Journal of Ecology 1998, **86**, 405–420

Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems?

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Summary

1 The development of general principles regarding biotic interactions involving plants, or plant species effects in ecosystems, is best achieved through simultaneous evaluation of several species. We utilized a comparative approach involving 20 dicotyledonous herbaceous species, to explore possible relationships between several plant ecophysiological traits and plant litter decomposition, interactions involving competition and herbivory, and plant species effects on soil properties.

2 Decomposition rates of plant stem and leaf litter were negatively related to plant mass, time until flowering and vegetative growth rate, and positively related to stem nitrogen content. Root decomposition was also related to several traits. Multiple regression relationships showed that 74% and 84% of the variation across species for stem and root litter decomposition, respectively, could be predicted by plant traits; this suggests that plant traits may be powerful predictors of decomposition and have potential as alternative predictors to the litter quality characteristics that previous studies have concentrated on.

3 Palatability of both seedlings and leaf discs by the invertebrate herbivores *Deroceras reticulatum* and *Listronotus bonariensis* were frequently related to plant traits. Those traits that showed the strongest relationships with the palatability data included various vegetative growth characteristics and (for the leaf disc data) nitrogen concentrations of flowering plant stems.

4 Competitive effects of the dicotyledonous species against a phytometer species, the grass *Lolium perenne*, were negatively related to leaf nitrogen concentration, and multiple regression relationships involving this trait in combination with others explained over 50% of the variation across species. The competitive response of both plant mass and total seed production to *L. perenne* was poorly related to plant traits.

5 The effects of plant species on soil properties including microbial biomass and activity, pH, nitrate concentration and total nitrogen were often closely related to various plant traits. Multiple regression relationships revealed that combinations of several traits were often important in determining these effects; the strongest relationships found were for effects of senescent plants on soil respiration and for the effects of flowering plants on soil nitrate. Plant traits were therefore clearly important in determining plant species effects on soils.

6 Our study emphasizes the importance of plant traits in understanding (and predicting) species interactions and effects in communities and ecosystems, and shows that properties considered at the whole plant level have the potential to manifest

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themselves over much larger scales. We therefore conclude that there are clear linkages between plant ecophysiological traits, biotic interactions involving plants, and ecosystem level properties and processes.

Keywords: comparative approaches, competition, decomposition, herbivory, plant traits

Journal of Ecology (1998) **86**, 405–420

Introduction

There is increasing recognition in ecology of the significance of individual species effects at the ecosystem-level of resolution, or 'what species do in ecosystems' (Lawton 1994). This development draws upon the principles of both population/community-level and ecosystem-level approaches to ecology (Jones & Lawton 1995). In order to understand the significance of an individual species on ecosystem properties and processes, it is firstly necessary to determine how that species interacts with both its biotic and abiotic environment, including both how the species responds to environmental factors, and the effect that the species has on those factors (Vitousek & Walker 1989; Wedin & Tilman 1990; Hobbie 1992; Vinton & Burke 1995). The vast majority of studies that have investigated biotic interactions in plant communities have concentrated on a relatively small number of species (Keddy 1992) and the same is also clearly true regarding most studies that have investigated ecosystem-level interactions. However, development of general principles of how such interactions operate requires simultaneous evaluation of several species under comparable or standardized conditions (Keddy 1992; Gaudet & Keddy 1995; Shipley 1995), and this is best achieved through the application of comparative approaches (Rorison *et al*. 1987; Grime *et al*. 1988). Since the relative performance of different species in any given interaction in a given environment is governed to a large degree by plant traits (Chapin *et al*. 1993; Gerry & Wilson 1995), a logical extension of the comparative approach is the utilization of plant traits across several species for predicting species performance (Poorter & Remkes 1990; Nieman *et al*. 1992; Poorter & Bergkotte 1992; Van de Werf *et al*. 1993). The utilization of several traits for several species, resulting in a traits × species matrix, may have considerable predictive power, but few such matrices exist (Keddy 1992).

Despite the historical recognition of the value of comparative approaches in enhancing our understanding of plant ecology (e.g. Clapham 1956; Grime 1965) and the apparent utility of such approaches for developing general principles regarding plant species interactions and effects in ecosystems, relatively few studies have actually used such approaches for addressing these sorts of issues. This is apparent, for example, in relation to plant litter decomposition, herbivore–plant interactions, interspecific competition and effects of plants on soil properties. With regard to decomposition, the comparative approach has been applied only sparingly, except in terms of using litter chemical constituents for predicting decomposition rates (Melillo *et al*. 1982; Taylor *et al*. 1989; Cadisch & Giller 1997). However, a recent screening of 125 British plant species (Cornelissen 1996) revealed that taxonomic status and, by implication, ecophysiological traits of plant species, was fundamental in explaining differences in decomposition between species. With herbivory, it is well recognized that plant species that differ in taxonomic status and ecological strategy also differ in terms of palatability and susceptibility to foliar feeders (Coley *et al*. 1985; Hanley *et al*. 1995). Despite this, there have been few attempts to use comparative approaches for testing such hypotheses, although some studies have used such approaches for investigating the likelihood of trade-offs in plants between investment in growth and investment in defence (Coley 1988; Van der Meijden *et al*. 1988; McCanny *et al*. 1990). Comparative approaches to competition have been restricted mainly to investigating whether competitive ability is related to habitat conditions (Van de Werf *et al*. 1993; Keddy *et al*. 1994; Gaudet & Keddy 1995), although there have been occasional attempts to relate competitive ability to selected key traits, principally plant biomass (Gaudet & Keddy 1988; Gerry & Wilson 1995) and shoot thrust (Campbell & Grime 1992). Despite the increasing interest in understanding the effects of individual plant species on nutrient cycling, soil properties and ecosystem processes (Vitousek & Walker 1989; Wedin & Tilman 1990; Hobbie 1992; Wedin & Pastor 1992) the use of comparative-type approaches for addressing this issue has been negligible, and restricted almost entirely to studying plant species effects on soil microbial biomass (Groffman *et al*. 1996; Wardle & Nicholson 1996); none has attempted to relate such effects to plant traits in a correlative manner.

The purpose of the present study was to investigate, through using a range of 20 herbaceous dicotyledonous grassland plant species and several ecophysiological traits measured for each of the species, the degree to which the various types of interactions outlined above were related to particular traits, and which combinations of traits may have potential for predicting outcomes of interactions involving plant species. The ultimate goal was to evaluate whether predictive comparative approaches could assist with

the generation of general principles about how ecophysiological traits may contribute to the performance and effects of plants at the ecosystem-level of resolution.

Methods

EXPERIMENTAL SET-UP

We selected 20 dicotyledonous herbaceous species (Table 1), all of which are abundant in New Zealand pasture/grassland ecosystems. All species were selected from the same 'functional group' in order to minimize discontinuities in the data. In this context, we regard dicotyledonous herbs as representing a discrete functional group, which is distinct from other functional groups present in the landscape, e.g. monocotyledonous species, dicotyledonous woody species, nitrogen-fixing species (e.g. Hooper & Vitousek 1997; Wardle & Barker 1997). Selection of this number of species appears appropriate in situations in which large numbers of measurements per species are performed (Keddy *et al.* 1994). Seeds from each species were collected in the field in the Waikato district of New Zealand (37°45′S, 175°19′E) between December 1993 and March 1994, and stored in air-dried conditions until further use.

The experiment was set up during June 1994, using the experimental protocol of Wardle & Nicholson (1996). Prior to initiation of the experiment, seedlings were sprouted in vermiculite and transplanted into pots before appearance of the first true leaf. Pots used were 12 cm diameter × 30 cm deep, and each contained ≈2.3 kg (dry weight basis) soil. The soil used was a Horotiu sandy loam (Vitric hapludand) with 6.0%C, 0.53%N, a pH of 6.0 and a sand:silt:clay ratio of 55:29:16. The experiment was arranged in a randomized block design with four replicate blocks. Within each block, four pots were set up for each species in monoculture, with one plant positioned in the centre of each pot. A further four pots per block were set up for each species in combination with the grass *Lolium perenne* L., for evaluation of competitive interactions (see below); each pot consisted of one dicotyledonous plant positioned in the centre, and three *Lolium* plants each positioned about 4 cm from the dicotyledonous plant in a radial pattern (Wardle & Nicholson 1996). Thirty pots were also established per block with three *Lolium* plants per pot but without the dicotyledonous species, to serve as *Lolium* monocultures for competition measurements. The densities and proportions of plant species we used for investigating competition between dicotyledonous plants and *Lolium* most closely resemble those found in the field, and have previously been shown to be appropriate for this type of study (Wardle & Nicholson 1996). We used a phytometer-based approach for studying competition, because of the convenience of this approach for investigating comparative competitive abilities of several plant species (Keddy *et al.* 1994; Gaudet & Keddy 1995). An additional 30 pots per block were set up but without plants, to serve as blanks for soil chemical and biological measurements (see below). For the experiment we intentionally set up more pots than we required, to enable us to accommodate losses due to plant mortality throughout the study.

All pots were maintained in glasshouse conditions; temperatures ranged from 15 to 30 °C in the summer and from 0 to 15 °C in the winter, while the corresponding day:night light ratios ranged from 14 h:10 h to 10 h:14 h. At the start of the experiment the soil was amended with urea (4 g kg^{-1} soil) and potassic superphosphate (4.6 g kg^{-1} soil). After 90 days the pots were amended every 8–10 days with a nutrient solution specifically designed for maintaining long-term plant growth in these sorts of experiments (Smith *et al.* 1983; Wardle & Nicholson 1996). All pots with *Lolium* were trimmed approximately monthly to maintain a mean grass height of 7 cm; this simulated field conditions under grazing (Wardle & Nicholson 1996). All clipped material was collected and its dry weight determined for each pot.

For each dicotyledonous species, pots were destructively harvested at three developmental stages, i.e. 'rosette stage', when plants had reached their maximum size immediately prior to flowering (Wardle & Nicholson 1996), full flowering stage and senescent stage. No flowering-stage measurements were made for *Cirsium*, since several of the plants succumbed to a severe fungal attack. The senescent stage was defined as when significant yellowing and browning of above-ground tissue had occurred. For those species capable of showing perennial tendencies (*Achillea*, *Cirsium*, *Rumex obtusifolius*) the majority of tissue had senesced after flowering in the first year. For each dicotyledonous species at each of the three stages, one pot per block was destructively harvested for each of the dicotyledonous plant monoculture, dicotyledonous plant and *Lolium* combination, *Lolium* monoculture and unplanted treatment, and determinations made as described below.

MEASUREMENT OF ECOPHYSIOLOGICAL TRAITS

In selecting plant traits to measure, we concentrated on traits that have previously been shown to be important in determining plant nutrient uptake, chemical composition, response to environmental conditions and ecological strategy (e.g. Grime 1979; Gaudet & Keddy 1988; Campbell & Grime 1989; Poorter & Remkes 1990; Nieman *et al.* 1992; Van de Werf *et al.* 1993). Only dicotyledonous monoculture pots were used for trait evaluation.

For each plant harvested at the rosette and flowering stages, the above-ground material was clipped off at ground level and separated into leaf, stem and

Table 1 Plant species investigated, together with information for some of the measured ecophysiological 'traits' (SD in parentheses)

Plant species	Family	Specific leaf area ($m^2\ kg^{-1}$)*	Leaf area ratio ($m^2\ kg^{-1}$)*	Root length to weight ratio ($m\ g^{-1}$)*	Shoot to root ratio*	Leaf N conc. (%)*	Total plant weight (g)†	Seed weight to plant weight ratio (%)†
Achillea millefolium L.	Asteraceae	10.2 (1.9)	4.1 (1.3)	79.3 (12.7)	0.68 (0.21)	1.86 (0.60)	41.5 (7.7)	4.1 (1.8)
Anthemis cotula L.	Asteraceae	16.3 (4.3)	9.3 (2.8)	145.0 (7.0)	3.25 (1.11)	2.66 (0.40)	84.5 (5.9)	19.2 (8.3)
Brassica rapa L. ssp. *sylvestris*	Brassicaceae	10.0 (2.2)	4.8 (0.5)	742.3 (149.0)	0.97 (0.37)	1.29 (0.24)	23.9 (9.0)	30.3 (12.3)
Carduus tenuifolius Curt	Asteraceae	9.9 (5.4)	5.9 (1.1)	95.5 (13.3)	1.81 (0.11)	0.72 (0.16)	64.5 (4.8)	ND‡
Cerastium glomeratum Thiul.	Caryophyllaceae	35.5 (6.8)	20.0 (3.6)	318.0 (58.0)	8.06 (1.44)	3.38 (0.07)	36.3 (11.8)	11.7 (10.8)
Chrysanthemum leucanthemum L.	Asteraceae	18.3 (3.3)	11.5 (2.7)	121.5 (42.0)	2.42 (0.52)	2.71 (0.33)	76.4 (3.3)	3.6 (1.3)
Cirsium arvense (L.) Scop.	Asteraceae	17.5 (3.2)	8.9 (3.1)	63.8 (13.1)	1.62 (0.57)	2.28 (0.35)	57.1 (6.5)	ND
Crepis capillaris (L.) Wallr	Asteraceae	16.6 (6.1)	9.9 (4.1)	138.3 (28.3)	1.10 (0.46)	1.17 (0.36)	36.6 (3.8)	3.4 (2.6)
Daucus carrota L.	Umbellifereae	18.5 (3.2)	11.4 (1.4)	207.0 (45.6)	1.66 (0.30)	1.63 (0.23)	56.1 (8.1)	33.8 (7.7)
Hypochaeris radicata L.	Asteraceae	17.4 (3.3)	8.9 (2.4)	210.3 (40.1)	1.14 (0.13)	1.53 (0.30)	51.6 (3.6)	10.4 (7.4)
Leontodon taraxacoides (Vill)	Asteraceae	31.2 (9.6)	24.9 (10.1)	237.7 (22.7)	4.06 (1.18)	3.81 (0.38)	28.0 (2.3)	7.0 (2.9)
Plantago lanceolata L.	Plantaginaceae	15.6 (5.7)	10.3 (3.3)	110.5 (21.3)	2.08 (0.51)	1.37 (0.29)	47.6 (4.4)	9.4 (1.4)
Ranunculus sardous Crantz	Ranunculaceae	35.7 (5.3)	12.5 (1.8)	170.0 (26.3)	2.38 (0.23)	2.11 (0.38)	30.5 (9.8)	35.2 (13.2)
Rumex obtusifolius L.	Polygonaceae	23.2 (6.5)	3.2 (0.8)	238.3 (19.0)	0.16 (0.02)	1.60 (0.34)	111.5 (9.0)	4.3 (3.4)
Rumex pulcher L.	Polygonaceae	28.0 (5.1)	4.0 (0.7)	312.5 (110.4)	0.17 (0.03)	2.68 (0.45)	65.1 (11.1)	13.4 (5.6)
Silene gallica L.	Caryophyllaceae	24.6 (3.0)	6.0 (0.4)	434.0 (125.0)	6.72 (1.52)	1.45 (0.19)	64.8 (8.3)	9.2 (4.2)
Sisymbrium officinale (L.) Scop.	Brassicaceae	12.7 (1.3)	7.6 (0.9)	914.3 (71.8)	1.52 (0.09)	4.64 (0.11)	18.2 (2.6)	22.2 (7.9)
Spergula arvensis L.	Caryophyllaceae	43.9 (17.3)	ND	ND	ND	5.06 (0.39)	13.2 (1.1)	41.1 (9.2)
Stellaria media (L.) Vill.	Caryophyllaceae	58.7 (8.3)	27.8 (1.2)	232.0 (77.9)	4.69 (0.53)	5.42 (0.30)	25.8 (7.3)	4.4 (1.0)
Taraxacum officinale Weber	Asteraceae	32.9 (8.3)	23.0 (4.3)	162.0 (35.1)	1.56 (0.45)	1.58 (0.29)	14.5 (3.7)	5.3 (2.8)

*Data for rosette plants immediately prior to initiation of flowering.
†Biomass data from plants in full flower.
ND, not determined.

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(where present) reproductive material. The soil was carefully removed from the root system, the roots thoroughly rinsed and the root material sorted into diameter size classes of <1 mm, 1–3 mm, 3–7 mm and >7 mm. Each of these above-ground and below-ground components was oven-dried (after certain measurements: see below) at 80 °C for 24 h and the dry weight determined.

Prior to drying, the number of leaves per plant was determined and 10–100 randomly selected leaves were assessed for mean leaf area using a LI-COR model LI-3000 area meter. The mean weight of each leaf was also determined. Based on these measurements and the plant weight data, we also determined the specific leaf area (i.e. leaf area/leaf weight), leaf weight ratio (i.e. total weight of leaves/total plant weight) and leaf area index (i.e. specific leaf area × leaf weight ratio) for each plant. Our plant weight data also enabled determination of the shoot to root ratio. The mean growth rate of plants during the entire vegetative stage was determined as the ratio of rosette plant weight to the time (in days) until first harvest.

Prior to drying the fine (<1 mm) roots, their total wet weight was determined, and a random subsample of root material (usually 0.10–1.00 g wet weight) was weighed, placed in blue dye and separated out on a sheet of A4-sized acetate. A photocopy of this acetate was then scanned, and the scanned image was evaluated using a customized MATLAB program (C. Hunt, AgResearch) written to implement the line intercept method for determining total root length (Newman 1966). The root length value obtained was used to determine the root length to dry weight ratio (note dry weight was determined as subsample wet weight × whole sample dry weight/whole sample wet weight), as well as the total length of roots per pot.

A subsample of the fine roots, stems and leaves from each plant for each of the three stages for each species was analysed for total nitrogen concentration by using a micro-Kjeldahl technique.

For each plant allowed to reach the senescent stage before harvest, the total number of seeds produced was estimated over the entire reproductive phase. The mean weight of several (usually 150–200) seeds per plant was also determined. A measure of the proportion of plant resources allocated to seeds, i.e. the ratio of the total weight of seeds produced (mean weight × total number) to the total weight of the plant at flowering, was determined for each species in each replicate block.

MEASUREMENT OF RESPONSE VARIABLES

For evaluating litter decomposition of each dicotyledonous species, senescent leaf, stem and root material was collected from each plant species from each of the four replicate blocks. This material was stored at room temperature in an air-dried condition prior to further use. Determination of decomposition rates of this senescent material was performed under standardized conditions. For each tissue investigated, a 9-cm diameter Petri dish was two-thirds filled with freshly collected soil (Horotiu sandy loam, described earlier) amended to 55% moisture content (dry weight basis); a disc of nylon mesh (1-mm holes) was placed on the soil surface. The litter (<1 cm fragments, 0.5 g dry weight) was placed on the surface of this, the Petri dish lid was sealed with tape, and the dish was incubated for 28 days at 22 °C. At the end of the incubation the litter was removed, rinsed, and the dry weight (80 °C, 24 h) remaining was determined.

The pots containing *Lolium* enabled determination of both the competitive effect and response of each of the dicotyledonous species. At each harvest period for the dicotyledonous monocultures, one pot of the dicotyledonous species + *Lolium* combination, and one of the *Lolium* monoculture pots, was also destructively harvested for each block; all the plants in each pot were clipped off at ground level. The *Lolium* material in each pot was oven-dried (80 °C, 24 h) and the weight of this material was added to the cumulative weight of all the prior trimmings of that pot, to determine the total production of *Lolium* during the experiment (Wardle & Nicholson 1996). The amount of *Lolium* production in the two-species pots, relative to that in the *Lolium* monoculture pots, was used as a measure of the net competitive effect of the dicotyledonous species against *Lolium* (Wardle & Nicholson 1996). The above procedure was followed for each of the three developmental stages for each species. The above-ground biomass of the dicotyledonous species present in the two species pots was determined for all plants harvested at the rosette, and at the full flower stages, and this was compared with the dicotyledonous monoculture dry weight (discussed earlier) to obtain a measure of competitive response to *Lolium*. Further, for the dicotyledonous plants grown in combination with *Lolium* that were allowed to reach the senescent stage, total seed production per plant was measured as described earlier for the dicotyledonous monocultures, to enable assessment of the response of reproductive output of each species to interference from *Lolium*.

For determining plant effects on soil biological and chemical properties, a soil subsample (≈ 100 g dry weight) was collected from each harvested dicotyledonous monoculture pot, as well as a corresponding plant-free pot from the same replicate block. For each soil sample, determinations were made on subsamples for microbial basal respiration and substrate-induced respiration (SIR; a relative measure of active microbial biomass), using approaches described by Anderson & Domsch (1978) and West & Sparling (1986) as modified by Wardle *et al.* (1993). For measuring basal respiration, one subsample of 15 g (dry weight) was amended to 55% moisture content (air-dry basis) either by gradual air-drying or by rewetting with a fine mist, placing it in a 169 ml airtight vessel

and incubating it at 22 °C. Evolution of CO_2-C between 1 h and 4 h was then determined by injecting 1-ml subsamples of headspace gas into an infrared gas analyser. Measurement of SIR was performed in the same way, but with amendment of the soil subsample with 90 mg glucose at the start of the incubation. A relative measure of the microbial metabolic quotient (qCO_2) or respiration to biomass ratio, a measure of microbial inefficiency, was calculated as the ratio of basal respiration to SIR (Anderson & Domsch 1985; Wardle & Ghani 1995). Subsamples of each sample were also analysed for concentrations of ammonium and nitrate using a Technicon auto-analyser, and soil pH was measured for each sample. For all the soil samples collected from pots with senescent plants, and the corresponding unplanted pots, total nitrogen concentration was also measured by using micro-Kjeldahl analysis. For each of the soil biological and chemical properties measured, the difference between the planted and unplanted pots was used as a measure of the effect of the plant on the property.

Parallel studies were set up to determine the palatability of the plants to two herbivorous invertebrates, i.e. *Listronotus bonariensis* (Kuschel) (Insecta: Coleoptera: Curculionidae) and *Deroceras reticulatum* (Müller) (Mollusca: Stylommatophora: Agriolimacidae). To investigate seedling palatability, two experiments were conducted, each with a different herbivore. For the first experiment, 20 pots, each 8.5 cm diameter × 9 cm deep, were set up for each dicotyledonous species; each was filled with about 110 g (dry weight) potting mix and one seedling was established in each pot. Immediately upon initiation of the first true leaf for that species, 10 adult *Listronotus* were confined to each of 10 of the pots by gauze mesh (0.3-mm holes); the other 10 pots were covered but kept herbivore-free. The pots were then placed in a randomized block design in a constant environment room (20 °C; day:night light ratio = 16 h:8 h) for 10 days, after which the plants were all cut at ground level and oven dried (80 °C, 24 h). The biomass of seedlings that were subjected to herbivory relative to those that were not was used as a relative measure of consumption of each species. The second experiment was conducted as described above, but with herbivory performed instead by one individual of *Deroceras* (body mass = 420–525 mg) per pot.

To test the palatability of plants at the rosette stage, two experiments were conducted. For the first, 10-mm diameter leaf discs were cut from leaves of rosette-stage plants of each species (except *Silene* and *Spergula*) in the field. For each species, sufficient leaf discs were placed into 10 9-cm diameter Petri dishes lined with moist filter paper to give 50 mg dry weight of material per dish (determined by predrying disc samples). Thirty adult *Listronotus* individuals were added to each of five of the dishes for each plant species; the other five were left insect-free. The Petri dishes were incubated in a growth chamber (18 °C; day:night light ratio = 16 h:8 h) in a randomized block design for 4 days. After incubation, all leaf discs were dried (100 °C, 24 h) and the dry weight remaining determined. The difference in dry weight remaining between the herbivore-treated and untreated leaf discs for each species was used as a measure of palatability for that species. The second experiment was conducted as for the first one (for all 20 plant species except *Leontodon*), except that 150 mg leaf disc material was used in each dish, three mature *Deroceras* (body weight 390–560 mg) were confined to each dish, and 10 replicates were used for the herbivore-amended and non-amended treatments.

Results

Although all plant species were selected from the same plant functional group there were large differences between species for all of the ecophysiological traits measured, and all traits except those based on tissue nitrogen concentration showed at least a 10-fold range across species (Table 1). There was no obvious evidence of discontinuities or clusters across the 20 species with regard to the traits we selected. Several of the traits were correlated with each other; it is apparent that plants that flowered the most rapidly and that were shorter lived also grew more slowly (Pearson's r between time until flowering and rosette growth rate = -0.563, $P = 0.015$), reached a smaller size (r between time and flowering plant weight = 0.493, $P = 0.032$) and contained more nitrogen in their tissues [r between time and rosette leaf and root nitrogen concentration = -0.692 ($P = 0.001$) and -0.626 ($P = 0.006$), respectively]. There were no significant correlations between either time until flowering and shoot to root ratio, proportion of mass allocated to seeds, number or mean weight of seeds, or any of the variables based on leaf area or root length. However, rosette growth rate was significantly negatively related to both leaf weight ratio ($r = -0.792$, $P < 0.001$) and leaf area ratio ($r = -0.750$, $P < 0.001$).

There were important differences between species with regard to leaf litter decomposition rates (Fig. 1), and leaf tissues tended to decompose faster than root or stem tissues. Decomposition rates of leaf and stem tissues were significantly correlated ($r = 0.626$, $P = 0.007$) but neither were correlated with root decomposition rate. Leaf and stem decomposition rates were also most closely correlated to the same traits, i.e. negatively with rosette weight and growth rate before flowering, and time before flowering, and positively with stem nitrogen concentration (Fig. 2). Root decomposition was negatively related to rosette growth rate and root length to weight ratio, and positively to leaf to weight ratio (Fig. 2). Multiple regression relationships revealed that for both stem and root litter, the vast majority of variation in the

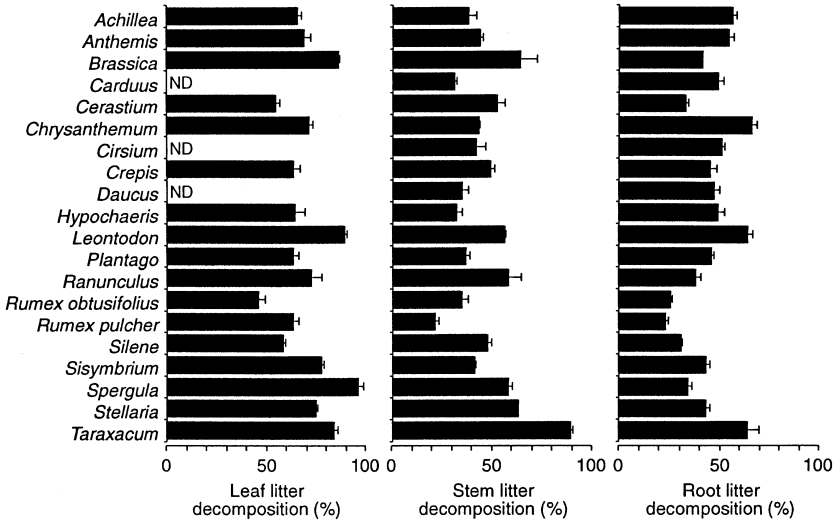

Fig. 1 Decomposition rates of leaf, stem and root litter for 20 herbaceous plant species. Horizontal bars represent standard errors. ND = not determined.

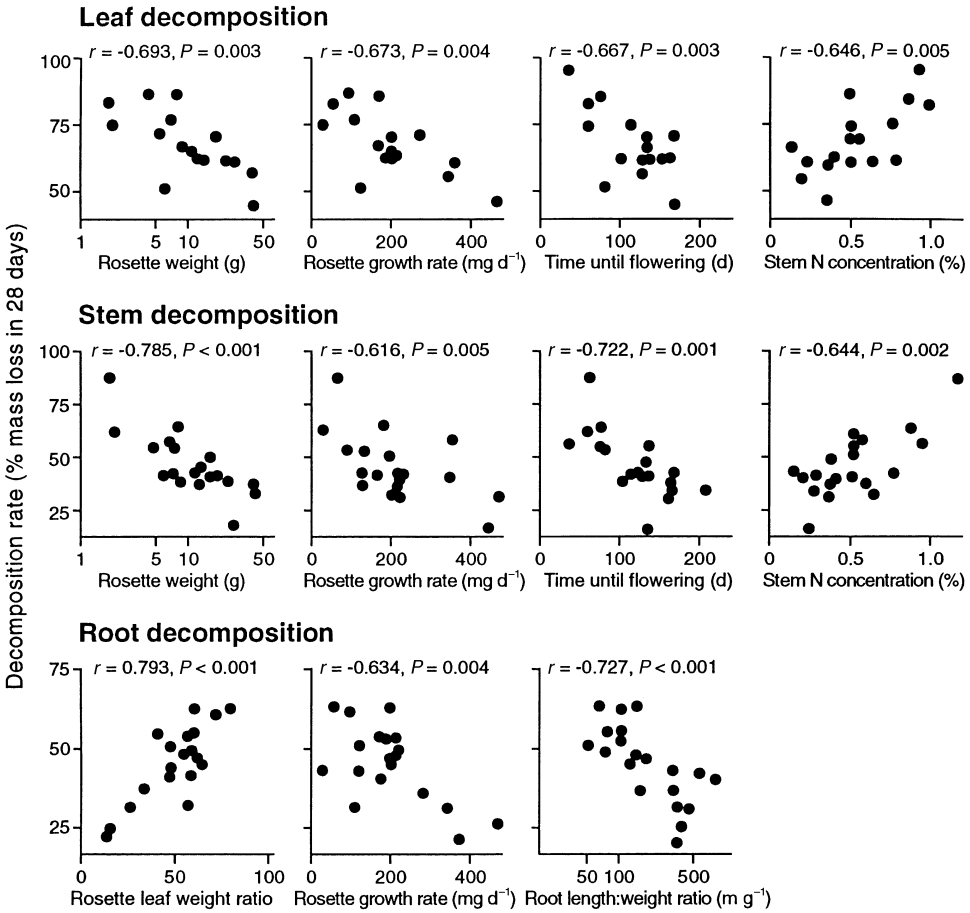

Fig. 2 Relationships between decomposition rates of leaf, stem and root litter and key ecophysiological plant traits. In each subgraph, each point represents a different plant species. Rosette weight applies to the above-ground biomass immediately prior to initiation of flowering; root length to weight ratios are presented for plants in full flower.

data set could be explained in terms of ecophysiological traits (Table 2).

Plant species varied considerably in their palatability by invertebrate herbivores in each of the four feeding experiments we conducted (Fig. 3). Palatability of leaf discs to *Deroceras* was significantly positively related to palatability of both leaf discs and seedlings to *Listronotus* [$r = 0.660$ ($P = 0.007$) and 0.561 ($P = 0.021$), respectively], but the results of no other pairs of feeding tests were significantly corre-

Table 2 Step-wise multiple regression relationships relating decomposition, palatability to invertebrate herbivores and aspects of plant competitiveness to plant ecophysiological traits across 20 plant species. Only terms (independent variables) that have a statistically significant slope at $P = 0.05$ are included in each relationship*

Dependent variable		Regression relationship†	R^2	P
Decomposition of:	leaf litter (% loss in 28 day)	$0.893 - 0.0903ln$(ROSWT)	0.481	0.003
	stem litter (% loss in 28 day)	$0.874 - 0.104ln$(ROSWT) $- 0.00136$(FLTIME)	0.739	<0.001
	root litter (% loss in 28 day)	$0.634 + 0.409$(LWRR) $- 0.731ln$(RLRF)	0.810	<0.001
Palatability of seedlings to	*Deroceras* (% consumption in 10 day)	$0.828 - 0.249ln$(SEEDWT) $+ 0.407$(LWRR)	0.461	0.014
	Listronotus (% consumption in 10 day)	$0.783 - 0.00114$(ROSPR)	0.303	0.022
Palatability of leaf discs to	*Deroceras* (% consumption in 4 day)	$1702e^{\text{ROSPR}}(\text{FLWT})^{-1.13}$	0.591	0.003
	Listronotus (% consumption in 4 day)	$-0.467 + 24.8$ (NS)	0.356	0.009
Competitive effect against *Lolium* by:	rosettes (% reduction)	$0.516 - 0.370ln$(RNL)	0.416	0.002
	flowering plants (% reduction)	$-0.260 + 0.134ln$(RLRR) $- 0.334$(FLN)	0.542	0.001
	senescent plants (% reduction)	$0.471 + 0.0411ln$(LARF) $+ 0.265ln$(FLN)	0.562	0.005
Competitive response to *Lolium* by:	rosettes (% reduction)	$0.764 + 0.00313$(FLTIME) $- 0.121ln$(RLRR)	0.574	0.003

*No significant terms for competitive response to *Lolium* by flowering plants or seed production per plant.
†ROSPR = mean production rate of rosette plant (mg day^{-1}1); ROSWT, FLWT = weight of plant (g) at rosette stage prior to flowering, and at full flower; LWRR = leaf weight ratio at rosette stage; LARF = leaf area ratio of flowering plant (m^2 kg^{-1}); FLTIME = time (day) until flowering; SEEDWT = mean weight of each seed (mg); RLRR, RLRF = root length to weight ratio (m g^{-1}) at rosette stage, and at flowering; RNL, FNL, NS = N concentration (%) of rosette leaves, leaves of flowering plants and stems of flowering plants.

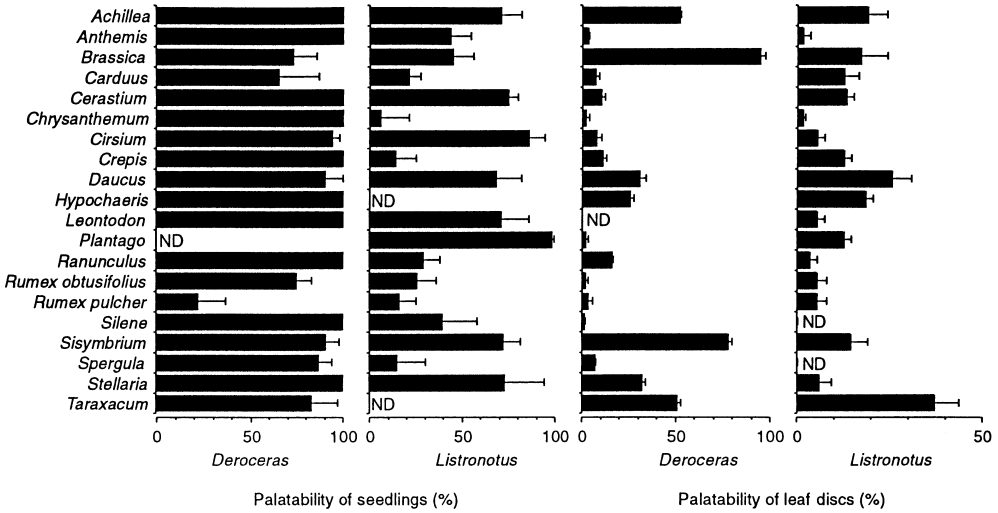

Fig. 3 Palatability (=percentage consumption) of seedlings (over 10 days) and leaf discs (over 4 days) of 20 plant species by invertebrate herbivores. Horizontal bars represent standard errors. ND = not determined.

lated. The data from all the consumption tests were significantly related to at least some plant traits, and palatability to *Deroceras* was related to a wider range of traits than was palatability to *Listronotus* (Table 3). The traits that appeared to show the strongest relationship with palatability were those associated with vegetative growth characteristics, and (for the leaf disc data) the nitrogen concentration of stems of flowering plants. Multiple regression analyses revealed strong relationships between seedling palatability to *Deroceras* and a three-parameter model incorporating the average weight of each seed produced by the plant and the rosette leaf weight ratio; and between leaf disc palatability to *Deroceras* and a three-parameter model incorporating rosette growth rate and total plant weight at flowering (Table 2). Leaf disc palatability was not significantly correlated with leaf litter decomposition at $P = 0.05$ for either herbivore, although the test using *Deroceras* was close (Fig. 4).

In most cases significant reduction of both *Lolium* and the dicotyledonous plants in the presence of each other was observed in the competition experiment (Fig. 5). However, there were instances where inhibition did not occur, and significant growth stimulation of *Lolium* by rosette plants of *Cerastium* also occurred. Generally flowering and senescent dicotyledonous plants inhibited *Lolium* production more than did rosette plants. There were marginally significant negative correlations between competitive responses of rosette plants to *Lolium* and effects of flowering plants ($r = -0.515$, $P = 0.034$) and senescent plants ($r = -0.513$, $P = 0.030$) on *Lolium*, but there were no significant relationships between any

Table 3 Correlation coefficients between palatability (proportion of plant material consumed) by invertebrate herbivores, and selected key plant ecophysiological traits, across 20 plant species

	Palatability of seedlings by		Palatability of leaf discs by	
Plant trait	*Deroceras*	*Listronotus*	*Deroceras*‡	*Listronotus*
Rosette plant weight just before flowering‡	−0.309	−0.463†	−0.716**	−0.336
Rosette growth rate	−0.426†	−0.550*	−0.650**	−0.311
Rosette shoot to root ratio	0.525**	0.256	0.124	0.130
Rosette leaf weight ratio	0.448*	0.388	0.518*	0.308
N concentration of stem (flowering plant)	0.020	0.195	0.620**	0.595**
Mean weight of each seed‡	−0.555**	0.100	0.094	0.084

†,*,** = correlation coefficient is significantly different to 0 at $P = 0.10$, 0.05 and 0.01, respectively.
‡Variate log-transformed.

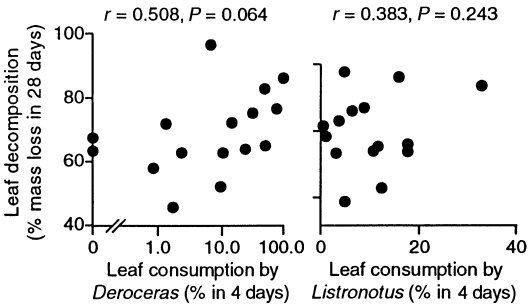

Fig. 4 Leaf litter decomposition rate vs. palatability of leaf discs by *Deroceras* and by *Listronotus*. Each point represents a different plant species. Correlation coefficients determined after ln $(x + 1)$ transformation of *Deroceras* data.

other pair of competition variables. For all of the three dicotyledonous developmental stages the competitive effects against *Lolium* were most closely correlated with leaf nitrogen concentration (Fig. 6); while this relationship was strong for rosette stage plants, it was only marginally significant at $P = 0.05$ for the flowering and senescent stages. However, much stronger relationships involving effects of flowering and senescent plants against *Lolium* were identified when leaf nitrogen concentration was included together with other traits in multiple regression relationships (Table 2). The competitive response of rosette plants to *Lolium* was best predicted by a three-parameter model incorporating time until flowering and root length ratio, but competitive response of flowering plant mass, or of total seed production per plant, could not be related to any of the traits we measured.

All plant species had stimulatory effects on both microbial basal respiration and SIR relative to the unplanted pots, and these effects were strongest for flowering and senescent plants (Table 4). For flowering plants, basal respiration was most closely related

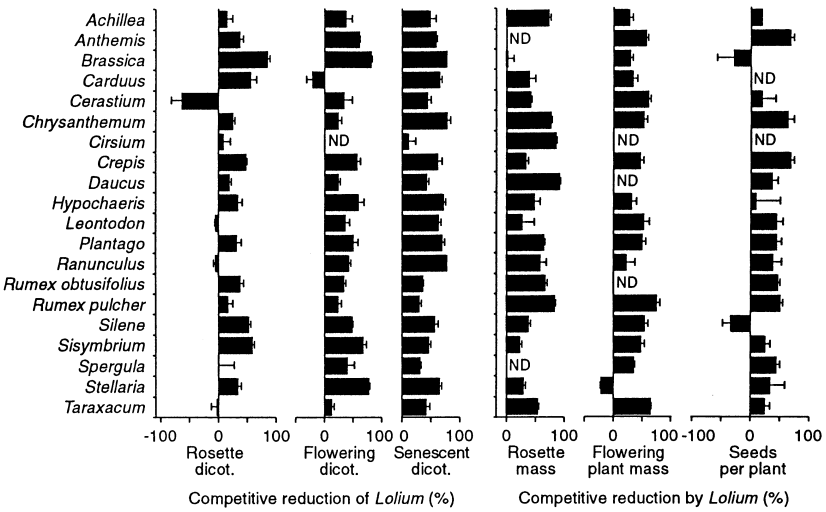

Fig. 5 Competitive response (=percentage suppression) of *Lolium* above-ground productivity by rosette, flowering and senescent dicotyledonous plants, and competitive reduction of above-ground rosette plant biomass (immediately before initiation of flowering), flowering plant biomass and total seed production of dicotyledonous plants. Horizontal bars represent standard errors. ND = not determined.

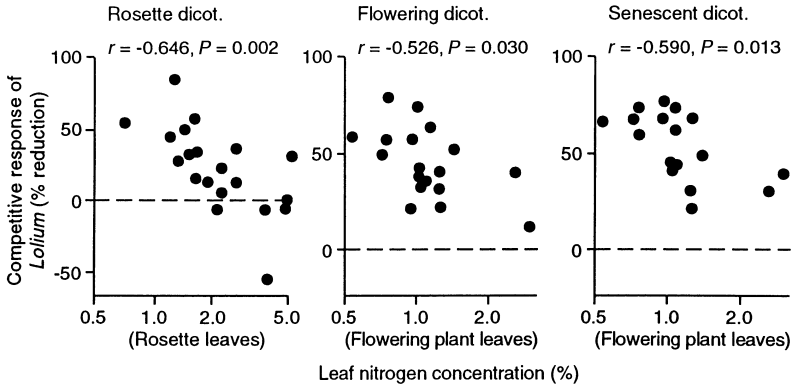

Fig. 6 Relationships between leaf nitrogen concentration, and competitive response of *Lolium* to rosette, flowering and senescent dicotyledonous plant species. Each point on each subgraph represents a different dicotyledonous species.

to plant leaf weight ratio and stem nitrogen concentration, while SIR was not related to any plant trait (Table 5). Plant traits had the strongest effects for these variables when plants were at the senescent stage; enhancement of both these variables was most closely related to the root length to weight ratio (flowering stage) and the total seed production per plant (Fig. 7), and both these terms were significant when incorporated into multiple regression relationships (Table 5). The ratio of basal respiration to SIR was always enhanced by rosette and flowering plants, though not always by senescent plants (Table 4). Enhancement of this ratio by flowering plants was negatively related to both the stem nitrogen concentration of flowering plants, and the proportion of plant mass allocated to seeds, and positively related to time until flowering (Fig. 8). Multiple regression analysis revealed that the effects of flowering plants on this ratio could be easily predicted by a four-parameter model encompassing four plant traits (Table 5). The effect of senescent plants on enhancing this ratio was less easily predicted by plant traits, although shoot to root ratio, and nitrogen concentration of senescent roots, both emerged as predictors (Table 5).

The plant species we considered all reduced soil nitrate concentrations relative to the unplanted pots, and this was most apparent for plants at the flowering stage (Table 6). Most plants also enhanced soil pH and total nitrogen concentration. Soil ammonium concentrations were always negligible and will not be considered further. Enhancement of soil pH and

Table 4 Effects of plant species at the full flowering and senescent stages on soil basal respiration, SIR and basal respiration to SIR ratio (SD in parentheses)

	Enhancement of basal resp. (μgCO_2-C h^{-1} g^{-1}) by		Enhancement of SIR (μgCO_2-C h^{-1} g^{-1}) by		Enhancement of basal resp. to SIR ratio by	
Plant species	Flowering plant	Senescent plant	Flowering plant	Senescent plant	Flowering plant	Senescent plant
Achillea	0.25 (0.13)	0.23 (0.08)	1.29 (0.72)	2.23 (0.52)	0.23 (0.40)	−0.03 (0.05)
Anthemis	0.80 (0.11)	1.10 (0.12)	0.70 (0.64)	1.71 (0.20)	0.11 (0.04)	0.20 (0.04)
Brassica	0.49 (0.19)	0.22 (0.14)	2.83 (0.38)	0.81 (0.65)	0.01 (0.01)	0.04 (0.01)
Carduus	0.91 (0.09)	0.66 (0.15)	1.16 (0.51)	2.59 (0.54)	0.11 (0.02)	0.05 (0.54)
Cerastium	0.45 (0.24)	0.18 (0.10)	2.13 (0.88)	1.09 (0.33)	0.02 (0.07)	0.00 (0.02)
Chrysanthemum	1.77 (0.15)	1.76 (0.54)	1.40 (0.44)	1.92 (0.62)	0.34 (0.04)	0.34 (0.07)
Cirsium	0.65 (0.20)	1.19 (0.25)	2.32 (0.43)	4.23 (0.16)	0.02 (0.06)	−0.04 (0.16)
Crepis	1.80 (0.46)	0.87 (0.20)	0.97 (0.16)	3.20 (0.30)	0.27 (0.09)	0.06 (0.01)
Daucus	1.18 (0.14)	0.49 (0.15)	1.15 (0.32)	2.62 (0.45)	0.14 (0.06)	−0.03 (0.05)
Hypochaeris	0.79 (0.16)	1.75 (0.12)	0.49 (0.31)	3.51 (0.31)	0.12 (0.03)	0.19 (0.03)
Leontodon	1.05 (0.20)	1.04 (0.10)	3.28 (0.79)	3.18 (0.39)	0.06 (0.03)	−0.21 (0.59)
Plantago	0.97 (0.32)	3.02 (0.09)	1.75 (0.37)	4.11 (0.37)	0.11 (0.03)	0.34 (0.02)
Ranunculus	0.47 (0.25)	0.32 (0.16)	1.30 (0.17)	0.85 (0.10)	0.06 (0.05)	0.05 (0.05)
Rumex obtusifolius	0.72 (0.10)	0.53 (0.32)	1.02 (0.33)	2.15 (0.85)	0.13 (0.03)	0.02 (0.04)
Rumex pulcher	0.00 (0.12)	0.85 (0.12)	0.35 (0.69)	2.02 (0.41)	0.03 (0.03)	0.12 (0.03)
Silene	1.03 (0.14)	0.47 (0.10)	1.58 (0.18)	0.97 (0.21)	0.13 (0.12)	0.07 (0.02)
Sisymbrium	0.57 (0.07)	0.39 (0.19)	1.70 (0.50)	1.29 (0.17)	0.06 (0.01)	0.05 (0.04)
Spergula	0.21 (0.31)	0.14 (0.13)	0.57 (0.22)	0.92 (0.39)	0.02 (0.06)	0.00 (0.21)
Stellaria	0.88 (0.13)	0.34 (0.15)	1.83 (0.25)	1.67 (0.33)	0.11 (0.02)	0.01 (0.02)
Taraxacum	0.43 (0.08)	1.07 (0.20)	0.10 (1.36)	3.07 (0.59)	0.06 (0.02)	0.10 (0.03)

Table 5 Step-wise multiple regression relationships relating plant species effects on soil properties to plant ecophysiological traits across 20 plant species. Only terms (independent variables) that have a statistically significant slope at $P = 0.05$ are included in each relationship*

Dependent variable		Regression relationship†	R^2	P
Enhancement of basal respiration by:	flowering plants (μgCO_2-C g^{-1} h^{-1})	$0.528 + 1.57$ (LWRR) $- 1.11$ (NS)	0.440	0.010
	senescent plants (μgCO_2-C g^{-1} h^{-1})	539 (RLRF)$^{-0.565}$ (NOSEED)$^{-0.419}$	0.638	<0.001
Enhancement of SIR by:	senescent plants (μgCO_2-C g^{-1} h^{-1})	$9.094 - 0.389ln$(NOSEED) $- 0.651ln$(RLRF)	0.491	<0.001
Enhancement of basal respiration to SIR ratio by:	flowering plants	$0.283e^{0.00968(\text{FLTIME})}$ (RLRF)$^{-0.440}$(PSEED)$^{-0.523}$	0.781	<0.001
	senescent plants	$0.270 - 0.0651ln$(SRF) $- 0.168$(NSR)	0.486	0.004
Enhancement of soil pH by:	flowering plants	$2.36 - 0.0219$ (FLTIME) $+ 0.156$(NRF)	0.731	<0.001
	senescent plants	$0.376 - 0.0891ln$(PSEED) $- 0.0972ln$(SRF) $+ 0.661$(LWRF)	0.724	0.001
Reduction of soil nitrate by:	flowering plants (μg g^{-1})	$41.7e^{0.474(\text{NS})+0.00594(\text{FLTIME})}$ (RNL)$^{-0.260}$	0.851	<0.001
	senescent plants (μg g^{-1})	$202.3e^{-0.842(\text{PSEED})}$	0.319	0.022
Enhancement of percentage soil N by:	senescent plants	$0.00121 - 0.00971ln$(LP)	0.423	0.003

*No significant terms for effects of flowering plants on SIR. Data not presented for rosette plants.
†Symbols in relationships as for Table 2. Additional symbols: FLA = mean area of leaf of flowering plant (cm^2); LWRF = leaf weight ratio of flowering plants (m^2 kg^{-1}); SRF = shoot to root mass ratio (flowering plants); LP = total length of rosette fine roots (km); RW = total weight of roots of rosette plant (g); NRF, NSR = nitrogen concentration of roots of flowering, and of senescent plants; PSEED = proportion of total plant mass allocated to seeds; NOSEED = number of seeds produced per plant.

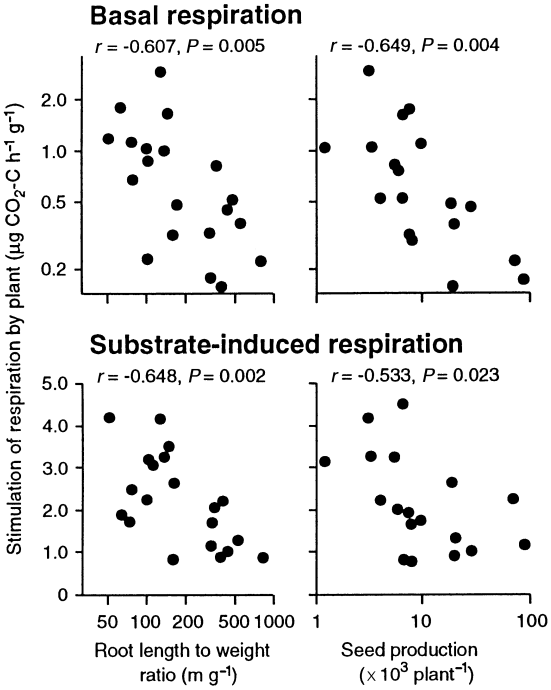

Fig. 7 Relationships between stimulation of soil basal respiration and SIR by plant species at the senescent stage, and root length to weight ratio and seed production per plant for the same plant species at the flowering or reproductive stage. Each point on each subgraph represents a different plant species.

reduction of soil nitrate levels were both significantly related to several traits indicative of plant mass and mass allocation, time until flowering, seeding characteristics and nitrogen concentrations of tissue (Table 7). Multiple regression relationships revealed strong relationships between effects of plants on soil pH or nitrate levels and combinations of these traits (Table 5). Enhancement of total soil nitrogen by senescent plants relative to the plant-free pots was most closely related to the total length of fine roots produced per plant at the rosette stage (Table 5).

Discussion

Our results show that within the plant functional group we identified there were large differences between plant species with regard to their traits. Several traits were also related to one another; plants that had an overall slower growth rate during the vegetative phase flowered earlier, reached a smaller size, had a higher tissue nitrogen concentration and had a lower leaf area per unit plant mass. Thus there were clear ecophysiological differences between those plant species that flowered first (i.e. *Spergula*, *Stellaria*) and those that flowered later (i.e. *Chrysanthemum*, *Rumex obtusifolius*). The close relationship we found between several of the traits we measured at least partially supports the conclusion of Reich *et al.* (1992) that co-variation in several interlinked traits provides a useful conceptual link between processes at leaf/whole plant scales, and ecosystem-level scales. The suite of ecophysiological traits we measured for each species thus provides a suitable gradient across which biotic interactions and ecosystem-level properties can be evaluated.

There is increasing recognition that those characteristics that determine plant ecological strategies are also likely to be important determinants of plant litter decomposition rates (Cornelissen 1996; Heal *et al.* 1997; Wardle & Lavelle 1997). We found several plant traits to be important in explaining litter decomposition rates. For stem and leaf litter, we found that plants which grew more slowly, reached a smaller size, were shorter lived and grew smaller also concentrated more nitrogen into their tissues and decomposed more

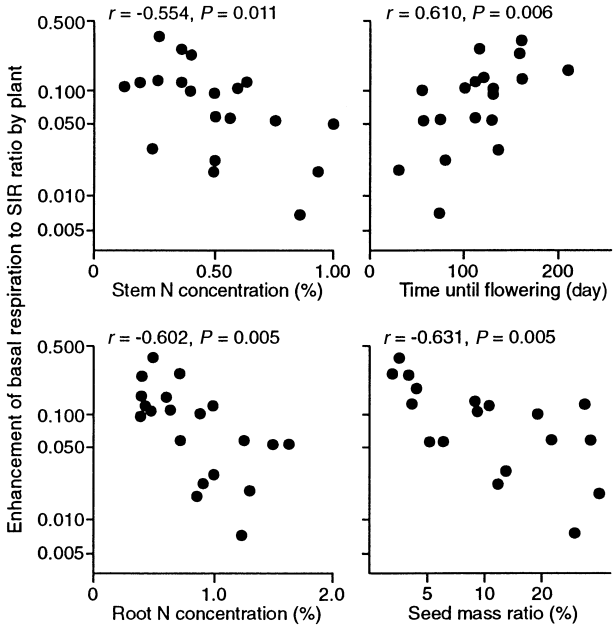

Fig. 8 Relationships between enhancement of the soil basal respiration to SIR ratio by plant species at the flowering stage, and key traits for the same plant species at the flowering or reproductive stage. Each point on each subgraph represents a different plant species.

rapidly. This appears consistent with plant strategy theory (Grime 1979; Coley *et al.* 1985), which predicts that longer lived species produce more recalcitrant tissue, as well as with modelling analyses presented by Tateno & Chapin (1997), which predict that slow growth rates can be associated with low C to N ratios. The likely significance of plant traits as controls of decomposition rates is demonstrated through combinations of traits being able to explain 74% and 81% of the variation in the stem and root decomposition, respectively (Table 2). It is unclear as to whether specific ecophysiological traits operate as direct or indirect controls of decomposition and we make no attempt at identifying mechanisms of causation; rather our point is that suites of ecophysiological traits are probably highly important in governing decomposition

Table 6 Effects of plant species at the full flowering and senescent stages on soil pH and nitrate levels, and senescent plants on total soil nitrogen concentration (SD in parentheses)

Plant species	Increase of soil pH by		Reduction of soil nitrate (μg g^{-1}) by		Enhancement of percentage soil nitrogen by senescent plant
	Flowering plant	Senescent plant	Flowering plant	Senescent plant	
Achillea	0.08 (0.15)	0.48 (0.15)	15.5 (5.1)	70.3 (48.0)	0.028 (0.040)
Anthemis	−0.13 (0.09)	0.03 (0.06)	15.5 (5.1)	2.7 (6.4)	0.000 (0.000)
Brassica	0.40 (0.00)	0.15 (0.17)	33.7 (6.5)	10.5 (4.5)	0.015 (0.026)
Carduus	−0.03 (0.05)	0.13 (0.05)	15.5 (5.7)	10.8 (5.8)	0.003 (0.022)
Cerastium	0.30 (0.12)	0.20 (0.08)	25.0 (14.8)	13.0 (0.8)	0.022 (0.022)
Chrysanthemum	−0.03 (0.05)	0.28 (0.15)	12.5 (5.5)	70.3 (48.0)	0.023 (0.015)
Cirsium	−0.30 (0.24)	0.87 (0.21)	52.8 (32.0)	40.3 (15.2)	0.043 (0.006)
Crepis	0.10 (0.12)	0.47 (0.15)	15.8 (5.5)	122.7 (34.1)	0.007 (0.025)
Daucus	−0.13 (0.05)	−0.10 (0.17)	15.5 (5.7)	25.0 (45.9)	0.000 (0.026)
Hypochaeris	0.00 (0.00)	0.43 (0.05)	13.3 (3.2)	142.5 (47.1)	0.003 (0.001)
Leontodon	0.23 (0.10)	0.50 (0.22)	37.0 (5.1)	142.5 (47.0)	0.005 (0.013)
Plantago	−0.03 (0.05)	0.48 (0.10)	12.5 (5.5)	142.5 (47.0)	−0.018 (0.010)
Ranunculus	0.03 (0.13)	0.07 (0.21)	15.0 (6.2)	5.3 (10.6)	0.010 (0.017)
Rumex obtusifolius	0.03 (0.06)	0.30 (0.61)	14.0 (4.4)	76.0 (108.3)	0.003 (0.059)
Rumex pulcher	0.03 (0.05)	0.25 (0.17)	13.0 (6.3)	43.5 (26.5)	−0.025 (0.010)
Silene	0.00 (0.00)	−0.05 (0.06)	15.3 (1.7)	12.3 (5.2)	−0.005 (0.017)
Sisymbrium	0.28 (0.10)	0.13 (0.10)	17.3 (6.6)	0.5 (8.3)	−0.010 (0.018)
Spergula	0.20 (0.08)	−0.03 (0.13)	53.5 (8.6)	10.5 (7.3)	0.125 (0.171)
Stellaria	0.35 (0.13)	0.00 (0.08)	48.3 (4.1)	11.8 (2.2)	0.020 (0.030)
Taraxacum	0.38 (0.10)	0.55 (0.06)	48.0 (3.9)	143.0 (47.0)	0.025 (0.010)

Table 7 Correlation coefficients between effects of plant species on soil pH or nitrate levels, and selected key plant traits, across 20 plant species

	Increase of soil pH by		Reduction of soil nitrate by	
Plant trait	Flowering plants	Senescent plants	Flowering plants‡	Senescent plants‡
Above-ground weight of flowering plant‡	−0.649**	−0.305	−0.502*	0.143
Shoot to root ratio of flowering plant‡	−0.144	0.563**	−0.242	0.517*
Time until full flowering	0.791***	−0.063	0.811***	−0.273
Number of seeds produced per plant‡	−0.218	−0.666**	0.184	0.543*
Proportion of biomass allocated to seeds‡	−0.053	−0.625**	−0.088	0.565*
N concentration of stems (flowering plants)‡	0.633**	0.176	−0.624**	0.048
N concentration of roots (flowering plants)‡	0.581**	0.045	−0.453*	0.289
Root length to weight ratio (flowering plants)‡	0.599*	0.562**	−0.078	0.245

†,*,**,*** = correlation coefficient is significantly different to 0 at $P = 0.10$, 0.05, 0.01 and 0.001, respectively.
‡Variate log-transformed.

processes in ecosystems, and some of these may be at least as relevant as the litter quality controls (cf. Swift, Heal & Anderson 1979; Cadisch & Giller 1997) on which nearly all studies concerned with predicting decomposition rates have concentrated.

Palatability of seedlings and leaf discs to *Deroceras*, and to a lesser extent to *Listronotus*, is clearly related to at least some of the key traits that we measured. It is apparent from both experiments involving *Deroceras* that plants which invest more resources into leaf tissues (or, in the case of seedlings, above-ground tissues) also have leaves of greater palatability. The data from the palatability tests also provide some support for theories that predict that larger, longer lived plants allocate a higher proportion of their resources to defence, and are therefore less palatable (Cates & Orians 1975; Dirzo 1980; Coley 1988; Van der Meijden et al. 1988; but see Rathcke 1985). Further, our data appear consistent with the view that faster growing plants sometimes produce tissues with poorer resource quality (Tateno & Chapin 1997); leaf disc palatability was positively related to stem nitrogen concentration for both herbivores, and stem nitrogen was in turn negatively related to mean growth rate. Both herbivores we investigated are generalists at the adult stage, although *Listronotus* is known to prefer high quality tissues with high concentrations of nitrogen and low levels of structural carbohydrates (Barker 1989), and *Deroceras* shows a clear preference for seedlings of certain dicotyledonous species, often operating as a major cause of their mortality (Hanley *et al*. 1995; Wardle & Barker 1997). Preferential feeding by these herbivores on certain species, as regulated by key plant traits, is therefore likely to be an important determinant of seedling establishment and ultimately plant community structure. Our study suggests that a better understanding of these types of relationships could contribute significantly to enhancing our understanding of interactions involving herbivores.

It is apparent from our data that the plant ecophysiological controls of leaf palatability are similar to those that control decomposition rate; this is consistent with the hypothesis that plants that herbivores avoid also produce inferior litter quality (Grime & Anderson 1986; Pastor *et al*. 1993) because both digestion and decomposition involve microbial breakdown of tissue (Chesson 1997). Grime *et al*. (1996) showed a strong relationship ($r = 0.75$) between leaf palatability and decomposition rate for 43 plant species; we failed to find such a close relationship (probably because we selected all our plant species within the same functional group rather than across several), although our results worked in the same direction and were almost significant at the $P = 0.05$ level for *Deroceras* (Fig. 4). In any case, any relationship between palatability and decomposition rate across plant species is likely to have important ecosystem-level implications, because herbivore-induced reduction of palatable species has the potential to lead to domination by plants that produce litter of poor quality, leading to retardation of ecosystem-level processes (Pastor *et al*. 1988, 1993).

The plant competition results were less closely related to the traits we measured than the other interactions we considered. The relative competitive effects of dicotyledonous species against *Lolium* were most closely related to their leaf nitrogen concentrations, and this implies that plants that accumulate a higher concentration of nitrogen in their leaves are less aggressive than other plants. Unlike Gaudet & Keddy (1988), we found no evidence that larger plants were inherently more competitive. However, our results generally agree with those of Gaudet & Keddy (1988) and Reynolds & Dantonio (1996) in indicating that most other key above-ground and below-ground plant traits are not closely related to plant competitive ability. We found few relationships between competitive effect and response, consistent with some studies (e.g. Goldberg & Landa 1991; Keddy *et al*. 1994) but not others (e.g. Goldberg & Fleetwood 1987; Panetta & Randall 1993). Further, both relative competitive effect and response clearly differed for

different plant developmental stages. This means that even though a given measure of competition may differ markedly between plant species, it is extremely difficult to generalize as to the relative competitive abilities of different species, and this is further confounded by competition showing weak, if any, relationships with many key ecophysiological traits.

Several studies have suggested that individual plant species effects are important determinants of ecosystem properties, and that these effects may override the importance of abiotic factors (Tamm 1991; Hobbie 1992; Wardle *et al.* 1997). Our results show that different plant species apparently adapted to similar habitats can have vastly differing effects on soil biological properties, presumably because plant species differ considerably in terms of release of rhizosphere compounds, efficiency of nutrient acquisition and root litter quality (Griffiths *et al.* 1992; Groffman *et al.* 1996). It has also been shown that plant species effects are important determinants of soil chemical properties including soil nitrate levels (Wedin & Tilman 1996); our results indicate that not only are plant species effects important, but that some ecophysiological traits are excellent predictors of the effects that plants have on such properties. This is especially the case for effects of flowering plants on soil nitrate levels, for which 85% of the variation across species could be explained by a combination of three key traits. We suggest that multiple combinations of traits may be extremely important in regulating how plants affect soils. Such effects are likely to be significant at the ecosystem-level of resolution, since they involve modification of the environment in terms of soil processes, nutrient dynamics and ultimately plant succession. It is also relevant that the plants we considered had mostly beneficial effects on soil quality, through enhancing microbial activity and biomass, increasing soil pH and reducing total soil nitrogen loss; this is in contrast to late successional plant species that are often classified as 'stress-tolerators' and frequently cause deterioration of these properties (Tamm 1991; Wardle *et al.* 1997). Ecophysiological traits of the short-lived plant species we considered could therefore conceivably alter the nature of subsequent plant colonization in the patches that they occupy.

Our study emphasizes the importance of plant traits in understanding plant species' interactions and effects in communities and ecosystems, and that properties at the whole plant level have the potential to manifest themselves at much larger scales, both spatially and temporally. The key plant traits we evaluated were most strongly related to the decomposition data and the soil property data, so it is intrinsically reasonable to conclude that plant traits determine soil ecosystem properties through individual plant species effects. Recent studies have shown the utility of comparative approaches for determining how plants respond to soil conditions (Keddy *et al.* 1994; Gaudet & Keddy 1995); our results also point to the utility of comparative studies in determining how below-ground properties can in turn be affected by plants. Ultimately, our study provides evidence for the existence of strong linkages between plant ecophysiological traits, biotic interactions involving plants, and ecosystem-level properties and processes.

Acknowledgements

We thank B. Ryburn and A. Firth for providing technical support for various aspects of this study. Special thanks also to C. Hunt and B. Campbell for use of their software for measuring root lengths and for introducing us to this 'short-cut' approach. B. Campbell and W. Lee offered constructive comments on an earlier version of this manuscript. This work was supported by the National Foundation of Research, Science and Technology.

References

Anderson, J.P.E. & Domsch, K.H. (1978) A physiologically active method for the quantitative measurement of microbial biomass in soils. *Soil Biology and Biochemistry*, **10**, 215–221.

Anderson, T.-H. & Domsch, K.H. (1985) Determination of ecophysiological maintenance requirements of soil microorganisms in a dormant state. *Biology and Fertility of Soils*, **1**, 81–89.

Barker, G.M. (1989) Grass host preferences of *Listronotus bonariensis* (Coleoptera: Curculionidae). *Journal of Economic Entomology*, **86**, 1807–1816.

Cadisch, G. & Giller, K.E. (eds) (1997) *Driven by Nature. Plant Litter Quality and Decomposition*. CAB International, Wallingford.

Campbell, B.D. & Grime, J.P. (1989) A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytologist*, **112**, 261–267.

Campbell, B.D. & Grime, J.P. (1992) Shoot thrust and its role in plant competition. *Journal of Ecology*, **80**, 633–641.

Cates, R.G. & Orians, G.H. (1975) Successional status and the palatability of plants to generalised herbivores. *Ecology*, **56**, 410–418.

Chapin, F.S. III, Autumn, K. & Pugnaire, F. (1993) Evolution of suites of traits in response to environmental stress. *American Naturalist*, **142**, 78–92.

Chesson, P. (1997) Plant degradation by ruminants: parallels with litter decomposition in soils. *Driven by Nature. Plant Litter Quality and Decomposition* (eds G. Cadisch & K. E. Giller), pp. 47–66. CAB International, Wallingford.

Clapham, A.R. (1956) Autecological studies and the biological flora of the British Isles. *Journal of Ecology*, **44**, 1–11.

Coley, P.D. (1988) Effects of plant growth rate and leaf lifetime on the amount and type of antiherbivore defense. *Oecologia*, **74**, 531–536.

Coley, P.D., Bryant, J.P. & Chapin, F.S. III (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.

Cornelissen, J.H.C. (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology*, **84**, 573–582.

Dirzo, R. (1980) Experimental studies on slug–plant interactions. I. The acceptability of thirty plant species to the slug *Agriolomax carunae*. *Journal of Ecology*, **68**, 981–998.

Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242–243.

Gaudet, C.L. & Keddy, P.A. (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology*, **76**, 280–291.

Gerry, A.K. & Wilson, S.D. (1995) The influence of initial plant size on the competitive responses of six plant species. *Ecology*, **76**, 272–279.

Goldberg, D.E. & Fleetwood, L. (1987) Competitive effect and response in four annual plants. *Journal of Ecology*, **75**, 1131–1143.

Goldberg, D.E. & Landa, K. (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013–1030.

Griffiths, B.S., Welschen, R., van Arendonk, J.J.C.M. & Lambers, H. (1992) The effect of nitrate-nitrogen on bacteria and the bacterial-feeding fauna in the rhizosphere of different grass species. *Oecologia*, **91**, 253–259.

Grime, J.P. (1965) Comparative experiments as a key to the ecology of flowering plants. *Ecology*, **45**, 413–415.

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

Grime, J.P. & Anderson, J.M. (1986) Environmental controls over organisational activity. *Forest Ecosystems in the Alaskan Taiga* (eds K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck & C.T. Dyrness), pp. 89–95. Springer-Verlag, Berlin.

Grime, J.P., Cornelissen, J.H.C., Thompson, K. & Hodgson, J.G. (1996) Evidence of a causal connection between anti-herbivore defense and the decomposition rate of leaves. *Oikos*, **77**, 489–494.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology: A Functional Approach to Common British Species*. Unwin-Hyman, London.

Groffman, P.M., Eagan, P., Sullivan, W.M. & Lemunyon, J.L. (1996) Grass species and soil type effects on microbial biomass and activity. *Plant and Soil*, **183**, 61–67.

Hanley, M.E., Fenner, M. & Edwards, P.J. (1995) The effect of seedling age on the likelihood of herbivory by the slug *Deroceras reticulatum*. *Functional Ecology*, **9**, 754–759.

Heal, O.W. Anderson, J.M. & Swift, M.J. (1997) Plant litter quality and decomposition: an historical overview. *Driven by Nature. Plant Litter Quality and Decomposition* (eds G. Cadisch & K. E. Giller), pp. 1–30. CAB International, Wallingford.

Hobbie, S.E. (1992) Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution*, **7**, 336–339.

Hooper, D.U. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.

Jones, C.G. & Lawton, J.H. (1995) *Linking Species and Ecosystems*. Chapman and Hall, New York.

Keddy, P.A. (1992) A pragmatic approach to functional ecology. *Functional Ecology*, **6**, 621–626.

Keddy, P.A., Twolan-Strutt, L. & Wisheu, I. (1994) Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments. *Journal of Ecology*, **82**, 635–643.

Lawton, J.H. (1994) What do species do in ecosystems? *Oikos*, **71**, 367–374.

McCanny, S.J., Keddy, P.A., Arnason, T.J., Gaudet, C.L., Moore, D.R.J. & Shipley, B. (1990) Fertility and the food quality of wetland plants: a test of the resource availability hypothesis. *Oikos*, **59**, 373–381.

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

Newman, E.I. (1966) A method of estimating the total length of roots in a sample. *Journal of Applied Ecology*, **3**, 139–145.

Nieman, G.J., Pureveen, J.B.M., Eijkel, G.B., Poorter, H. & Boon, J.J. (1992) Differences in relative growth rate in 11 grasses correlate with differences in chemical composition as determined by pyrolysis mass spectrometry. *Oecologia*, **89**, 567–573.

Panetta, F.D. & Randall, R.P. (1993) *Emex australis* and the competitive hierarchy of a grazed annual pasture. *Journal of Applied Ecology*, **30**, 373–379.

Pastor, J., Dewey, B., Naiman, R.J., McInnes, P. & Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, **74**, 467–480.

Pastor, J., Naiman, R.J., Dewey, B. & McInnes, P. (1988) Moose, microbes and the Boreal forest. *BioScience*, **38**, 770–777.

Poorter, H. & Bergkotte, M. (1992) Chemical composition of 24 wild species differing in relative growth rate. *Plant, Cell and Environment*, **15**, 221–229.

Poorter, H. & Remkes, C. (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia*, **83**, 553–559.

Rathcke, B. (1985) Slugs as generalist herbivores: tests of three hypotheses on plant choices. *Ecology*, **66**, 828–836.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365–392.

Reynolds, H.L. & Dantonio, C. (1996) The ecological significance in plasticity in root weight ratio in response to nitrogen. *Plant and Soil*, **185**, 75–97.

Rorison, I.H., Grime, J.P., Hunt, R., Hendry, G.A.F. & Lewis, D.H. (1987) Frontiers of comparative plant ecology. *New Phytologist*, **106**, 1–300.

Shipley, B. (1995) Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms. *Functional Ecology*, **9**, 312–319.

Smith, G.S., Johnson, C.M. & Cornforth, I.S. (1983) Comparisons for nutrients for plants in sand culture. *New Phytologist*, **94**, 537–548.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*. Blackwell, Oxford.

Tamm, C.O. (1991) *Nitrogen in Terrestrial Ecosystems*. Springer, Berlin.

Tateno, M. & Chapin, F.S. III (1997) The logic of carbon and nitrogen interactions in terrestrial ecosystems. *American Naturalist*, **149**, 723–744.

Taylor, B.R., Parkinson, D. & Parsons, W.F.J. (1989) Nitrogen and lignin as predictors of litter decay rates: a microcosm test. *Ecology*, **70**, 97–107.

Van de Werf, A., van Neunen, M., Visser, A.J. & Lambers, H. (1993) Contribution of physiological and morphological plant traits to a species' competitive ability at high and low nutrient supply. *Oecologia*, **94**, 434–440.

Van der Meijden, E., Wijn, M. & Verkaar, H.G. (1988) Defense and regrowth, alternative plant strategies and the struggle against herbivores. *Oikos*, **51**, 355–363.

Vinton, M.A. & Burke, I.C. (1995) Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology*, **76**, 1116–1133.

Vitousek, P.M. & Walker, L.R. (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs*, **59**, 247–265.

Wardle, D.A. & Barker, G.M. (1997) Competition and herbivory in establishing grassland communities: implications for plant biomass, species diversity and soil microbial activity. *Oikos*, **80**, 470–480.

Wardle, D.A. & Ghani, A. (1995) A critique of the microbial metabolic quotient (qCO_2) as a bioindicator of disturbance and ecosystem development. *Soil Biology and Biochemistry*, **27**, 1601–1610.

Wardle, D.A. & Lavelle, P. (1997) Linkages between soil biota, plant litter quality and decomposition. *Driven by Nature. Plant Litter Quality and Decomposition* (eds G. Cadisch & K. E. Giller), pp. 107–124. CAB International, Wallingford.

Wardle, D.A. & Nicholson, K.S. (1996) Synergistic effects of grassland plant species on soil microbial biomass and activity: implications for ecosystem-level effects of enriched plant diversity. *Functional Ecology*, **10**, 410–416.

Wardle, D.A., Yeates, G.W., Watson, R.N. & Nicholson, K.S. (1993) Response of the soil microbial biomass and plant litter decomposition to weed management strategies in maize and asparagus cropping systems. *Soil Biology and Biochemistry*, **25**, 857–868.

Wardle, D.A., Zackrisson, O., Hörnberg, G. & Gallet, C. (1997) The influence of island area on ecosystem properties. *Science*, **277**, 1296–1299.

Wedin, D. & Pastor, J. (1992) Nitrogen mineralisation dynamics in grass monocultures. *Oecologia*, **96**, 186–192.

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

Wedin, D. & Tilman, D. (1996) Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science*, **274**, 1720–1723.

West, A.W. & Sparling, G.P. (1986) Modifications to the substrate-induced respiration method to permit measurement of microbial biomass in soils of differing water content. *Journal of Microbiological Methods*, **5**, 177–189.

Received 23 June 1997
revision accepted 30 September 1997