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Linkages of plant traits to soil properties and the functioning of temperate grassland

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Summary

1. Global change is likely to alter plant community structure, with consequences for the structure and functioning of the below-ground community and potential feedbacks to climate change. Understanding the mechanisms behind these plant–soil interactions and feedbacks to the Earth-system is therefore crucial. One approach to understanding such mechanisms is to use plant traits as predictors of functioning.

2. We used a field-based monoculture experiment involving nine grassland species that had been growing on the same base soil for 7 years to test whether leaf, litter and root traits associated with different plant growth strategies can be linked to an extensive range of soil properties relevant to carbon, nitrogen and phosphorus cycling. Soil properties included the biomass and structure of the soil microbial community, soil nutrients, soil microclimate and soil process rates.

3. Plant species with a high relative growth rate (RGR) were associated with high leaf and litter quality (e.g. low toughness, high nitrogen concentrations), an elevated biomass of bacteria relative to fungi in soil, high rates of soil nitrogen mineralization and concentrations of extractable inorganic nitrogen, and to some extent higher available phosphorus pools.

4. In contrast to current theory, species with a high RGR and litter quality were associated with soils with a lower rate of soil respiration and slow decomposition rates. This indicates that predicting processes that influence carbon cycling from plant traits may be more complex than predicting processes that influence nitrogen and phosphorus cycling.

5. Root traits did not show strong relationships to RGR, leaf or litter traits, but were strongly correlated with several soil properties, particularly the biomass of bacteria relative to fungi in soil and measures relating to soil carbon cycling.

6. *Synthesis*. Our results indicate that plant species from a single habitat can result in significant divergence in soil properties and functioning when grown in monoculture, and that many of these changes are strongly and predictably linked to variation in plant traits associated with different growth strategies. Traits therefore have the potential to be a powerful tool for understanding the mechanisms behind plant–soil interactions and ecosystem functioning, and for predicting how changes in plant species composition associated with global change will feedback to the Earth-system.

Key-words: bacteria:fungi ratio, carbon cycling, leaf traits, nutrient cycling, plant growth strategy, relative growth rate, root traits, soil microbial community structure

Introduction

One of the most likely impacts of global change on ecosystems is a change in plant species distributions, and therefore in the structure of the plant community (Bardgett, Freeman & Ostle 2008; Cornwell *et al*. 2008; Wookey *et al*. 2009). Such changes in plant community structure have an impact on the soil microbial community and the processes they mediate, and this in turn is likely to feedback to global climate change by altering the storage and loss of soil carbon (C) and primary production

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(Wardle 2002; Bardgett, Freeman & Ostle 2008; De Deyn, Cornelissen & Bardgett 2008; Bardgett, De Deyn & Ostle 2009). Understanding the mechanisms behind these effects and being able to predict how ecosystems may respond to global change are therefore of importance. One emerging approach aimed at gaining a more mechanistic understanding of how plant species affect ecosystem functioning is to study relationships of plant traits to ecosystem properties (Grime 2001; Lavorel & Garnier 2002; Chapin 2003; Diaz *et al*. 2007; De Deyn, Cornelissen & Bardgett 2008). Indeed, links of plant traits to litter decomposition and net nitrogen (N) mineralization have already been demonstrated (Tilman & Wedin 1991; Cornelissen *et al*. 1999; van der Krift & Berendse 2001; Garnier *et al*. 2004; Kazakou *et al*. 2006; Cornwell *et al*. 2008; Fortunel *et al*. 2009). Given the strong inter-dependence of the above-ground and below-ground subsystems, it is likely that plant traits could also be useful for predicting how, and understanding the mechanisms by which, plants influence C and phosphorus (P) cycling (Wardle *et al*. 2004; Eviner, Chapin & Vaughn 2006; De Deyn, Cornelissen & Bardgett 2008; van der Heijden, Bardgett & van Straalen 2008). However, very few studies have comprehensively examined whether plant traits can be related to a broad range of key soil properties.

Plant species influence the below-ground subsystem primarily by determining the quantity and quality of leaf litter and root inputs that enter the soil (Gill & Jackson 2000; Norby & Jackson 2000; Wardle 2002; De Deyn, Cornelissen & Bardgett 2008). Theory and recent global-scale studies show that the quality of leaf litter inputs to soil is strongly related to evolutionary trade-offs in plant growth strategies to maximize resource gain or to conserve nutrients (Reich *et al*. 1998; Grime 2001; Wright *et al*. 2004). Species that maximize resource gain are more typical of fertile soils, tend to have a fast growth rate and produce high-quality, short-lived, N-rich leaves and subsequently high-quality litter. These plant traits are thought to promote bacterial-based food webs with a corresponding fast and 'open' nutrient cycle, which results in a positive feedback to plant growth and the quality of litter inputs by maintaining high nutrient availability, but reduces soil C storage because of fast decomposition rates. Species that conserve nutrients show the opposite trends: they are more typical of infertile soils, tend to have slower growth rates and produce long-lived, low-N leaves. These plant traits are thought to promote a fungal-based food web with slow and conservative rates of nutrient cycling, which maintains low soil fertility levels, slow plant growth rates and low-quality litter inputs, but leads to high C storage because of low decomposition rates (Reich *et al*. 1998; Grime 2001; Wardle *et al*. 2004; Wright *et al*. 2004). Although these theories emphasize the fertility of the soil as a key determinant of plant growth strategies, it is also clear that species with very different strategies can coexist on soils of the same initial fertility (Bowman *et al*. 2004; Personeni & Loiseau 2004; Ward *et al*. 2009).

The degree to which root traits show the same evolutionary trade-offs as above-ground traits is uncertain: some studies demonstrate that root traits may fall along a similar growth rate continuum (Grime *et al*. 1997; Wahl & Ryser 2000; Craine *et al*. 2002; Tjoelker *et al*. 2005; Roumet, Urcelay & Diaz 2006), but others show that relationships of leaf traits to root traits are weak (Craine *et al*. 2005) and that the same plant can have above-ground traits associated with the opposite growth strategy to that of its roots (Personeni & Loiseau 2004). Roots may also influence nutrient and C cycling through their exudates. The quantity of these is thought to be higher for faster-growing species (van der Krift *et al*. 2001; De Deyn, Cornelissen & Bardgett 2008), which may contribute to the proposed faster C and N cycling under these species through priming effects (van der Krift *et al*. 2001; Kuzyakov 2006). However, higher levels of root exudation may also result in reduced N cycling rates due to higher net N immobilization (Kuzyakov 2006). These results suggest that where root traits align with leaf traits, they could strengthen feedbacks between above-ground traits and soil properties, but that they also have the potential to weaken these feedbacks where they show different trends to above-ground traits, or where they have opposite effects on soil functioning. Although links of plant traits to N cycling in particular have been shown (Wedin & Tilman 1990; Scott & Binkley 1997; Eviner, Chapin & Vaughn 2006), to date no study has tested the proposed links with the soil microbial community, or comprehensively examined a wide range of leaf, litter and root traits and soil properties within a single study.

The overall goal of our study was to test whether differences in the traits of co-existing grassland species with different growth strategies are sufficient to cause divergence in soil properties when species are grown on the same initial soil, and whether this divergence is associated with leaf, litter and root traits in a predictable, consistent way. We aimed to cover an extensive range of soil properties relevant to below-ground ecosystem functioning, including soil microbial community structure, soil microclimate and C, N and P cycling. Specifically, we tested the hypotheses that: (i) plant traits associated with fast-growing species (e.g. high-quality leaves and litter) are associated with bacterial-dominated soil microbial communities and fast rates of soil C, N and P cycling, which in turn results in high nutrient availability and low C sequestration; and (ii) root traits show the same evolutionary trade-offs as leaf traits, and will therefore show similar relationships to soil properties as those of above-ground traits. These hypotheses were tested by sampling a unique, long-term field experiment at Sourhope, Scotland, UK (established in 1999/2000), which involves monoculture plots of common herbaceous species of semi-natural upland grassland that vary significantly in their nutrient requirements and growth strategies.

Materials and methods

FIELD SITE

This study was carried out on a semi-natural *Festuca ovina–Agrostis capillaris–Galium saxatile* grassland, classified as a *Luzula multiflora–Rhytidiadelphus loreus* sub-community [National Vegetation Classification Ud4 (Rodwell 1992)] at Sourhope in Scotland (55°28′32″N

and 2°14′43″W). The site is at 309 m a.s.l., on a slope of about 6° and has a mean annual rainfall of 954 mm. The soil is characterized as acid brown forest soil belonging to the Sourhope series. Further details on the site are given by Usher *et al.* (2006).

The site was fenced to exclude grazing animals in 1999, and experimental plots were established between autumn 1999 and spring 2000. Plots were 1 m^2 and were laid out using a randomized block design with eight replicates. Treatments consisted of bare plots with all vegetation removed, undisturbed plots where the natural vegetation remained intact, and monocultures of common herbaceous species at the Sourhope site [namely *Agrostis capillaris* L., *Anthoxanthum odoratum* L., *Festuca ovina* L., *Festuca rubra* L., *Luzula multiflora* (Ehrh.), *Nardus stricta* L., *Rumex acetosa* L. and *Trifolium repens* L.], and *Lolium perenne* L., which is present in agriculturally improved areas of pasture. The top 2–3 cm of turf was removed from each plot, and monocultures of all species (except for *L. perenne*, which was established by sowing 60 g of seed per plot) were created by planting individuals collected from the natural vegetation within the enclosure. This approach has the advantage of mostly avoiding the vagaries associated with seed germination, and ensures that existing soil and rhizosphere biota were present and that plants were growing in their natural setting. Black plastic barriers were placed around the plots to a depth of 10 cm to restrict ingress of roots from non-planted species. The treatments were maintained by regular hand-weeding and mowing. Plant trait and soil property measurements were made on six of the eight blocks between May 2007 and 2008, 7–8 years after the plots were established.

PLANT TRAITS

Plant traits were measured on fresh leaf, litter and root material collected from each plot. Total C, N and P were measured on all plant material, using an Elementar Vario EL elemental analyzer (Hanau, Germany) for C and N, and an auto-analyser (Bran + Luebbe Autoanalyser 3, Northampton, UK) following acid digestion for P (Allen 1989). We also measured specific leaf area (SLA) and leaf dry matter content (LDMC) on fresh leaves (Cornelissen *et al.* 2003), the decomposability of litter of each species and root biomass. Litter decomposability was measured in a laboratory assay, based on the methods described in Wardle *et al.* (1998). Leaf litter (0.5 g) was placed in a Petri dish containing soil collected from Sourhope [15 g dry wt at 107% moisture content (MC) equivalent to 60% water-holding capacity (WHC), determined using the methods of Orwin, Wardle & Greenfield (2006)], and incubated at 25 °C for 2 months. The percentage mass loss over that time period will be referred to as litter decomposability from here onwards. Root biomass was determined by extracting roots from a core of known volume (40 mm diameter × 60 mm depth). Because very little leaf litter could be obtained for *R. acetosa* and *T. repens*, litter from several blocks was pooled to give two replicates for *R. acetosa* and one replicate for *T. repens* for both decomposition and litter chemistry measurements. Values for relative growth rate (RGR) were taken from the literature (Grime, Hodgson & Hunt 2007), and values for leaf thickness and toughness were supplied by J.G. Hodgson. The list of plant traits used and their values is given in the Supporting Information (Table S1).

SOIL PROPERTIES

In May 2007, 10 soil cores were taken to 10 cm depth from each plot, pooled and sieved to 4 mm. These soil samples were stored at 4 °C and chemical analyses on fresh soils performed within 7 days. To determine how plant traits are related to soil properties that have an impact on the ecosystem functions of C, N and P cycling, we measured soil microbial biomass and community structure, soil C, N and P pools, various measures of soil microbial activity directly related to biogeochemical cycling, and the soil microclimate.

Soil microbial biomass and community structure

Soil microbial C (MOC) and microbial N (MON) concentrations were analysed using the fumigation–extraction technique (Vance, Brookes & Jenkinson 1987; Ross 1992), as described by Bardgett *et al.* (2007). The resulting microbial C and N flushes were converted to MOC and MON using a conversion factor of 0.35 (Sparling *et al.* 1990) and 0.54 (Brookes *et al.* 1985) respectively. Soil microbial community structure was analysed using phospholipid fatty acid analyses (PLFA) using the methods described by Bardgett, Hobbs & Frostegård (1996), which are based on the methods of Bligh & Dyer (1959). Phospholipid fatty acids used to represent bacteria were cy-17:0, cy-19:0, i-15:0, a-15:0, i-16:0, i-17:0 and 16:1ω7. A relative measure of the bacteria : fungi ratio was calculated by dividing summed bacterial PLFAs by the fungal PLFA marker (18:2ω9,12) (Bardgett, Hobbs & Frostegård 1996). All identified peaks were summed to form a measure of total PLFA. Changes in community structure were also summarized using Principal Components Analysis (PCA). The first two principal components from this analysis explained 28.95% and 20.26% of the variation; scores along both axes were included as response variables in subsequent analyses (see below).

Soil properties related to C cycling

We measured five soil properties that are related to C cycling: soil % C, dissolved organic C (DOC), *in situ* soil CO_2 efflux (termed *in situ* respiration from here onwards), basal respiration and the ability of each soil to decompose a standard substrate (soil decomposability). Soil % C was measured using the same methods as those described for leaf and litter % C, and DOC was measured on water extracts (1 g soil: 7 mL dH_2O), using a Shimadzu 5000A TOC analyser (Asia Pacific, Kyoto, Japan) (Bardgett *et al.* 2007). *In situ* respiration gives a measure of root and microbial respiratory activity, and was determined on each plot on the same day as cores were collected, using a portable infra-red gas analyser [IRGA; Li-6400 fitted with a Glen Spectra soil respiration chamber (Li-Cor Biosciences, Lincoln, NE, USA)]. Green vegetation was clipped from 10 cm diameter circles and the chamber placed directly onto the plot surface. Basal respiration is an index of soil microbial respiration in the absence of roots, and was measured by determining the amount of CO_2 evolved from 1 g dry wt equivalent of soil in a sealed McCartney bottle after incubation at 25 °C for 24 h, using an IRGA (model ADC-225-MK3; Analytical Development Co. Ltd, Hoddesdon, UK). Soil decomposability assesses microbial activity in the presence of a standard, fresh-litter substrate and was determined using the same approach described above for litter decomposability. Each soil was adjusted to 60% WHC, and 15 g dry wt equivalent placed in a Petri dish. One g of air-dried litter (*Nothofagus fusca*) was placed on the soil surface and incubated at 25 °C for 4 months. Mass loss was calculated after this period.

Soil properties related to N cycling

We measured seven soil properties that are related to N cycling: soil % N, dissolved organic N (DON), ammonium (NH_4^+), nitrate (NO_3^-), total inorganic N, net N mineralization and net nitrification. Total soil N was measured as for leaf total N, and DON was measured on the same water extracts as DOC (Bardgett *et al.* 2007).

Inorganic N concentrations were measured on 1 M KCl extracts (using a ratio of 1 g soil : 5 mL KCl) (Blakemore, Searle & Daly 1987), and along with DON were analysed using a Bran + Luebbe Autoanalyser 3. Net N mineralization was estimated as the net release of inorganic N (NH_4^+-N and NO_3^--N) over a 14-day incubation of field-moist samples (5 g) at 25 °C, followed by KCl extraction as detailed above (Bardgett *et al.* 2007). Net nitrification was estimated by subtracting nitrate concentrations at the beginning from concentrations at the end of the same incubation.

Soil properties related to P cycling

We measured six properties that are related to P cycling: total soil P, NaOH–EDTA extractable reactive P, NaOH–EDTA extractable unreactive P, the proportion of NaOH–EDTA extractable unreactive P, water-extractable inorganic P (W.E. inorganic P from here onwards) and phosphatase activity. Total soil P contents were analysed as for leaf P, and W.E. inorganic P was measured on the same water extracts as DON, on a Bran + Luebbe Autoanalyser 3 (Bardgett *et al.* 2007). Remaining analyses of soil P pools were done on air-dried soil samples sieved to 2 mm. Soil (1.50 ± 0.01 g) was extracted in 30 mL of a solution containing 0.25 M NaOH and 50 mM EDTA (1:20 solid to solution ratio) for 16 h shaking time at ambient laboratory temperature. Extracts were centrifuged at 8000 *g* for 30 min and a 1 mL aliquot was neutralized using phenolphthalein indicator and 3 M H_2SO_4, and then diluted to 20 mL with deionized water. NaOH–EDTA reactive P was determined by molybdate colorimetry and flow injection analysis. Interference by organic matter was corrected by analysing samples with acid only (i.e. no reagents). Total phosphorus was determined by inductively-coupled plasma optical-emission spectrometry. NaOH–EDTA unreactive P, which includes organic P and inorganic polyphosphates (including pyrophosphate), was determined by calculating the difference between total and reactive P concentrations (Turner, Mahieu & Condron 2003). Phosphatase activity was measured using the methods described in Tabatabai & Bremner (1969), using *para*-nitrophenyl phosphate as a chromogenic substrate. This measurement was performed on soil collected in June 2008. Because *T. repens* had a very low biomass at the time of this measurement, this treatment was not included in analyses.

Soil properties related to general soil conditions

We measured four soil properties that describe aspects of soil conditions: soil pH, temperature, MC and WHC. Soil pH was measured in water (1 g soil: 2.5 dH_2O). Soil temperature was determined using a temperature probe during *in situ* respiration measurements. Gravimetric soil MC was measured on sieved field-moist soils, and WHC was measured as described in Orwin, Wardle & Greenfield (2006).

STATISTICAL ANALYSES

The effects of plant species on each soil property were analysed using analysis of variance with block as a random factor and species as a fixed factor. We also analysed standardized data using PCA to gain a clearer picture of how plant species affected soil properties. To explore how plant traits and soil properties were related to each other, we estimated the slope of the relationships between each trait and soil property using a Generalized Linear Mixed Model (SAS proc mixed; Little *et al.* 2000), with plant traits as fixed effects, soil properties as the response variable and species identity as a random blocking variable. This approach means that we can assess how individual plant traits affect individual soil properties while taking into account that the values of individual plant traits are correlated within species and hence that their relationships to soil properties are not independent of each other. The slopes derived from the mixed models were used to create a matrix where each entry expressed the strength of the mixed-model regression relationship between traits and soil properties. This matrix was analysed using PCA. This PCA allows us to assess whether the plant traits that we might expect to group together due to their association with different growth strategies have similar relationships to soil properties, and similarly whether soil properties that we might expect to have similar relationships to plant traits do in fact do so. Data were standardized before analysis by subtracting the mean of each variable and dividing by the standard deviation, to ensure that absolute differences in the magnitude of plant traits and soil properties did not influence the clustering of slope coefficients along PCA axes. Mean trait values for each plant species were used in place of missing data as required. For each PCA, including for the PCA summarizing PLFA data, we ran a parallel analysis first to determine how many components to extract (Franklin *et al.* 1995), and excluded any components that explained less than 10% of the variation. We used a correlation matrix for all PCAs and used a varimax rotation where it helped interpretation. All PCAs were run in SPSS.

Results

The PCA summarizing plant species effects on soil properties indicated that most species had resulted in divergence of soil properties from their initial state and that most of the planted soils were different to the bare soils (Fig. 1). The first axis of this PCA primarily reflected differences in microbial biomass and soil moisture, and the second reflected differences in inorganic N contents, N mineralization rates, *in situ* respiration and microbial community structure (Table S2). The first axis explained 28.9% of the variation and the second 14.3%. Monocultures of *T. repens* and *L. multiflora* resulted in the greatest divergence in soil properties from the natural, initial state, but had the least effect on soil properties compared to

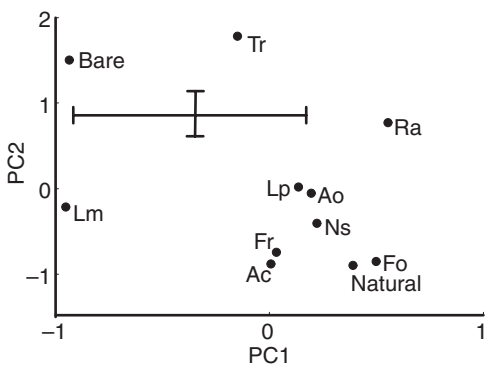

Fig. 1. Effect of plant species on soil properties as analysed by principal component analysis using the entire data set and raw values. Circles represent mean scores, error bars are least significant differences for each axis ($P < 0.05$). The first axis explains 28.9% of the variation and the second 14.3%. Ns = *Nardus stricta*; Ao = *Anthoxanthum odoratum*; Fo = *Festuca ovina*; Lm = *Luzula multiflora*; Fr = *F. rubra*, Tr = *Trifolium repens*; Lp = *Lolium perenne*; Ac = *Agrostis capillaris*; Ra = *Rumex acetosa*.

the bare soil. Analysis of variance of each soil property indicated that plant species treatments had a significant effect on 19 of the 29 soil variables measured (Table 1). The variables that did not show a significant response to plant species treatments were fungal biomass, most P-cycling-related variables and soil % C and % N (Table 1).

RELATIONSHIPS AMONG PLANT TRAITS AND AMONG SOIL PROPERTIES

The slopes used in the PCA aimed at determining how relationships of plant traits to soil properties group together are given in Table S3, along with their statistical significance. PCA of this traits × soil property slope matrix identified two axes, which explained 38.6% and 16.04% of the variation respectively. Axis 1 was primarily associated with positive relationships of soil properties to leaf N and litter N and negative relationships to leaf toughness (Fig. 2). Positive relationships of soil properties to SLA, RGR, litter C and leaf C, and negative relationships to LDMC were also related to this axis but to a lesser extent. Therefore, axis 1 appears to primarily reflect relationships of soil properties to changes in leaf and litter quality. Axis 2 was associated with positive relationships of soil properties to leaf P, root C, root N and leaf thickness (Fig. 2).

Graphing the PCA scores from this analysis allows us to look for soil properties that show similar relationships to the same plant traits. The position of a soil property along each PCA axis reflects both the strength and direction of its relationship to the plant traits most strongly associated with that axis. Soil properties positioned on the left of the *x*-axis or the bottom of the *y*-axis indicate a strong negative relationship, and those positioned on the right of the *x*-axis or the top of the *y*-axis indicate a strong positive relationship. Any PCA scores that are close to zero indicate a weak relationship to the plant trait associated with that axis. Axis 1 described the strongest relationships of plant traits to soil properties, and indicated that soil inorganic N pools, soil microbial community structure and soil temperature were related strongly to high levels of leaf and litter N and low toughness (Fig. 3, Table S3). The bacteria : fungi ratio, W.E. inorganic P, and net rates of N mineralization and nitrification were also positively associated with these traits, but to a lesser extent than inorganic N pools. In contrast, total microbial and fungal biomass, soil moisture, pH, phosphatase, and measures of C-related process rates (i.e. respiration and soil decomposability) were strongly and negatively related to leaf and litter N, and positively related to leaf toughness. Soil properties relating to organic C, N or P pools were only weakly related to leaf and litter N and leaf toughness (Fig. 3, Table S3).

Axis 2 generally reflected weaker relationships of plant traits to soil properties and did not show easily interpretable groupings of soil properties to traits. The clearest trend along PCA axis 2 was that leaf P was positively related to NaOH–EDTA reactive P, and negatively related to phosphatase activity and the proportion of NaOH–EDTA unreactive P. Axis 2 also highlighted the negative relationship of root C and N to the bacteria : fungi ratio (Fig. 3, Table S3). The relationships of other root traits to soil properties were largely independent of those highlighted by the PCA, but did nevertheless show some significant relationships to soil properties ($P < 0.05$) (Table S3). The strongest trend amongst these was that root biomass was relatively consistently related to measures of C cycling [soil decomposability ($\beta = 0.32$), *in situ* respiration ($\beta = 0.49$) and soil C ($\beta = 0.29$)].

Discussion

LINKS AMONG PLANT TRAITS

The weighting of traits along the first axis identified by PCA of the slopes data set supported the concept that evolutionary trade-offs in plant growth strategies result in species with a faster growth rate, such as *R. acetosa*, also being associated with higher leaf and litter quality, as assessed in this study by leaf and litter N, litter P, SLA, leaf toughness and LDMC (Reich *et al.* 1998; Grime 2001; Wright *et al.* 2004). The traits expressed by a given species are likely to depend on how the plant interacts with the soil that it is growing in. Because of this dependence, it is likely that the traits and rankings of plant species will vary depending on the length of time a plant has been growing in a particular patch and differences in soil fertility (e.g. Craine & Reich (2001). The fact that RGR measured in non-limiting conditions (Grime, Hodgson & Hunt 2007) was related to increases in leaf and litter nutrients measured *in situ* in our study suggests that feedbacks between plant species and the soil beneath them can allow species to express traits that reflect their underlying growth strategies, given sufficient time.

In contrast to leaf and litter traits, there was very little evidence that root traits showed the same evolutionary trade-offs as none of the root traits were strongly related to the first axis of the PCA (Fig. 2), and the species with the fastest growth rate, *R. acetosa*, had a very similar root C, N and P content to *N. stricta*, the species with the slowest growth rate (Table S1). This supports the finding of Craine *et al.* (2005) that root traits are not strongly linked to leaf traits, but contradicts the findings of others that root traits follow patterns similar to leaves in grassland species (Craine *et al.* 2002; Tjoelker *et al.* 2005). The lack of consistent patterns among studies focusing on similar species suggests that the strength of relationships of root to leaf traits may depend on other factors, such as seasonal differences in nutrient allocation among roots and shoots and disturbance regimes (Bardgett *et al.* 2002; Craine *et al.* 2005).

LINKS AMONG SOIL PROPERTIES AND PLANT TRAITS

We hypothesized that the traits associated with fast-growing plant species promote bacterial-dominated soil microbial communities and fast rates of soil C, N and P cycling, which in turn results in high nutrient availability and low C sequestration. Our data strongly support this hypothesis for N cycling, with increases in the bacteria : fungi ratio, inorganic N pools, and net rates of N mineralization and nitrification all showing positive and often strong relationships to axis 1 of the PCA of the slopes data set, which reflected increases in leaf and litter

Table 1. Mean effects of plant species on soil properties, as analysed by analysis of variance (ANOVA) with block and treatment as explanatory variables. Relative growth rate increases from left to right for the monoculture treatments

	Bare	Natural	Ns	Ao	Fo	Lm	Fr	Tr	Lp	Ac	Ra	*F*-value
Soil microbial community												
MOC†	1.68c	4.25a	3.40a	3.68a	3.65a	2.37b	3.43a	2.32b	3.24ab	3.64a	3.28ab	5.58***
MON†	0.01d	0.31a	0.21bc	0.33a	0.16b	0.09cd	0.24ab	0.12cd	0.20bc	0.21bc	0.24ab	4.94***
Total PLFA	212.9d	418.5a	344.7abc	367.0abc	392.5ab	281.1cd	335.5abc	304.2bcd	352.4abc	362.2abc	339.2abc	2.14*
Total fungi	28.7	50.1	51.9	42.8	63.9	39.1	47	40.8	49.1	50.9	46.6	NS
Total bacteria	84.7c	166.7a	131.4ab	147.9ab	144.4ab	110.2bc	127.5ab	122.9bc	136.6ab	137.9ab	135.4ab	2.058*
Bacteria:fungi†	3.19	3.25	2.66	4.1	2.4	3.07	2.73	3.09	2.84	2.72	3.02	NS
PLFA PC1	1.88a	−0.63de	−0.57de	−0.03cd	−0.71e	0.38c	−0.69e	1.07b	−0.45de	−0.75e	0.49bc	16.02***
PLFA PC2	0.29	−0.13	−0.04	0.02	0.51	−0.5	−0.13	0.18	−0.23	−0.19	0.23	NS
Variables related to carbon cycling												
% C	12.2	13.8	13.2	13.4	15.7	10.8	11.9	12.6	13.9	12.8	14.8	NS
DOC†	0.28a	0.22ab	0.19bc	0.23bc	0.21b	0.17c	0.20bc	0.16c	0.22ab	0.21b	0.22ab	3.06**
In situ respiration	2.26e	6.14a	4.61bcd	4.70bcd	5.58b	4.00d	4.80bcd	2.79e	4.09cd	5.08bc	4.23cd	10.27***
Basal respiration	1.44cd	3.09ab	2.30abc	2.34abc	2.26abc	1.40d	2.90a	1.82bcd	2.35abc	2.63ab	2.02abcd	2.21*
Soil decomposability	13.0e	29.2a	29.7a	15.0de	20.0bcde	18.0cde	24.5abc	16.0de	21.2bcd	25.3ab	28.8a	5.44***
Variables related to nitrogen cycling												
% N	0.85	0.94	0.89	0.89	0.96	0.73	0.81	0.89	0.93	0.83	1.0	NS
DON†	58.8ab	61.5ab	101.6ab	66.3ab	32.5c	30.2c	90.1ab	56.8abc	58.6ab	56.8bc	93.8a	2.46*
Ammonium†	14.68b	3.43de	4.41de	5.30cd	1.84f	6.12cd	2.59ef	28.29a	9.10bc	2.97def	12.02b	16.91***
Nitrate†	6.58a	1.41b	3.14b	3.69b	2.22b	3.39b	2.84b	23.63a	2.51b	1.87b	3.68b	11.14***
N mineralization†	1.78bc	1.46cd	2.48b	1.74bc	0.22e	1.29cd	0.83de	4.15a	2.25bc	0.80de	2.58b	9.30***
Net nitrification†	0.86a	0.08bc	0.94ab	0.52abc	0.06c	0.35abc	0.11bc	1.11a	0.08bc	0.04c	0.43abc	2.10*
Variables related to phosphorus cycling												
Total soil P	1.73a	1.52b	1.41b	1.37b	1.51b	1.37b	1.37b	1.45b	1.48b	1.38b	1.50b	2.30*
N-E Unreactive P	0.70	0.71	0.73	0.73	0.65	0.67	0.67	0.68	0.69	0.66	0.65	NS
N-E reactive P	50.4	36.1	62	57.2	51.5	42.7	58.3	56	53.7	40.6	73.2	NS
W.E. inorganic P[a]	2.29	1.82	2.08	1.74	2.36	2.57	2.49	2.59	3.88	2.77	3.25	NS
Phosphatase activity	2.48	3.03	3.39	3.32	3.1	2.86	3.29	ND	3.51	3.18	2.85	NS
General soil conditions												
Soil pH	4.75a	4.80a	4.79a	4.82a	4.76a	4.89a	4.82a	4.40b	4.92a	4.90a	4.70a	2.61*
Temperature (°C)	13.00a	9.27g	9.19g	10.43de	9.50fg	11.01cd	10.42de	12.04b	10.05ef	9.92efg	11.31bc	19.55***
Moisture (%)	58.7d	79.8abc	89.1a	84.1abc	90.5a	66.0cd	90.0a	67.3bcd	82.0abc	80.9abc	87.0ab	2.40*
WHC (%)	107c	178a	177a	163ab	184a	140bc	177a	138bc	156ab	181a	168ab	3.72***

Microbial carbon (MOC), microbial nitrogen (MON) and dissolved organic carbon (DOC) were measured in mg g^{-1} dry wt; total phospholipid fatty acids (Total PLFA), fungi and bacteria in nmol g^{-1}; *in situ* respiration in μmol CO_2 m^{-2} s^{-1}; basal respiration in μg CO_2-C g^{-1} h^{-1}; soil decomposability as % mass loss; dissolved organic N (DON), ammonium, nitrate and water-extractable (W.E.) inorganic P in μg g^{-1} dry wt; net N mineralization in μg NO_3^--N + NH_4^+-N g^{-1} day^{-1}; net nitrification in (μg NO_3^--N g^{-1} day^{-1}; total soil phosphorus (P) and NaOH–EDTA unreactive P (N-E unreactive P) in mg g^{-1}; NaOH–EDTA reactive P (N-E reactive P) in mg kg^{-1}; and phosphatase activity in μmol pNP g^{-1} s^{-1}. PLFA PC1 and PC2 refer to principal component scores (axes 1 and 2 respectively), calculated from proportional PLFA data, and WHC = water holding capacity. Ns = *Nardus stricta*; Ao = *Anthoxanthum odoratum*; Fo = *Festuca ovina*; Lm = *Luzula multiflora*; Fr = *F. rubra*; Tr = *Trifolium repens*; Lp = *Lolium perenne*; Ac = *Agrostis capillaris*; Ra = *Rumex acetosa*. Means in rows followed by the same letter are not significantly different from each other at $P < 0.05$.

†Log-transformed for analysis. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

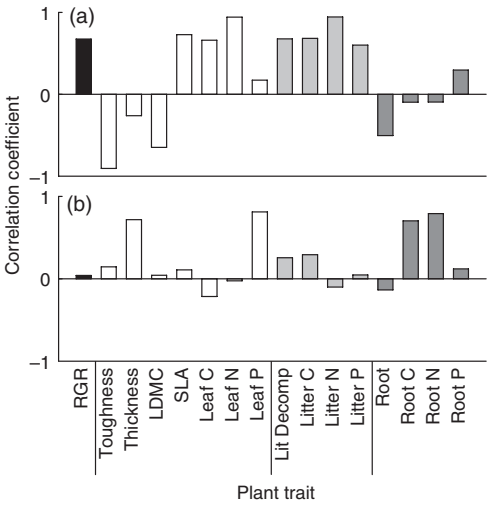

Fig. 2. Correlation coefficients of plant traits to axis 1 (a) and axis 2 (b) identified by PCA of the slopes describing the relationships of plant traits to soil properties. Open bars represent leaf traits, pale grey bars represent litter traits and dark grey bars represent root traits. RGR = relative growth rate; Toughness = leaf toughness (N mm^{-1}); Thickness = leaf thickness (mm); LDMC = leaf dry matter content (%); SLA = specific leaf area (mm^2 mg^{-1}), Lit Decomp = litter decomposition rate (% mass loss); Root = root biomass (g dry wt m^{-2} to a depth of 6 cm). Carbon (C), nitrogen (N) and phosphorus (P) contents were measured in mg g^{-1}.

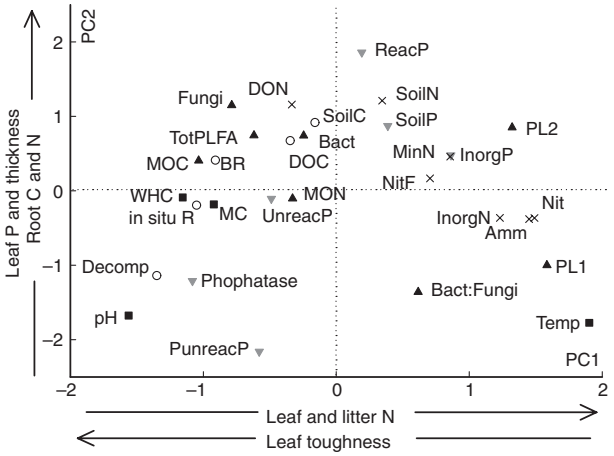

Fig. 3. Principal component scores for each soil property, calculated by PCA of the slopes describing the relationships of plant traits to soil properties. Loadings of plant traits on each axis are given in Fig. 2, and the traits with the highest loading for each axis are indicated. The position of a soil property along each PCA axis reflects both the strength and direction of its relationship to the plant traits most strongly associated with that axis. Soil properties positioned on the left of the *x*-axis or the bottom of the *y*-axis indicate a strong negative relationship to the plant traits associated with the axis, and those positioned on the right of the *x*-axis or the top of the *y*-axis indicate a strong positive relationship. Any PCA scores that are close to zero indicate a weak relationship to the plant trait associated with that axis. ▲ = microbial community variables; × = soil N cycling variables; ▼ = soil P cycling variables; ○ = C cycling variables; ■ = general soil condition variables. Amm = ammonium; Bact : Fungi = bacteria : fungi ratio; BR = basal respiration; Decomp = soil decomposability; in situ R = *in situ* respiration; inorgP = W.E. inorganic P; MinN = net mineralizable N; Nit = nitrate; NitF = net nitrification; InorgN = total inorganic N; PL1 and PL2 = PLFA PCA1 and 2 respectively; PunreacP = proportion of NaOH–EDTA unreactive P; ReacP = NaOH–EDTA reactive P; Temp = temperature; TotPLFA = total PLFA content; Bact = total bacterial fatty acids; Fungi = total fungal fatty acids; unreacP = NaOH–EDTA unreactive P.

quality associated with increases in RGR (Fig. 3). Unsurprisingly, these relationships were driven in part by the large effect of the N fixer *T. repens* on soil properties relating to N cycling. However, they were also influenced by other species with higher leaf and litter N contents and low toughness (i.e. *R. acetosa* and to some extent *L. multiflora*). This suggests that, even excluding the large effects of legumes on soil N, positive feedbacks between plant traits and soil properties had become sufficiently well established to result in predictable effects of traits on soil properties relating to N cycling. These findings extend those of other studies that have linked litter quality or RGR to inorganic N pools and N mineralization (Wedin & Tilman 1990; Scott & Binkley 1997; Berendse 1998; van der Krift & Berendse 2001; Bertiller *et al.* 2006; Eviner, Chapin & Vaughn 2006; McIntyre 2008) by demonstrating across-species relationships of RGR to the quality of plant inputs to soil and the composition of the soil microbial community, as well as the availability of plant growth-limiting nutrients.

Significant relationships of plant traits to soil properties related to P cycling were few and weak compared to those to soil properties related to N cycling (Fig. 3, Table S3). This may have been because the amount of soil P in our system was at the high end of the range of values typically found in UK pasture soils (Turner, Mahieu & Condron 2003), resulting in a reduced probability that plant species could strongly influence the relatively coarse-scale soil P pools measured (Eviner, Chapin & Vaughn 2006). Nevertheless, the general trends found provided support for at least some aspects of the proposed link of RGR to high leaf and litter quality, bacterial-dominated microbial communities, and high levels of activity and available nutrients. The weak positive relationship of W.E. inorganic P to the changes in leaf and litter quality represented by axis 1 of the PCA of the slopes data set, and the stronger positive relationship of NaOH–EDTA reactive P to leaf P along axis 2 (Fig. 3, Table S3), suggest that there were sufficient feedbacks between soil properties and leaf and litter P to result in the maintenance of higher amounts of soil P in a relatively available form. This trend was particularly strong for *R. acetosa*, which has the highest RGR and leaf P content of the species measured, and was associated with soils with comparatively high W.E. inorganic P and NaOH–EDTA reactive P contents. The tendency for phosphatase activity to be negatively related to leaf and litter quality and leaf P contents (Fig. 3, Table S3) may also provide some support for the proposed links between plant traits and soil properties, in that low soil P availability induces plants and microbes to invest in enzymes such as phosphatase to acquire P (Treseder & Vitousek 2001).The higher phosphatase activity in low-litter-quality systems may therefore indicate that these

systems were associated with reduced P availability, as predicted. It is, however, unclear how greater phosphatase activity is likely to affect rates of P mineralization and feedbacks between plants and soil P pools, given that organic P mineralization appears to be limited by substrate availability rather than by phosphatase activity (Tarafdar & Claassen 1988). Our results showed that high phosphatase activity was associated with a low bacteria : fungi ratio, but this may be because phosphatase activity was associated with low litter quality rather than being indicative of a direct link between a greater abundance of fungi relative to bacteria and elevated phosphatase activity.

In contrast to the results for soil properties related to P and N cycling, the increase in leaf and litter quality represented by PCA axis 1 of the slopes data set was negatively related to measures of C-related process rates, and showed no strong relationships to soil C pools (Fig. 3, Table S3). There are two likely reasons why we did not find the expected trends. First, it is possible that high-quality litter results in high temporal variation in C-related process rates because the litter is decomposed quickly, whereas lower-quality litter might result in a more consistent level of microbial activity due to the longer residence time of the litter in soil. This in turn suggests that the direction of relationships between C cycling and leaf and litter quality may oppose each other depending on whether measurements are made shortly or a long time after inputs of litter. Because our measurements were made early in the growing season, it is possible that they coincided with a period of low microbial activity in high litter quality systems due to a lack of recent litter inputs. Secondly, other factors that co-varied with leaf and litter quality may have been more important drivers of C-related process rates. For example, plant species that produced litter of lower quality, such as *F. ovina*, were also associated with a higher root biomass (albeit weakly) and with soils with high MCs and a high microbial biomass, all of which can have an impact on C-related process rates (van der Krift *et al.* 2001; Chapin 2003; Scott-Denton, Sparks & Monson 2003; Bahn *et al.* 2006; Bardgett, Freeman & Ostle 2008). Overall, these results suggest that rates of C cycling are unlikely to be predictable based solely on leaf and litter quality, and therefore that predicting C cycling from plant traits is likely to be a complex task.

We also hypothesized that root traits would show similar relationships to the soil microbial community and C, N and P cycling as leaf and litter traits. However, in accordance with the lack of relationship of root traits to leaf and litter traits, there were few indications that this was true. Root C, N and P were not strongly related to measures of N and P cycling, and only root C showed some relationships to variables related to C cycling (Table S3). This suggests that live root N and P contents give a poor indication of the nutrient content of root litter, or that the nutrient content of roots have less of an impact on nutrient cycling than above-ground litter. This finding is consistent with some other studies, which have found that grass root chemistry is not strongly related to its decomposition rate (van der Krift *et al.* 2001; Vivanco & Austin 2006). Despite the lack of relationships to C, N and P cycling-related processes, root C and N showed some of the strongest relationships to the biomass of the soil microbial community and the bacteria : fungi ratio (Table S3). This suggests that root quality (as measured by C and N contents) may co-vary with other factors that are likely to influence the microbial community through different pathways to litter, such as the amount and type of root exudates produced (Griffiths *et al.* 1999; van der Krift *et al.* 2001; De Deyn, Cornelissen & Bardgett 2008).

In contrast to measures of root quality, root biomass showed many significant relationships to soil properties, especially to variables related to C cycling (Table S3). The positive correlation of root biomass with soil respiration rates and soil decomposability is likely to be due to stimulation of soil microbial biomass and activity in the rhizosphere through exudate production, and to direct contributions of root respiration to *in situ* respiration (van der Krift *et al.* 2001; Baudoin, Benizri & Guckert 2003; Kuzyakov 2006). This result highlights the importance of focusing on the quantity as well as the quality of inputs to soils as key drivers of soil C cycling.

CONCLUSION

Our results show that plant species that coexist in a single grassland ecosystem vary sufficiently in their traits to result in soils with divergent properties within 7 years of replacing the original vegetation with monocultures, and that many of the soil properties measured showed strong correlations with co-varying suites of plant traits linked to plant growth strategies. Our data strongly support the theory that plants with a high growth rate are associated with high leaf and litter quality that in turn promote the bacterial component of the soil microbial community, high N availability and high rates of N mineralization. Relationships of growth rate and leaf and litter quality to soil properties related to soil P cycling were weaker, but were in the direction expected. This suggests that similar mechanisms may be operating for P cycling as for N cycling, but that feedbacks between plant traits and soil P cycling were not as strongly expressed because of the relatively high P content of the soil used in this study. In contrast and contrary to predictions, high levels of microbial respiration and soil decomposability tended to be negatively related to leaf and litter quality, suggesting that relationships of plant traits to C cycling may be more complex than for N and P cycling. Root traits were not strongly related to leaf and litter traits, and high root quality did not show the same relationships to soil properties related to C, N and P cycling as high leaf and litter quality did. This dichotomy highlights the difficulty of fully understanding how plant traits drive soil functioning in natural systems, as leaf, litter and root traits may vary in their importance for different soil functions, and co-varying plant traits may affect the same functions in opposing directions. Nevertheless, our results indicate that there is strong potential for plant traits to be useful for predicting how changes in plant species composition might affect below-ground communities and the functions that they drive, and for studies linking plant traits to soil properties to increase our understanding of the mechanisms behind plant–soil interactions. It is important to note that our

study was based on measures taken at a single time point and on monocultures, and as such represents only a simple ecosystem. Although our findings extend our understanding of the behaviour of systems driven by the traits of dominant species, a fuller understanding of how traits and soil properties interact in natural systems will require studies across multiple time points and in multi-species communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of mean plant species traits.

Table S2. Correlation coefficients of each soil property to the axes identified by the PCA of the raw data set.

Table S3. Slopes describing the relationships of plant traits to all soil properties, and statistical significance.

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