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Interspecific interactions and biomass allocation among grassland plant species

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Although a handful of studies have shown how interspecific interactions may influence plant shoot to root ratios, the issue of how these interactions influence biomass partitioning among coexisting plant species remains largely unexplored. In this study, we determined whether a given plant species could induce other plant species to allocate relative biomass to each of four zones (aboveground, and three soil depth layers) in a different manner to what they would otherwise, and whether this may influence the nature of competitive or facilitative interactions amongst coexisting plant species. We used a glasshouse study in which mixtures and monocultures of ten grassland plant species were grown in cylindrical pots to determine the effects of plant species mixtures versus monocultures on the production of shoots and of roots of other species for each of three soil depths. Across all experiments, stimulation of production in mixtures was far less common than suppression of production. Different plant species shifted their allocation to shoots or roots at different depths, suggesting that interspecific interactions can either: (1) increase the ratio of deep to shallow roots, perhaps because competition reduces root growth in the uppermost part of the soil profile; or (2) decrease this ratio by reducing plant vigour to such an extent that the plant cannot produce roots that can reach deep enough to exploit resources at lower depths. Further, these results suggest that there are instances in which competition may have the potential to enforce resource partitioning between coexisting plant species by inducing different species to root at different depths to each other.

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Coexistence between different plant species is determined by the balance between competition and resource partitioning. It has frequently been proposed that a major mechanism by which coexisting plant species partition resources is through different species allocating tissues in such a way as to exploit resources differently, leading to a greater overall exploitation of resources (Walter 1985, Bazzaz 1996, Huber-Sannwald et al. 1996, Grime 2001). This could occur, for example, through different plant species producing shoots with different architectures so as to result in a more complete capture of incoming light, or producing foraging roots at differing depths in the soil profile so as to enable greater total nutrient uptake by the plant community (Mahall and Callaway 1992, Naeem et al. 1994, Hooper 1998, Köchy and Wilson 2000). Further, it has been suggested that when plant species which, when grown in monoculture which utilise the same resources are grown in combination, they may produce foliage at different heights or root at different depths to what they would otherwise so as to avoid competition (Walter 1954, 1985, Grime 1979, 2001, Bazzaz 1996). This leads to an enforced resource partitioning, which may result in a greater productivity of mixtures than monocultures. Despite the potential importance of such a mechanism in maintaining species coexistence, this issue has been addressed in very few studies. Tremmel and Bazzaz (1995) found that competition among neigh-

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bouring plants of different species was generally unimportant in influencing aboveground architecture. However, while some data seem to show that coexistence in natural systems may be influenced by differences in rooting depths among species (Sala et al. 1989, Nobel 1997), there have been no studies on how plant species may allocate tissues belowground when they are grown in combination versus when they are grown in monoculture (but see suggestions by Goldberg 1994). Such information is, however, essential in understanding the mechanistic basis behind the structuring of plant communities.

Wardle and Nicholson (1996) conducted a glasshouse study in which pairs of grassland plant species were grown in cylindrical pots (together with appropriate monoculture pots) to determine the effects of plant species mixtures versus monocultures on soil microbiological properties and processes. In their study, data were also collected on biomass production of shoots, and of roots for each of three soil depths, for each species of each species pair in mixture and in monoculture. This data set can also be used to evaluate how plant species allocate biomass when grown in combination with other plant species relative to that which occurs when grown in monoculture. While a few investigators which have examined how shoot: root ratios for individual species may be affected by interspecific interactions (Berendse 1982, reviewed by Wilson 1988, Bazzaz 1996, Casper and Jackson 1997), to our knowledge the issue of how interspecific interactions influence biomass partitioning among coexisting species remains largely unexplored. In this study, we specifically sought to determine whether a given plant species could induce other plant species to allocate relative biomass to each of four zones (aboveground, and three soil depth layers) in a different manner from what they would otherwise, and whether this may influence the nature of competitive or facilitative interactions amongst plant species.

Materials and methods

The experiments used for the present analysis are the same as those used by Wardle and Nicholson (1996). These experiments were based on mixtures of the perennial C_3 grass *Lolium perenne* and nine herbaceous dicotyledonous plant species common in managed grasslands in the Waikato area of northern New Zealand, i.e. *Rumex obtusifolius*, *Carduus nutans*, *Leucanthemum vulgare*, *Senecio jacobaea*, *Cirsium vulgare*, *Taraxacum officinale*, *Crepis capillaris*, *Ranunculus sardous* and *Cirsium arvense*. An additive design was used because it enabled us to quantify the total net effects of a given species on another species in a two species system (Goldberg and Scheiner 1993); this approach is more appropriate than a replacement series design which confounds intraspecific and interspecific interactions (Snaydon 1991). Each experiment consisted of four replicate pots of each of three combinations: (i) three *L. perenne* plants arranged in an equilateral triangle 8 cm apart, (ii) one dicotyledonous plant in the centre of the pot, and (iii) three *L. perenne* plants and one dicotyledonous plant. Different experiments were focused on different dicotyledonous plant species; all experiments were set up in a randomised block design. The arrangement of plants within the pots in each experiment closely resembles field conditions; *L. perenne* grows in swards while the dicotyledonous species occur as isolated plants (Wardle and Nicholson 1996). All experiments were set up in April 1992, in cylindrical pots (12 cm diam. $\times$ 30 cm depth); the depth of pots used make them appropriate for evaluating depthwise distributions of plant roots. The growth medium used was a 1:2 mixture of fine pumice and Horotiu sandy loam soil (Vitric hapludand; soil C = 6.0%; N = 0.53%, P = 0.18%; pH = 6.0); 2.3 kg of this medium was added to each pot. Seedlings were sprouted in vermiculite before planting, and transplanted to the pots prior to the formation of the first true leaf. For three species (*L. vulgare*, *C. nutans* and *C. vulgare*) the experiment was set up in duplicate so that two separate temporal assessments could be made; for a fourth species (*R. obtusifolius*) it was set up in triplicate to enable three separate temporal assessments. Although *L. perenne* biomass and hence the potential for interspecific interactions will increase over time (i.e. with increasing plant age and size), we are interested in the outcome of interactions on biomass partitioning at different stages within individual plant species and do not compare these effects directly among species.

The experiments were maintained in a glasshouse. Prior to setup the soil was amended with urea (4 g kg^{-1} soil) and potassic superphosphate (4.6 g kg^{-1} soil). After 90 days all pots were amended every 8–10 days for the remainder of the experiment with 100 ml of a nutrient solution developed specifically for glasshouse experiments using the types of plant species and soil used in the present study (Smith et al. 1983). All *L. perenne* plants were trimmed approximately monthly to a 3 cm height so as to maintain their height at a mean of approximately 7 cm. The reason for this is that in managed grasslands in the Waikato area of New Zealand, livestock closely graze *L. perenne* (often on a one month rotation) and leave the dicotyledonous species largely untouched, meaning that the experimental conditions used here therefore resemble those that are observed in the field (Wardle et al. 1995, Wardle and Nicholson 1996). All clipped grass was removed and its dry mass determined for each pot. We recognize that clipping of aboveground vegetation may alter biomass allocation to roots (Bardgett et al. 1998) but emphasize that clipping was applied equally to *L. perenne* plants

grown in monoculture and in mixture, reducing the prospect of treatment-related biases.

When the plants of each dicotyledonous species had reached their full (vegetative) rosette size prior to initiating flowering, pots were destructively harvested for each of the three combinations of that mixture experiment; this occurred after 78 days for *R. obtusifolius*, 111 days for *L. vulgare* and *C. nutans*, 139 days for *S. jacobaea*, 171 days for *T. officinale* and *C. capillaris*, 199 days for *R. sardous* and *C. arvense*, and 411 days for *C. vulgare*. For the three mixture experiments that were set up in duplicate, pots were also destructively harvested when the dicotyledonous species were in full flower, i.e. 171 days for *L. vulgare*, 199 days for *C. nutans*, and 502 days for *C. vulgare*. For *R. obtusifolius*, in which the experiment was set up in triplicate, pots were also destructively harvested when *R. obtusifolius* plants were in full flower (139 days) and when they were senescent (220 days).

Upon harvest, the soil in each pot was sliced into three depth layers, 0–10 cm, 10–20 cm and 20–30 cm; in each depth layer all roots were carefully separated from the soil. These depths capture the majority of roots and most important interactions among plant species (Casper and Jackson 1997). All roots derived from the two species mixture pots were then carefully hand sorted into the component species based on appearance and comparison with roots of each of the component species with roots of those species removed from the monoculture pots. Generally *L. perenne* roots are more fibrous (and often differ in colour) in comparison with those of the dicotyledonous species used in this study, enabling separation of roots into those of component species with a reasonable level of accuracy. Roots were then washed to remove adhering soil, and all shoot and root material obtained from each pot oven dried at 80°C for 24 h for mass determination. Aboveground net productivity for each *L. perenne* pot over the course of the experiment was calculated by adding the aboveground dry weight at the time of harvest to the weights of all the previous trimmings from that pot.

For each of the 14 experiments (each experiment consisting of four replicate monocultures of a dicotyledonous plant species, four replicates of *L. perenne* and four replicate two species mixtures), the data were analysed to determine the shoot to root productivity ratio of each plant species when grown with the other species, relative to its shoot to root ratio in monoculture. The root data were also analysed to determine whether *L. perenne* influenced the depthwise distribution of roots of each herbaceous species. These trends were then related to measures of competition among the species. For each experiment competitive balance indices were determined separately for each of the four replicate blocks in each experiment; the index used is that presented by Wilson (1988) (modified from De Wit and Goudriaan 1974) which ranges from -1 to $+1$, and is increasingly positive or negative depending upon which of the two species in the mixture has the competitive advantage; a value of 0 indicates that neither species has a competitive advantage. Indices were calculated separately using shoot productivity data only, root productivity data only, and total plant productivity data. Variation in biomass among pots will contribute to variation in the effects of *L. perenne* on other species, but this source of variation was averaged across replicates rather than quantifying per-gram or per-individual effects of *L. perenne* (Goldberg and Scheiner 1993). Root-binding was not commonly observed during these experiments and hence did not contribute to variation in *L. perenne* biomass among replicate pots. The index of competition intensity presented by Wilson (1988) was also determined separately for each replicate block in each experiment; this index has a value of 0 in the absence of competition and becomes increasingly positive as competition among the two species becomes more intense whereas negative values indicate facilitation or net stimulation of production in mixtures. Indices were calculated separately for shoot and root data, as well as separately for root biomass data from each of the three rooting depths.

Our study involved comparison of plants grown in monoculture and in mixture, so for each biomass response variable within each species the significance of differences between these treatments was tested using a paired-sample Student's t-test. The Student's t-test was also used to test whether values of the competitive balance for each species pair differed significantly from zero (meaning that one species had a significant competitive advantage over the other), and whether competition intensity indices were significantly greater than 1 (i.e. the mixture is significantly less productive than the mean of the monocultures) or significantly less than 0 (i.e. significant net stimulation of the two species by each other).

Results

When the monoculture treatments of each experiment were considered, a range of allocation patterns across species were detected (Table 1). For dicotyledonous plants, all species except *C. vulgare* and *T. officinale* produced more aboveground than belowground tissue, and three species *C. nutans* (vegetative stage), *R. sardous* and *C. capillaris* produced at least three times as much shoot material as root material. For all dicotyledonous species in monoculture, roots were present in all depth layers, but the relative amounts of roots in the three depth layers varied considerably among species (Table 1); *L. vulgare* (vegetative and flowering stages), *C. vulgare* (vegetative and flowering stages) and *R.*

Table 1. Total production (aboveground + belowground) (g d.w. per pot), and percentage of total production allocated to aboveground tissues, and roots in each of three soil depth layers, for monocultures of each dicotyledonous plant species, and for corresponding monocultures of *L. perenne* plants which were harvested at the same time as for the dicotyledonous plant species. Numbers in brackets are Standard Errors.

Dicotyledonous	Dicotyledonous plants					*Lolium perenne*				
	Total production (g/pot)	% of total production in:				Total production (g/pot)	% of total production in:			
		Shoots	Roots (0–10cm)	Roots (10–20cm)	Roots (20–30cm)		Shoots	Roots (0–10cm)	Roots (10–20cm)	Roots (20–30cm)
Vegetative phase										
Rumex obtusifolius	8.1 (1.0)	70.5 (1.7)	17.1 (3.0)	7.2 (0.8)	5.3 (0.9)	4.8 (0.8)	79.5 (4.2)	10.9 (1.4)	6.7 (1.0)	2.9 (0.6)
Carduus nutans	8.2 (1.3)	75.7 (3.2)	13.7 (2.6)	5.4 (0.7)	5.3 (0.4)	20.9 (1.1)	84.8 (2.1)	7.7 (0.9)	4.1 (1.0)	3.5 (0.6)
Leucanthemum vulgare	4.7 (0.3)	71.0 (3.6)	14.2 (0.5)	6.7 (0.7)	8.0 (1.6)	20.9 (1.1)	84.8 (2.1)	7.7 (0.9)	4.1 (1.0)	3.5 (0.6)
Senecio jacobaea	5.3 (1.7)	69.9 (1.4)	20.7 (0.8)	4.8 (0.3)	5.0 (0.7)	47.0 (1.5)	86.5 (0.8)	6.4 (0.3)	3.2 (0.4)	3.5 (0.3)
Cirsium vulgare	236.6 (7.6)	39.1 (1.6)	20.7 (0.9)	20.8 (1.0)	19.4 (1.9)	185.3 (3.5)	80.7 (0.8)	13.3 (0.9)	3.4 (0.4)	2.5 (0.7)
Taraxacum officinale	5.3 (0.2)	39.4 (2.0)	41.2 (0.6)	13.7 (0.2)	5.8 (0.9)	93.7 (3.5)	72.7 (0.4)	20.8 (0.8)	3.8 (0.3)	2.8 (0.3)
Crepis capillaris	15.8 (0.8)	86.7 (1.0)	10.0 (0.4)	1.7 (0.1)	1.7 (0.1)	93.7 (3.5)	72.7 (0.4)	20.8 (0.8)	3.8 (0.3)	2.8 (0.3)
Ranunculus sardous	26.7 (1.0)	77.6 (0.4)	15.7 (0.3)	5.6 (0.3)	1.1 (0.2)	130.0 (4.1)	79.0 (1.1)	15.0 (0.9)	4.0 (0.4)	1.3 (0.2)
Cirsium arvense	71.5 (4.4)	59.3 (0.7)	20.3 (0.8)	12.0 (0.7)	8.4 (0.6)	130.0 (4.1)	79.0 (1.1)	15.0 (0.9)	4.0 (0.4)	1.3 (0.2)
Flowering phase										
Rumex obtusifolius	209.0 (11.9)	55.7 (1.5)	20.8 (0.6)	12.0 (0.7)	8.4 (0.6)	47.0 (1.5)	86.5 (0.8)	6.4 (0.3)	3.2 (0.4)	3.5 (0.3)
Carduus nutans	32.3 (2.3)	72.4 (1.2)	14.2 (0.6)	7.6 (0.7)	5.8 (0.4)	130.0 (4.1)	79.0 (1.1)	15.0 (0.9)	4.0 (0.4)	1.3 (0.2)
Leucanthemum vulgare	84.7 (5.0)	81.4 (1.4)	8.8 (0.9)	4.1 (0.1)	5.8 (0.8)	93.7 (3.5)	72.7 (0.4)	20.8 (0.8)	3.8 (0.3)	2.8 (0.3)
Cirsium vulgare	238.1 (8.0)	47.4 (1.4)	21.6 (0.6)	16.2 (0.8)	14.9 (0.3)	197.7 (4.5)	87.0 (0.5)	8.2 (0.3)	3.4 (0.9)	1.4 (0.6)
Senescent phase										
Rumex obtusifolius	224.4 (8.0)	73.0 (1.2)	12.5 (0.4)	7.3 (0.5)	7.3 (1.4)	142.8 (6.1)	78.5 (1.9)	14.7 (0.9)	3.8 (0.6)	2.9 (0.6)

obtusifolius (senescent stage) each produced at least half the mass of roots in the 20–30 cm depth layer than they did in the 0–10 cm depth layer, while *S. jacobaea*, *C. capillaris* and *R. sardous* all produced fewer than one fifth the amount of roots in the 20–30 cm depth layer than they did in the 0–10 cm depth layer. In all cases *L. perenne* plants in monoculture allocated over 70% of their production to shoot material, and always produced at least twice as much root material in the 0–10 cm depth layer as in the 20–30 cm depth layer (Table 1).

Lolium perenne had a statistically significant effect on the production of some tissues by dicotyledonous plants in mixed plantings for all but one of the 14 experiments (Fig. 1). *L. perenne* significantly reduced aboveground production of five species in the vegetative phase (*C. nutans*, *C. vulgare*, *C. capillaris*, *R. sardous* and *C. arvense*), two species in the flowering phase (*L. vulgare* and *C. vulgare*), and *R. obtusifolius* in the senescent phase. In contrast, *L. perenne* significantly increased shoot production of two species (*S. jacobaea* and *T. officinale*). In all nine experiments involving dicotyledonous plants in the vegetative phase, *L. perenne* significantly influenced dicotyledonous plant root production in the 0–10 cm soil depth layers; these effects were negative in all but two cases in which stimulation occurred (i.e. for *T. officinale* and *S. jacobaea*). For five of the nine cases, *L. perenne* also significantly reduced dicotyledonous plant root production at lower depth layers. In addition, *L. perenne* reduced root production of flowering *L. vulgare* plants (20–30 cm depth layer) and flowering *C. vulgare* plants (all depth layers), and stimulated root production of senescent *R. obtusifolius* plants (10–20 cm depth layer).

Dicotyledonous plants also significantly altered biomass production of *L. perenne* in several instances. Four of the nine dicotyledonous plant species in the vegetative stage significantly reduced *L. perenne* shoot production (i.e. *S. jacobaea*, *C. vulgare*, *R. sardous* and *C. arvense*), and all species in the flowering or senescent phase significantly reduced *L. perenne* shoot production; the only exception to this pattern was in the case of *C. nutans* (vegetative stage), which stimulated *L. perenne* shoot production. Five dicotyledonous species in the vegetative stage significantly reduced *L. perenne* root production in the 0-10 cm depth layer (Fig. 1); however two species in the vegetative phase (*R. obtusifolius* and *C. nutans*) stimulated root production of *L. perenne*. Two species in the vegetative stage also reduced *L. perenne* root production at lower soil depths. Flowering *R. obtusifolius* plants stimulated *L. perenne* root production, but the other species in the flowering or senescent stages reduced *L. perenne* root production for at least some soil depth layers.

Lolium perenne significantly increased the shoot to root production ratio of six of the nine dicotyledonous species, and for all but one of these cases the effect was positive (Table 2). *L. perenne* also significantly increased shoot to root ratios of *R. obtusifolius* and *C. vulgare* at the flowering phase, and reduced this ratio for *R. sardous* at the senescent phase. Six of the dicotyledonous species at the vegetative phase also significantly increased the shoot to root production ratio of *L. perenne* (Table 2); and in two cases (i.e. for *T. officinale* and *C. capillaris*) the dicotyledonous plants stimulated the ratio for *L. perenne* by a factor of over two. Three dicotyledonous species (i.e. *C. nutans*, *C. vulgare* and *L. vulgare*) at the flowering phase also increased shoot: root ratios of *L. perenne*; only one species, *R. obtusifolius*, caused the opposite trend in both the flowering and senescent phases by significantly reducing the shoot to root production ratio for *L. perenne*.

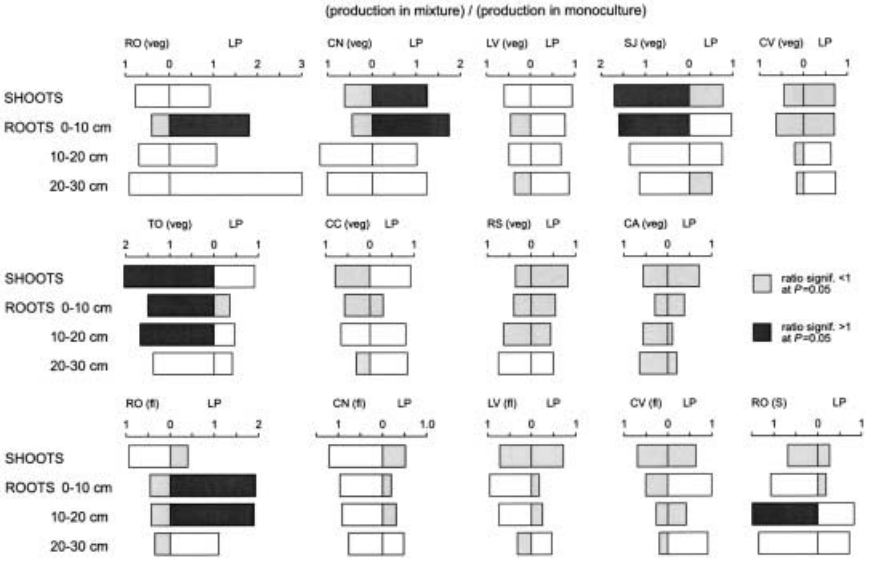

Fig. 1. Productivity of shoots and roots (in each of three soil depth layers; 0–10 cm, 10–20 cm and 20–30 cm) for nine dicotyledonous plant species and the grass *Lolium perenne* in two species mixtures, expressed as a proportion of their productivity in monoculture. Production ratios > 1 indicate underyielding whereas ratios < 1 indicate overyielding. Abbreviations: CA = *Cirsium arvense*; CC = *Crepis capillaris*; CN = *Carduus nutans*; CV = *Cirsium vulgare*; LP = *Lolium perenne*; LV = *Leucanthemum vulgare*; RO = *Rumex obtusifolius*; RS = *Ranunculus sardous*; SJ = *Senecio jacobaea*; TO = *Taraxacum officinale*. Veg = vegetative stage; fl = flowering stage; s = senescent stage.

Table 2. Shoot to root production ratios for dicotyledonous plant species and *Lolium perenne* grown in monoculture and together in mixture. See Table 1 for details.

Dicotyledonous species	Dicotyledonous plants			*Lolium perenne*		
	Monoculture pots	Mixture pots	Significance of difference (t-value)	Monoculture pots	Mixture pots	Significance of difference (t-value)
Vegetative phase						
Rumex obtusifolius	2.39 (0.19)	3.06 (0.37)	1.5	3.87 (0.49)	2.01 (0.38)	3.2*
Carduus nutans	3.11 (0.51)	2.54 (0.40)	1.5	5.57 (1.30)	4.98 (0.28)	0.9
Leucanthemum vulgare	2.45 (0.24)	3.67 (0.50)	2.9*	5.57 (1.30)	7.26 (1.07)	3.6*
Senecio jacobaea	2.32 (0.14)	2.71 (0.49)	0.6	6.41 (0.45)	6.32 (0.43)	0.2
Cirsium vulgare	0.64 (0.04)	0.86 (0.03)	4.0**	4.18 (0.44)	4.41 (0.43)	0.0
Taraxacum officinale	0.65 (0.06)	0.85 (0.03)	8.0***	2.66 (0.05)	6.43 (019)	22.1***
Crepis capillaries	6.51 (0.61)	9.40 (0.71)	4.0**	2.66 (0.05)	5.83 (0.47)	6.7***
Ranunculus sardous	3.46 (0.08)	2.61 (0.08)	5.4**	3.76 (0.24)	5.97 (0.22)	9.4***
Cirsium arvense	1.46 (0.04)	1.82 (0.08)	6.2***	3.76 (0.24)	8.14 (0.78)	19.0***
Flowering phase						
Rumex obtusifolius	1.26 (0.05)	2.83 (0.08)	11.9***	6.41 (0.45)	1.55 (0.20)	12.4***
Carduus nutans	2.62 (0.18)	3.48 (0.25)	2.1	3.76 (0.24)	8.29 (0.78)	4.4**
Leucanthemum vulgare	4.37 (0.36)	4.47 (0.09)	0.2	2.66 (0.05)	9.10 (1.54)	4.1**
Cirsium vulgare	0.90 (0.06)	1.80 (0.08)	12.3***	6.69 (0.18)	9.29 (0.24)	10.3***
Senescent phase						
Rumex obtusifolius	2.70 (0.17)	1.47 (0.10)	10.5***	3.65 (0.41)	2.57 (0.40)	4.7**

*, **, *** indicates that t-values are significantly different to 0 at $P = 0.05$, 0.01 or 0.001 respectively.

In many cases, the depthwise distribution of roots was altered by other plant species (Fig. 2). *Lolium perenne* significantly increased the ratio of root mass in the 10–20 cm depth layer to that in the 0–10 cm depth layer for *R. obtusifolius*, *C. nutans*, *R. sardous* and *C. arv*ense at the vegetative phase, and significantly re-

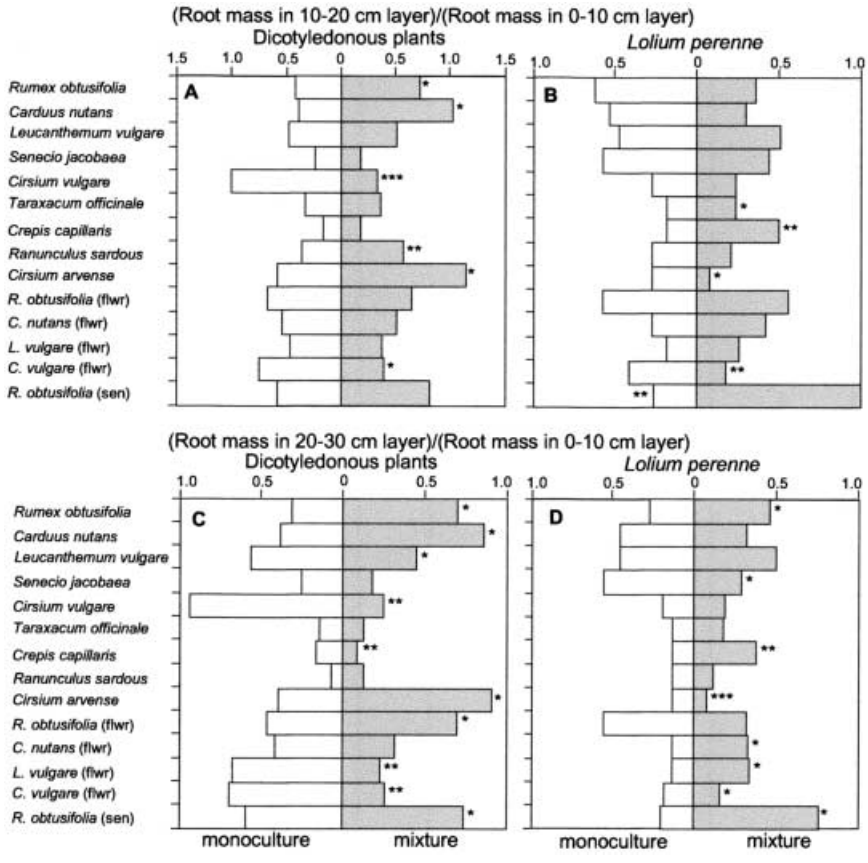

Fig. 2. Ratios of root mass in the 10–20 cm (top panels) and 20–30 cm soil depth layers (bottom panels) to that in the 0–10 cm depth layer, for dicotyledonous plant species (A, C) and *Lolium perenne* (B, D) grown in monoculture (open bars) or together in mixture (filled bars). *, **, ***: indicates that mixtures vs. monocultures are significantly different at $P = 0.05$, 0.01 and 0.001 respectively according to the paired sample Student's t-test. Flwr = flowering stage; sen = senescent stage.

duced this ratio for *C. vulgare* at both the vegetative and flowering stages (Fig. 2). *L. perenne* also significantly increased the ratio of root mass in the 20–30 cm depth layer to that in the 0–10 cm depth layer for *C. nutans* and *C. arvense* at the vegetative phase and *R. obtusifolius* at all three phases, and significantly reduced it for *L. vulgare*, *C. vulgare* and *C. capillaris* at the vegetative phase and *L. vulgare* and *C. vulgare* at the flowering phase. Further, *T. officinale* and *C. capillaris* at the vegetative phase and *R. obtusifolius* at the senescent phase increased the ratio for *L. perenne* of root mass in the 10–20 cm depth layer to that in the 0–10 cm depth layer; *C. arvense* at the vegetative phase and *C. vulgare* at the flowering phase substantially reduced this ratio for *L. perenne* (Fig. 2). The ratio of *L. perenne* root mass in the 20–30 cm depth layer to that in the 0–10 cm depth layer was significantly increased by *R. obtusifolius* and *C. capillaris* at the vegetative phase, *C. nutans* and *L. vulgare* at the flowering phase, and *R. obtusifolius* at the senescent phase but significantly decreased by *S. jacobaea* and *C. arvense* at the vegetative phase and *C. vulgare* at the flowering phase.

The competitive balance indices among species indicated that while some dicotyledonous species had the competitive advantage when grown with *L. perenne*; the reverse was true for other dicotyledonous species (Table 3). When shoot production data was considered, *S. jacobaea* and *T. officinale* at the vegetative phase, *R. obtusifolius* and *C. nutans* at the flowering phase, and *R. obtusifolius* at the senescent phase all had a significant competitive advantage over *L. perenne* whereas *L. perenne* plants had a significant advantage over vegetative plants of *C. nutans*, *C. vulgare* and *R. sardous* (Table 3).

With regard to root production data, *S. jacobaea* and *T. officinale* at the vegetative phase, *C. nutans* and *L. vulgare* at the flowering phase, and *R. obtusifolius* at the senescent phase all had a competitive advantage over *L. perenne*, while *L. perenne* had a competitive advantage over *C. vulgare* and *R. sardous* at the vegetative phase, and *R. obtusifolius* and *C. vulgare* at the flowering phase (Table 3). When combinations of flowering dicotyledonous plants and *L. perenne* were considered, there were large differences between aboveground and belowground competitive balance values in three out of four cases; combinations of *L. perenne* and *L. vulgare* or *C. vulgare* had competitive balance values which differed greatly from 0 when root data, but not shoot data, were considered; the direction of competitive balance between *L. perenne* and *R. obtusifolius* worked in entirely opposite directions depending upon whether shoot data or root data were considered.

The indices of competition intensity varied considerably among the different species combinations, but more importantly also varied within species combinations depending upon which plant parts were considered (Table 4). With regard to the shoot production data, competition intensity indices were significantly greater than 0 for only one of the nine combinations of *L. perenne* and vegetative dicotyledonous plants, but for all combinations of *L. perenne* and flowering or senescent dicotyledonous plants. However, for four of the nine combinations between vegetative dicotyledonous plants and *L. perenne*, competition intensity values were significantly greater than 0 in the 0-10 cm soil depth layer; two of the four combinations of flowering dicotyledonous plants and *L. perenne* also showed significant competition intensity values at this depth.

Table 3. Competitive balance indices between *Lolium perenne* and dicotyledonous plants using shoot production data only, root production data only, and total plant production data. Indices are calculated as according to Wilson (1988) and are increasingly positive or negative as the dicotyledonous plant or *L. perenne* respectively has the competitive advantage.

Dicotyledonous species	Shoot dry weight	Root dry weight	Total plant dry weight
Vegetative phase			
Rumex obtusifolius	−0.201	−1.205	−0.488
Carduus nutans	−0.726*	−0.564	−0.660
Leucanthemum vulgare	−0.450	−0.638	−0.514
Senecio jacobaea	0.785*	0.654*	0.757**
Cirsium vulgare	−0.488**	−0.722**	−0.611***
Taraxacum officinale	0.759*	1.394***	0.794*
Crepis capillaris	−0.176	0.255	−0.057
Ranunculus sardous	−0.863*	−1.295*	−0.717
Cirsium arvense	−0.238	0.434	−0.189
Flowering phase			
Rumex obtusifolius	0.853**	−1.197**	0.289
Carduus nutans	0.845*	1.247*	0.897**
Leucanthemum vulgare	0.008	1.170**	0.208
Cirsium vulgare	−0.006	−0.691**	−0.281*
Senescent phase			
Rumex obtusifolius	0.942**	1.200**	1.063***

*, **, *** indicates that competitive balance values are significantly different to 0 at $P = 0.05$, 0.01 or 0.001 respectively (Student's t-test).

Table 4. Competition intensity indices for interactions between *Lolium perenne* and dicotyledonous species, calculated as according to Wilson (1988). The index is 0 in the absence of competition and becomes increasingly positive as competition intensity increases. An index value of greater than one indicates that the mixture is less productive than the mean of the monocultures and a negative value is indicative of net stimulation of the species by each other. Values greater than 0 and less than 1 indicate some net competitive reduction but also partial resource partitioning.

Dicotyledonous species	Shoot dry weights	Root dry weights				Total plant dry weights
		Total roots	0–10cm depth	10–20 cm depth	20–30 cm depth	
Vegetative phase						
Rumex obtusifolius	0.347	0.127	0.271	0.294	−0.176	0.282
Carduus nutans	−0.086	−0.151	−0.183	−0.016	0.145	−0.090
Leucanthemum vulgare	0.130	0.470	0.456	0.563	0.419	0.180
Senecio jacobaea	0.178	0.099	−0.103	0.290	0.693	0.165
Cirsium vulgare	0.635	1.455*	0.543*	2.928*	3.536 #	0.897*
Taraxacum officinale	0.058	0.962	1.123*	0.515	0.803	0.221
Crepis capillaris	0.128	1.334	2.177*	0.266	0.288	0.294
Ranunculus sardous	0.399*	0.943*	0.936	1.075	0.935	0.431*
Cirsium arvense	0.490	1.682*	1.928*	1.598	1.168*	0.701*
Flowering phase						
Rumex obtusifolius	0.250*	0.655*	0.550	1.034	0.336	0.364*
Carduus nutans	0.545*	1.404	2.104 #	0.998	0.668	0.687*
Leucanthemum vulgare	0.390*	1.484*	1.617	1.042*	1.715*	0.543*
Cirsium vulgare	0.507*	1.415 #	0.690*	2.576*	3.325 #	0.787*
Senescent phase						
Rumex obtusifolius	0.970*	0.040	0.453	−0.237	−0.190	0.609*

*, #: index significantly greater than 0.0 and 1.0 respectively at $P = 0.05$.

For four combinations (*L. perenne* with *C. vulgare* or *C. arvense* at the vegetative stage and with *L. vulgare* or *C. vulgare* at the flowering stage) competition intensity indices were also significantly (and considerably) greater than 0 at greater soil depths (20–30 cm > 0–10 cm depths). For combinations of *L. perenne* and *C. vulgare* (both at the flowering and vegetative stages), competition intensity increased with soil depth, and at the lowest soil depth the index was greater than 1.0, indicative of substantial underyielding. No competition indices were significantly less than 0, meaning that there were no combinations in which net overall stimulation of production occurred.

Discussion

Differences among species

Biomass allocation to different tissues, i.e. shoots vs roots, and roots near the surface vs deeper roots, varied widely among the ten study species (Table 1). For example, *Crepis capillaris* allocated 86.7% of its production to shoots and produced most roots in the 0-10 cm rooting zone. In contrast, *Cirsium vulgare* and *Taraxacum officinale* both allocated ca 40% of their biomass aboveground, but *C. vulgare* allocated biomass to roots equally at all depths whereas *T. officinale* concentrated its roots in the top 10 cm of soil. These contrasting patterns of biomass allocation among species suggests that there is the amplitude for resource partitioning to occur. We focus on the responses of biomass allocation here, but recognize that shifts in plant morphology and biomass allocation can be linked to patterns of resource uptake and use with the appropriate experimental design (Caldwell and Richards 1986, Campbell et al. 1991, Jolliffe 2000; reviewed by Aarssen and Keogh 2002).

Biomass allocation patterns often shifted in the presence of other plant species (Table 2, Fig. 2); therefore the potential for species coexistence and more complete resource utilization in multispecies systems is also possible. Almost no previous studies have investigated whether greater productivity in mixtures than in monocultures may be attributable to divergences in the rooting depths of species between monoculture and mixtures. The best previous test of this idea was by Berendse (1982) who found some evidence for aboveground overyielding in a replacement series experiment using a relatively deep-rooted herb (*Plantago lanceolata*) and a common, shallow-rooted grass species (*Anthoxanthum odoratum*). Future research will need to ascertain the resource supply to demand ratio in mixtures to determine whether shifts in biomass partitioning reflect resource complimentarity in mixtures of species (Jolliffe 2000, Aarssen and Keogh 2002).

Although we did not design the present study to examine niche segregation along environmental gradients, our results suggest that strong niche segregation, i.e. changes in biomass allocation, may not necessarily occur in response to interspecific interactions (Table 2, Fig. 2). Despite a long interest by ecologists in how competition influences niche widths and community organization (Schoener 1974, Rosenzweig 1978, Connell 1980, 1983, Silvertown and Law 1987), our findings that many species do not alter their patterns of biomass allocation in mixtures (Table 2, Fig. 2) support the

alternative hypothesis that competition does not usually cause niche differentiation in plants (reviewed by Bazzaz 1996). This may occur for several reasons: plant species may have shared rather than distinct habitat or niche preferences (Harper 1977, Wisheu 1998), niches may be partitioned temporally rather than spatially (Grubb 1977, Bazzaz 1996), or niches may be less important than other ecological factors for species coexistence (Shmida and Ellner 1984, Chesson 1991). Separating niche differentiation from the intensity of interspecific interactions or resource partitioning requires more detailed information on resource availability and demand for plant species in mixture (for details see Jolliffe 2000, Aarssen and Keogh 2002).

Shoot vs root responses

The shoot, root and total biomass responses of dicotyledonous plants to *L. perenne* were similar across all of the plant developmental stages examined, i.e. vegetative, flowering and senescent phases (Table 3). Competitive interactions influenced the relative allocation to different tissues among species. In the case of the shoot:root ratio, most significant effects involved stimulation of this ratio by the other species (Table 2), meaning that root production is more adversely affected by competition than is shoot production. In the present study, we quantified the total net effects of interactions (i.e. the sum of cumulative competitive and facilitative interactions, Goldberg et al. 1999) on biomass allocation of a species, but are unable to determine what the separate effects of above- and belowground interactions are on biomass allocation (discussed by Cahill 1999). *Lolium* tended to suppress herbaceous species, but was only suppressed itself in two cases, at least during the vegetative stage (Table 3). There was also some evidence for facilitation between species. In six cases, one plant species stimulated the productivity of another plant species in at least part of the rooting zone (Fig. 1). Our results demonstrate that both competition and facilitation can vary in their effects on biomass allocation both aboveground and through the soil profile, meaning that the outcome of interspecific interactions can vary spatially, perhaps promoting species coexistence (Aarssen 1989, Kleb and Wilson 1997).

Root allocation responses

Interspecific interactions were important in influencing depthwise rooting patterns of plants. In many cases competition intensity indices were greatest in the 0–10 cm soil depth layer because suppressed plants tended to show a significant reduction in root biomass in the 0–10 cm layer but not in deeper soil layers (Fig. 2, Table 4). This means that plants having a higher proportion of their roots in deeper layers are therefore presumably obtaining a higher proportion of their soil resources from a deeper layer than they would otherwise. In contrast, competition between *L. perenne* and *C. nutans* reduced root biomass mostly in the 20–30 cm depth layer, and a pattern of transgressive underyielding of roots in this layer appears to occur; there are also instances of other species producing fewer roots at greater depths due to competition (Fig. 1, 2).

Differences in the rooting patterns of co-occurring plant species are often taken as evidence for niche segregation among species. For example, Nobel (1997) examined the rooting depths of three co-dominant Sonoran desert perennials: the C_3 subshrub *Encelia farinosa*, the C_4 bunchgrass *Pleuraphis rigida* and the CAM leaf succulent *Agave deserti*. Mean rooting depths were only 9–10 cm for isolated individuals of all species (Nobel's Fig. 1). However, roots of interspecific pairs were 2–3 cm shallower than this for *Agave deserti*, but 2–3 cm deeper than this for the other two species, suggesting partial spatial separation of their root niches when in competition. In contrast, a pattern analysis of nearest neighbours in the Chihauhuan desert by Briones et al. (1996) showed that belowground root niche differentiation is not sufficiently important to avoid the negative effects of competition among coexisting perennial desert plants such as the shrub *Larrea tridentata*, tussock grass *Hilaria mutica* and the succulent *Opuntia rastrera*. In more mesic US old-fields, Mou et al. (1995) showed that the root systems for individual plants of the tree species *Liquidambar styraciflua* and *Pinus taeda* tended to avoid interplant overlap in the top 60 cm of soil. These studies together with our results showing that different plant species can shift their allocation to shoots or to roots at different depths in response to competition suggest that interspecific interactions can either: (1) increase the ratio of deep to shallow roots, perhaps because competition reduces root growth to a greater extent in the uppermost part of the soil profile; or (2) decrease this ratio by reducing plant vigour to such an extent that the plant cannot produce roots that can reach deep enough to adequately exploit resources at lower depths.

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