thesis, University of Groningen.

Harley, J.L. & Harley, E.L. (1987): A checklist of mycorrhiza in the British flora. *New Phytol.* 105 (Supplement): 1–102.

Harley, J.L. & Smith, S.E. (1983). *Mycorrhizal Symbiosis.* Academic Press, London/New York.

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

Hartnett, D.C., Samenus, R.J., Fischer, L.E. & Hetrick, B.A.D. (1994): Plant demographic responses to mycorrhizal symbiosis in tallgrass prairie. *Oecologia* 99: 21–26.

Haselwandter, J., Bobleter, O. & Read, D.J. (1990): Utilization of lignin by ericoid and ectomycorrhizal fungi. *Arch. Microbiol.* 153: 352–354.

Helm, D.J., Allen, E.B. & Trappe, J.M. (1996): Mycorrhizal chronosequence near Exit Glacier, Alaska. *Can. J. Bot.* 74: 1496–1506.

Hetrick, B.A.D., Wilson, G.W.T. & Hartnett, D.C. (1989): Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. *Can. J. Bot.* 67: 2608–2615.

Hobbie, S.E. (1992): Effects of plant species on nutrient cycling. *TREE* 7: 336–339.

Hobbs, N.T. (1996): Modification of ecosystems by ungulates. *J. Wildl. Manage.* 60: 695–713.

Högberg, P., Högbom, L., Schinkel, H., Högberg, M., Johannisson, C. & Wallmark, H. (1996): ^{15}N abundance of surface soils, roots and mycorrhizas in profiles of European forest soils. *Oecologia* 108: 207–214.

Huston, M.A. & DeAngelis, D.L. (1994): Competition and coexistence: the effects of resource transport and supply rates. *Am. Nat.* 144: 954–977.

Jackson, R.B. & Caldwell, M.M. (1989): The timing and degree of root proliferation in fertile soil microsites for three cold-desert perennials. *Oecologia* 81: 149–153.

Jackson, R.B. & Caldwell, M.M. (1993): The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* **74**: 612–614.

Jackson, R.B. & Caldwell, M.M. (1996): Integrating resource heterogeneity and plant plasticity: modelling nitrate and phosphate uptake in a patchy soil environment. *J. Ecol.* **84**: 891–903.

Jackson, R.B., Manwaring, J.H. & Caldwell, M.M. (1990): Rapid physiological adjustment of roots to localized soil enrichment. *Nature* **344**: 58–60.

Jalal, M.A.F. & Read, D.J. (1983): The organic acid composition of *Calluna* heathland soil with special reference to phyto- and fungi-toxicity. I. Isolation and identification of organic acids. *Plant Soil* **70**: 257–272.

Kamminga-Van Wijk, C., Prins, H.B.A. & Kuiper, P.J.C. (1992): Mycorrhizal and non-mycorrhizal Douglas fir grown in hydroculture. The effect of nutrient concentration on the formation and functioning of mycorrhiza. *Acta Bot. Neerl.* **41**: 481–495.

Keller, G. (1996): Utilization of inorganic and organic nitrogen sources by high-subalpine ectomycorrhizal fungi of *Pinus cembra* in pure culture. *Mycol. Res.* **100**: 989–998.

Kuiters, A.T. (1987): *Phenolic acids and plant growth in forest ecosystems.* PhD thesis, Free University Amsterdam.

Kuiters, A.T. (1990): Role of phenolic substances from decomposing forest litter in plant–soil interactions. *Acta Bot. Neerl.* **39**: 329–348.

Kuyper, T.R.W. (1990): Some effects of forest fertilization on ectomycorrhizal fungi and ectomycorrhizas: implications for tree responses to nitrogen pollution. In: Persson, H. (ed.): *Above and below-ground interactions in forest trees in acidified soils,* pp. 63–73. Air Pollution Research Report 32. Commission of the European Communities, Brussels.

Last, F.T., Dighton, J. & Mason, P.A. (1987): Succession of sheating mycorrhizal fungi. *TREE* **2**: 157–161.

Leake, J.R., Shaw, G. & Read, D.J. (1989): The role of ericoid mycorrhiza in the ecology of ericaceous plants. *Agric. Ecosyst. Environm.* **29**: 237–250.

Leake, J.R. & Read, D.J. (1990): Chitin as a nitrogen source for mycorrhizal fungi. *Mycol. Res.* **94**: 993–995.

Lodge, D.J. (1989): The influence of soil moisture and flooding on formation of VA-endo- and ectomycorrhizae in *Populus* and *Salix. Plant Soil* **117**: 243–253.

Lodge, D.J. & Wentworth, T.R. (1990): Negative associations among VA-mycorrhizal fungi and some ectomycorrhizal fungi inhibiting the same root system. *Oikos* **57**: 347–356.

Malloch, D. & Blackwell, M. (1992): Dispersal of fungal diaspores. In: Carroll, G.C. & Wicklow, D.T. (eds): *The Fungal Community: its organization and role in the ecosystem,* 2nd edn, pp. 631–652. Marcel Dekker, New York.

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

Marschner, H. & Dell, B. (1994): Nutrient uptake in mycorrhizal symbiosis. *Plant Soil* **159**: 89–102.

McLellan, A.J., Fitter, A.H. & Law, R. (1995): On decaying roots, mycorrhizal colonization and, the design of removal experiments. *J. Ecol.* **83**: 225–230.

Melillo, J.M., Aber, J.D. & Muratore, J.F. (1982): Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**: 621–626.

Newman, E.I. (1988): Mycorrhizal links between plants: their functioning and ecological significance. *Adv. Ecol. Res.* **18**: 243–270.

Newman, E.I. (1991): The role of root-inhabiting fungi in mixed-species plant communities. In: Atkinson, D. (ed.): *Plant Root Growth,* pp. 437–451. Blackwell Scientific Publications, Oxford.

Newman, E.I., Devoy, C.L.N., Easen, N.J. & Fowles, K.J. (1994): Plant species that can be linked by VA mycorrhizal fungi. *New Phytol.* **126**: 691–693.

Newman, E.I. & Reddell, P. (1988): Relationship between mycorrhizal infection and diversity in vegetation: evidence from the Great Smoky Mountains. *Funct. Ecol.* **2**: 259–262.

Newsham, K.K., Fitter, A.H. & Watkinson, A.R. (1995a): Multi-functionality and biodiversity in arbuscular mycorrhizas. *TREE* **10**: 407–411.

Newsham, K.K., Watkinson, A.R., West, H.M. & Fitter, A.H. (1995b): Symbiotic fungi determine plant community structure: changes in a lichen-rich community induced by fungicide application. *Funct. Ecol.* **9**: 442–447.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B. & Allen, T.F.B. (1986): *A Hierarchical Concept of Ecosystems.* Princeton University Press, New Jersey.

Pärtel, M., Zobel, M., Zobel, K. & Van der Maarel, E. (1996): The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* **75**: 111–117.

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

Pegtel, D.M. (1987): Soil fertility and the composition of seminatural grassland. In: Van Andel, J., Bakker, J.P. & Snaydon, R.W. (eds): *Disturbance in Grasslands,* pp. 51–66. Junk Publishers, Dordrecht.

Perotto, S., Coisson, J.D., Perugini, I., Cometti, V. & Bonfante, P. (1997): Production of pectin-degrading enzymes by ericoid mycorrhizal fungi. *New Phytol.* **135**: 151–162.

Perry, D.A., Amaranthus, M.P., Borchers, J.G., Borchers, S.L. & Brainerd, R.E. (1989a): Boot-strapping in ecosystems—internal interactions largely determine productivity and stability in biological systems with strong positive feedback. *BioScience* **39**: 230–237.

Perry, D.A., Bell, T. & Amaranthus, M.P. (1992): Mycorrhizal fungi in mixed-species forests and other tales of positive feedback, redundancy and stability. In: Cannell, M.R., Malcolm, D.C. & Robertson, P. (eds): *The Ecology of Mixed Species Stands of Trees*, pp. 151–179. Blackwell Scientific Publications, Oxford.

Perry, D.A. & Choquette, C. (1987): Allelopatic effects on mycorrhizae: influence on structure and dynamics of forest ecosystems. In: Waller, G.R. (ed.): *Allelochemicals: role in agriculture and forestry*, pp. 185–194. Am. Chem. Soc., Washington, DC.

Perry, D.A., Margolis, H., Choquette, C., Molina, R. & Trappe, J.M. (1989b): Ectomycorrhizal mediation of competition between coniferous tree species. *New Phytol.* **112**: 501–511.

Pickett, S.T.A., Kolasa, J., Armesto, J.J. & Collins, S.L. (1989): The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* **54**: 129–136.

Read, D.J. (1991): Mycorrhizas in ecosystems. *Experientia* **47**: 376–391.

Read, D.J., Francis, R. & Finlay, R.D. (1985): Mycorrhizal mycelia and nutrient cycling in plant communities. In: Fitter, A.H., Atkinson, D., Read, D.J. & Usher, M.B. (eds): *Ecological Interactions in Soil*, pp. 193–217. Blackwell Scientific Publications, Oxford.

Read, D.J., Leake, J.R. & Langdale, A.J. (1989): The nitrogen nutrition of mycorrhizal fungi and their host plants. In: Boddy, L., Marchant, R. & Read, D.J. (eds): *Nitrogen, Phosphorus and Sulphur Utilization by Fungi*, pp. 181–204. Academic Press, London.

Reddell, P. & Malajczuk, N. (1984): Formation of ectomycorrhizae by jarrah (*Eucalyptus marginata* Donn. ex. Smith) in litter and soil. *Aust. J. Bot.* **32**: 435–444.

Robertson, G.P., Crum, J.R. & Ellis, B.G. (1993): The spatial variability of soil resources following long term disturbance. *Oecologia* **96**: 451–456.

Robertson, G.P., Huston, M.A., Evans, F.C. & Tiedje, J.M. (1988): Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* **69**: 1517–1524.

Robertson, G.P. & Gross, K.L. (1994): Assessing the heterogeneity of belowground resources: quantifying pattern and scale. In: Caldwell, M.M. & Pearcy, R.W. (eds): *Exploitation of Environmental Heterogeneity by Plants*, pp. 237–253. Academic Press, London.

Robinson, D. (1991): Roots and resource fluxes in plants and communities. In: Atkinson, D. (ed.): *Plant Root Growth*, pp. 103–130. Blackwell Scientific Publications, Oxford.

Rosenzweig, M.L. (1995): *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Rosenzweig, M.L. & Abramsky, Z. (1993): How are diversity and productivity related? In: Ricklefs, R.E. & Schluter, D. (eds): *Species Diversity in Ecological Communities*, pp. 52–65. The University of Chicago Press, Chicago and London.

Rossi, R.E., Mulla, D.J., Journal, A.G. & Franz, E.H. (1992): Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecol. Monogr.* **62**: 277–314.

Stark, J.M. (1994): Causes of soil nutrient heterogeneity at different scales. In: Caldwell, M.M. & Pearcy, R.W. (eds): *Exploitation of Environmental Heterogeneity by Plants*, pp. 255–284. Academic Press, London.

St John, T.V., Coleman, D.C. & Reid, C.P.P. (1983): Growth and spatial distribution of nutrient-absorbing organs: selective exploitation of soil heterogeneity. *Plant Soil* **71**: 487–493.

Stuefer, J.F. (1996): Potentials and limitations of current concepts regarding the response of clonal plants to environmental heterogeneity. *Vegetatio* **127**: 55–70.

Tilman, D. (1982): *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.

Tilman, D. (1985): The resource ratio hypothesis of succession. *Am. Nat.* **125**: 827–852.

Tilman, D. (1990): Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* **58**: 3–15.

Tilman, D. (1994): Competition and biodiversity in spatially structured habitats. *Ecology* **75**: 2–16.

Tilman, D. & Pacala, S. (1993): The maintenance of species richness in plant communities. In: Ricklefs, R.E. & Schluter, D. (eds): *Species Diversity in Ecological Communities*, pp. 13–25. The University of Chicago Press, Chicago/London.

Timbal, J., Gelpe, J. & Garbaye, J. (1990): Étude préliminaire sur l'effet dépressif de la molinie (*Molinia caerulea*) sur la croissance et l'état mycorhizien de semis de chêne rouge (*Quercus rubra*). *Ann. Sci. For.* **21**: 643–649.

Tinker, P.B., Durall, D.M. & Jones, M.D. (1994): Carbon use efficiency in mycorrhizas: theory and sample calculations. *New Phytol.* **128**: 115–122.

Trappe, J.M. (1987): Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an ecolutionary standpoint. In: Safir, G.R. (ed.):

Ecophysiology of VA Mycorrhizal Plants, pp. 5–25. CRC Press, Boca Raton, USA.

Van Andel, J. & Van den Bergh, J.P. (1987): Disturbance in grasslands—outline of the theme. In: Van Andel, J., Bakker, J.P. & Snaydon, R.W. (eds): *Disturbance in Grasslands*, pp. 3–13. Junk Publishers, Dordrecht.

Van Andel, J., Bakker, J. & Grootjans, A.P. (1993): Mechanisms of vegetation succession: a review of concepts and perspectives. *Acta Bot. Neerl.* **42:** 413–433.

Van Breemen, N. (1995): Nutrient cycling strategies. *Plant Soil* **168/169:** 321–326.

Van Duin, W.E., Griffioen, W.A.J. & Ietswaart, J.H. (1991): Occurrence and function of mycorrhiza in environmentally stressed soils. In: Rozema, J. & Verkleij, J.A.C. (eds): *Ecological Responses to Environmental Stresses*, pp. 114–123. Kluwer Academic Publishers, Dordrecht.

Van Oorschot, M.M.P. (1996): *Effects of the vegetation on carbon, nitrogen and phosphorus dynamics in English and French riverine grasslands.* PhD thesis, Utrecht University.

Visser, S. (1995): Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytol.* **129:** 389–401.

Waalend, M.E. & Allen, E.B. (1987): Relationship between VA mycorrhizal fungi and cover following surface mining in Wyoming. *J. Range Mgt* **40:** 271–276.

Wallander, H. & Nylund, J.-E. (1992): Effects of excess nitrogen and phosphorus starvation on the extramatrical mycelium of ectomycorrhizas of *Pinus sylvestris*. L. *New Phytol* **120:** 495–503.

Weaver, J.E. (1958a): Summary and interpretation of underground development in natural grassland communities. *Ecol. Monogr.* **28:** 55–78.

Weaver, J.E. (1958b): Classification of root systems of forbs of grassland and consideration of their significance. *Ecology* **39:** 393–401.

Wedin, D.A. & Tilman, D. (1990): Species effects on nutrient cycling: a test with perennial grasses. *Oecologia* **84:** 433–441.

Wedin, D.A. & Tilman, D. (1993): Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecol. Monogr.* **63:** 199–229.

Wilkins, D.A. (1991): The influence of sheathing (ecto-) mycorrhizas of trees on the uptake and toxicity of metals. *Agric. Ecosys. Environm.* **35:** 145–260.

Wilson, S.D. & Tilman, D. (1993): Plant competition and resource availability in response to disturbance and fertilization. *Ecology* **74:** 599–611.

Yasman, I. (1995): *Dipterocarpaceae: tree–mycorrhiza–seedling connections.* PhD thesis, Wageningen Agricultural University.

Zak, J.C. (1992): Response of soil fungal communities to disturbance. In: Carroll, G.C. & Wicklow, D.T. (eds): *The Fungal Community: its organization and role in the ecosystem*, 2nd edn, pp. 631–652. Marcel Dekker, New York.

Zobel, M. & Moora, M. (1997): Plant coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind. *Oikos* **78:** 202–208.