Plant and Soil (2006) 280:101–114
DOI 10.1007/s11104-005-2612-x

Aggregative root placement: A feature during interspecific competition in inland sand-dune habitats

Maik Bartelheimer[1], Tom Steinlein & Wolfram Beyschlag
Chair of Experimental and Systems Ecology, University of Bielefeld, Universitätsstr. 25, 33615, Bielefeld, Germany. [1]*Corresponding author**

Received 7 March 2005. Accepted in revised form 30 August 2005

Key words: aggregation, competition, *Conyza canadensis*, root distribution, sand ecosystems, segregation

Abstract

Segregation of roots is frequently observed in competing root systems. However, recently, intensified root growth in response to a neighbouring plant has been described in pot experiments [Gersani M, Brown J S, O'Brien E E, Maina G M and Abramsky Z 2001. J. Ecol. 89, 660–669]. This paper examines whether intense root growth towards a neighbour (aggregation) plays a role in competitive interactions between plant species from open nutrient-poor mid-European sand ecosystems. In a controlled field-competition experiment, root distribution patterns of intra- and interspecific pairs as well as single control plants of *Corynephorus canescens*, *Festuca psammophila*, *Hieracium pilosella*, *Hypochoeris radicata* and *Conyza canadensis* were investigated after one growing season. Under intraspecific competition plants tended to segregate their root systems, while under interspecific competition most species tended to aggregate roots towards their neighbours even at the expense of root development at the opposite competition-free side of the target. Preference of a root aggregation strategy over the occupation of competition-free soil in interspecific competition emphasizes the importance of contesting between individuals in relation to mere resource acquisition. It is suggested that in the presence of a competitor the plants might use root aggregation as a defensive reaction to maintain a strong competitive response and exclusive access to the resources of already occupied soil volumes.

Introduction

Competitive interactions are one of the major forces influencing abundance and distribution of plant species. Depending on the resource limitations of the respective ecosystem, either above- or belowground competition is prevalent (Casper and Jackson, 1997). In early successional stages of temperate open sand ecosystems, belowground resources are typically limiting for plant growth (Boorman, 1982; Weigelt et al., 2005). Mechanisms and traits contributing to belowground competitive abilities of plants are not yet fully understood and a matter of intense debate, particularly because competitive strength is composed of both, the ability to tolerate neighbours (competitive response) and the ability to affect neighbours (competitive effect, Goldberg and Fleetwood, 1987). For instance, the retention of resources, especially nutrients (Aerts, 1999) is of high importance concerning a plant's competitive response, while most traits considered to determine competitive effect in resource-poor habitats rather emphasize the acquisition of resources. The extension of a root system (Cahill and Casper, 2000) and its spatial influence (Casper et al., 2003) as well as root architecture (Fitter et al., 2002), mycorrhizal symbiosis (Smith and Read, 1997) and root uptake capacities (Caldwell et al.,

---

* FAX No: +49-521-1066038.
E-mail: maik.bartelheimer@uni-bielefeld.de

1985) are traits widely accepted to be determining for belowground competitive strength (but see Cahill Jr., 2003b), since their impacts on resource acquisition are rather evident. Recently, the plasticity of root systems seems to increasingly move into the focus of interest: forage capacities (Bliss et al., 2001; Hutchings et al., 2003), the importance of plastic responses of specific root length (SRL) (Huber-Sannwald et al., 1996) as well as root/shoot ratio or root proliferation (Robinson et al., 1999) are just a few examples which clearly show the reactivity of root systems to external influences. As size-symmetric division of resources according to the relative proportion of roots is the principle underlying most belowground competitive processes (Weiner, 1986), a target plant cannot expect high resource-pay-off for high amounts of roots produced in the vicinity of an adjacent root system (Novoplansky and Cohen, 1997; Sachs et al., 1993). It is therefore not surprising that roots typically avoid each other (Schenk et al., 1999). However, recent findings suggest that such segregative root placement is only one aspect of possible reactions of roots towards neighbouring roots: In pot-experiments with intraspecific competition between soybean individuals, Gersani et al. (2001) showed that the presence of neighbour roots induced and intensified root growth. Due to space restrictions (McConnaughay and Bazzaz, 1991) the option of avoidance was limited, and the authors argued that under these circumstances the possibility to 'steal' resources from a neighbour encourages additional root production. Segregation is the well-known phenomenon of roots preferentially growing into unoccupied soil, thereby avoiding proliferation in the presence of neighbouring roots. We will call the opposite phenomenon aggregation. Aggregation thus means that a plant develops an uneven root distribution in response to a neighbour, exhibiting a higher rooting density towards the neighbour compared to directions without competitive influence. So segregation or aggregation within a target's rooting zone can be detected by comparing the rooting density of the competing plants in two soil compartments that only differ in their relative position (proximal or distal) to a neighbouring plant.

In this paper we investigate the relative importance of aggregation and segregation under semi-natural conditions. In a controlled field experiment we planted intra- and interspecific pairs of five common plant species from the early successional stages of mid-European sand ecosystems and examined the following questions by fractional excavation of their roots after one growing season

1. Do the species exhibit root segregation or aggregation patterns in the presence of competing roots?
2. Are the different modes of reaction species-specific?
3. Which belowground plant traits can be identified to be responsible for the competitive strength of the examined species?

Methods

Study site

The experiments were carried out during the 2002 vegetation period on a sandpit near the University of Bielefeld, Germany where plant roots were not subjected to any kind of spatial restrictions. The sand pit is designed to mimic the natural situation of early successional stages of mid-European sand ecosystems. It consists of four chambers of 5×6 m area filled with river sand of 1.20 m depth. All chambers are separately lined with PVC film and contain an effective draining system. For further details see Weigelt et al. (2005).

Soil analyses

Soil samples (soil cores from the margin between three adjacent plots, 15 cm depth, volume: 47 cm^3) were taken monthly (June–September). For each chamber of the sandpit five cores were taken in a cross pattern covering all parts of the chamber. Then all five were pooled into one sample per chamber. $CaCl_2$-extracted (0.01 *M*) nitrate and ammonium were analysed with a continuous flow analyser (FIA-LAB II, MLE Engineering GmbH, Germany). Extractable nitrate content varied from 1.19 ± 0.11 mg NO_3^--N kg^{-1} (means ± SE for $n=4$) in June to 2.18 ± 0.13 mg NO_3^--N kg^{-1} in July. Ammonium contents were considerably lower, ranging from

0.20 ± 0.002 mg NH_4^+-N kg^{-1} (June) to 0.50 ± 0.03 mg NH_4^+-N kg^{-1} (September).

Soil water potential of all chambers was continuously recorded with equitensiometers (EQ2 Delta-T Devices Ltd, UK) in 15 cm soil depth. The lowest soil water potential was recorded in July (−31.9 kPa). Typically soil water potentials barely fell below −25 kPa. The mean value of all recorded data was -15.4 ± 5.8 kPa (mean ± SD).

Climate

Precipitation, soil water potential, soil temperature and PFD were monitored by an automatic weather-station (Campbell Scientific Inc., UK), next to the sand-pit. Monthly total precipitation during the course of the experiment was recorded as follows. April: 67 mm, May: 46 mm, June: 31 mm, July: 143 mm, August: 60 mm, September: 37 mm, October: 110 mm. Soil temperature was measured with a Pt 100 sensor in 5 cm depth. The highest soil temperature was reached in July (35.7 °C) and the lowest value was recorded in October (4.0 °C).

Species description and preparation of experimental plants

Corynephorus canescens (L.) P.B is a bunchgrass occurring on open sand and is frequently socialised with the perennial rosette species *Hieracium pilosella* L. and *Hypochoeris radicata* L. (both Asteraceae). With ongoing succession, *Festuca psammophila* (Hack. ex Čelak.) Fritsch a perennial bunch grass from Eastern Europe (Pless, 1995) can also emerge at these sites. *Conyza canadensis* (L.) Cronq. is an annual to biennial Asteracee, which was naturalized to Europe since 1700. It is nowadays very common in disturbed or ruderal communities and on sandy soils (Hegi, 1979).

Plants were grown from seeds (Seed sources: *C. canescens*, *H. pilosella*: collections from former sand-pit plants which were grown from seeds collected from approximately 20 maternal plants in a sand dune area near Bielefeld (08°40′ E 51°57′ N), *F. psammophila*: Botanical Garden of Gießen (Germany), *H. radicata*: Botanical Garden of Strassburg (Belgium), *C. canadensis*: Botanical Garden of Jena (Germany)), first raised in a glasshouse (about 4 weeks) and subsequently in a cold frame (2 weeks) and then cultivated next to the sand pit for two weeks before planting. On April 22 and 23, plants were washed out of the soil (potting-soil-amended sand), pruned for homogenous size of above- and belowground plant parts and then planted into the experimental plots on the sandpit. Mean total dry weight at planting was measured on representative plants (means ± SE, $n = 20$) and was 0.043 ± 0.003 g for *C. canescens*, 0.027 ± 0.002 g for *F. psammophila*, 0.114 ± 0.005 g for *C. canadensis*, 0.090 ± 0.004 g for *H. pilosella* and 0.111 ± 0.005 g for *H. radicata*. Although the forbs showed higher biomass values, their sizes before drying appeared rather similar to the grasses.

One experimental plot consisted of a 50×40 cm rectangle with either a pair of plants in the centre or a single control plant (simple additive design). Plots were arranged in a brick pattern directly adjacent to each other without any soil dividers that could have restricted root growth. The distance between plants from neighbouring plots was 42 cm within rows or 44 cm between rows, as plant pairs within one plot were planted 7.5 cm apart. Plant positions (left or right hand side) were chosen by random. In the case of control plants, the neighbouring space remained unoccupied. The controls and all possible intra- and interspecific combinations were planted with 2 replications into each of the 4 chambers of the pit, resulting in a total of initially 160 plots for 20 combinations and 8 replicates.

Plant harvest

From October 15 to October 26 five replicates of each treatment were harvested, i.e. one of each sandpit chamber plus one additional replicate, which had been randomly chosen. Aboveground biomass was cut-off at the soil surface, oven-dried and weighted. Belowground biomass was differentially harvested by a modified monolith-method (Böhm, 1979; Caldwell and Richards, 1986; Kücke et al., 1995). The volume of interest was partitioned into strata consisting of bigger lateral and smaller central cuboids (Figure 1). To fix soil and roots in their defined position, an open steel cube of $30.0 \times 22.5 \times 15.0$ cm was

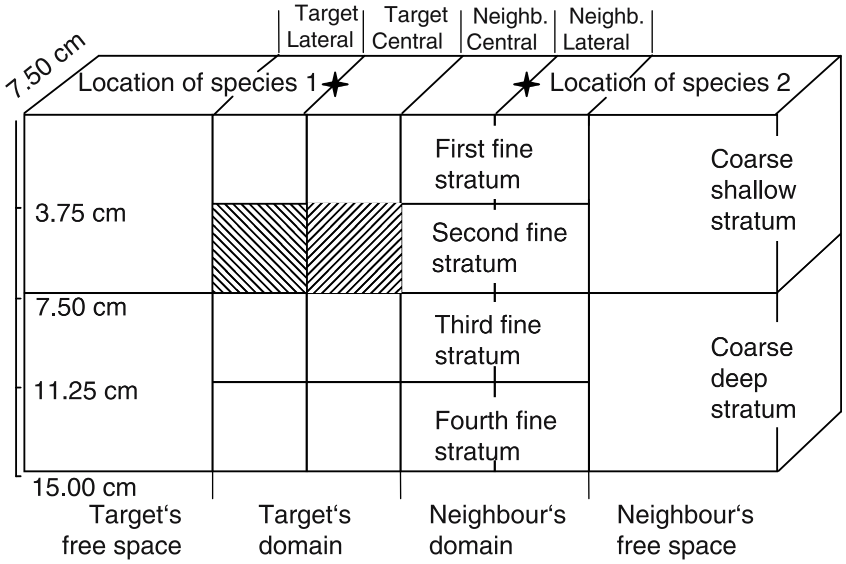

Figure 1. Schematic overview of the partitioning and denomination of the collected soil-cuboids. The stars denote the position of the target (or control) and (if present) its respective neighbour plant. Lateral spheres are divided into coarse cuboids (7.5×7.5×7.5 cm); the central sphere is divided into finer cuboids (3.75×7.5×3.75 cm). The two hatched cuboids exemplarily show a pair of a lateral and a central cuboid as it was typically used for the relative comparisons described in the text.

pushed into the soil. By application of sharpened, one-sided open steel forms (7.5×7.5×7.5 cm for bigger cuboids and 3.75×7.50×3.75 cm for smaller cuboids) and sharpened spatulas, defined volumes were cut out of the sand. A few thicker roots, which were not properly cut by the steel frames, were thoroughly cut by scissors, and the resulting parts assigned to the respective soil cuboids. Roots were immediately washed out of the cut soil fragments (1 mm steel-sieves) and stored in water at 4 °C until scanning (Figure 1).

The obtained root samples were further cleaned from adhering soil particles etc. by tweezers and thoroughly spread on a glass recording tray (Richner et al., 2000), which was then placed on a flatbed scanner with transparency lighting system (Snap Scan 1236, AGFA, Belgium). Maximum scanning root density as recommended by Bouma et al. (2000) (0.5 mm root length/mm^2 scanner surface) was typically not exceeded. Scanning was performed with 300 dpi in colour mode. Root analysis was done with WinRhizo Pro Software (Version 2002c; Regent Instruments Inc., Quebec, Canada). Program adjustments were set to ignore objects smaller than 0.01 cm^2 and discriminate roots from background based on grey levels with a threshold of 235 as was found to consistently deliver clear identifications. Attempts to separate the various root-fragments according to species proved infeasible.

Data processing and analysis

Having an additive experimental design, the Relative Neighbour Effect (RNE) was chosen as a quantitative measure of competitive strength. RNE is a modification of the relative competitive intensity (RCI, Wilson and Keddy, 1986) which is identical to the RCI in the case of competitive interactions but differs in the case of facilitative interaction.

$$\begin{aligned} \text{RNE} &= \frac{(P_{\text{control}} - P_{\text{mix}})}{x} \\ \text{with } x &= P_{\text{control}} \text{ if } P_{\text{control}} > P_{\text{mix}}; \\ x &= P_{\text{mix}} \quad \text{if } P_{\text{mix}} > P_{\text{control}} \end{aligned} \tag{1}$$

when P_{control} is the control plant's performance while P_{mix} is the performance of the target plant in the competition treatment. The RNE can vary between –1 and +1, i.e. it is symmetric with respect to zero (Markham and Chanway, 1996). The performance parameter used in the present study was aboveground biomass, since, due to the above described fractionized harvest, plant-specific root biomass was not available. For plots with intraspecific pairs, dependencies of samples were avoided by randomly choosing one plant from each pair (following Law and Watkinson, 1987). From plots with interspecific pairs, aboveground biomass of each plant was used for the calculation of the respective RNE. The competitive response of a certain species was calculated as mean RNE of that species in all interspecific treatments irrespective of the neighbour species, with high RNE values indicating weak competitive performance. Conversely, the competitive effect of a species was calculated as mean RNE imposed by that species on the various neighbours. Here high RNE values indicate a strong competitive performance (Goldberg and Fleetwood, 1987).

Unfortunately there was no way to distinguish between the roots of the two competing species in the competition treatments. So all roots within each cuboid were analysed together and subsequently related to a calculated theoretical control value for root area. This theoretical control was used as the reference corresponding to the null-hypothesis that neighbouring plants would not at all affect each other's root distribution. It was calculated by simply adding the root surface area (RSA) data of the control experiments, where the species were grown without a competitor. In other words: the root surface area found within the cuboids of the control experiments of the respective species was added according to the equation:

$$\mathrm{RSA(species1;2)}_0 = \frac{1}{n} \times \sum_{i=1}^{n} \mathrm{RSA(species1)}_i + \frac{1}{n} \times \sum_{i=1}^{n} \mathrm{RSA(species2)}_i \tag{2}$$

with $\mathrm{RSA(species1;2)}_0$: Theoretical control for the root area in a certain cuboid in a certain species combination calculated according to the null-hypothesis.

This theoretical control value was then used as reference value for the interpretation of the root data from the respective cuboids of the competition experiment.

For the examination of a neighbour's influence on a plant's horizontal root distribution we used the cuboids in the Target's domain (see Figure 1), i.e. for each fine scale stratum the Target Central cuboid was compared to the Target Lateral cuboid (see hatched cuboids in Figure 1), representing one adjacent and one distal soil sphere with respect to the neighbour plant. For each stratum, the applied test always involved a relative comparison between the two cuboids. The compared values were percent values calculated as the actual root area in relation to the above described theoretical control for H_0:

$$\mathrm{Percentage_{RSA}}[\%] = \left(\frac{\mathrm{RSA(species1;2)}}{\mathrm{RSA(species1;2)}_0}\right) \times 100 \tag{3}$$

with $\mathrm{Percentage_{RSA}}$: Achieved percentage in relation to the theoretical control. RSA(species1;2): Root area actually present in a certain cuboid. $\mathrm{RSA(species1;2)}_0$: root area of the theoretical control for this cuboid according to the null-hypothesis.

Due to competition, the values should typically be below 100%, as the plants in the competitive situation are typically smaller than those growing without competition. The conducted relative comparisons between cuboids should be robust against such a size bias. Higher values in the Target Lateral cuboid (e.g. 80%) over the Target Central cuboid (e.g. 60%) are interpreted as segregative root placement. Conversely, higher values in the Target Central cuboid to the Target Lateral cuboid indicate aggregation: both values are reduced in relation to the theoretical control, but the reduction is less intense in the Target Central cuboid.

To test for changes in vertical root placement, percentage values of the four fine strata were compared. This analysis was restricted to the Target Central cuboids only, where the intermingling of roots is presumably most intense.

When analysing reactions in root distribution of individual target species (Figures 5 and 6), we used all values of that species in interspecific treatments irrespective of the neighbour species.

Statistical analyses were carried out with STATISTICA 6.0 (StatSoft, Inc., Tulsa, USA). To test the influence of species and the influence of central and lateral soil cuboids, we used two-way ANOVAs, while paired *t*-tests were applied for species-specific comparisons. For other comparisons one-way ANOVAs with post-hoc

Fischer LSD-tests were applied. If assumptions of normality or homogeneity of variances were not fulfilled, log- or square-root-transformed data were used instead.

Results

Evaluation of competitive effects and responses

To relate competitive interactions to root distribution and altered root placement, we evaluated intensity of intra- and interspecific competition and root distribution in the presence and absence of neighbours.

Intraspecific competition (Figure 2A) was quite intense for the two grass species *F. psammophila* and *C. canescens* as well as for *C. canadensis*, while *H. pilosella* and especially *H. radicata* exhibited low net intraspecific competition. Due to high data variability, differences were not significant, though. The interspecific competitive strength of a species was characterized by its ability to affect other plants (competitive effect) and by the ability to tolerate the influence of neighbours (competitive response (Goldberg and Fleetwood, 1987). Figure 2B shows both components for the five examined species.

Ranking the five examined species according to their general competitive effect (Figure 2C), *F. psammophila* was found to be the strongest effect competitor; *C. canadensis* and *C. canescens* and *H. radicata* showed intermediate effects upon their various neighbours, while *H. pilosella* imposed no net effect. Most differences were not significant, which was again mostly due to high standard errors resulting from pooling the values of a species from all competition experiments i.e. from experiments with four different neighbour species. Nevertheless, this generalized view still gives a clear overview of competitive abilities, particularly for the competitive response. As outlined in the methods, and in contrast to the RNE values of the competitive effect, high RNE values of competitive response represent poor competitive strength. So *F. psammophila* was found to be a strong effect – but a poor response-competitor. The second grass, *C. canescens*, behaved similarly

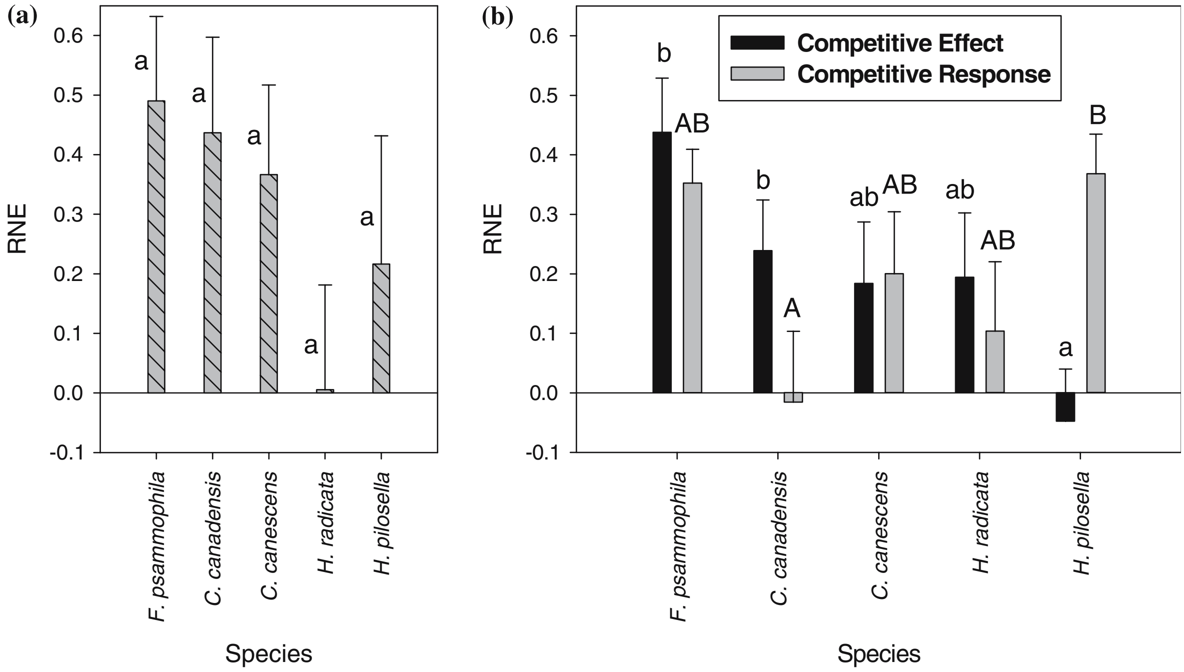

Figure 2. General competitive abilities of the five examined species, expressed as Relative Neighbour Effect RNE calculated from aboveground biomass (means + SE for $n = 25$) in (a): intraspecific competition and (b): interspecific competition. Values with the same letters are not significantly different by ANOVA and Fischer LSD-test ($P < 0.05$): a, b for species comparisons concerning competitive effect; A, B for species comparisons concerning competitive response.

at a lower RNE level. *C. canadensis* was a rather good effect and response competitor, and the values for *H. radicata* were within a similar range. *H. pilosella* showed both poor competitive effect and response.

Comparative morphology of control root systems (without neighbours)

Root distribution patterns

Figure 3 gives detailed information of the vertical and horizontal distribution of roots, which is needed for the analysis of the impact of competition on root placement. Concerning the vertical distribution, *F. psammophila* displayed high root area in the top stratum, while the decline with depth was steep (entire bottom stratum = 9.0% of entire top stratum). *C. canadensis* showed a gentle decline (bottom stratum = 25.9% of top stratum). *C. canescens* appeared to have a similar root distribution as *F. psammophila*, though the decline with depth (bottom stratum = 3.6% of top stratum) was even stronger.

H. radicata and *H. pilosella* have small allorhizous root systems (Kutschera and Lichtenegger, 1992) with their maximum rooting intensities in the second stratum. It should be noted that the species with the highest root area values within the top stratum (*F. psammophila*, *C. canadensis* and *C. canescens*) were the species with the strongest general competitive effect (see Figure 2).

Horizontal root distribution

F. psammophila: A high degree of horizontal root spread was observed in the uppermost stratum as the roots exhibited comparatively high root area values in the neighbour domains (Neighbour Central and Neighbour Lateral). This indicates a high potential for competitive interaction with neighbouring plants. In deeper strata, the horizontal distance from the tussock was not associated with reduced root area. *C. canadensis:* In the first stratum and close to the shoot this species developed quite high root densities (about 100 cm^2 per cuboid in the target domain) with significantly fewer roots growing into the neighbour domain. In deeper strata, though, root distribution was rather even across the different spheres.

C. canescens: This species displayed very high root densities in the top stratum, with a significant decline towards the neighbour domain. Beside this, *C. canescens* showed similar patterns as *F. psammophila*, but it is noteworthy that, due to a steep vertical decline, from the second stratum downwards the values are lower than those of *F. psammophila*. With increasing distance from the sprout, the root area of *H. radicata* and *H. pilosella* declined only smoothly in the first stratum. In the second and, in the case of *H. pilosella*, also in the third stratum, however, the decline with distance was significant.

Comparative morphology of competing root systems

Root area within the target domain

To find out whether there are tendencies for horizontal segregation or aggregation in response to a neighbouring root system, we carried out a two-way ANOVA to compare the relative changes (related to the theoretical control) within all the Target Lateral Spaces and all Target Central Spaces, with the target species as an additional factor. Since high root densities were solely found in the two top strata (data not shown, but compare Figure 3), the analyses were restricted to these strata. Two separate analyses were carried out for intraspecific or interspecific combinations, respectively. For none of these analyses (Table 1) differences between central and lateral cuboids were significant, but interestingly analyses revealed different tendencies of horizontal root segregation (in intraspecific combinations) or aggregation (in interspecific combinations) in response to the presence of a neighbour: segregation is represented by a stronger reduction in the Target Central than in the Target Lateral Space (intraspecific combinations in stratum 1 and especially 2), while aggregation is represented by a stronger reduction in the Target Lateral than in the Target Central Space (interspecific combinations in both strata). In contrast, there were significant differences for the influence of the target species hinting at species specific tendencies to segregate or to aggregate.

For the interspecific competition experiments each target-species was examined separately.

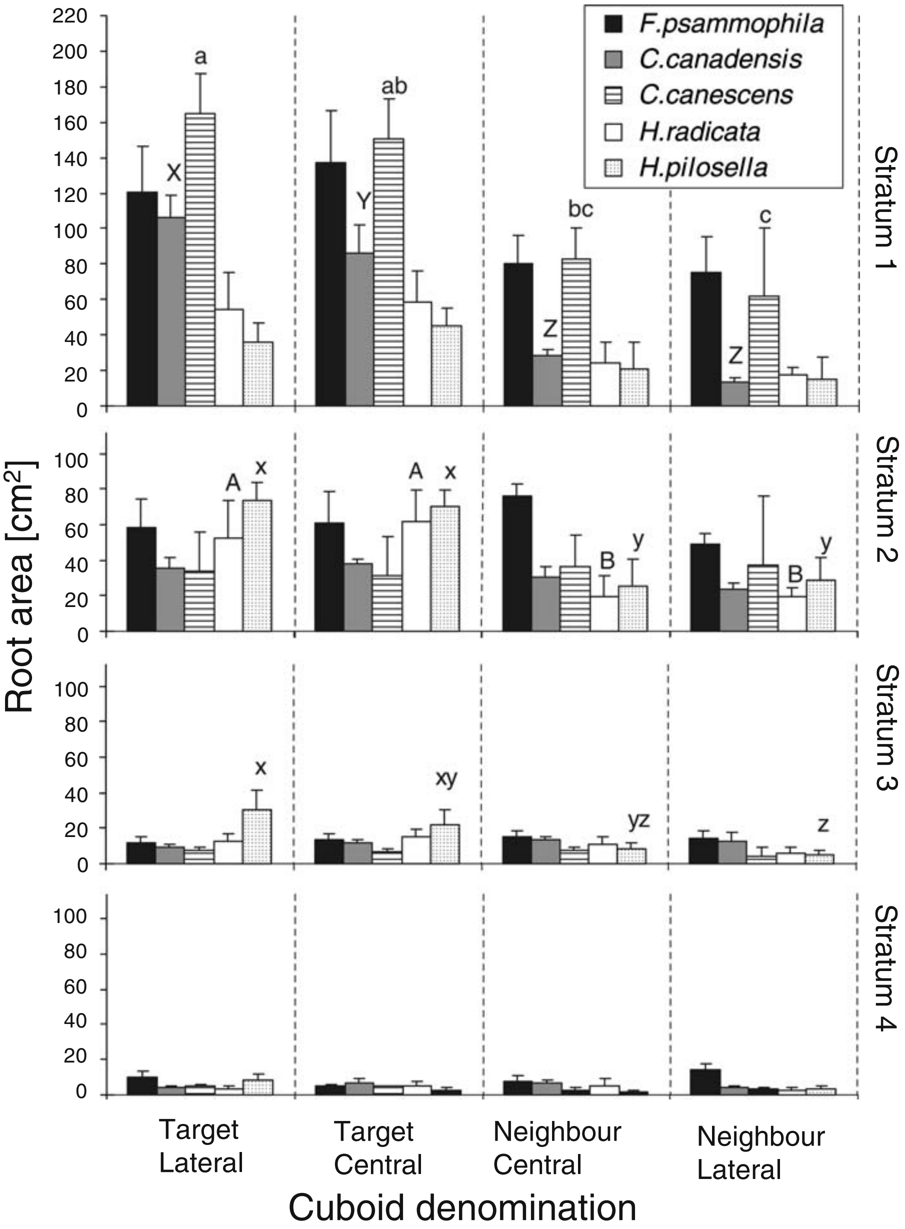

Figure 3. Fine scale distribution of root surface area for the control treatments (means + SE, $n = 5$). For means of comparison, all species are assumed to have grown on the left hand side (target domain). ANOVA comparisons and Fischer LSD-test always refer to one species within one layer. Different letters denote statistically significant differences with a, b, c referring to *C. canescens*, X, Y, Z referring to *C. canadensis*, x, y, z referring to *H. pilosella* and A, B referring to *H. radicata*. Items without letters had no within-layer significances at all.

Figure 4 shows a consistent aggregation of *C. canadensis*, *C. canescens* and *H. pilosella* in both examined strata, while *F. psammophila* showed no consistent response and *H. radicata* rather exhibited segregation.

The fact that *H. radicata* consistently exhibited root segregation can now be used to examine whether high percentage values in the Target Central space can be predominantly attributed to the target plants or whether they are

Table 1. Overview of analyses concerning the alterations in horizontal root placement of the targets in response to a neighbouring root system in intra- or interspecific competition, respectively. Displayed percent values are percentages of produced root area in comparison to the corresponding theoretical control (means ± SE).

Type of competition	Soil-layer	Fine scale cuboid [%]		*n*	ANOVA factors					
		Target Lateral	Target Central		Cuboid			Target species		
					df	*F*	*P*	df	*F*	*P*
Intraspecific	1	68.28 ± 7.49	66.55 ± 7.01	22	1	0.02	0.8911	4	3.71	0.0125
Intraspecific	2	75.56 ± 7.75	67.03 ± 7.37	24	1	0.49	0.4840	4	3.93	0.0044
Interspecific	1	79.45 ± 4.35	82.76 ± 4.33	99	1	0.85	0.3565	4	1.94	0.1049
Interspecific	2	74.02 ± 2.97	77.31 ± 3.82	99	1	1.23	0.2694	4	5.96	0.0001

the result of the activities of both competitors (Figure 5).

With *H. radicata* as the target species, the Target Space indicates segregation (Figure 5A). With *H. radicata* as the neighbour species (Figure 5B), the Target Space indicates aggregation. Thus, since *H. radicata* generally segregates, the increase in root area in the target space can be attributed to the target species.

Vertical segregation and aggregation

Additional to the horizontal dimension, we examined possible alterations of root placement in the vertical dimension. For this purpose, the analysis was restricted to the Target Central Space, where the root systems overlap and interaction should be most intense. Nevertheless, neither a segregation- nor an aggregation-tendency could be identified when the pooled responses of all target species to all neighbour species were analysed (data not shown). Only the target species *C. canadensis* showed a clear response of vertical aggregation in the upper soil strata (Figure 6).

Discussion

Numerous authors point out that, particularly under field conditions, much too little is known about belowground processes and still a lot of things remain to be clarified (e.g. Agrawal, 2003; Schenk, 2004; Zobel, 2003). Studies like the present one, at least showing some clear tendencies, can hint at so far unexplored interactions and can in so far be an appropriate way to achieve some scientific progress in this area.

Segregation or aggregation?

Our results suggest that segregation of roots occurs under intraspecific competition, while aggregation seems to result from the interaction of different species. In fact, as reviewed by Schenk et al. (1999) segregation is predominantly, though not exclusively, documented for intraspecific competition, suggesting that avoiding competition is particularly advantageous among taxonomically closely related plants. Proximate factors of segregation are thought to involve at least two processes, the avoidance of depleted soil (Bunce et al., 1977; Novoplansky and Cohen, 1997; Schenk et al., 1999) and the avoidance of repressive or toxic root exudates like prunasin or phloricin (Gur and Cohen, 1989; Inderjit and Weston, 2003; Webb et al, 1967). However, some recent papers showed exciting results for roots in intraspecific competition, which by space restrictions were forced to grow together: (i) Gersani et al. (2001) found that root growth of such competing plants was increased instead of decreased; (ii) Falik et al. (2003) and Gruntman and Novoplansky (2004) could show that such increase was the stronger the less related (from clonally integrated ramets over genetically identical but divided ramets to genetically different plants) the competing plants were. The role of self-/non-self recognition becomes evident here. Root exudates may play a role as mediators (Bais et al., 2004), as e.g. soyasaponin 1 could be shown to enhance root growth of wheat seedlings (Oleszek et al., 1999) and Falik et al. (2005) could prove a case where the direction and the redirectioning of root growth were governed by the roots' own exudates.

The present results, pointing towards root aggregation for interspecific competition correspond nicely with the findings of Falik et al. (2003) and Gruntman and Novoplansky (2004). A way of species recognition is necessary for this behaviour and in fact, several cases of species recognition in the rhizosphere, also involving root exudates, have already been documented (Mahall and Callaway, 1991, 1992). Especially the case of *Pseudoroegneria spicata*, increasing SRL and root-shoot ratio in response to the presence of *Agropyron desertorum* but not to the presence of a conspecific neighbour (Huber-Sannwald et al. 1996) supports the present results and also calls for the involvement of species recognition. As far as our results are concerned, we can speculate that conspecific neighbours tend to segregate their roots, because the evenness of the joint root systems would cause intense scramble competition and, thus, reduced

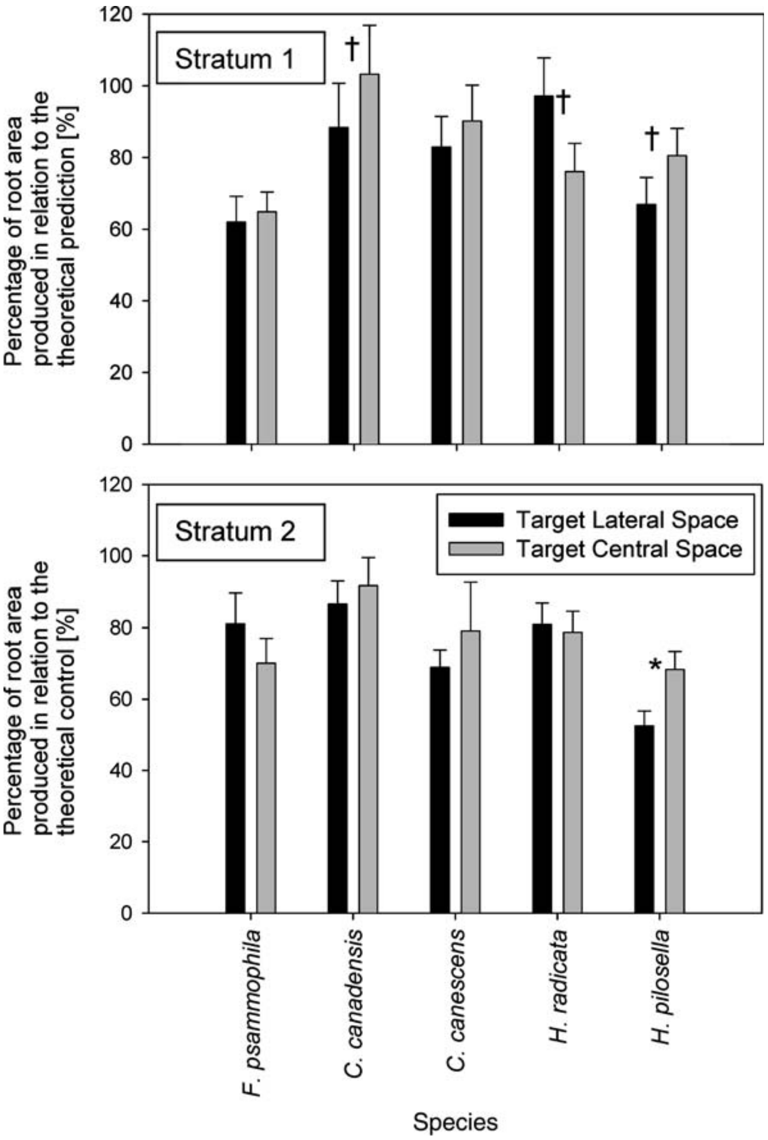

Figure 4. Species specific comparison of Target Lateral and Target Central cuboids for detection of possible alterations in horizontal root placement of the targets in response to a neighbouring root system (means ± SE with $n = 20$ for each species). Asterisks and crosses denote statistically significant differences in paired *t*-tests between lateral and central cuboids with †: $P < 0.1$, *: $P < 0.05$.

fitness. On the other hand, plant individuals from different species might have good biological reasons to aggregate roots against the competitor, since it is known that by strong competitive pressure weak neighbours of other species can be forced to place their roots into less favourable spheres (Berendse, 1982; McKane et al., 2002).

For the discussion of the biological sense of aggregation, it is important to note that the examined interactions were competitive, not facilitative (Figure 2). Therefore, the possible existence of favourable micro-sites close to neighbouring roots, involving interactions with mycorrhiza (Zobel and Moora, 1997) or hydraulic lift (Caldwell et al., 1998) does not seem to be of major importance. Decreased evaporation from soil spheres in-between the plants can be ruled out as well, as the aboveground plant parts shaded only very small parts of the soil surface.

Aggregation might be explained by a statement of d'Antonio and Mahall (1991), who suggested that plants might proliferate roots with the intent of directly discouraging intrusions from other individuals into their own root zone. Depleted soil can certainly preclude other plants from profitably foraging there (Novoplansky and Cohen, 1997), and such a pre-emption is even more conceivable for plants from different spe-

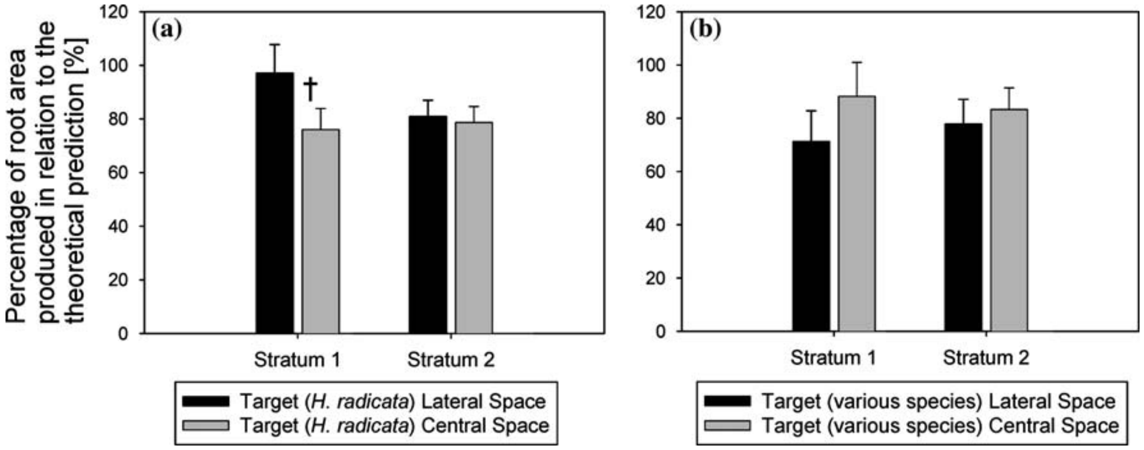

Figure 5. Differential horizontal root placement within the target domain when *H. radicata* is (a), the target plant or (b), the neighbour plant in interspecific competition. Data of all examined species were pooled and expressed as percentage of root area relative to the according theoretical controls (means + SE; $n = 23$ for stratum 1 and $n = 24$ for stratum 2). Crosses indicate marginally significant differences in paired *t*-tests with †: $P < 0.1$.

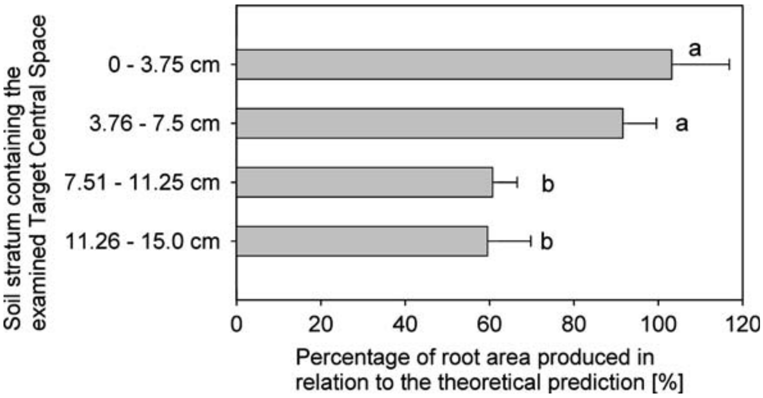

Figure 6. Vertical response in root placement of the target species *C. canadensis* towards the presence of a neighbour of another species expressed as percentage of root area within the Target Central Space as compared to the according theoretical controls (means + SE; $n = 24$). Different minor letters indicate statistically significant differences in ANOVA-comparisons and *post hoc* Fischer LSD-test with $P < 0.05$.

cies, typically exhibiting differences in their morphological and physiological traits (Robinson et al., 1999). Thus, aggregation might also be looked at as a defensive reaction, as by the development of high root densities an effective barrier to foreign roots is formed.

In a pot experiment Gersani et al. (2001), found an increase in root biomass for competing root systems. Based on their results they made some predictions for optimal resource capture including the importance of the utilization of unoccupied soil. In the present case aggregation took place although there was plenty of unoccupied soil space available at the back side of the target plant (Target's Free space, Figure 1), so our plants did not prefer the unoccupied soil, where neither own nor foreign roots were present, but rather the occupied soil (Target Central cuboids), where interactions with the neighbouring root system were most intense. This strongly illustrates the higher importance of resource contesting (Callaway, 2002) compared to resource matching (producing roots according to the availability of resources). Maintaining resources and 'stealing resources from the neighbour' (Maina et al., 2002) seems to be the underlying principle of such behaviour. In a competitive situation, the loss of a resource to a neighbour can be of greater implication than the mere loss to the abiotic surroundings (e.g. leaching (Lundell et al., 2001)). Thus, depriving a neighbour of resources could be a rather advantageous strategy (Callaway, 2002).

Species specificity?

If we want to attribute the different root placement patterns to individual species, we need to show that rooting intensities in the Target Central cuboids are mostly caused by the target's and not to the neighbour's root placement. While there is no way to prove it statistically, we get a good hint from the case of *H. radicata*, the species that showed segregation in the Target's domain (see Figure 5). In contrast, when *H. radicata* was the neighbour species, aggregation was found in the Target's domain. In this case at least, aggregation was found even though the neighbour could only scarcely place roots in the Target Central cuboid and we take this as a good hint that our attribution of aggregational or segregational behaviour to certain species (Figures 4 and 6) is valid. Doing so, a tendency for horizontal aggregation was confirmed for *C. canadensis*, *C. canescens* and *H. pilosella*. It should be noted that within the scale of the examined root traits (root system type, vertical or lateral spread (Figure 2), root diameter (data not shown) these species have hardly any common features. Thus, the ability to aggregate roots was not correlated with root morphology. Vertically, only the species *C. canadensis* showed aggregative root placement (Figure 6). So in summa a rather high species specificity of the observed effects can be stated.

Competitive strength and belowground traits

Trying to find connections between competitive performance of species and their root traits, we analysed intra- and interspecific competition as well as various root traits. Interspecific competitive strength was divided into competitive effect and competitive response (Goldberg, 1990) and we found no close connection between these two components. This finding is similar to what has been reported by Keddy et al. (1994), who stress the importance of investigating the traits connected with competitive effect and competitive response. We therefore differentiated between plant traits conferring advantages in the two components. Especially for intraspecific competition we found an apparent link between competitive strength and the amount of root area formed within the upper two soil strata by the species' control plants (see Figures 2 and 3). This result corresponds with other competition experiments on nutrient-poor sandy soil (Weigelt, 2001). A strong relationship between competitive effect and root system size has often been shown before (Cahill Jr and Casper, 2000; Caldwell et al., 1996; Purves and Law, 2003), suggesting that high root overlap with the neighbour is the most important feature, here.

For the competitive response, high root overlap with the neighbour might be disadvantageous (Cahill Jr., 2003a). Concordantly we found neither a connection of competitive response and root size nor any other hint from root morphology. On the other hand we could show that the species with the strongest competitive response (*C. canadensis* and *H. radicata*) showed the most pronounced reactions in root placement, when a neighbour was present. The advantage in the segregation of *H. radicata* is certainly the avoidance of depleted soil (Schenk et al., 1999). For *C. canadensis* our interpretation is different: the fact that *C. canadensis* shows the clearest aggregation in response to a neighbouring root system and at the same time is the strongest response-competitor (Figure 2) reinforces the above hypothesis that aggregation is partly a defensive strategy.

Conclusions

Under field-like conditions root-placement alterations in reaction to neighbours are an important component of the competitive strength of a species. Root aggregation towards a neighbour seems to be an important but up to now mostly unrecognised phenomenon in this connection. The fact that it occurs even when unoccupied soil is available stresses the importance of resource contesting in comparison to the mere resource acquisition.

Acknowledgements

The authors gratefully acknowledge the extensive field-work of Holger Abel, Marcel Austenfeld, Jürgen Birtsch, Elke Furlkröger, Gunther Klippel, Sven Luhmann and Birgit Peperkorn. They would further like to thank Ronald J. Ryel (Logan, UT) for statistical advice and Alexandra Weigelt (Jena) and two anonymous reviewers for their very helpful comments.

References

Aerts R 1999 Interspecific competition in natural plant communities: Mechanisms, trade-offs and plant-soil feedbacks. J. Exp. Bot. 50, 29–37.

Agrawal A 2003 Underground processes in plant communities. Ecology 84, 2256–2257.

Bais H P, Park S-W, Weir T L, Callaway R M and Vivanco J M 2004 How plants communicate using the underground information superhighway. Trends Plant Sci. 9, 26–32.

Berendse F 1982 Competition between plant populations with different rooting depths III. Field experiments. Oecologia 53, 50–55.

Bunce J A, Miller L N and Chabot B F 1977 Competitive exploitation of soil water by five eastern North American tree species. Bot. Gaz. 138, 168–173.

Bliss K M, Jones R H, Mitchell R J and Mou P P 2001 Are competitive interactions influenced by spatial nutrient heterogeneity and root foraging behavior? New Phytol. 154, 409–417.

Böhm W 1979 Methods of Studying Root Systems. Springer Verlag, Heidelberg, Berlin, New York 183 p.

Boorman L A 1982 Some plant growth patterns in relation to the sand dune habitat. J. Ecol. 70, 607–614.

Bouma T J, Nielsen K L and Koutstaal B 2000 Sample preparation and scanning protocol for computerized analysis of root length diameter. Plant Soil 218, 185–196.

Cahill J F Jr 2003a Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. J. Ecol. 91, 532–540.

Cahill J F Jr 2003b Neighbourhood-scale diversity, composition and root crowding do not alter competition during drought in a native grassland. Ecol. Lett. 6, 599–603.

Cahill J F Jr and Casper B B 2000 Investigating the relationship between neighbor root biomass and belowground competition: Field evidence for symmetric competition belowground. OIKOS 90, 311–320.

Caldwell M M, Dawson T E and Richards J H 1998 Hydraulic lift: Consequences of water efflux from the roots of plants. Oecologia 113, 151–161.

Caldwell M M, Eissenstat D M, Richards J H and Allen F M 1985 Competition for Phosphorus: Differential uptake from dual-isotope-labeled soil interspaces between shrub and grass. Science 229, 384–386.

Caldwell M M, Manwaring J H and Durham S L 1996 Species interactions at the level of fine roots in the field: Influence of soil nutrient heterogeneity and plant size. Oecologia 106, 440–447.

Caldwell M M and Richards J H 1986 Competing root systems: Morphology and models of absorption. *In* On the Economy of Plant Form and Function. Ed. T J Givnish. pp. 251–273. Cambridge University Press, Cambridge.

Callaway R M 2002 The detection of neighbors by plants. Trends Ecol. Evol. 17, 104–105.

Casper B B and Jackson R B 1997 Plant competition underground. Annu. Rev. Ecol. Syst. 28, 545–570.

Casper B B, Schenk H J and Jackson R B 2003 Defining a plant's belowground zone of influence. Ecology 84, 2313–2321.

Falik O, Reides P, Gersani M and Novoplansky A 2003 Self/non-self discrimination in roots. J. Ecol. 91, 525–531.

Falik O, Reides P, Gersani M and Novoplansky A 2005 Root navigation by self inhibition. Plant Cell Environ. 28, 562–569.

Fitter A H, Williamson L, Linkohr B and Leyser O 2002 Root system achitecture determines fitness in an *Arabidopsis* mutant in competition for immobile phosphat ions but not for nitrate ions. Proc. R. Soc. Lond. 269, 2017–2022.

Fu X D and Harberd N P 2003 Auxin promotes *Arabidopsis* root growth by modulating giberillin response. Nature 421, 740–743.

Gersani M, Brown J S, O'Brien E E, Maina G M and Abramsky Z 2001 Tragedy of the commons as a result of root competition. J. Ecol. 89, 660–669.

Goldberg D E 1990 Components of resource competition in plant communities. *In* Perspectives on Plant Competition. Eds. J B Grace and D Tilman. pp. 27–49. Academic Press, San Diego, London.

Goldberg D E and Fleetwood L 1987 Competitive effect and response in four annual plants. J. Ecol. 75, 1131–1143.

Gruntman M and Novoplansky A 2004 Physiologically mediated self/non-self discrimination in roots. Proc. Natl. Acad. Sci. USA 101, 3863–3667.

Gur A and Cohen Y 1989 The peach replant problem – some causal agents. Soil Biol. Biochem. 21, 829–834.

Hegi G 1979 Illustrierte Flora von Mittel-europa. Verlag Paul Parey, Berlin, Hamburg.

Holzapfel C and Alpert P 2003 Root cooperation in a clonal plant: Connected strawberries segregate roots. Oecologia 134, 72–77.

Huber-Sannwald E, Pyke D and Caldwell M M 1996 Morphological plasticity following species-specific recognition and competition in two perennial grasses. Am. J. Bot. 83, 919–931.

Hutchings M J, John A J and Wijesinghe D K 2003 Toward understanding the consequences of soil heterogeneity for plant populations and communities. Ecology 84, 2322–2334.

Inderjit Weston L A 2003 Root Exudates: An overview. *In* Root Ecology. Eds. H De Kroon and E J W Visser. pp. 235–251. Springer-Verlag, Berlin, Heidelberg.

Keddy P A, Twolan-Strutt L and Wisheu I C 1994 Competitive effect and response rankings in 20 wetland plants: Are they consistent across three environments? J. Ecol. 82, 635–643.

Kücke M, Schmid H and Spiess A 1995 A comparison of four methods for measuring roots of field crops in three contrasting soils. Plant Soil 172, 63–71.

Kutschera L and Lichtenegger E 1992 Wurzelatlas mitteleuropäischer Grünlandpflanzen. Fischer, Stuttgart.

Lamont B B 2003 Structure, ecology and physiology of root clusters – a review. Plant Soil 248, 1–19.

Law R and Watkinson A R 1987 Response-surface analysis of two-species competition: An experiment on *Phleum arenarium* and *Vulpia fasciculata*. J. Ecol. 75, 871–886.

Lundell Y, Johannisson C and Högberg P 2001 Ion leakage after liming or acidifying fertilization of Swedish forests – a study of lysimeters with and without active tree roots. Forest Ecol. Manag. 147, 151–170.

Mahall B E and Callaway R M 1991 Root communication among desert shrubs. Proc. Natl. Acad. Sci. USA 88, 874–876.

Mahall B E and Callaway R M 1992 Root communication mechanisms and intracommunity distribution of two Mojave shrubs. Ecology 73, 2145–2151.

Maina G M, Brown J S and Gersani M 2002 Intra-plant versus inter-plant root competition in beans: Avoidance, resource matching or tragedy of the commons. Plant Ecol. 160, 235–247.

Markham J H and Chanway C P 1996 Measuring plant neighbour effects. Funct. Ecol. 10, 548–549.

McConnaughay K D M and Bazzaz F A 1991 Is physical space a soil resource? Ecology 72, 94–103.

McKane R B, Johnson L C, Shaver G R, Nadelhoffer K J, Rastetter E B, Fry B, Biblin A E, Kielland K, Kwiatkowske B L, Laundre J A and Murray G 2002 Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415, 68–71.

Novoplansky A and Cohen D 1997 The mutual distribution of competing root systems. *In* Biology of Root Formation and Development: Proceedings of the Second International Symposium on the Biology of Root Formation and Development, held June 23. Eds. A Altman and Y Waisel. pp. 353–364. Plenum Press, New York.

Oleszek W A, Hoagland R E and Zablotowicz R M 1999 Ecological significance of plant saponins. *In* Priciples and Practices in Plant Ecology: Allelochemical Interactions. Eds. Inderjit, K M M Dakshini and F Chester. pp. 451–465. CRC Press LLC, Boca Raton.

Pless H 1995 Pflanzensoziologische Untersuchungen der Trockenrasen an den Hängen des Odertales zwischen Seelow und Frankfurt (Oder). Naturschutz und Landschaftspflege in Brandenburg 3, 27–31.

Purves D W and Law R 2003 Experimental derivation of functions relating growth of *Arabidopsis thaliana* neighbour size and distance. J. Ecol. 90, 882–894.

Richner W, Liedgens M, Bürgi H, Soldati A and Stamp P 2000 Root image analysis and interpretation. *In* Root Methods: A Handbook. Eds. A L Smit, A G Bengough, C Engels, M van Noordwijk, S Pellegrin and S C Van de Geijn. pp. 305–341. Springer Verlag, Berlin, Heidelberg.

Robinson D, Hodge A, Griffiths B and Fitter A H 1999 Plant root proliferation in nitrogen-rich patches confers competitive advantage. Proc R. Soc. Lond. 266, 431–435.

Sachs T, Novoplansky A and Cohen D 1993 Plants as competing populations of redundant organs. Plant Cell Environ. 16, 765–770.

Schenk H J 2004 Vertical vegetation structure below ground: Scaling from root to globe. *In* Progress in Botany. Eds. K Esser, U Lüttge, W Beyschlag and J Murata. pp. 341–373. Vol. 66 Springer-Verlag, Berlin Heidelberg.

Schenk H J, Callaway R M and Mahall B E 1999 Spatial root segregation: Are plants territorial? Adv. Ecol. Res. 28, 145–180.

Smith S E and Read D J 1997 Mycorrhizal Symbiosis. Academic Press, San Diego, London.

Webb L J, Tracey J G and Haydock K P 1967 A factor toxic to seedlings of the same species associated with living roots of the non-gregarious subtropical rain forest tree *Grevillea robusta*. J Appl Ecol 4, 13–25.

Weigelt A 2001 Plant competition on inland dunes: Influence of water availability, nitrogen supply and the role of belowground processes. Ph.D. thesis. University of Bielefeld.

Weigelt A, Steinlein T and Beyschlag W 2005 Competition in inland dunes: The impact of water availability on belowground processes. Plant Ecol. 176, 57–68.

Weiner J 1986 How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. Ecology 67, 1425–1427.

Wilson S D and Keddy P A 1986 Measuring diffuse competition along an environmental gradient: Results from a shoreline plant community. Am. Nat. 127, 862–869.

Zobel M and Moora M 1997 Plant coexistence in the interactive environment: Arbuscular mycorrhiza should not be out of mind. OIKOS 78, 202–208.

Zobel R 2003 Fine roots – discarding flawed assumptions. New Phytol. 160, 276–279.

Section editor: P.J. Gregory