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Horizontal and vertical distribution of root absorption zones of four common grass species in a mountain grassland

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Summary

• Horizontal distance between shoots and the place of nutrient absorption as a function of depth of the absorption zone was studied using a pointwise application of a non-radioactive tracer (strontium). The tracer was applied to three different soil depths in a mountain grassland and the biomass was sampled at the fine-scale.

• Vertical distribution of absorption zones differed between the species; in *Deschampsia flexuosa, Festuca rubra* and *Anthoxanthum alpinum* the amount of strontium absorbed decreased with increasing application depth; no such decrease took place in *Nardus stricta*.

• The horizontal distance of maximum strontium concentration from the application point increased with increasing depth of application in *Festuca* and, to a lesser extent, in *Anthoxanthum*. The absorbing zone therefore had essentially a conical shape, widening with increasing depth. No similar increase in horizontal-uptake distance with depth occurred in *Nardus* or *Deschampsia*; their absorption zones were more cylindrical. This indicates that shapes of root absorption zones differ between the component grass species.

• The differences in shapes of root absorption zones can be attributed to different gross morphologies of roots and rhizomes. The horizontal extent of root absorption zones is large relative to the grain of interspecific spatial pattern in the grassland.

Key words: interaction range, non-radioactive tracer, spatial patterns, strontium, uptake, weighted average.

Introduction

Species co-existence in resource-poor communities such as unproductive grasslands is strongly determined by below-ground processes, namely competition for water and/or nutrients (Caldwell, 1987). Since mobility of some of these resources in soil is limited, their exploitation depends critically on size, shape and spatial arrangement of root absorption zones (Fitter & Hay, 1989). Root systems extend beyond the canopy of almost all plants (Weaver, 1926; Anderson, 1927) although data from mixed stands of many species and habitats with very dense root systems such as grasslands are limited. Most studies have concentrated on thicker roots or total root biomass, but the spatial distribution of the absorption zone of a species typically differs from that of the total root biomass (Dumortier, 1991; Robinson, 1991). By contrast to biomass, which is rather easy to determine, absorption zones are more difficult to identify. Non-radioactive elements (strontium, rubidium) that mimic the uptake of common elements (calcium, potassium) have been used as markers of the absorption zone (Veresoglou & Fitter, 1984; Fitter, 1986; Dumortier, 1991; Mamolos *et al.*, 1995; McLellan, 1995).

Spatial arrangement of absorption zones can be an important element in species co-existence. Success in acquiring soil-based resources is determined by placement of roots in resource-rich and low-competition patches. In particular, different plant species may co-exist by exploiting spatially and/or temporally separated soil patches. Absorption zones of roots of different species may occupy different depths of the soil profile (Veresoglou & Fitter, 1984; Fitter, 1986; Mamolos

et al., 1995), and peaks of absorption in time may differ among species (Veresoglou & Fitter, 1984; Fitter, 1986). In addition to vertical and temporal separation of resource uptake, horizontal fine-scale spatial pattern has often been invoked as another mechanism for niche separation in plants (Grubb, 1977; Tilman, 1982; Palmer, 1994). Plant communities are never perfectly homogeneous in the horizontal dimensions. Above-ground spatial pattern is a direct outcome of the fact that space can be filled by limited numbers of individuals; consequently, the number of opportunities for plant individuals to interact is reduced by this spatial pattern (Keeling, 1999). For obvious reasons, most of the data on spatial pattern come from studies of above-ground parts of plants. However, this spatial pattern should also have a bearing on the ways in which plants interact and exploit soil resources. Since roots and rhizomes are of finite length, the spatial pattern of plant individuals/ramets above ground constrains their ability to exploit below-ground resources (Oborny, 1994; Wijesinghe & Hutchings, 1997). The spatial arrangement of absorption zones thus reflects the distance (horizontal and vertical) that roots and rhizomes may reach. This type of spatial separation may thus add a further dimension for niche differentiation between plants in the soil in addition to differentiation in the vertical dimension and in time.

Understanding and quantifying the role of below-ground horizontal spatial pattern is hampered by lack of knowledge on the vertical and horizontal distance that separates the position of a ramet from the position of the absorption zones. McLellan (1995) showed, using non-radioactive tracers at a single depth in soil, that species differed in horizontal distance between shoot position and position of the absorption zones. As the roots of different species often occupy different depths in soil (Anderson, 1927; Linkola & Tiirikka, 1936; Kutschera & Lichtenegger, 1982; Berendse, 1983), it is likely that the horizontal extent of the uptake zone will change with depth and that this change will differ between plant species. Indeed, an earlier study of fine-scale spatial pattern of roots and rhizomes (Pecháčková *et al.*, 1999) showed that individual species differed in the size of root patches and in the distance between these patches and their above-ground parts. Moreover, this distance changed with soil depth.

The current study therefore aims to identify the horizontal and vertical distance between root absorption zones and ramets supplied by the resources from these absorption zones. In particular, we were interested in species-specific differences in how the horizontal absorption distance changes with soil depth. We used a mountain grassland with four major species as a model system (see Herben *et al.*, 1993) where data on root morphology and spatial distribution of roots and rhizomes were available (Pecháčková *et al.*, 1999). We used Sr as a tracer element. Earlier studies (Boehm, 1979; Clarkson & Hanson, 1980; Fitter, 1986; Mamolos *et al.*, 1995) have shown that Sr is a good tracer, since: its chemical behaviour is very similar to calcium; it moves rather slowly in the soil, particularly if the soil is humus-rich and of low pH; and its uptake takes place in young unsuberized root parts. Calcium is mainly absorbed by passive processes, and its uptake thus reflects its ambient concentration in the soil; the absorption pattern of the very similar Sr can be expected to be similar.

We used point-wise application of strontium chloride to three different soil depths. This permitted us to identify the horizontal distance between rooted above-ground shoots and the place of nutrient absorption as a function of depth of the absorption zone. The main questions here are: what is the horizontal distance between the ramet and its absorption zones changed as the function of depth; and whether component species differ in the shapes of their absorption zones.

Methods

Study site

The study site is located in a mountain grassland in the Krkonoše Mts., North Bohemia, Czech Republic (Severka settlement, *c.* 3 km NW of Pec pod Sněžkou, latitude 50°41′42″ N, longitude 15°42′25″ E, altitude *c.* 1100 m, NE facing slope of inclination 18). This grassland was established several centuries ago; traditional management was by mowing once a year and manuring once in several years. The experiment was done in a species-poor stand with prevailing *Nardus stricta* and *Deschampsia flexuosa* (association Sileno–Nardetum, alliance Nardo-Agrostion; Krahulec, 1990) and *c.* 6–10 species/50 × 50 cm and 2–4 species/3 × 3 cm. There are only four common grass species: *Anthoxanthum alpinum* Å. Löve et D. Löve (hereafter *Anthoxanthum*), *Deschampsia flexuosa* (L.) Trin. (hereafter *Deschampsia*), *Festuca rubra* L. (hereafter *Festuca*), *Nardus stricta* L. (hereafter *Nardus*). The only other species of importance was *Polygonum bistorta* L.; its density was so low that it had to be excluded from the analyses.

Field experiment and data collection

Twelve 33 × 33 cm plots were established in the study grassland. The plot size was selected to conform with other analyses done in the same grassland. All four major grass species were present in all plots, except for *Nardus*, which was missing in one plot, and had < 5% frequency in three further plots. Frequency (recorded in 100 3.3 × 3.3 cells) of these species varied from plot to plot (*Deschampsia* 32–81, *Festuca* 15–70, *Nardus* 0–31, *Anthoxanthum* 29–83). On 3 June 1994, we applied 1.5 ml of water solution of $SrCl_2$ (concentration 3 mg ml^{-1}) to the soil in the centre of each of these plots. At first a hollow was made using a thin (3 mm in diameter) nail inserted to the required depth. Then a syringe with a long needle was used to deliver the solution into the bottom of the hollow. The solution was applied to three different depths: soil surface below the litter layer, 6 cm below

the surface and 12 cm below the surface; each depth was thus replicated at four plots. Individual treatments were spatially arranged in an incomplete Latin square; distances between individual treatment plots were *c.* 1 m. For the purpose of this study, the soil surface was defined as the top of the humus layer immediately below the litter layer. The depths were selected on the basis of an earlier morphological study of the root and rhizome distribution in the experimental grassland (Pecháčková *et al.*, 1999). Root density and soil organic matter content declined with depth (Pecháčková *et al.*, 1999).

After 20 d of incubation, 33 × 33 cm grids were established around the points of application. These grids were divided into cells 3.3 × 3.3 cm in size so that the point of application lay directly in the centre of the grid. All plants rooting in individual cells (100 cells per plot) were harvested and their spatial positions in the grid recorded. They were sorted to species immediately after sampling, and dried at 60°C for 24 h. Daily precipitation values (mm) during the exposure period were 2, 1.4, 7.1, 1.4, 0, 0, 4.2, 0.3, 0, 0, 0, 0, 0, 8.4, 0, 7.6, 0, 0, 0, 0, 0 (recorded at a climatological station Pec pod Sněžkou, 1.5 km apart).

Individual plants of each species sampled in each grid cells were pooled and analysed for Sr if their dry mass exceeded 0.1 g. The dried biomass was ground using a vibration agate grinder to a powder of maximum particle size 0.1 mm. Up to 200 mg of the sample was mineralized in 0.4 ml 65% HNO_3 p.a and 0.4 ml 30% H_2O_2 p.a. in a microwave mineralizator Millestone 1200 Standard. The resulting solution was vacuum-filtered and diluted to a volume of 25 ml. The Sr content was determined using atomic absorption spectrophotometry using a Unicam 9200X machine, and expressed as Sr concentrations per unit biomass for each species in each cell. Altogether 2073 values were measured (out of 1200 cells and four species, i.e. 4800 potential values).

Since uptake of Sr is species- and organ-specific (Dumortier, 1991), it cannot be used directly for comparison across species. Therefore we always tested positions of absorption zones *relative* to other patches for the same species (i.e. species-standardized values). This treatment also removes the effect of phenological differences in uptake (Fitter, 1986) provided that the rate of absorption changed through the season in the same way at all positions of the root system.

Background strontium values

Two separate data sets were collected to determine the background Sr concentration in the species tested. First, stored samples of above-ground plant parts taken from close to the experimental site (*c.* 10 m distance) taken in July 1990 were subsampled; four samples of sterile shoots were analysed for each species. Second, samples of above-ground biomass were taken in a grassland upslope *c.* 100 m away in July 1999. The upslope position was to ensure that no transport of Sr could have taken place from the application site. Three replicates of each these samples were analysed for Sr concentration as above; three replicates within each sample were analysed; the data used are means from these replicates. The background Sr concentrations were (mean ± SD; n = 11, ppm) 4.13 ± 0.30 (*Deschampsia*). 5.91 ± 1.27 (*Festuca*), 2.56 ± 0.87 (*Nardus*), 4.71 ± 1.46 (*Anthoxanthum*).

Data analysis

Since the values in different cells within one grid are not independent, they cannot be treated as separate observations and subjected to the usual statistical tests. Therefore, randomization tests were used to determine whether plants with high Sr concentrations were aggregated close to the application point. For the purpose of this test, we defined a measure of aggregation of high Sr values around the application point, and tested whether this measure was systematically shifted relative to the values expected if the application point were randomly positioned within the grid. Average radial distance between the application point and all occurrences of that species, weighted by the Sr concentration at each occurrence, was used as the measure of radial distribution of high Sr concentration values in each grid. This weighted average distance is determined primarily by the cells with plants of high concentration; weighting by concentration means that cells where the species has zero or negligible Sr concentration do not contribute to the resulting value of the weighted average distance. The weighted average (radial) distance was thus calculated as:

$$m = \frac{\sum_i c_i x_i w(x_i)}{\sum_i c_i w(x_i)} \qquad \text{(Eqn 1)}$$

where c_i is the Sr concentration in the species in question in the cell i, x_i is the radial distance from the cell i to the point of Sr application, and $w(x_i)$ is the weight of the distance class to which the cell i belongs. This weight was defined as the inverse of the number of observations of that species in all cells in the grid in the distance class to which x_i belongs. For this purpose, distance was divided into classes 3.3 cm (i.e. one cell) in width. The weighting had to be introduced since the number of observations in individual distance classes were unequal, both due to geometric effects and absence of the species in some cells. When calculating the distance no account was taken of the direction of slope; preliminary analysis of the data showed no effect of slope inclination on the spatial distribution of the high concentration points.

This weighted average is a measure of aggregation of high Sr concentration values around the point of application. Its numerical value depends on the background level of Sr (shown by artificial data, not presented here). It increases with increased distance of high concentration values from the point of application (it increases from Fig. 1a to all other arrangements), and with decreasing difference between low

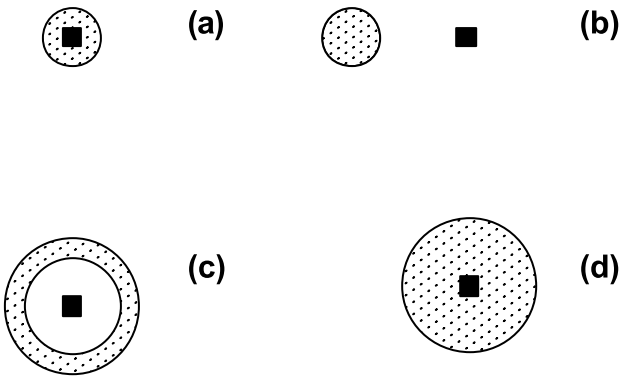


Fig. 1 Schematic drawing of several possible configurations of high Sr values around the point of application (viewed from above) and significance of weighted average and variance using artificial data of that structure. The little square indicates point of application; shaded areas indicate regions with non-zero Sr values. (a) Weighted average low and significant, variance high and significant (if background non-zero); (b) weighted average non-significant, variance non-significant; (c) weighted average non-significant, variance low and significant; (d) both weighted average and variance low and significant.

and high values (it increases from Fig. 1a–c). This was checked by using artificial data (full results not shown).

In addition to the weighted average of distance, weighted variance of distance was used to measure the spread of high values from the mean distance to the application point. It was calculated using the formula:

$$\text{var} = \frac{\sum_i c_i (x_i - m)^2 w(x_i)}{\sum_i c_i w(x_i)} \qquad \text{(Eqn 2)}$$

where m is defined by the formula (1). Weighted variance is low if samples at one distance have similar concentration values (it is lowest in spatial arrangement shown at Fig. 1c).

Properties of the weighted mean and, in particular, weighted variance, were tested using artificially generated data with properties shown in Fig. 1. This showed that weighted variance is low if high Sr values are at equal non-zero distances from the point of application in all directions (compare Fig. 1c,f), and if differences between low and high Sr values are high; it is high when there is no marked peak in Sr concentrations or if the high values are at highly variable distances from the point of application (Fig. 1). Due to the radial definition of distance the variance changes if a pattern of high values around the centre is shifted within the grid. This feature can be used to test equidistant distribution of the points of high concentration around the application point. Artificial data also showed that it is high when the peak was directly at the point of application in a background of non-zero values (results not shown).

These two measures (weighted average and weighted variance), calculated with the measured Sr values, were tested for deviation from the null hypothesis of random distribution of Sr concentration in the grid by a Monte Carlo randomization, which consisted in shifting the position of the point of application relative to the grid of measured concentration values. Each species was treated separately. Under the null hypothesis, any distribution of Sr values in the grid is equally probable (under the constraints of a given plant distribution in the grid) and the expected distribution of each of the two measures can thus be generated by randomization of the point of application in the grid, assuming periodic boundary condition (toroidal surface). In the randomization tests, all plots of the same depth of Sr application were analysed together. However, the randomization was done within each plot separately. A total of 500 randomizations (positional shifts done independently in each grid) were made to generate a distribution of values of weighted average and weighted variance under the null hypothesis. One-tailed tests (testing only for the aggregation of high values) were used for the weighted average; two-tailed tests were used for the variance. Negative deviation of the weighted average was taken as an indication of high Sr values close to the point of application; negative deviation of the weighted variance was taken as an indication of a 'circle' of high Sr values around the point of application; positive deviation of the weighted variance was taken as an indication of a moderately high concentration very close to the point of application.

The null hypotheses of equality of distance of maximum concentration across species and application depths were tested by a repeated measurements ANOVA (species as the within-factor) of plot-wise weighted averages.

The analyses were done on untransformed values of measured Sr concentrations; these represent the background Sr levels plus the increase due to root absorption from the experimental application. The effect of the background values did not seem to affect the results; if the same set of analyses was run on the values reduced by subtracting the 95% upper confidence limit of the background Sr level (calculated from the sterile plants, negative values replaced by zero), very similar statistical results were obtained (data not shown).

Results

Sr concentrations in individual plant samples differed by almost two orders of magnitude; whereas most values lay in the range of 0.5–5 ppm (i.e. close to background values), there were Sr values as high as 80 ppm (Fig. 2). Tests among species and application depths showed that differences in weighted averages between application depths were marginally significant using repeated measurements ANOVA ($F = 3.72$, d.f. = 2, 8, $P = 0.072$). Differences between species were highly significant ($F = 7.15$, d.f. = 3, 24, $P = 0.001$); interaction was not significant ($F = 1.87$, d.f. = 6, 24, $P = 0.128$). In separate tests of each species, average Sr concentration decreased with the depth of application in all species except *Nardus*; this indicated that in these species the uptake was lower from deeper soil layers (tests for differences in means between depths: *Deschampsia*: $F = 4.2$, d.f. = 2, 9, $P = 0.051$, *Festuca*:

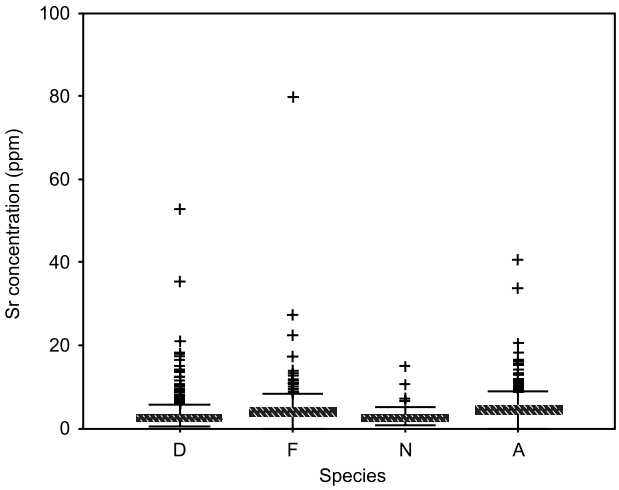


Fig. 2 Distribution of Sr concentrations in individual species. D, *Deschampsia* (n = 786); F, *Festuca* (n = 431); N, *Nardus* (n = 171); A, *Anthoxanthum* (n = 685). All treatments and all plots are pooled. Boxes cover 50% of all values (interquartile range); lines cover values closer than 1.5 box length. Crosses indicate observations > 1.5 box lengths from the median.

F = 4.7, d.f. = 2, 9, P = 0.040, *Nardus*: F = 3.0, d.f. = 2, 8, P = 0.106, *Anthoxanthum*: F = 7.2, d.f. = 2, 9, P = 0.013). The same was true for number of extreme values per grid (data not shown). Plot #3 (application depth 12 cm) was exceptional, since mean Sr concentration in all species was higher than in other plots with the same application depth.

Spatial distribution of high Sr values was quite pronounced (see Fig. 3 for an example). The Sr concentration in *Deschampsia*, *Festuca* and *Anthoxanthum* decreased with the horizontal distance from the application point (Fig. 4). This decrease was strongest in plots where the tracer was applied to surface layers of the soil and this decrease is significant using randomization tests (Table 1). This indicates that in these three species, the absorption zones close to the soil surface are always attached to nearby shoots. Weighted variances were higher than expected, indicating clustering of high Sr values close to the application point (cf. Fig. 1). In *Nardus*, there was no clear pattern of distribution of high values relative to the application point.

With greater application depths, the clustering of high values became weaker in *Anthoxanthum* and *Festuca*. For the application depth of 6 cm, it was significant for *Anthoxanthum* and *Deschampsia*; in *Anthoxanthum*, also the weighted variance was (marginally) significant, indicating strong clustering of high values around the application point. For the application depth of 12 cm it was still significant for *Deschampsia* and non-significant for the other species. This indicates that the horizontal range of the absorption zone widens with increasing depth in *Festuca* (and, to a lesser degree, in *Anthoxanthum*, where the widening takes place in greater depths) while it remains rather narrow in *Deschampsia*. Weighted

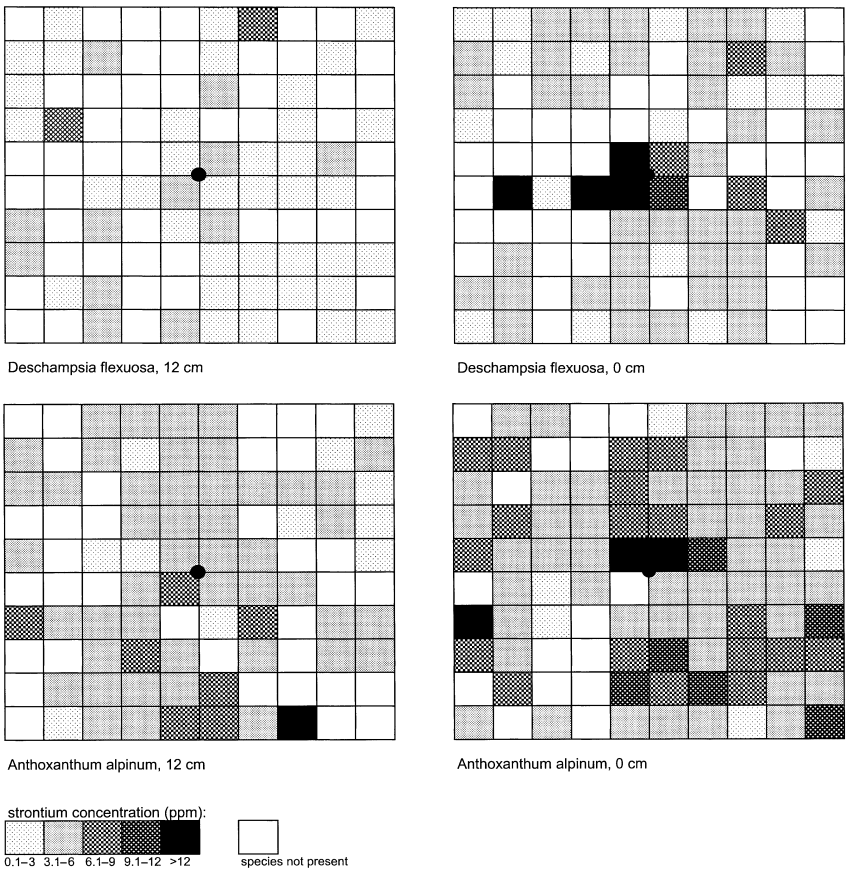


Fig. 3 Examples of spatial distribution of Sr concentrations in *Anthoxanthum* and *Deschampsia* in two plots. One plot with Sr application to 0 cm and one plot with Sr application to 12 cm are shown. Black dots indicate points of Sr application.

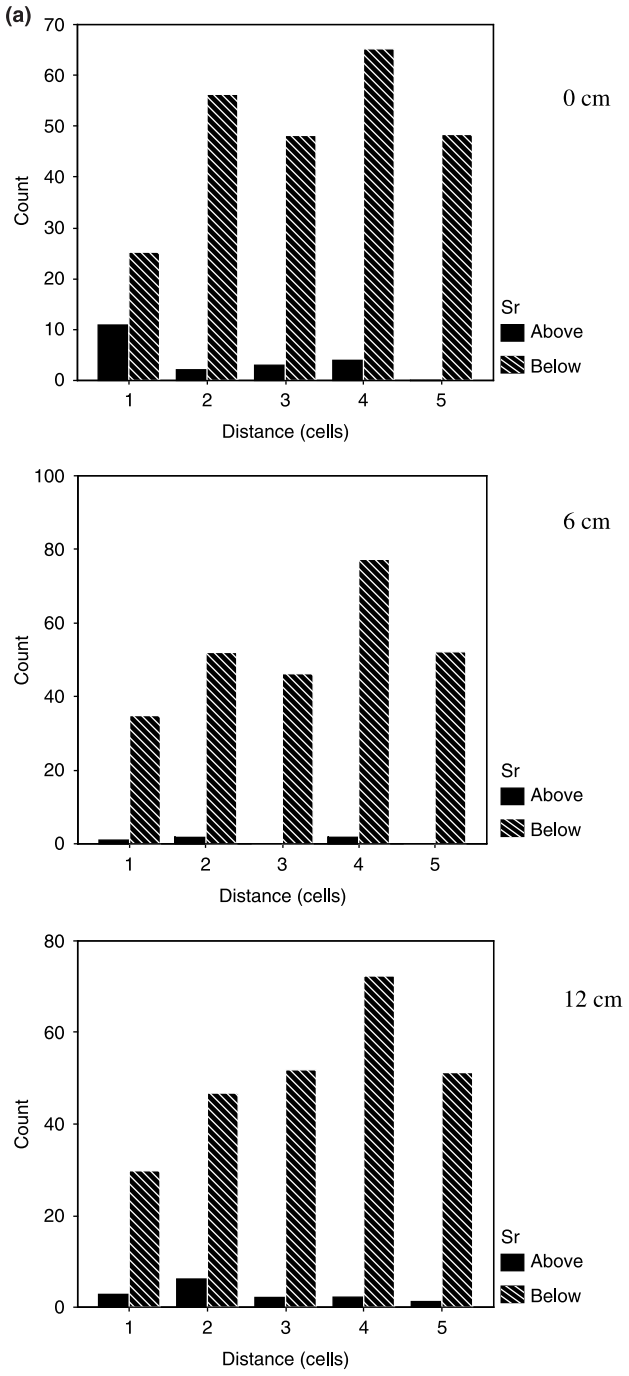


Fig. 4 Distribution of extreme Sr concentrations as a function of distance to the point of application. Above, number of cells with Sr concentration in biomass greater than 95% quantile of the background values for the given species; below, Number of cells with Sr concentration in biomass smaller than 95% quantile of the background values for the given species. Distance classes: 1, cells 0–1 cell from the application point; 2, cells 1–2 cells from the application point, etc.; one cell equals 3.3 cm. (a) *Deschampsia*; (b) *Festuca*; (c) *Nardus*; (d) *Anthoxanthum*. All plots within one treatment are pooled.

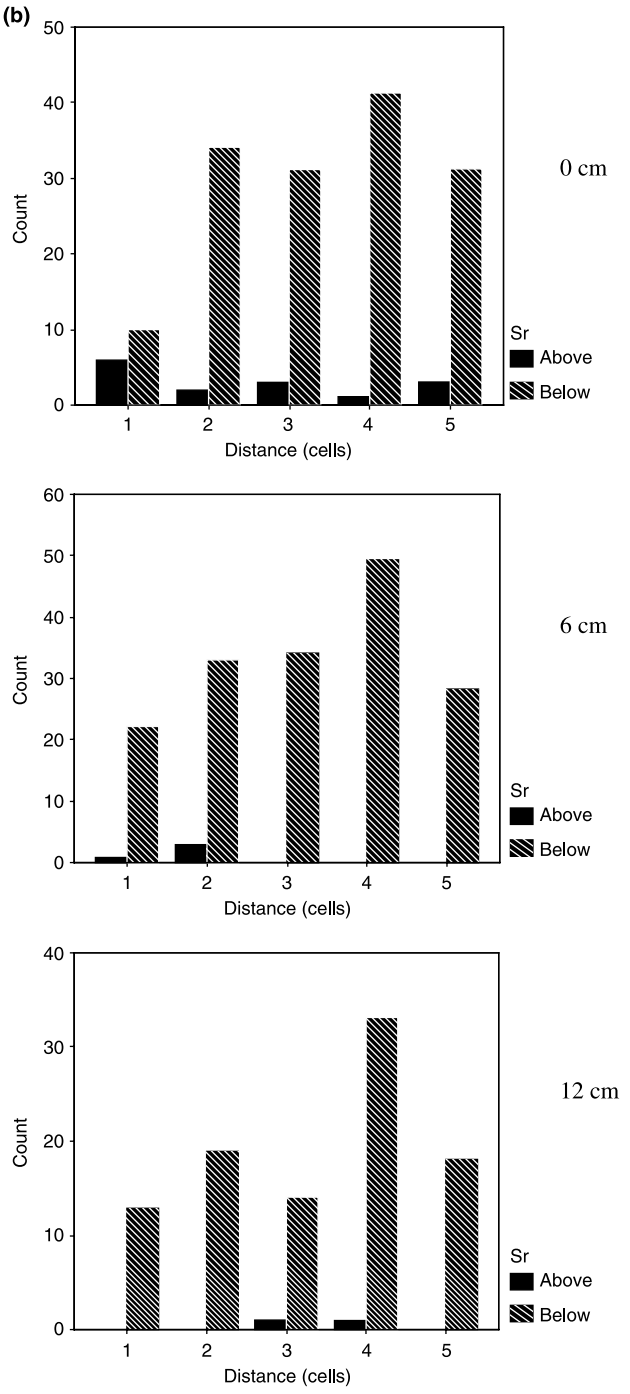
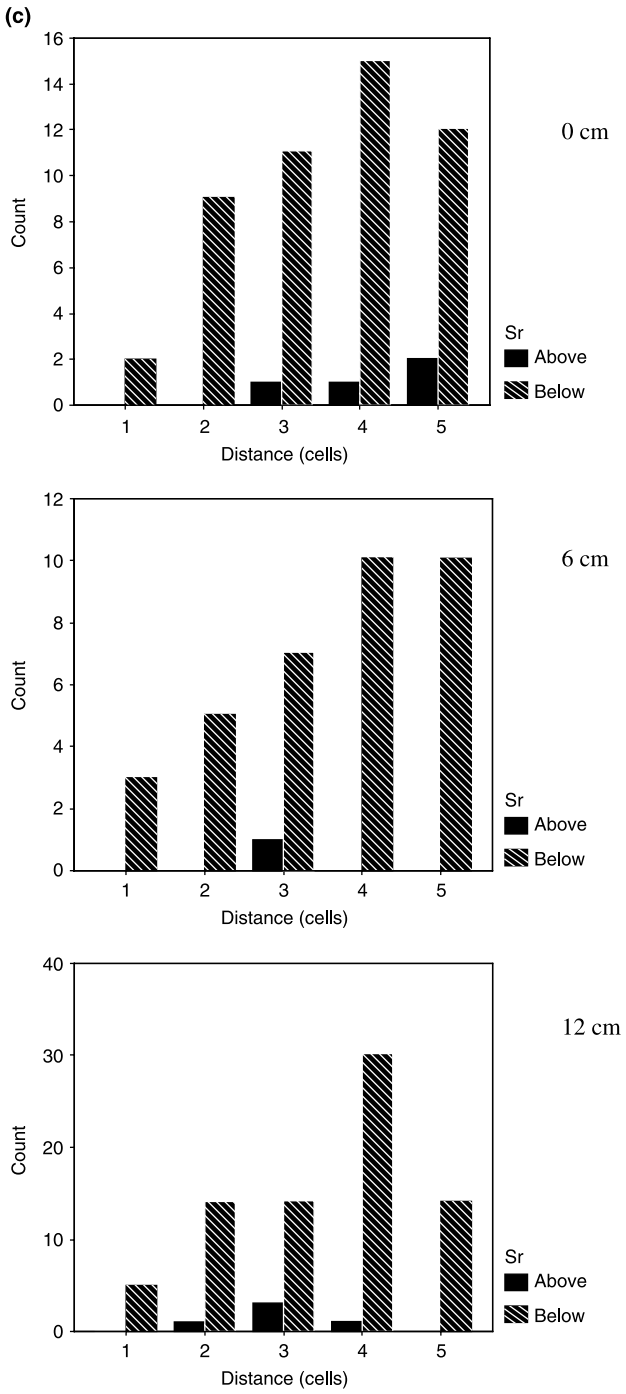


Fig. 4 *Continued*

variance was never significantly lower than expected in these three species. This indicates that the distribution of high Sr values in plant biomass was never circular around the application point (as in Fig. 1c). Instead, it peaked in individual plants at variable distance from the application point (Fig. 1a,b).

Nardus showed a very different pattern from the three remaining species since there is no indication of clustering of high-Sr values around the application point, irrespective of



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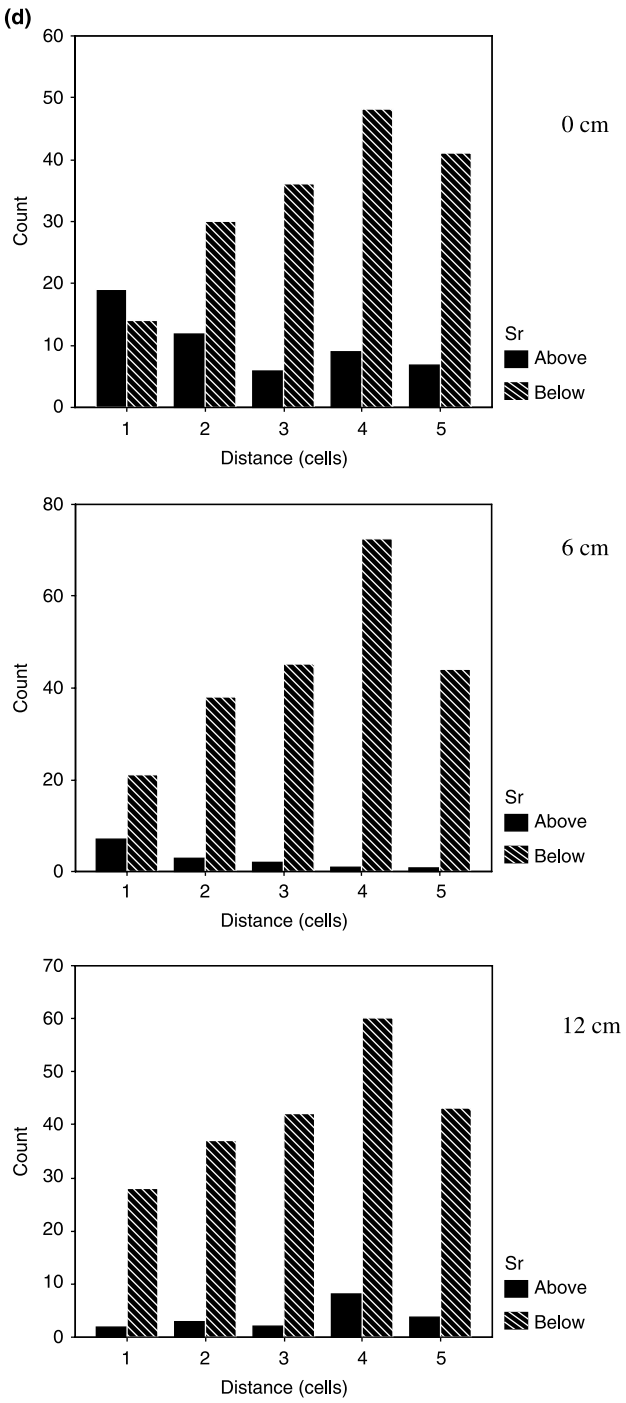

Fig. 4 *Continued*

application depth. Also, neither its concentration-weighted average distance nor weighted variance changed with the application depth.

Discussion

The results confirm earlier findings that species differ in the proportion of their absorbing roots that are in the upper and deeper soil layers (Veresoglou & Fitter, 1984; Fitter, 1986; Mamolos *et al.*, 1995). In three species (*Deschampsia*, *Festuca* and *Anthoxanthum*), but not in *Nardus*, the amount of Sr absorbed decreased with increasing application depth (Figs 2 and 4). This difference is probably due to a change in the mean density of absorbing roots with depth, and corresponds well with data on species-specific root distribution along the

Table 1 Monte Carlo tests of non-random distribution of high strontium (Sr) values in individual cells

Species	Depth	Weighted average true value	Significance	Variance true value	Significance
Deschampsia	0	3.00	**0.00**	2.64	**0.99**
Deschampsia	6	3.31	**0.02**	2.51	0.93
Deschampsia	12	3.32	**0.05**	2.39	0.68
Festuca	0	2.59	**0.00**	3.18	**0.99**
Festuca	6	3.46	0.16	2.38	0.64
Festuca	12	3.56	0.50	2.09	0.13
Nardus	0	3.66	0.74	2.16	0.39
Nardus	6	3.48	0.28	1.72	0.23
Nardus	12	3.58	0.49	1.92	0.16
Anthoxanthum	0	2.88	**0.00**	2.71	**0.98**
Anthoxanthum	6	3.34	**0.00**	2.55	0.97
Anthoxanthum	12	3.51	0.32	2.41	0.71

In each test, the weighted average and variance around this average are used as measures of high values around the point of application; their true value is compared with the distribution of values obtained by randomly shifting the grids. Note that the tests of weighted average and variance within one species are not independent, since they are based on one set of randomizations. Weighted average and variance are expressed using number of cells as units; they should be multiplied by 3.3 to yield cm. Randomization test is done separately for each species and each application depth. Values significant at $\alpha = 0.05$ (one tail for average and two tail for variance) are shown in bold.

Table 2 Shape of the of strontium (Sr) absorption zone of a shoot and the structure of the rhizome system

	Rhizomes long	Rhizomes short
Absorption zone widens with increasing depth (conical shape)	*Festuca* (transport by roots and possibly rhizomes)	*Anthoxanthum* (transport by roots and possibly short rhizomes)
Absorption zone does not widen with increasing depth (cylindrical shape)	*Deschampsia* (transport mainly by roots?)	*Nardus* (transport by roots)

Data on rhizome lengths from Pecháčková *et al*. (1999) and unpublished data by S. Pecháčková and R. Wildová.

depth gradient (Pecháčková, unpublished data). These findings might not be consistent at other times in the growing season, since the root activity has been shown to shift to deeper layers through the growing season (Fitter, 1986). The experiment also cannot distinguish direct transport by roots and rhizomes, passive Sr transport in the soil, and Sr transport by mycorrhizal hyphae, which can transport some ions over distances longer than 3 cm (Johansen *et al*., 1992; Thingstrup *et al*., 2000). However, hyphal transport may be considered to extend the absorption zone by the root and can thus be included into a generalized concept of an absorption zone.

Spatial analysis of shapes and positions of root absorption zones revealed that the species differed in the horizontal distance over which Sr was absorbed at each depth. As a rule, the horizontal distance of points of maximum Sr concentration in the plant from the application point increased with increasing depth; the increase was highest in *Festuca*, smaller in *Anthoxanthum* and non-significant in *Deschampsia* and *Nardus* (Fig. 4).

The species-specific variation is attributable to differences in architecture of the root and rhizome systems of the four species (Pecháčková, unpublished data). A plant may reach a horizontally and vertically distant nutrient-rich patch by two very different morphologies: by inclined growth of roots; or roots that grow vertically from horizontal rhizomes. In the former case the root system is formed *after* the above-ground part (ramet) has established at its current position, whereas in the latter case the rhizome with its associated roots is as a rule formed *before* the ramet and occurs mainly in clonal plants with persistent rhizome structures. *Anthoxanthum* possesses short rhizomes only and it is likely that most of the Sr is acquired by root transport. By contrast, *Deschampsia* and *Festuca* possess long rhizomes, but they have different Sr uptake patterns. While the spatial range of *Festuca* widens with increasing depth, there is no similar increase in *Deschampsia.* This implies that *Deschampsia* is not able to use the rhizome system to transport Sr; *Festuca* may be able to do so, but horizontal transport entirely due to inclined roots also cannot be excluded (Table 2). The low importance of the rhizome system

in translocation is also indicated by the very low horizontal transport when Sr was applied to the surface. Uptake of Sr in the surface layer far from the position of the ramet would require extensive transport along the rhizome.

The peculiar behaviour of *Nardus* is also due to distinct features of its below-ground organs. It has no extensive rhizome system that would allow it to cross longer horizontal distances. It has two types of roots: thick and long roots that often grow almost vertically; and short roots in the surface layer. Owing to these structures it is the only species out of the four studied here where ramet presence at a microsite is correlated with root presence in deeper layers exactly below the same microsite (Pecháčková *et al.*, 1999). The long vertical roots are likely to account for the uptake deep in the soil directly below the ramet; indeed, really high Sr concentrations in *Nardus* occurred only in the plots where Sr was applied at 12 cm depth. Short shallow roots absorb from the surface and enable the plant to get nutrients from a larger radius in the surface layer, but this uptake is never as great as the uptake by the thick roots from the greater depth. By contrast to the other three species, the amount of short surface roots is lower than the amount of long roots going deep into the soil; this is likely to account for the rather low absorption from the surface relative to that from deeper layers in *Nardus*.

The present data also show that the spatial range of below-ground interactions is much larger than the spatial range of above-ground interactions. Since the current study shows that the Sr root uptake may occur at a distance of 10–15 cm from the ramet, two ramets at a distance of 20–30 cm may interact by absorbing simultaneously from a given soil microsite. Above ground, the prime resource is incident light; two ramets interact if they change the light environment of each other (Smith *et al.*, 1990). This effect is much more restricted in space. There was no identifiable correlation between light levels below the canopy (either red light or the red/far red ratio) and the above-ground ramet presence over distances larger than 3.3 cm at the field site (Skálová *et al.*, 1999), almost an order of magnitude less than the absorption range detected here. In the soil environment therefore, plant individuals may interact with a much higher number of neighbours than above ground. The spatial extent of absorption zones has to be compared with the scale of above-ground structure at the same locality. Earlier studies have shown one of the studied species has clumps extending over more than 7(−10) cm in diameter (Herben *et al.*, 1995). This means that the spatial extent of roots permits most of the patches below ground to be reached by any of the species, and means that the fine-scale pattern observed above ground is therefore of much less importance for species interactions that often assumed. This may also explain rather large interaction ranges found in several grassland species (McLellan *et al.*, 1997); the same study also showed that both close and distant plants may be important. It is very likely that below-ground interactions are responsible for the latter interactions. This implies that competition above ground and below ground cannot be represented using one neighbourhood size.

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