

CENTENARY SYMPOSIUM SPECIAL FEATURE

ESSAY REVIEW

Root responses to nutrients and soil biota: drivers of species coexistence and ecosystem productivity

Hans de Kroon^{1*}, Marloes Hendriks¹, Jasper van Ruijven², Janneke Ravenek¹, Francisco M. Padilla¹, Eelke Jongejans¹, Eric J. W. Visser¹ and Liesje Mommer^{1,2}

¹Experimental Plant Ecology, Institute for Water and Wetland Research, Radboud University Nijmegen, PO Box 9010, 6500 GL Nijmegen, The Netherlands; and ²Nature Conservation and Plant Ecology, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands

Summary

1. Although a major part of plant biomass is underground, we know little about the contribution of different species to root biomass in multispecies communities. We summarize studies on root distributions and plant responses to species-specific soil biota and formulate three hypotheses to explain how root responses may drive species coexistence and ecosystem productivity.
2. Recent studies suggest that root growth of some species may be stimulated in species mixtures compared with monocultures without hampering the growth of other species, leading to below-ground overyielding. Further studies suggest that these responses are the result of reduced impairment of growth by species-specific plant pathogens that accumulate in monocultures.
3. First, we hypothesize that due to pathogen-constrained growth, monocultures are 'under-rooted', i.e. they do not have enough roots for optimal acquisition of nutrients. Although elevated root production in mixtures represents a cost to the plant, improved nutrition will eventually result in improved plant performance.
4. Second, due to the plant species specificity of the soil biotic communities, we suggest that plant species in mixtures develop an intransitive competitive network in which none of the species is competitively superior to all other species. Competitive intransitivity is proposed as a mechanism of species coexistence.
5. As a final hypothesis, we suggest that pathogen-mediated root overproduction in species mixtures determines the patterns of community productivity and overyielding, both directly, by improving plant performance, and indirectly, by releasing more carbon into the soil, resulting in enhanced availability of nutrients.
6. *Synthesis.* Recent evidence suggests that species coexistence and ecosystem productivity may be the result of an interplay between pathogen-driven plant responses and nutritional consequences. We suggest that responses of the roots are an important yet mostly overlooked intermediary between soil biota and plant community responses to biodiversity.

Key-words: biodiversity, ecosystem functioning, intransitive competition, niche differentiation, plant–soil (below-ground) interactions, root distributions, root ecology, soil nutrient availability, transgressive overyielding

Introduction

In most ecosystems, a large part of plant biomass is below-ground, with estimates of up to 80% for temperate grasslands, tundra and deserts (Jackson *et al.* 1996; Mokany, Raison & Prokushkin 2006). Roots are a major contributor to ecosystem

productivity, but despite numerous studies on the effects of biodiversity on ecosystem productivity (see Cardinale *et al.* 2007 for a meta-analysis), few have considered the effects on root mass (Tilman *et al.* 2001; Gastine, Scherer-Lorenzen & Leadley 2003; Dimitrakopoulos & Schmid 2004; Reich *et al.* 2004; Bessler *et al.* 2009; Fornara, Tilman & Hobbie 2009; Brassard *et al.* 2011). Because roots of different coexisting species cannot usually be distinguished by visual inspection,

*Correspondence author. E-mail: h.dekroon@science.ru.nl

we had until recently almost no information on species-specific spatial distributions of roots within diverse plant communities. As a consequence, we do not know whether species responses to biodiversity below-ground are similar to those above-ground. We also do not know the extent to which roots contribute to so-called overyielding, the generally higher biomass that plant communities develop with increasing species richness compared with monocultures (Cardinale *et al.* 2007). It is now common to statistically partition net overyielding into species complementarity effects and selection effects (Loreau & Hector 2001; Fargione *et al.* 2007), but results are incomplete at best because the below-ground plant mass is not included in the calculations.

Two sets of hypotheses prevail in the current literature on overyielding. The first set considers niche differentiation through differences between species in rooting depth (Parrish & Bazzaz 1976; Berendse 1983; Mamolos, Elisseeu & Veresoglou 1995) or differential use of nutrient forms (McKane *et al.* 2002; von Felten *et al.* 2009). Until recently, the lack of information on root distributions of species in mixed communities hampered appropriate tests, especially of the spatial niche hypothesis. The other set of hypotheses is based on effects of species-specific soil biota, in particular the negative effects of pathogenic bacteria and fungi, reminiscent of effects in agriculture where higher productivity is realized in intercropping systems than in monocultures (Trenbath 1974; Vandermeer 1989). While hypotheses about the way in which soil microbial communities may affect plant species coexistence have been around for some time (Bever 1994; Mills & Bever 1998; Westover & Bever 2001; Reynolds *et al.* 2003; Petermann *et al.* 2008; Fitzsimons & Miller 2010), a number of recent studies have focussed on the way in which soil biota may affect ecosystem productivity (van der Heijden, Bardgett & van Straalen 2008; Bever *et al.* 2010; Maron *et al.* 2011; Schnitzer *et al.* 2011). As soil pathogens first and foremost affect the growth and vitality of the roots (van der Putten, Breteler & van Dijk 1989; van Dam 2009), the effects of pathogenic soil biota on the plant community must operate through effects on root growth, root distributions and nutrient uptake. However, as in most other biodiversity–ecosystem functioning studies, the effects of soil biota are typically evaluated above-ground, not below-ground.

The goal of this review was to evaluate the extent and significance of root responses in the studies of plant biodiversity. We summarize findings about root distributions and root interactions in diverse plant communities, discuss the mechanisms that control them and formulate hypotheses on their significance for species coexistence and the relationship between biodiversity and ecosystem functioning.

We start by summarizing current knowledge on root responses to soil resources and competition, and hypotheses on niche differentiation below-ground. Next, these hypotheses are juxtaposed to previous work on root distributions and tracer studies as well as our recent results on quantitative root distributions below-ground, based on a molecular method. We argue that the patterns observed are inconsistent with interpretations that assume that they have a basis in resource

competition. We follow by summarizing recent findings on effects of soil biota on plant growth and how these may be responsible for the root distributions observed. We conclude by proposing three hypotheses to explain how effects of species-specific soil biota on root interactions and root distributions may influence niche differentiation, plant nutrient availability and productivity in species-rich plant communities.

What root distributions are predicted by root responses to soil resources and competition?

Roots are dynamic plant structures in a very dynamic soil environment. Water and mineral nutrients are heterogeneously distributed, but roots are well able to forage for these resources, i.e. to locate hotspots and express morphological and physiological responses to exploit the local resource (Hutchings & de Kroon 1994; Hodge 2004; McNickle, St. Clair & Cahill 2009). The ability to proliferate roots in resource-rich soil patches is thought to be particularly beneficial in competition: the plant that occupies a patch first will pre-empt the available resource at the expense of a plant that arrives later (Robinson *et al.* 1999), leading to competitive advantage (Schwinning & Weiner 1998; de Kroon, Mommer & Nishiwaki 2003). Current evidence suggests that the critical ability is obtaining high root densities (or more precisely a large root surface area) in resource hotspots in time. Such high densities can be realized in different ways. Placing roots preferentially into the hotspots is one option, but high biomass allocation to thin roots (generally roots with high specific root length) without selective root placement may confer a similar competitive advantage in heterogeneous soils (Mommer *et al.* 2011a). As a result of root foraging activities, root densities will be higher and competition between plants more intense in favourable soil patches (Hutchings, John & Wijesinghe 2003). Because activities of different roots on a single plant are well coordinated (de Kroon *et al.* 2005, 2009), plants may avoid locations of intense competition by shifting their root growth to relatively unexplored soil volumes (Gersani, Abramsky & Falik 1998; Semchenko, John & Hutchings 2007; Mommer *et al.* 2011b). In this way, plasticity may allow species to adjust to their neighbours and promote coexistence (Callaway, Pennings & Richards 2003).

Walter (1971) was one of the first to suggest that competition for soil resources could be reduced by partitioning of rooting space. In particular, he suggested a two-layer model for subtropical savanna in which deep-rooting woody plants and shallow rooting grasses could coexist on spatially separated water sources (see Kulmatiski *et al.* 2010). Parrish & Bazzaz (1976) hypothesized that below-ground competition acted as a selective agent in prairie vegetation lowering the overlap in rooting profiles, particularly between more shallow rooted grasses and deeper rooted forbs. Berendse (1979) developed the theoretical foundation of this idea by predicting that a combination of species with different rooting patterns can stably coexist, can explore a broader niche space and can produce more biomass than the mean biomass of each of the constituent monocultures, i.e. it can show overyielding. He confirmed

his predictions in pot and field experiments with a shallow rooting grass and a deep-rooting forb species (Berendse 1981, 1983). Root spatial niche differentiation has thus long been considered an important mechanism for species coexistence (McKane *et al.* 2002; Fargione & Tilman 2005; Levine & HilleRisLambers 2009).

What is known about root distributions in the field?

We have reasonably good understanding of vertical root distributions of whole communities across biomes. Compiling data from root excavation studies, often from individual plants, Schenk, Jackson and co-workers (Jackson *et al.* 1996; Schenk & Jackson 2002b,a) found that most roots develop in the upper soil layers, with a global average of 75% of all roots in the top 40 cm across all ecosystems. Temperate grasslands possess the shallowest root profiles, with 80–90% of their roots in the top 30 cm of soil. Globally, differences between perennial grasses and forbs are minor, both in rooting profile and in maximum rooting density, although much variability exists between species (Schenk & Jackson 2002b).

While it is clear that most of the root biomass of co-occurring species is located in the top soil layers, our information is limited as to how the roots of different species are distributed relative to each other within this stratum (see de Kroon, Mommer & Nishiwaki 2003, for an overview). Examining root distributions at the millimetre to centimetre scale by identifying the species in cut surfaces of frozen root cores, Caldwell, Manwaring & Durham (1991, 1996) showed that roots of shrub and grass species from cold desert tended to be segregated. In desert shrub populations, individuals have been shown to avoid contact, leading to the formation of individual plant root territories (Schenk, Callaway & Mahall 1999). For example, analyses of horizontal rooting patterns of a *Larrea tridentata* population suggested that intense overlap of rooting systems between individuals was avoided and compensated by enhanced root growth in neighbour-free areas, resulting in a more even filling of soil space (Brisson & Reynolds 1994, 1997), as predicted by the root responses to competition described in the previous section.

However, root segregation in the horizontal or vertical plane between coexisting species appears to be the exception rather than the rule (Casper, Schenk & Jackson 2003; de Kroon, Mommer & Nishiwaki 2003). Results from field tracer studies suggest that roots of different species are well intermingled. Roots of individual plants spread out wider laterally than the above-ground canopy (Pecháčková *et al.* 1999; Schenk & Jackson 2002b; Casper, Schenk & Jackson 2003), suggesting intense below-ground interaction with neighbouring plants. Results of local tracer application in a mountain grassland led Pecháčková *et al.* (2003) to conclude that none of the patches within the rooting zone, irrespective of horizontal or vertical position, was out of reach to any of the coexisting species. In grassland communities of different species richness, von Felten *et al.* (2009) found a large overlap between species in tracer uptake from different soil layers, and all species primarily took

up N from shallow soil irrespective of community diversity. Even Walter's classical two-layer hypothesis has sometimes been difficult to prove, with intense rooting of both shrubs and grasses in the upper soil layers (Rodríguez, Bertiller & Bisigato 2007), limited partitioning of soil resources between these life-forms (Kulmatiski *et al.* 2010) and reduced grass growth due to root competition with trees for water in the upper soil layers (Ludwig *et al.* 2004). However, a considerable number of tracer studies have demonstrated differences in nutrient or water uptake patterns in time or space between coexisting species (Fitter 1986; McKane, Grigal & Russelle 1990; Mamolos, Elisseou & Veresoglou 1995; McKane *et al.* 2002; Pecháčková *et al.* 2003; Fargione & Tilman 2005).

Results from these tracer studies have been supplemented recently by two field studies examining root distributions with molecular tools that allowed identification to species level of root fragments from small soil cores taken at different (5 or 10 cm) depths. In two grasslands in Yellowstone National Park, Frank *et al.* (2010) found little evidence for species segregation. Roots of up to eight species co-occurred in the small cores, and species frequency was not influenced by depth for nearly all species. Species associations were random except for the roots of two dominant grasses that tended to segregate spatially in one soil layer in one of the grasslands. By contrast, in a Canadian old-field community, Kesanakurti *et al.* (2011) found significant species segregation between soil cores, particularly between grasses and composites, although there was also a large overlap in rooting profiles. Because both studies examined the presence and absence of species in soil cores, rather than their abundance, they do not provide information on the distribution of root biomass. In quantitative terms, therefore, species segregations may either be much stronger or weaker than the studies imply.

Overall, these studies show that rooting is concentrated in shallow soil, and soil resources may not be partitioned between species in all ecosystems, or it may take place at such small distances that it is not recorded in all studies (Kulmatiski *et al.* 2010). However, several tracer studies do report results that are consistent with the spatial niche differentiation hypotheses detailed earlier (Walter 1971; Parrish & Bazzaz 1976; Berendse 1979). In the absence of quantitative information on the patterns of root distribution in the soil, these long-standing hypotheses remain essentially untested.

Unexpected and unexplained quantitative root distributions in species mixture

To examine quantitative root distributions of different species below-ground, we developed a novel molecular technique by which roots in a mixed sample can be separated into proportions of each of the component species (Mommer *et al.* 2008). The method is based on a real-time PCR of parts of the genomic DNA of the roots that are unique to each species. The first experiment to which the technique was applied was a straightforward biodiversity experiment with four species, two grasses and two forbs, grown in monocultures and in a four-species mixture (Mommer *et al.* 2010), carried under the near-ambient

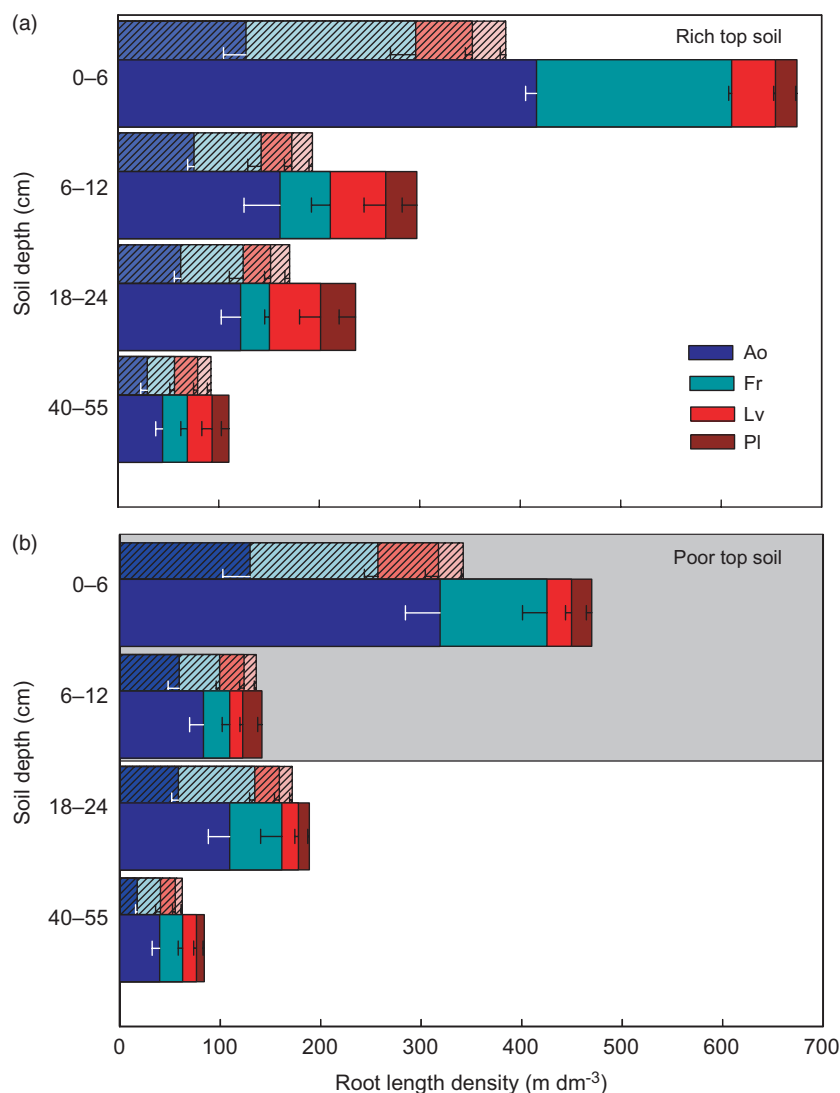


Fig. 1. Root overproduction in a biodiversity experiment. In four soil layers, root length density was determined in monocultures and in 1:1:1:1 four-species mixtures. Expected values for the root length densities in the mixtures (1/4th of the root mass in the monocultures) are given as the hatched bars at the background. Actual root densities, determined from total root densities and species proportions derived using the molecular method of Mommer *et al.* (2008), are given as the solid bars at the foreground. The monocultures and mixtures were grown on either rich top soil up to 55 cm deep (a) or a poor top soil layer of 12 cm deep (grey area) above rich soil in the deeper layers (b). The rich top soil containers had a similar poor soil layer at 55–67 cm depth. Species names are *Anthoxanthum odoratum* (Ao), *Festuca rubra* (Fr), *Leucanthemum vulgare* (Lv) and *Plantago lanceolata* (Pl). *A. odoratum* produced 3–4 times more roots in mixtures than expected from its monoculture, especially in the most densely rooted top layer, and irrespective of the soil nutrient richness of this top layer. Means \pm SE ($n = 4$ –5) are shown for the first year of the experiment. After Mommer *et al.* (2010).

conditions of the Nijmegen Phytotron (<http://www.ru.nl/phytotron>). We included two species (*Anthoxanthum odoratum* and *Plantago lanceolata*) from the studies of Berendse (1981, 1983) for which he demonstrated positive effects of below-ground niche differentiation on above-ground biomass. We thus expected that, due to competition, root distributions of species would start to segregate over time with the grasses rooting predominantly in the top soil layers, and the dicots predominantly in the deeper soil layers, and that this would be accompanied by overyielding below-ground.

Although overyielding of 35% was found below-ground in the first year of the experiment, a quantitative analysis of root distributions showed that roots of different species hardly segregated over different soil depths (Fig. 1). Thus, there was no evidence for niche differentiation in the vertical plane. The below-ground overyielding appeared predominantly due to the overproduction of one of the species, the grass *Anthoxanthum odoratum*, producing three to four times more roots in mixtures than expected from its monocultures (Fig. 1a). This implies that in mixture, approximately the same length of *A. odoratum* roots was produced by only one-quarter of the number of plants in monoculture. This overproduction was

strongest in the top soil layers, where the other species were also most densely rooted. Rooting densities of these other species, however, were similar to the expected values from monocultures (Fig. 1a) and thus hardly affected by the boost in *A. odoratum* root growth. Overall rooting densities doubled in the second year of the experiment and roots tended to be even more concentrated in the top soil layers, in contrast to our expectations (Mommer *et al.* 2010).

To speed up nutrient depletion in the densely rooted top layers, half of the treatments were established with a nutrient-poor top soil (12 cm deep). We expected that the dicot species would more quickly forage for the nutrient-rich deeper layers than the grasses in this treatment (Mommer *et al.* 2010). However, the distributions of roots with respect to depth were almost the same in both treatments (Fig. 1b). In the nutrient-poor top layer, *A. odoratum* also overproduced roots, which tended to concentrate more in the top layers in the second year, in a similar way to the treatment with the nutrient-rich top layer (Mommer *et al.* 2010).

These root growth stimulation results are supported by results from other studies (de Kroon 2007). Semchenko, John & Hutchings (2007) found that *Fragaria vesca* root growth was

stimulated by contact with competing *Glechoma hederacea* roots. For species from nutrient-poor sand ecosystems, Bartelheimer, Steinlein & Beyschlag (2006) reported that the roots of neighbouring plants tended to be aggregated under interspecific competition, whereas under intraspecific competition, roots tended to segregate. When different crops were grown together in an intercropping system, root length densities were significantly greater over all soil depths than when they grew in monocultures, suggestive of interspecific root growth stimulation (Li *et al.* 2006). Brassard *et al.* (2011) recently reported elevated root biomass of some tree species in mixed- compared with single-species stands, leading to higher fine root biomass of all species combined, especially in the densely rooted organic top layer. Although contrasting results have been reported (Mahall & Callaway 1992; Krannitz & Caldwell 1995 and references in Mommer *et al.* 2010; Brassard *et al.* 2011), evidence is accumulating that interspecific root growth stimulation is common and that spatial niche differentiation underground is inconsistent with this phenomenon.

The notion that root distributions of species in mixtures are driven by responses to soil nutrients is contradicted by evidence demonstrating the intermingling, rather than segregation, of roots of different species; the overproduction of roots of some species without affecting the root growth of co-occurring species; and a minor role of local soil nutrient availability. Indeed, an analysis of minirhizotron observations through time in the Phytotron experiment of Mommer *et al.* (2010) showed that root growth stimulation in mixture was already apparent in the first 3 months of the experiment, when soil nutrients were still in ample supply (F. M. Padilla, L. Mommer & H. de Kroon, unpubl. data).

Species-specific soil biota as drivers of root responses and overyielding

How can these increased root densities in species-rich communities be explained if soil resources are not the main drivers? It is well known that a myriad of chemical substances and soil biota (micro-organisms, fungi and nematodes) affect roots either by reducing growth through pathogenicity or herbivory or by directly stimulating growth (Bais *et al.* 2006; Raaijmakers *et al.* 2008; van Dam 2009; Bever *et al.* 2010). At least in the short term, the overall effect of the microbial community that plant species accumulate in their rhizosphere is overwhelmingly negative, as plants generally grow much better when all living soil biota are removed, e.g. through sterilization (Brinkman *et al.* 2010). In addition, plants are less constrained in growth by the soil biota of other species than by the soil biota that accumulate in their own rhizosphere (e.g. Bever, Westover & Antonovics 1997; Kardol *et al.* 2007; Kulmatiski *et al.* 2008; Petermann *et al.* 2008; Harrison & Bardgett 2010). This would imply that growth of any species in mixtures, confronted with a cocktail of soil biota of its own and those of other species, would be greater than in monocultures where roots are subjected to only their own soil biota.

Two recent studies provide support for this notion: Maron *et al.* (2011) and Schnitzer *et al.* (2011) manipulated the soil

biota by soil fungicide treatment or sterilization and found that overyielding in mixtures disappeared because monocultures increased in biomass relative to the mixtures. We thus hypothesized that the root overproduction seen in our biodiversity experiment (Fig. 1) and the concomitant below-ground overyielding were the result of species-specific build-up of pathogenic effects of soil biota suppressing root growth in monocultures.

We tested this hypothesis in a plant–soil feedback experiment in which soils were conditioned by pre-growing plants of a given species to accumulate the species-specific rhizosphere communities, after which the soils were used as substrate for the same or different plant species to examine the feedback of the soil community on plant growth (M. Hendriks, L. Mommer, W. H. van der Putten and H. de Kroon, unpubl. data). Plant growth on these soils was compared with growth on exactly the same soils following sterilization after the conditioning phase to exclude the living soil biota. We were able to repeat the main results from our longer-term outdoor biodiversity experiments: a mixture of four plant species grown on a mixture of the soils conditioned by each of the four species significantly overyielded compared with the averages of the four plant monocultures grown on each of their own soils. Overyielding completely disappeared when soils were sterilized, with the same average root and shoot growth in monocultures and mixtures, irrespective of soil conditioning. Further analyses revealed species-specific effects of soil biota underlying these results. The dicots performed better on soils of grasses and the grasses performed better on soils of the dicots (see also Petermann *et al.* 2008), but effect sizes were highly dependent on the species pair involved. Particularly striking was the major growth-stimulating (or less limiting) effect of the *Leucanthemum vulgare* soil biota on the growth of *Anthoxanthum odoratum*, especially in species mixture, compared with the growth of any other plant species–soil biota combination (M. Hendriks, L. Mommer, W. H. van der Putten and H. de Kroon, unpubl. data). The *A. odoratum* root growth stimulation in the mixtures of our Phytotron experiment (Fig. 1) may thus be largely due to the stimulatory effects of the *L. vulgare* soil biota.

Echoing Maron *et al.* (2011) and Schnitzer *et al.* (2011), we conclude that overyielding and species-specific contributions seen in our previous study (Fig. 1; Mommer *et al.* 2010) can be largely explained by the operation of species-specific plant–soil interactions. In the remainder of this review, we propose three hypotheses explaining how roots may act as an intermediary between soil biota and plant community responses to biodiversity.

The significance of root responses for biodiversity and ecosystem productivity: three hypotheses

We have reasons to assume that the early root responses seen in the experiments discussed above persist in the long run. In the 2-year biodiversity experiment reported above (Fig. 1), the mixtures did not yet produce signs of above-ground overyielding. Such a delay has been shown before, particularly in

the absence of legumes. In the long-term experiment of van Ruijven & Berendse (2005, 2009 and unpubl. data), four-species mixtures (including the combination of species used in the Phytotron experiment) started to overproduce above-ground in the second year and consistently produced 60% more biomass than the average of monocultures of the constituent species from the fourth year onwards. This increase was mirrored below-ground: harvesting the roots in a subset of the plots 8 years after the start of the experiment showed 47% below-ground overyielding in four-species mixtures, with *A. odoratum* as the species contributing the most to this effect (L. Mommer and J. van Ruijven, unpubl. data). These results suggest that the early root overproduction seen in our Phytotron experiment (Fig. 1) precedes and underlies the overyielding of species-rich communities.

How can root growth stimulation in species mixtures, induced by plant species-specific cocktails of soil biota, be the driving force for positive effects on community productivity when elevated root growth is considered a cost that trades off with above-ground growth and reproduction (Gersani *et al.* 2001; O'Brien & Brown 2008)? Our first hypothesis addresses this paradox. The second and third hypotheses further suggest how the root and plant growth responses may promote species coexistence and may explain elevated ecosystem productivity under increasing levels of plant diversity seen in field experiments.

Hypothesis 1

If root densities of a species in monoculture are constrained by accumulated soil pathogens, these root densities may be 'suboptimal' for acquiring soil nutrients. Partial release from pathogens in species mixtures will result in increased root density, higher uptake of limited nutrients by the plant and ultimately, increased plant performance.

If root growth in monoculture is strongly constrained by the pathogens that a species accumulates in its rhizosphere, plants in monoculture may well be 'under-rooted', i.e. their root densities may be lower than optimal for nutrient acquisition and above-ground growth. If the apparent root overproduction in species mixtures is triggered by a partial release from the negative effects of these pathogens, higher root densities may ultimately result in improved plant performance. If so, roots are strictly speaking not 'overproduced' in mixtures; instead, root densities are less suppressed by pathogens. As such, elevated root production directly increases resource acquisition and may ultimately result in higher production above-ground, rather than trading off with above-ground growth.

While root growth may immediately be enhanced in mixtures compared with monocultures, the proposed benefit of the higher root densities in mixtures (elevated shoot growth) appears to take effect later (van Ruijven & Berendse 2009). There may be two reasons for this. First, increased growth of the root system over the first few years in biodiversity experiments is costly in terms of carbon investment. In the experiment of Mommer *et al.* (2010), root mass increased by 77% from the first to the second year, while shoot mass was reduced

by 50% over the same time period. Second, this larger root system is formed over the course of the first experimental growing season when the readily available nutrients in fresh soils are already immobilized or taken up (Fransen & de Kroon 2001), lowering immediate growth benefits. In conclusion, initial costs of root production and maintenance are likely to be high and initial returns in terms of nutrient acquisition will be modest. This may be why net benefits of elevated root production in mixtures take time before becoming apparent above-ground.

Hypothesis 2

Release from conspecific pathogenic constraints on root growth in interspecific neighbourhoods results in an intransitive competitive network between plant species. Competitive intransitivity between species in a community, in turn, results in species coexistence.

If we assume that competition below-ground is indirect through effect and response to shared soil resources (Tilman 1982; Goldberg 1990; Casper & Jackson 1997), competition inevitably leads to a competitive hierarchy between species. This implies that when species A is competitively superior to species B, and B to species C, species A will also win in competition with species C ($A > B$; $B > C$; $\Rightarrow A > C$). Indeed, if species compete for a limited soil resource, it is inconceivable that a superior competitor A that wins in competition with a species B will lose in competition with species C that is itself competitively inferior to species B (Lankau *et al.* 2011). The opposite of hierarchical competition is 'intransitive competition', implying that competitive abilities of different species cannot be ranked along a hierarchy in which a single species gains competitive dominance (Gilpin 1975; Buss 1980). An example of an intransitive competitive network is when species A is superior to species B, and B superior to C, but C is superior to species A ($A > B$; $B > C$; $C > A$; Laird & Schamp 2006).

Interestingly, an increasing number of studies have shown that competitive relationships between species are not hierarchical but intransitive (Keddy & Shipley 1989; Taylor & Aarssen 1990; Shipley 1993; Rejmanek & Leps 1996; Suding & Goldberg 2001; Fortner & Weltzin 2007). This means that factors other than resources must determine the outcome of interactions between plants. Lankau *et al.* (2011) recently suggested that intransitive competitive networks may be mediated by soil biota. As discussed earlier, because of their species specificity, plant species on average grow better with soil biota of other species than with their own soil biota. As shown for grasses and forbs (Petermann *et al.* 2008), the effects may well be reciprocal, with species A growing better on soils of species B and species B growing better on soils of species A, possibly leading to competitive intransitivity.

As proof of concept, Lankau and co-workers (Lankau & Strauss 2007; Lankau *et al.* 2011) showed how genetic variation in exudation of allelochemicals and species-specific dependence on mycorrhiza contribute to competitive intransitivity amongst a group of plant species. Theory further suggests that competitive intransitivity results in species coexis-

tence. If all species frequently interact in a community, none will win in an intransitive network. Models of spatial distributions of individuals and populations suggest that intransitive competitive relationships result in coexisting populations (Gilpin 1975; Laird & Schamp 2006; Edwards & Schreiber 2010; Murrell 2010; Rojas-Echenique & Allesina 2011), consistent with general community theory explaining species coexistence from underlying population dynamics of co-occurring species (Chesson 2000).

This second hypothesis on intransitive networks implies that species coexist through Janzen–Connell effects (Gilbert 2002; Bever 2003; Petermann *et al.* 2008; Fitzsimons & Miller 2010), i.e. negative density dependence arising from species-specific enemies, as originally proposed for rain forests. Current plant–soil feedback experiments are only a starting point in the investigation of these effects. Testing of the hypothesis could be conducted by carrying out experiments (see Casper & Castelli 2007; Lankau & Strauss 2007) in soils with or without soil biota to examine whether species-specific soil biota allow competitively inferior species to invade neighbourhoods dominated by superior competitors.

Hypothesis 3

Pathogen-induced root responses qualitatively and quantitatively explain elevated ecosystem productivity under increasing levels of plant diversity. Release from species-specific soil pathogens in species mixtures induces root overproduction, which underlies overyielding by increasing plant production, and enhances C and N inputs into the soil, enabling overyielding to be sustained in the long run.

Effects of biodiversity on ecosystem functioning are now well synthesized in several papers (Hooper *et al.* 2005; Cardinale *et al.* 2007), but the mechanisms are still debated. If species complementarity (overyielding) seen in biodiversity experiments is due to pathogen niches rather than resource niches (Petermann *et al.* 2008; Maron *et al.* 2011; Schnitzer *et al.* 2011), we propose that it is the result of two effects related to root production that operate in concert: first, species-specific pathogen sensitivity stimulating plant growth in mixture and, second, increased soil C and N fertilization in mixture as a result of increased root biomass.

If pathogen-constrained root densities are suboptimal for nutrient acquisition in monocultures, as we proposed in Hypothesis 1, and if total root densities increase in species mixtures due to the release from species-specific soil pathogens, higher production of mixtures compared with the average of the monocultures (i.e. overyielding) is to be expected. Predictions for transgressive overyielding are less straightforward. Transgressive overyielding occurs when species mixtures outperform the most productive monoculture (Loreau 1998). Evidence for transgressive overyielding is mixed and seems particularly associated with the presence of legumes, which increases soil N availability (Cardinale *et al.* 2007; Fargione *et al.* 2007; Schmid *et al.* 2008; Marquard *et al.* 2009). Although the legume-free mixtures in the experiment of van Ruijven & Berendse (2009) quickly showed overyielding with

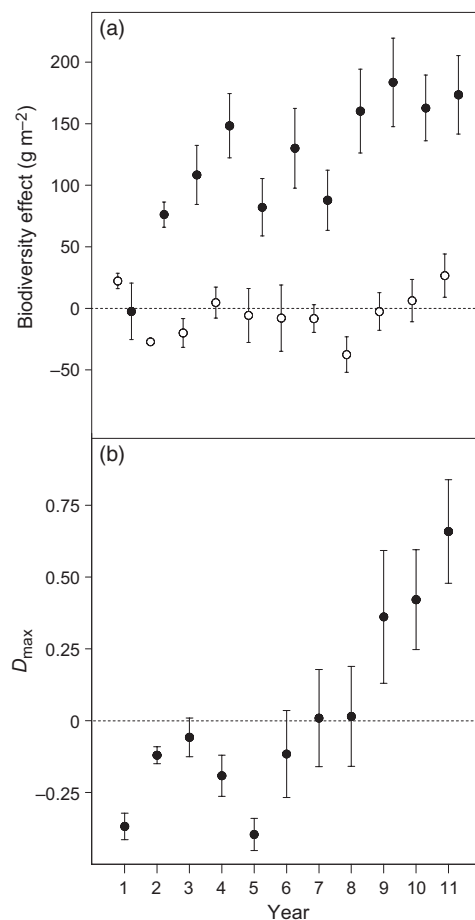


Fig. 2. (a) Complementarity (filled circles) and selection effects (open) in eight-species mixtures over time and (b) transgressive overyielding (measured as D_{\max} , which measures the difference between the mix and the best monoculture, scaled by the best monoculture; Loreau 1998) in the long-term biodiversity experiment of van Ruijven & Berendse (2005). Although overyielding (measured as the net effect, which is the sum of the complementarity and selection effect) already occurred in the second year of the experiment, transgressive overyielding was not observed until the last 3 years of the experiment. Note that selection effects were generally negative, but switched to positive in the last years, when transgressive overyielding occurred.

significant species complementarity effects (Fig. 2a), they did not show transgressive overyielding until the ninth year of the experiment (Fig. 2b).

The lack of transgressive overyielding is remarkable in the light of niche differentiation mechanisms. If all species have a unique realized resource niche, one would expect that a species mixture combining these niches would have a higher productivity than any of the monocultures. Mixtures would cover niche space more completely, and transgressive overyielding should occur. von Felten *et al.* (2009) already falsified this notion in their field tracer study, showing that at least some monocultures had a similar niche breadth as six-species mixtures. Given the wide overlap in rooting depths between species (Fig. 1; von Felten & Schmid 2008) as well as the overlap in the use of different chemical forms of N (von Felten *et al.* 2009), densely rooted monocultures of highly productive species will continue to perform as well as, or even better, than

species mixtures in terms of productivity, with a lack of transgressive overyielding as a result. Accordingly, in our Phytotron experiment, root biomass of *Anthoxanthum odoratum* was markedly higher in mixtures than expected from root masses in their monocultures (Fig. 1), but total root mass in mixtures remained lower than the root mass of the densest monoculture (*Festuca rubra*; Mommer *et al.* 2010).

Interestingly, from year nine onwards in the biodiversity experiment of van Ruijven & Berendse (2009), transgressive overyielding did appear (Fig. 2b). In these years, monocultures further declined in biomass compared with the years before (results not shown), whereas mixture biomass levels were maintained. The species with the highest biomass in monoculture in nearly all years in this experiment (*Centaurea jacea*) was shown to have very low negative plant soil feedback (Petermann *et al.* 2008). It seems that eventually this most productive monoculture may also have become limited by its own pathogens reducing its root densities and above-ground biomass. Clearly, strongly limited production caused by pathogens in all monocultures will lead to transgressive overyielding if pathogen limitation remains alleviated in mixtures.

Root overproduction in mixtures may also contribute indirectly to increased biomass production in more diverse communities over time through effects on soil nutrient availability. Given the high turnover rates of roots [average root life spans of grasses are between 3 months and 1 year (van der Krift & Berendse 2002)], a consistently higher root mass production in species mixtures will lead to increased carbon input into the soil. Indeed, after 4 years in the Jena Biodiversity Experiment, carbon stocks were significantly higher in plots with higher species diversity (Steinbeiss *et al.* 2008). It has been demonstrated that, over time, this additional carbon input increases mineralization and N availability (Fornara, Tilman & Hobbie 2009), which in turn is held responsible for the higher productivity in more diverse plant communities. We thus suggest that the long-term effects of biodiversity on ecosystem productivity are the result of a combination of direct influences of pathogen release on root and shoot production and indirect effects of increased root production on soil nutrient availability.

Final remarks

The hypotheses put forward in this paper propose an interplay between pathogen-driven plant responses and consequences for plant growth and soil nutrient availability. Plant species identity determines the community of soil biota that accumulates in the substrate, and this is suggested to result in a cascade of effects on root distributions, root production and eventually species coexistence and biodiversity-ecosystem functioning relationships. More work is needed to examine how this proposed interplay depends on abiotic conditions such as soil fertility, water availability and drought. As these conditions affect root distributions, they may also alter opportunities for root foraging, spatial niche differentiation as well as pathogenic interactions. Experiments combining species that differ in root foraging ability, nutrient competitive ability and pathogen sensitivity should indicate how important pathogen versus

resource niches are for plant community characteristics seen in the field.

A particular challenge will be to assess the extent to which the root responses of the individuals in mixed communities are responsible for community responses as a whole. Tests will require new experimental work, e.g. mixing species that do and do not show root growth stimulation, combined with modelling by which responses of the individual are used to predict community processes. Models have been developed recently that compute the way in which the plasticity of the individual affects population growth rates through changes in growth, survival and reproduction of individuals (Jongejans, Huber & de Kroon 2010). Population dynamics of coexisting species in turn determine biodiversity mechanisms (Adler, Ellner & Levine 2010). Mechanistic population models can thus be used in the future to bridge the gap between responses of the individual, biodiversity experiments and coexistence theory.

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