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Root morphological plasticity and nitrogen uptake of 59 plant species from the Great Plains grasslands, U.S.A.

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Abstract

We investigated 59 plant species from the Great Plains grasslands with the following objectives: (1) Determine the ability of individual plant species to: (a) redirect root surface area growth to patches with high N and P concentrations; and (b) alter their root:shoot ratio in response to a non-uniform distribution of soil N and P. (2) Determine how a patchy distribution of soil N and P within a plant's rooting zone affects biomass, total root surface area, N uptake, %N in plant tissue, and N uptake per unit of root surface area. Results showed a diversity of responses with some important common patterns. (1) Root responses (defined as total RSA, allocation of RSA, and R:S ratio) were twice as prevalent as whole plant responses (defined as total N uptake, %N in plant tissue, and plant biomass). (2) The percentage of species with the ability to allocate their RSA to nutrient rich patches was 9 times higher in forbs than in grasses, but there were proportionally more grasses than forbs that increased their R:S ratios in response to nutrient patchiness. (4) The proportions of late successional forbs that responded to nutrient patchiness was higher than that of mid successional ones, but the size of the response was substantially larger in the latter. (4) We found a very weak coupling between root plasticity and plant performance. (5) Our results tend to suggest that: (a) most plants have sufficient plasticity in root system development to track the scale of soil nutrient heterogeneity and thus show similar performance regardless of the degree of nutrient patchiness; and (b) the benefits of root plasticity may be more critical for subdominant species as a general adaptation to compete for soil nutrients in mixed plant communities regardless of the extent of soil nutrient heterogeneity.

Wir haben 59 Pflanzenarten der Prärie in den Great Plains mit folgenden Zielen untersucht: (1) Feststellung der Fähigkeiten der einzelnen Pflanzenart in Bezug auf: (a) die Steuerung des Wurzelwachstums in den oberflächennahen Bodenschichten in Bereiche mit hohem N- and P-Gehalt; und (b) Veränderung des Verhältnisses Wurzelmasse: Pflanzenmasse als Reaktion auf eine uneinheitliche Verteilung des N und P im Boden. (2) Festzustellen, wie die Verteilung der verschiedenen Zonen des N- und P-Gehaltes innerhalb der Wurzelzone einer Pflanze sich auf die Biomasse, die gesamte durchwurzelte Fläche , die N-Aufnahme, den N-Gehalt (%) in der Pflanzenmembran und die N-Aufnahme pro Einheit der Wurzeloberfläche auswirkt. Die Ergebnisse zeigten eine Vielfalt an Reaktionen mit einigen wichtigen allgemeinen Mustern. (1) Wurzelreaktionen (definiert als Total RSA, Lokalisierung der RSA und R:S ratio) waren doppelt so ausgeprägt wie die Reaktionen der gesamten Pflanze (definiert als Gesamt N-Aufnahme, N-Gehalt (%) in der Pflanzenmembran und Biomasse der Pflanze). (2) Die Prozentzahl der Arten mit der Fähigkeit, ihre

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RSA in nährstoffreiche Bodenzonen zu dirigieren war bei Blattpflanzen neunmal höher als bei Gräsern, aber es waren propotional mehr Gräser als Blattpflanzen,die ihr R:S ratio als Reaktion auf die Nährstoffverteilung veränderten. (3) Die Reaktion derjenigen Blattpflanzen, die sich erst später ansiedeln war größser als die der Mittelansiedler, wobei die Anzahl der Reaktionen unter den letzteren überwog. (4) Wir stellten eine sehr schwache Verknüpfung zwischen Wurzelflexibilität und der Leistung der Pflanze fest. (5) Unsere Ergebnisse lassen folgende Schlüsse zu: (a) die meisten Pflanzen haben eine ausreichende Flexibilität in ihrer Wurzelsystementwicklung um Nährstoffuneinheitlichkeiten im Boden zu begegnen und zeigen deshalb unveränderte Leistungsfähigkeit unabhängig von der Nährstoffverteilung; und (b) der Nutzen der Wurzelflexibilität kann für nichtdominante Arten entscheidender sein, da in gemischten Pflanzenpopulationen generell die einzelnen Arten in Konkurrenz um die Nährstoff stehen unabhängig von der inhomogenen Nährstoffverteilung.

Key words: Great Plains grasslands – N uptake – root:shoot ratio – root foraging – root plasticity – root surface area

Introduction

Soil nutrients exist in complex spatial patterns because of variations in the rate of organic matter decomposition, amount of microbial activity, temperature, moisture availability, and nutrient concentrations. The result of this complexity is a degree of heterogeneity that can range from a scale of millimeters to the landscape level (Caldwell et al. 1996, Robertson et al. 1997). While heterogeneity at scales larger than the plants rooting area can affect plant diversity and biomass distribution at the landscape level (Tilman 1988, Palmer 1992), it is fine scale heterogeneity that has the greatest impact in belowground interactions among plants, and thus plant competition (Casper &Jackson 1997). Campbell et al. (1991) have gone so far as to suggest that small scale heterogeneity is more important than average soil nutrients in determining competitive outcomes.

Plants can respond to soil nutrient heterogeneity through root proliferation in nutrient rich patches (morphological plasticity) and/or by increases in the uptake kinetics of roots exposed to high nutrient concentrations (physiological plasticity) (Caldwell 1994, Robinson 1994, van Vuuren et al. 1996). A series of studies in recent years have attempted to empirically determine how root plasticity affects plant performance and composition in patchy environments, and how the spatial distribution of nutrients themselves alter biomass allocation to roots and root architecture (Campbell et al. 1991, Caldwell et al. 1992, Gross et al. 1993, Van de Vijver 1993, Larigauderie & Richards 1994, Bilbrough & Caldwell 1995, Caldwell et al. 1996, van Vuuren et al. 1996, Fransen et al. 1998). Reviews by Fitter (1994), Robinson (1994), and Reynolds & D'Antonio (1996), however, have pointed out the very limited number of species for which data is available and the overrepresentation of crop species in these data sets. Grime et al. (1991) and Campbell et al. (1991) have conducted some of the most extensive studies involving native grasses and forbs but mostly with species common to the UK. Consequently, for many of the species from the Great Plains grasslands there is a dearth of data on root plasticity and more broadly on the whole question of the morphological and physiological responses of plants subjected to an heterogeneous soil nutrient environment.

Empirical and theoretical studies by Biondini & Grygiel (1994) and Jackson & Caldwell (1996), among others, have highlighted the important role that small scale soil nutrient heterogeneity and root plasticity play in both nutrient acquisition and plant competition. Therefore, realistic simulations of plant species growth, competition, diversity, and composition require models with spatially explicit mechanisms for root growth, plasticity, and nutrient uptake. This study was designed to provide some of the pertinent information required by such models by investigating 59 plant species from the Great Plains grasslands with the following objectives:

1. Determine the ability of individual plant species to: (a) redirect root surface area growth to patches with high nitrogen (N) and phosphorus (P) concentrations; and (b) alter their root:shoot ratio in response to a non-uniform distribution of soil N and P.
2. Determine how a patchy distribution of soil N and P within a plant's rooting zone affects biomass, total root surface area, N uptake, % N in plant tissue, and N uptake per unit of root surface area.

Materials and methods

Experimental design

The experiment was conducted in the greenhouse and organized as a completely randomized design. Fifty nine species (Tab. 1) were used in 2 treatments, with 5 replications per treatment. Treatment 1 consisted of an even distribution of all major plant nutrients, while in treatment 2, N and P were applied in a non-uniform (patchy) pattern with the rest of the macro- and micronutrients distributed evenly. Thirty nine of the species used in this study were dicotyledonous hemicryptophytes, 3 dicotyledonous chamaephytes, and 17 monocotyledonous hemicryptophytes. The species in Table 1 were further classified into mid and late successional ones. The subdivision was made on two bases: (**a**) years during secondary succession when the species in question are more abundant: 1–10 years for mid and beyond 10 years for late successional species (Kuchler 1964); and (**b**) relative growth rate (RGR). Species classified as mid succession dicotyledonous have a higher average RGR than late successional ones: 0.12 $g \cdot g^{-1} \cdot d^{-1}$ vs. 0.09 $g \cdot g^{-1} \cdot d^{-1}$ ($P = 0.027$). For monocotyledonous the corresponding RGR values for mid and late successional species are 0.13 $g \cdot g^{-1} \cdot d^{-1}$ vs. 0.10 $g \cdot g^{-1} \cdot d^{-1}$ ($P = 0.046$).

Plants were grown in individual pots (1 plant per pot) utilizing pure silica sand as a growth medium to guarantee total control over the nutrient supply. Pots had a diameter of 21 cm with a height of 20.5 cm and were filled to 19 centimeters. Two horizontal plastic grid panels (0.5 cm^2 grid size) were located at 10 and 15 cm from the base of each pot to keep the roots in place

Table 1. List of species used in the experiment. Nomenclature and authorities follows the Great Plains Flora Association (1986).

Dicotyledonous (Forbs and Shrubs)		**Monocotyledonous (Grasses)**	
(shrubs and/or legumes are identified in brackets)		**Cool Season (C_3)**	**Warm Season Grasses (C_4)**
Mid Successional Species	**Late Successional Species**	**Mid Successional Species**	**Mid Successional Species**
Achillea millefolium L.	*Allium stellatum* Ker.	*Agropyron cristatum* (L.) Gaertn.	*Sporobolus cryptandrus* (Torr.) A. Gray
Artemisia dracunculus L.	*Amorpha canescens* Pursh [shrub, legume]	*Bromus inermis* Leyss.	**Late Successional Species**
Artemisia frigida Willd.	*Anaphalis margaritacea* (L.) Benth. & Hook.	*Hordeum jubatum* L.	*Andropogon gerardii* Vitman
Asclepias verticillata L.	*Artemisia tridentata* Nutt. [shrub]	**Late Successional Species**	*Bouteloua curtipendula* (Michx.) Torr.
Cirsium arvense L.	*Aster ericoides* L.	*Agropyron spicatum* (Pursh) Scribn. & Sm.	*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths
Erigeron philadelphicus L.	*Astragalus canadensis* L. [legume]	*Elymus canadensis* L.	*Calamovilfa longifolia* (Hook) Scribn.
Gaillardia aristata Pursh.	*Campanula rotundifolia* L.	*Koeleria cristata* (Lam.) Beauv.	*Panicum virgatum* L.
	Chrysopsis villosa (Pursh) Nutt.	*Poa pratensis* L.	*Schizachyrium scoparium* (Michx.) Nash-Gould
Melilotus officinalis L. [legume]	*Coreopsis lanceolata* L.	*Stipa comata* Trin. & Rupr.	*Sorghastrum nutans* L.
Oenothera biennis L.	*Dalea purpurea* Vent. [legume]	*Stipa viridula* Trin.	
Ratibida columnifera (Nutt.) Woot. & Standl.	*Galium boreale* L.		
Rudbeckia hirta L.	*Geum triflorum* Pursh		
Solidago missouriensis Nutt.	*Grindelia squarrosa* Pursh.		
Tragopogon dubius Scop.	*Helianthus rigidus* (Cass.) Desf.		
Verbena stricta Vent.	*Helianthus maximiliani* Schrad.		
Vicia americana Muhl. ex Willd. [legume]	*Heuchera richardsonii* R. Br.		
	Liatris punctata Hook.		
	Linum perenne L.		
	Lupinus perennis S. Wats. [legume]		
	Oxytropis lambertii Pursh. [legume]		
	Potentilla arguta Pursh.		
	Psoralea esculenta Pursh. [legume]		
	Rosa arkansana Porter. [shrub]		
	Solidago rigida L.		
	Sphaeralcea coccinea (Pursh) Rydb.		
	Taraxacum officinale Weber.		
	Viola pedatifida G. Don.		

during harvest after the sand had been removed. To compensate for variability of conditions within the greenhouse, the pots were randomly located within a 20 × 3 m bench. The temperature of the greenhouse ranged between 25–30 °C. Day length was maintained at 16 hours for the duration of the study, with the light being supplied by Son Agro 430W High Pressure Sodium lamps configured to produce 5000 lux at plant height.

Seedlings were germinated in flat trays, using pure silica sand as a medium, and then transplanted to the experimental pots. Some of the species used in this experiment required stratification and/or scarification of seeds for germination. Stratification is an artificial cold period mimicking winter conditions, and was implemented by mixing seeds and sand into Ziploc bags, moistening the sand, and storing it in a refrigerator for a 2 month period. Scarification involves abrasion (or some other breach) of the seed coat to promote seedling growth. Scarification was done by slightly abrading the seed coats with sandpaper prior to placement of the seed in the flat trays.

The design of nutrient treatments followed the recommendation of Robinson (1994). Robinson (1994), after an extensive review of published experiments, recommended that control treatments be uniformly nutrient rich, since otherwise there would be no way of empirically determining how plants subjected to a patchy distribution of soil nutrients would perform relative to plants grown under minimal nutrient constraints. Consequently, the even N and P treatment (Treatment 1) was implemented by applying 30 ppm of N (NO_3^{-1}), 10 ppm of P ($H_2PO_4^{-1}$), and macro and micronutrients from a 10% strength Rorison solution (8 ppm Ca^{2+}, 2.4 ppm Mg^{2+}, 7.8 ppm K^{+}, 0.3 ppm Fe^{2+}, 0.05 ppm Mn^{2+}, 0.05 ppm B^{3+}, 0.01 ppm Mo^{+6}, 0.01 ppm Zn^{2+}, and 0.01 ppm Cu^{2+}) evenly on both the left and right side of the experimental pots. In the patchy N and P treatment (Treatment 2), the same N and P levels were applied to the right side of the pot while the left side received 5 ppm of N and 1 ppm of P. As in Treatment 1, the rest of the macro- and micronutrients were applied evenly to both sides of the pot using a 10% strength Rorison solution. The pH of the solution was maintained between 5.5 and 6.0.

To create localized nutrient patches we used an experimental set-up based on the one developed by Campbell & Grime (1989). Like in Campbell & Grime (1989) nutrients were applied using an automated drip irrigation system. According to Campbell & Grime (1989), by dripping the nutrient solution at a constant rate through a cylindrical, free-draining container, uniform patches of nutrients can be constantly maintained at the desired nutrient concentration. Our design, however, was sufficiently different from the Campbell & Grime (1989) one that further testing was required to determine its effectiveness in both creating and maintaining nutrient patches. In the Campbell & Grime (1989) experiment the nutrient patches were maintained for only 14 days, the soil column was 2.5 cm in depth, and nutrients were applied continuously at a rate of 20 ml · hr^{-1} per emitter. Our design introduced 3 major modifications: (**1**) the length of the experiment was extended so nutrient patches had to be maintained for at least 60 days; (**2**) the soil column was 19 cm in depth; and (**3**) nutrients were to be applied every day but with the dripping lasting only until the entire soil solution was replaced. The last item was a practical constraint imposed by the size of our experiment. With 590 pots, using the Campbell & Grime (1989) design of continuous dripping for 60 days, with 4 emitters per pot, would have required about 68.000 l of nutrient solutions. Under continuous dripping, nutrient patches can be maintained because lateral diffusion of nutrients is overcome by vertical mass flow (Campbell 1985). The question raised by discontinuous dripping is whether diffusion can be strong enough to undo nutrient patchiness during the non dripping period. The average linear distance of diffusive movement of an ion with time, under water saturation conditions, is approximately equal to $\sqrt{2D_e t}$ where D_e is the diffusion rate and t is time (Barber 1984). For N and P which have average diffusion rates of 2.5×10^{-6} $cm^2 \cdot s^{-1}$ and 2.3×10^{-9} $cm^2 \cdot s^{-1}$ respectively, the maximum expected movement per day would amount only to about 0.66 cm for N and 0.02 cm for P. In theory, therefore, patches could be maintained under a daily dripping regime designed to only replace the soil solution. To test whether this would hold under experimental conditions we built a testing bed that consisted of a 60 × 60 × 30 cm plastic container equipped with 36 emitters located at 10 cm intervals (Fig. 1). The emitters were connected to 2 Dosatron injectors with the dripping rate set at 1.9 l · hr^{-1} (Fig. 1). We used as a medium pure, fine grain, silica sand with no plants. The objective of the design was to determine whether we could generate and maintain a regular chessboard pattern of nutrient/no-nutrient (an extreme case of patchiness) with a discontinuous dripping regime. We conducted two experiments. The first experiment was designed to visually determine if patchiness could be maintained for 60 days to a soil depth of 20 cm. For that purpose one of the injectors was set to deliver a fluorescent water soluble red dye (FWT Red dye manufactured by Formulabs) while the other delivered only water. Dripping was applied daily for 30 minutes. As shown in Figure 1, the experiment resulted in a regular chessboard pattern of red surfaces and clear surfaces to a depth of 20 cm. The second experiment was designed to test whether actual N patchiness could be maintained for 60 days. For this purpose one injector was

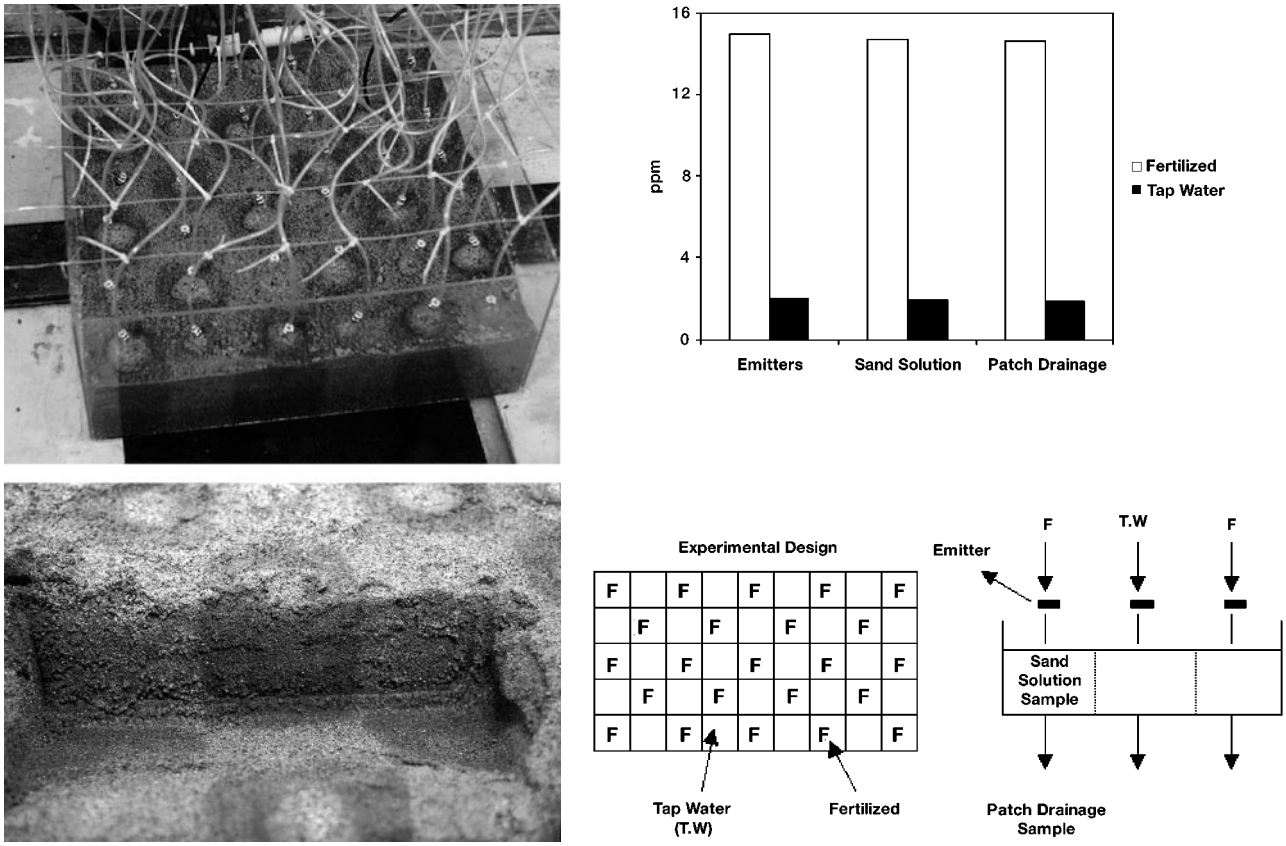

Fig. 1. Testing bed results. The pictures on the left shows the testing bed itself and the chessboard pattern from the fluorescent water soluble red dye (dark squares) experiment. The graphs on the right show the experimental design and summary results from the $NaNO_3$ dripping experiment. See text for details.

set up to deliver $NaNO_3$ at concentrations of 15 ppm of N while the other delivered tap water (0.95 ppm of N) (Fig. 1). We chose N for a test due to its high diffusion rate. We dripped the solutions for 30 minutes per day (the time required to replace the soil solution) for 60 consecutive days. We collected samples every 3 days from both the emitters and drainage holes and every 10 days from the actual soil solution. Like the first one, this experiment also generates a regular chessboard pattern of N concentrations (Fig. 1). We are therefore very confident that this dripping design can generate and maintain nutrient patches.

The actual experimental design we settle for consisted of 2 Dosatron injectors connected to 4 emitters per pot that delivered the appropriate nutrient solutions. Nutrients in each pot were dripped from 4 microtubes (4 mm inside diameter) placed at the four corners of a 10 cm × 10 cm square, with the seedlings placed directly in the center of the square. In Treatment 1, all 4 microtubes delivered the high nutrient solution (30 ppm of N, 10 ppm P), while in Treatment 2, the 2 microtubes located in the right side of the pot delivered the high nutrient solution while the 2 in the left side of the pot delivered the low nutrient solution (5 ppm of N and 1 ppm of P). The entire system was regulated by a programmable Rain Bird Controller with dripping applied daily for 30 minutes to totally replace the soil solution.

Data collection

Plants were harvested after 60–80 days of growth (depending on the plant growth rate). Fast growing plants were harvested early while slow growing plants were harvested later. At harvest time, the sand was removed from each pot by washing it out through slits cut into the sides of the pots. The grids held the roots in place as the sand was removed. Plant biomass was divided into the above- and belowground component, with the roots further separated into the portions from the left and right side of the pot. Roots were floated in water, digitized with a high resolution Hewlett Packard scanner, and the images analyzed for total root surface area with the use of a Delta-T Scan imaging system (Delta-T Devices Ltd). All biomass components were then dried at 60 °C and weighed. Above- and belowground samples from each plant and replication were analyzed for N content using the Kjeldahl method (Nelson & Sommers 1980).

Statistical Analysis

Differences in root surface area between the right and left hand side of the pot were tested for each species and treatment using a pair sample t-test employing a null hypothesis of 0.5:0.5 (Snedecor & Cochran 1967).

For each species, treatment differences in root:shoot ratio, biomass (g), total root surface area (m^2), N uptake (gN), %N in plant tissue, and N uptake per unit of RSA ($gN \cdot m^{-2}$) were tested using an unequal variance t-test (Snedecor & Cochran 1967). N uptake, %N in plant tissue, and N uptake per unit of root surface area were calculated as:

$$N\ uptake\ (gN) = \frac{AGB*\%N\ AGB + BGB*\%N\ BGB}{100}$$

$$\%N = \frac{N\ uptake}{AGB+BGB} * 100$$

$$N\ uptake\ per\ unit\ per\ RSA\left(\frac{gN}{m^2}\right) = \frac{N\ uptake}{Total\ RSA}$$

$$Total\ RSA = RSA\ in\ the\ left\ side\ of\ the\ pot + RSA\ in\ the\ right\ side\ of\ the\ pot$$

where AGB and BGB are above- and belowground biomass (g), and %N AGB and %N BGB are the percentage of N in above- and belowground biomass tissue.

Results

Allocation of root surface area

Twenty one species, 19 dicotyledonous hemicryptophytes (from now on described as forbs), 1 dicotyledonous chamaephytes (from now on described as shrubs), and 1 monocotyledonous hemicryptophytes (from now on described as grasses), showed a significant change in the allocation of their root surface area (RSA) as a result of a patchy distribution of soil N and P (Tab. 2). In all of them, RSA was higher in the right side of the experimental pot (high nutrient patch) than in the left side (low nutrient patch) (Tab. 2). There were, however, substantial differences among species with different life forms and successional status in the magnitude of the change in RSA allocation patterns. The increase in RSA in the nutrient rich patch visa vis

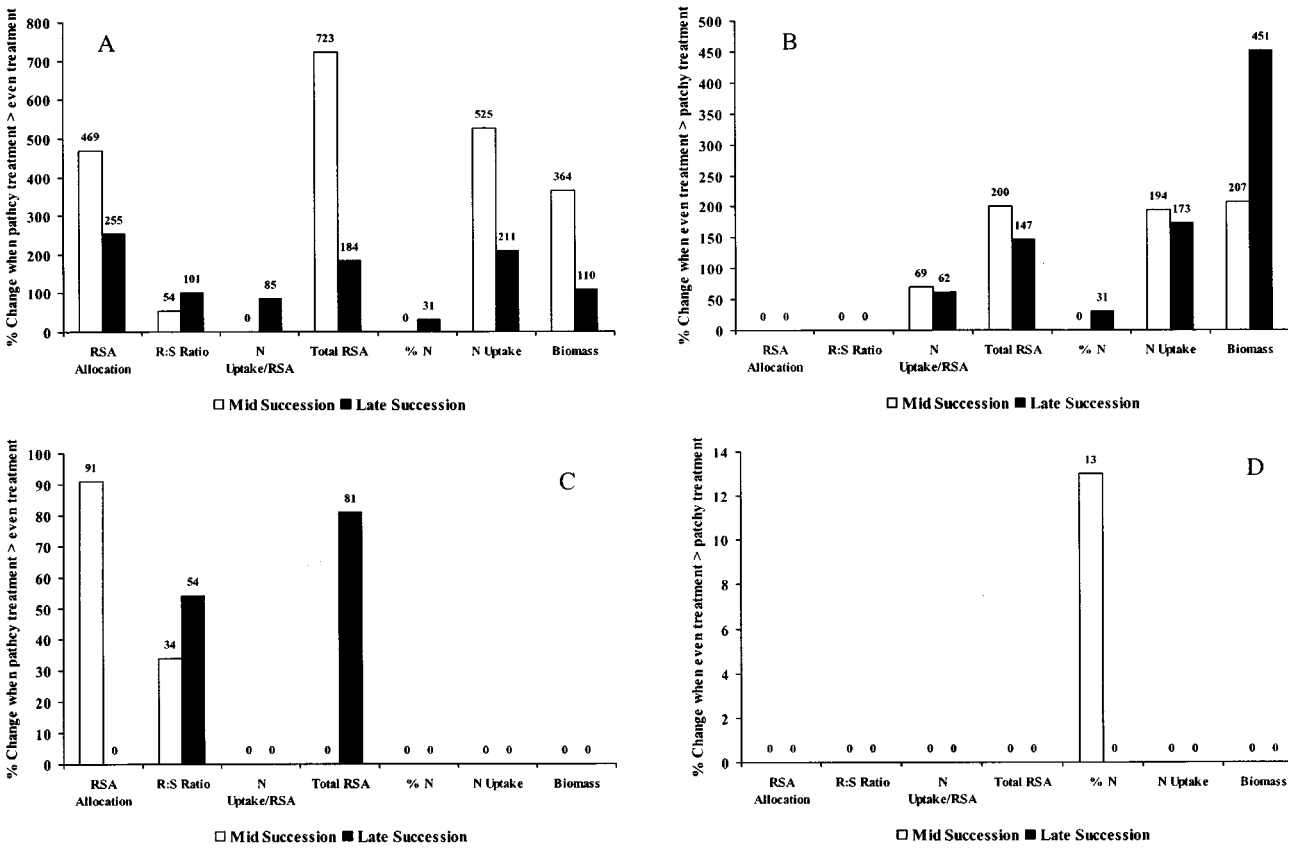

Fig. 2. Average response size (in %) for dicotyledonous, and monocotyledonous to the spatial distribution of N and P as measured by root surface area (RSA) allocation, root:shoot (R:S) ratio, N uptake per RSA, total RSA, %N in plant tissue, N uptake, and plant biomass. **A.** Dicotyledonous: case when the patchy soil nutrient treatment was higher ($P < 0.05$) than the even one. **B.** Dicotyledonous: case when the even soil nutrient treatment was higher ($P < 0.05$) than the patchy one. **C.** Monocotyledonous: case when the patchy soil nutrient treatment was higher ($P < 0.05$) than the even one. **D.** Monocotyledonous: case when the even soil nutrient treatment was higher ($P < 0.05$) than the patchy one. For treatment details see text.

Table 2. Average root:shoot (R:S) ratio and root surface area (right and left side of the experimental plots). Right and left are the sides of the experimental pots from were roots were harvested. High and low represent the concentrations of N and P nutrients (High = 30 ppm of N and 10 ppm of P; Low = 5ppm of N and 1 ppm of P). For treatment details see text. Only numbers in bold for between treatment (R:S) or within treatment comparison (root surface area in the right vs. left side of the experimental pot) are statistically significant at the $P < 0.05$ level.

				Average Allocation of Root Surface Area Per Plant					
				Even N and P Distribution			Patchy N and P Distribution		
Species	R:S for Even N & P Distribution	R:S for Patchy N & P Distribution	P-value	Root Surface Area (m^2) Right (High)	Root Surface Area (m^2) Left (High)	P-value	Root Surface Area (m^2) Right (High)	Root Surface Area (m^2) Left (Low)	P-value
Dicotyledonous Hemicryptophytes Mid Succession									
Grindelia squarrosa	0.347	0.397	0.390	0.00320	0.00240	0.30	**0.00390**	**0.00090**	**0.007**
Achillea millefolium	0.444	0.609	0.256	0.00154	0.00169	0.83	**0.00236**	**0.00045**	**0.009**
Erigeron philadelphicus	0.420	0.478	0.390	0.00800	0.00490	0.25	**0.04510**	**0.01810**	**0.023**
Rudbeckia hirta	0.383	0.518	0.360	0.02320	0.01470	0.17	**0.05070**	**0.01200**	**0.033**
Oenothera biennis	1.182	1.048	0.660	0.09530	0.10210	0.92	**0.05290**	**0.01940**	**0.050**
Solidago missouriensis	**0.348**	**0.409**	**0.050**	0.00320	0.00400	0.62	**0.01120**	**0.00310**	**0.050**
Verbena stricta	**0.370**	**0.540**	**0.010**	0.01780	0.00920	0.14	**0.02920**	**0.00170**	**0.050**
Ratibida columnifera	**0.217**	**0.407**	**0.001**	0.00360	0.00240	0.40	0.00640	0.00260	0.125
Gaillardia aristata	0.683	0.660	0.900	0.00160	0.00130	0.35	0.00230	0.00050	0.126
Asclepias verticillata	**0.665**	**0.941**	**0.030**	**0.00210**	**0.00150**	**0.02**	0.00080	0.00040	0.132
Taraxacum officinale	0.654	0.711	0.640	0.00560	0.00340	0.20	0.01510	0.00510	0.143
Artemisia frigida	0.232	0.266	0.500	0.00090	0.00100	0.80	0.00630	0.00140	0.168
Melilotus officinalis	**0.549**	**0.948**	**0.050**	0.01470	0.00590	0.13	0.00510	0.00260	0.414
Artemisia dracunculus	0.275	0.350	0.180	0.00110	0.00090	0.11	0.01310	0.01000	0.562
Tragopogon dubius	0.572	0.888	0.130	0.00140	0.00180	0.24	0.00120	0.00140	0.743
Cirsium arvense	0.359	0.460	0.110	0.02440	0.02360	0.91	0.01470	0.01390	0.959
Dicotyledonous Hemicryptophytes Late Succession									
Aster ericoides	0.923	0.445	0.310	0.00140	0.00150	0.37	**0.00540**	**0.00220**	**0.006**
Lupinus perennis	0.422	0.424	0.980	0.00440	0.00530	0.74	**0.00630**	**0.00080**	**0.011**
Helianthus maximiliani	**0.190**	**0.653**	**0.001**	0.00140	0.00100	0.64	**0.00640**	**0.00150**	**0.018**
Dalea purpurea	0.533	0.463	0.540	0.00040	0.00040	0.77	**0.00110**	**0.00030**	**0.021**
Sphaeralcea coccinea	0.479	0.536	0.360	0.00260	0.00220	0.62	**0.00270**	**0.00120**	**0.030**
Astragalus canadensis	0.552	0.574	0.790	0.00300	0.00360	0.61	**0.00910**	**0.00330**	**0.032**
Vicia americana	0.367	0.521	0.230	0.00550	0.00640	0.58	**0.00870**	**0.00210**	**0.033**
Linum perenne	0.525	0.700	0.260	0.00360	0.00440	0.64	**0.01110**	**0.00690**	**0.040**
Anaphalis margantacea	0.280	0.347	0.150	0.00443	0.00483	0.25	**0.00740**	**0.00240**	**0.044**
Psoralea esculenta	3.009	2.649	0.330	0.00060	0.00100	0.39	**0.00130**	**0.00070**	**0.044**
Helianthus rigidus	0.285	0.583	0.110	0.00120	0.00140	0.83	**0.00780**	**0.00150**	**0.046**
Chrysopsis villosa	**0.202**	**0.371**	**0.010**	0.00140	0.00080	0.17	**0.00700**	**0.00180**	**0.050**
Solidago rigida	0.361	0.553	0.280	0.00430	0.00410	0.65	0.00360	0.00170	0.139
Campanula rotundifolia	0.614	0.724	0.640	0.00030	0.00030	0.96	0.00070	0.00050	0.143
Potentilla arguta	**0.319**	**0.424**	**0.030**	**0.00660**	**0.00490**	**0.05**	0.00640	0.00410	0.147
Galium boreale	0.372	0.498	0.140	0.00290	0.00260	0.51	0.00410	0.00260	0.153
Oxytropis lambertii	0.340	0.353	0.820	0.00050	0.00080	0.08	0.00080	0.00040	0.160
Allium stellatum	1.732	2.110	0.150	0.00140	0.00120	0.61	0.00190	0.00160	0.164
Coreopsis lanceolata	0.264	0.210	0.290	0.00260	0.00290	0.65	0.00540	0.00290	0.194
Geum triflorum	0.272	0.230	0.302	0.00498	0.00580	0.62	0.00199	0.00109	0.220
Heuchera richardsonii	0.337	0.649	0.120	0.00490	0.00480	0.88	0.01460	0.00750	0.222
Liatris punctata	**2.057**	**2.927**	**0.050**	0.00020	0.00010	0.15	0.00030	0.00010	0.230
Viola pedatifida	0.350	0.408	0.420	0.00090	0.00110	0.42	0.00120	0.00080	0.388
Dicotyledonous Chamaephytes Late Succession									
Artemisia tridentata	0.493	0.537	0.610	0.00350	0.00300	0.39	**0.00340**	**0.00110**	**0.043**
Rosa arkansana	0.179	0.223	0.230	0.01030	0.00830	0.34	0.05000	0.00720	0.107
Amorpha canescens	0.319	0.826	0.220	0.00260	0.00370	0.23	0.00220	0.00200	0.361

Table 2. continued

Species	R:S for Even N & P Distribution	R:S for Patchy N & P Distribution	P-value	Average Allocation of Root Surface Area Per Plant					
				Even N and P Distribution			Patchy N and P Distribution		
				Root Surface Area (m^2) Right (High)	Root Surface Area (m^2) Left (High)	P-value	Root Surface Area (m^2) Right (High)	Root Surface Area (m^2) Left (Low)	P-value
Monocotyledonous Hemicryptophytes Mid Succession									
Sporobolus cryptandrus	0.280	0.311	0.770	0.00180	0.00120	0.49	**0.00210**	**0.00110**	**0.036**
Hordeum jubatum	0.280	0.317	0.540	0.00610	0.00450	0.24	0.00620	0.00380	0.148
Agropyron cristatum	0.612	0.705	0.427	0.00262	0.00258	0.96	0.00491	0.00295	0.210
Bromus inermis	**0.530**	**0.706**	**0.005**	0.02137	0.01859	0.57	0.02919	0.02512	0.458
Monocotyledonous Hemicryptophytes Late Succession									
Sorghastrum nutans	**0.397**	**0.582**	**0.010**	0.00560	0.00560	0.97	0.00870	0.01160	0.096
Andropogon gerardii	**0.253**	**0.353**	**0.050**	0.00530	0.00610	0.43	0.00710	0.00620	0.598
Panicum virgatum	**0.286**	**0.471**	**0.050**	0.00170	0.00130	0.55	0.00290	0.00190	0.334
Stipa viridula	**0.373**	**0.616**	**0.050**	0.00120	0.00090	0.32	0.00070	0.00080	0.720
Elymus canadensis	0.492	0.433	0.212	0.00207	0.00168	0.24	0.00384	0.00208	0.129
Calamovilfa longifolia	0.427	0.802	0.250	0.00190	0.00230	0.41	0.00330	0.00210	0.551
Schizachyrium scoparium	0.353	0.283	0.260	0.00090	0.00110	0.77	0.00070	0.00040	0.145
Agropyron spicatum	0.543	0.674	0.340	0.00170	0.00190	0.85	0.00330	0.00260	0.166
Bouteloua gracilis	1.534	0.608	0.370	0.00130	0.00090	0.20	0.00210	0.00360	0.515
Stipa comata	0.632	1.677	0.430	0.00100	0.00090	0.83	0.00080	0.00050	0.232
Koehlaria cristata	0.291	0.388	0.470	0.00040	0.00030	0.80	0.00050	0.00030	0.197
Poa pratensis	0.711	0.627	0.740	0.00090	0.00100	0.85	0.00060	0.00030	0.204
Bouteloua curtipendula	0.487	0.494	0.910	0.00200	0.00200	0.80	0.00250	0.00240	0.920

the nutrient poor patch was much larger in mid successional forbs when compared with late successional forbs: 469% vs. 255% (Fig. 2A). For the only grass showing a response, *Sporobulus cryptandrus* (a mid successional grass) the increase was only 91% (Fig. 2C).

Under an even nutrient distribution of N and P, only 2 species, both forbs, differed from the null hypotheses of 50%:50% RSA ratio between the right and left side of the experimental pots, which under this treatment were both nutrient rich (Tab. 2): *Asclepias verticillata* (a mid successional forb) and *Potentilla arguta* (a late successional forb) had on average 38% more RSA in the right side of the pot than in the left side.

A total of 9 species (2 mid successional forbs, 5 late successional forbs, 1 shrub, and 1 late successional grass) responded to a patchy distribution of soil N and P by increasing their total RSA (Tab. 3). There were, again, substantial differences among species with different life forms and successional status in terms of the magnitude of their response to nutrient patchiness: for mid successional forbs a patchy distribution of soil N and P resulted in a 723% increase in total RSA when compared to the even distribution one, while the equivalent numbers for late successional forbs and shrubs was 184% (Figs. 2A–B), and for the only grass showing a treatment response (*Sorghastrum nutans*) it was only 81% (Fig. 2C). In *Erigeron philadelphicus* (mid successional forb) and 5 of the late successional forbs (*Aster ericoides, Chrysopsis villosa, Dalea purpurea, Helianthus maximilliana,* and *Linum perenne*) the increases in total RSA (Tab. 3) were also accompanied by significant reallocation of roots toward nutrient rich patches (Tab. 2).

Root to shoot ratio

Fourteen species (5 mid successional forbs, 4 late successional forbs, 1 mid successional grass, and 4 late successional grasses) changed their biomass allocation in response to a patchy distribution of soil N and P (Tab. 2). In all cases, the result was a higher R:S ratio for plants grown under a non-even distribution of soil N and P than under an even one (Tab. 2). As usual, there were differences involving life forms and successional status. The increases in the R:S ratio averaged 54% for mid successional forbs, 101% for late successional forbs, and an average of 50% for both mid and late successional grasses (Figs. 2A and 2C). An interesting point to note is that the R:S ratio was one of

only two measurements (the other being %N) where grasses had a proportionally higher response to nutrient patchiness than forbs: 30% vs. 22% (Fig. 3A).

Plant biomass

Only 8 species (3 mid successional forbs, 4 late successional forbs, and 1 shrub) showed any significant response in plant growth as a result of N and P patchiness (Tab. 3). Six of these species had more biomass under a patchy distribution of soil N and P than under an even one with the increases being substantially larger for mid successional species: an average of 364% for mid successional forbs (*Artemisia dracunculus*, and *Erigeron philadelphicus*, *Linum perenne*) vs. an average of 110% for late successional forbs (*Aster ericoides*, *Chrysopsis villosa*, and *Rosa Arkansan*, Figs. 2A–B). For the other 2 species (one of them a legume), *Geum triflorum*, and *Melilotus officinalis*, biomass was on average 330% higher under the uniform nutrient regime (Fig. 2C).

Nitrogen uptake

A total of 9 species (2 mid successional forbs, 6 late successional forbs, and 1 shrub) had significant differences in total N uptake in response to a patchy vs. an even distribution of soil N and P (Tab. 4). Four species (two of them legumes), *Artemisia tridentata*, *Geum triflorum*, *Melilotus officinalis*, and *Vicia americana* averaged 178% higher N uptake under an even distribution of N and P than under a patchy one with no major differences in response among live forms and successional status (Fig. 2B). For 5 species, *Artemisia dracunculus*, *Aster ericoides*, *Chrysopsis villosa*, *Helianthus maximilliana*, and *Linum perenne*, the reverse was the case with N uptake being, on average, higher under the patchy distribution of N and P when compared to the even nutrient regime (Tab. 4). In this case the only mid successional species (*Artemisia dracunculus*) had a 525% increase in N uptake when subjected to a patchy distribution of soil N and P visa vis a patchy one, while for the other 4 the increase was 211% (Fig. 2A).

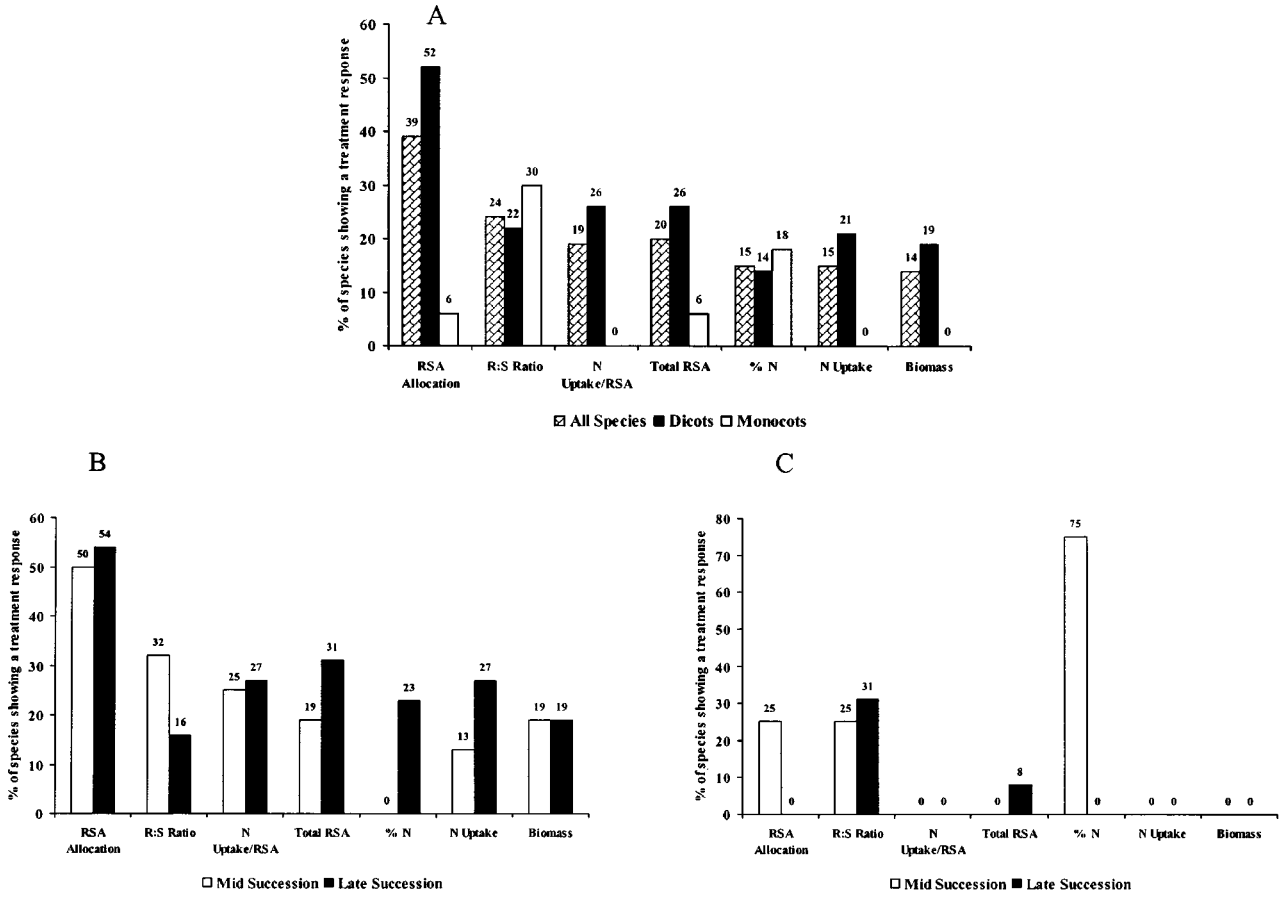

Fig. 3. Percentage of plant species that had significant ($P < 0.05$) responses to the spatial distribution of N and P as measured by root surface area (RSA) allocation, root:shoot (R:S) ratio, N uptake per RSA, total RSA, %N in plant tissue, N uptake, and plant biomass. **A.** All species. **B.** Mid and late successional dicotyledonous. **C.** Mid and late successional monocotyledonous. For treatment details see text.

Table 3. Plants average biomass and total root surface area. For treatment details see text. Only numbers in bold for between treatment comparison are statistically significant at the $P < 0.05$ level.

Species	Biomass (g) for Even N & P Distribution	Biomass (g) for Patchy N & P Distribution	P-value	Total Root Surface Area (m^2) for Even N & P Distribution	Total Root Surface Area (m^2) for Patchy N & P Distribution	P-value
Dicotyledonous Hemicryptophytes Mid Succession						
Artemisia dracunculus	**0.256**	**1.675**	**0.001**	**0.00200**	**0.02310**	**0.001**
Asclepias verticillata	0.251	0.212	0.590	**0.00360**	**0.00120**	**0.041**
Erigeron philadelphicus	**1.394**	**3.813**	**0.040**	**0.01290**	**0.06320**	**0.047**
Melilotus officinalis	**3.452**	**1.123**	**0.010**	0.02060	0.00770	0.110
Artemisia frigida	0.307	0.674	0.100	0.00190	0.00770	0.113
Solidago missouriensis	0.766	1.273	0.170	0.00720	0.01430	0.141
Taraxacum officinale	1.094	1.140	0.940	0.00900	0.02020	0.230
Ratibida columnifera	0.657	0.582	0.670	0.00600	0.00900	0.252
Oenothera biennis	8.676	4.568	0.250	0.19740	0.07230	0.259
Cirsium arvense	2.965	1.739	0.300	0.04800	0.02860	0.316
Rudbeckia hirta	2.511	2.790	0.830	0.03790	0.06270	0.423
Tragopogon dubius	0.258	0.257	0.990	0.00320	0.00260	0.499
Achillea millefolium	0.284	0.181	0.308	0.00324	0.00281	0.719
Grindelia squarrosa	0.628	0.509	0.520	0.00560	0.00480	0.755
Verbena stricta	1.786	1.350	0.450	0.02700	0.03090	0.782
Gaillardia aristata	0.611	0.497	0.750	0.00290	0.00280	0.912
Dicotyledonous Hemicryptophytes Late Succession						
Aster ericoides	**0.219**	**0.577**	**0.010**	**0.00290**	**0.00760**	**0.006**
Helianthus maximiliani	0.349	0.544	0.300	**0.00240**	**0.00790**	**0.027**
Geum triflorum	**1.511**	**0.274**	**0.046**	**0.01078**	**0.00309**	**0.030**
Chrysopsis villosa	**0.329**	**0.662**	**0.050**	**0.00220**	**0.00880**	**0.038**
Dalea purpurea	0.098	0.190	0.150	**0.00080**	**0.00140**	**0.049**
Linum perenne	**0.227**	**0.519**	**0.020**	**0.00800**	**0.01800**	**0.049**
Heuchera richardsonii	1.578	2.533	0.160	0.00970	0.02210	0.082
Astragalus canadensis	1.214	1.196	0.960	0.00660	0.01240	0.106
Liatris punctata	0.016	0.019	0.250	0.00030	0.00040	0.120
Helianthus rigidus	0.375	0.641	0.410	0.00260	0.00930	0.128
Anaphalis margantacea	0.363	0.392	0.750	0.00926	0.00980	0.150
Sphaeralcea coccinea	0.570	0.582	0.930	0.00480	0.00390	0.288
Allium stellatum	0.124	0.123	0.900	0.00260	0.00350	0.324
Psoralea esculenta	0.241	0.293	0.410	0.00160	0.00200	0.328
Campanula rotundifolia	0.345	0.349	0.960	0.00060	0.00120	0.360
Solidago rigida	1.159	0.579	0.140	0.00840	0.00530	0.403
Coreopsis lanceolata	0.612	0.868	0.360	0.00550	0.00830	0.417
Lupinus perennis	1.303	0.997	0.560	0.00970	0.00710	0.462
Galium boreale	0.273	0.252	0.840	0.00550	0.00670	0.632
Vicia americana	1.813	1.268	0.160	0.01190	0.01080	0.750
Potentilla arguta	1.394	1.199	0.740	0.01150	0.01050	0.863
Oxytropis lambertii	0.283	0.293	0.930	0.00130	0.00120	0.927
Viola pedatifida	0.790	0.814	0.560	0.00200	0.00200	0.950
Dicotyledonous Chamaephytes Late Succession						
Rosa arkansana	**3.225**	**4.654**	**0.042**	**0.01860**	**0.05720**	**0.030**
Artemisia tridentata	0.420	0.275	0.120	**0.00650**	**0.00450**	**0.039**
Amorpha canescens	0.640	0.614	0.910	0.00630	0.00420	0.085
Monocotyledonous Hemicryptophytes Mid Succession						
Agropyron cristatum	0.896	1.525	0.100	0.00520	0.00786	0.381
Bromus inermis	3.091	4.106	0.248	0.03997	0.05431	0.355

Table 3. continued

Species	Biomass (g) for Even N & P Distribution	Biomass (g) for Patchy N & P Distribution	P-value	Total Root Surface Area (m^2) for Even N & P Distribution	Total Root Surface Area (m^2) for Patchy N & P Distribution	P-value
Hordeum jubatum	1.039	0.868	0.630	0.01060	0.01000	0.803
Sporobolus cryptandrus	1.447	1.317	0.870	0.00300	0.00320	0.927
Monocotyledonous Hemicryptophytes Late Succession						
Sorghastrum nutans	0.579	1.061	0.110	**0.01120**	**0.02030**	**0.041**
Panicum virgatum	0.594	0.878	0.200	0.00300	0.00480	0.155
Elymus canadensis	1.441	2.225	0.164	0.00375	0.00592	0.175
Bouteloua gracilis	0.176	0.262	0.500	0.00220	0.00570	0.191
Schizachyrium scoparium	1.059	0.625	0.450	0.00200	0.00110	0.215
Poa pratensis	0.328	0.150	0.350	0.00190	0.00090	0.352
Stipa viridula	0.443	0.398	0.850	0.00210	0.00150	0.392
Stipa comata	0.274	0.271	0.980	0.00190	0.00130	0.413
Bouteloua curtipendula	0.394	0.355	0.720	0.00400	0.00490	0.443
Agropyron spicatum	0.472	0.433	0.640	0.00360	0.00590	0.520
Calamovilfa longifolia	0.445	0.646	0.540	0.00420	0.00540	0.689
Koehlaria cristata	0.136	0.195	0.470	0.00070	0.00080	0.925
Andropogon gerardii	1.328	1.179	0.730	0.01140	0.01330	0.955

The response of grasses to a patchy distribution soil N and P was manifested mainly in terms of %N in plant tissue and was confined to mid successional species (Tab. 4). The %N in the plant tissue of 3 mid successional grasees, *Agropyron cristatum*, *Hordeum jubatum*, and *Sporobolus cryptandrus*, was on average 13% higher when the plants were grown with an even distribution of soil N and P vis a vis a patchy one (Fig. 2D).

When N uptake was scaled by root surface area ($gN \cdot m^{-2}$), 10 species (4 mid successional forbs, 6 late successional forbs) showed a significant response to the spatial distribution of soil N and P (Tab. 4). The 10 species in question had on average a 65% higher N uptake per unit of RSA when grown under an even distribution of soil N and P than under a patchy one with no appreciable differences between successional status (Fig. 2B). Only one species, *Anaphalis margantacea* (late successional forb) had higher uptake per unit of RSA when grown under an even distribution of soil N and P than under a patchy one (Tab. 4).

Discussion

Root responses (defined as total RSA, allocation of RSA, and R:S ratio) were more prevalent than overall plant responses (defined as total N uptake, %N in plant tissue, and plant biomass): 58% of all species showed some root response to variations in the spatial distribution of soil nutrients as opposed to only 31% showing some overall plant response (Fig. 3A). There were, however, pronounced differences between monocotyledonous (grasses) and dicotyledonous (forbs) as well as between mid and late successional species in how they responded to soil nutrient patchiness. For most of the plant measurements used in this study, the proportions of forbs that responded to a patchy distribution of nutrients was on average substantially larger than that of grasses, the only exception being the R:S ratio and %N in plant tissue where the reverse was the case (Fig. 3A). Within forbs (but not grasses) the proportions of late successional species that had either a root or an overall plant response to a patchy distribution of nutrients was higher than that of mid successional ones (Fig. 3B), but the size of the response was substantially larger in the latter (Fig. 2A), a result that is fairly consistent with other studies (e.g. Campbell et al. 1991, Fransen et al. 1998) showing that, on average, fast growing plants (in our case mid successional forbs) can more rapidly and thoroughly exploit nutrient patches than slower growing ones (in our case late successional forbs).

The higher propensity of forbs to reallocate RSA, and grasses to alter their R:S ratio in response to a patchy distribution of nutrients that we found in this study was not totally unexpected. Robinson (1994) in a review of the literature found that 40% of all the species showed various degrees of root plasticity (defined as a redirection of root growth to nutrient rich patches) in response to a non uniform distribution of soil nutrients, a number that is very close to the 39%

Table 4. Average N uptake, %N in plant tissue, and N uptake per unit of root surface area. For treatment details see text. Only numbers in bold for between treatment comparison are statistically significant at the P < 0.05 level.

Species	N Uptake (gN) for Even N & P Distribution	N Uptake (gN) for Patchy N & P Distribution	P-value	% N for Even N & P Distribution	% N for Patchy N & P Distribution	P-value	N Uptake per Root Surface Area ($gN.m^{-2}$) Even N & P Distribution	N Uptake per Root Surface Area ($gN.m^{-2}$) Patchy N & P Distribution	P-value
Dicotyledonous Hemicryptophytes Mid Succession									
Erigeron philadelphicus	0.045	0.130	0.132	3.30	3.27	0.916	**3.46**	**2.10**	**0.002**
Ratibida columnifera	0.023	0.019	0.521	3.44	2.73	0.477	**4.08**	**2.19**	**0.012**
Artemisia frigida	0.007	0.015	0.097	2.38	2.32	0.466	**4.00**	**2.56**	**0.026**
Artemisia dracunculus	**0.008**	**0.050**	**0.030**	2.98	3.03	0.120	**3.81**	**2.27**	**0.030**
Rudbeckia hirta	0.083	0.063	0.515	3.28	2.64	0.213	2.26	1.24	0.094
Taraxacum officinale	0.030	0.030	0.989	2.98	2.78	0.596	3.38	1.86	0.095
Achillea millefolium	0.008	0.005	0.346	2.64	2.82	0.331	2.21	1.83	0.148
Cirsium arvense	0.097	0.043	0.105	3.27	3.09	0.616	2.13	1.71	0.149
Asclepias verticillata	0.007	0.006	0.543	2.81	2.86	0.820	2.88	5.04	0.165
Grindelia squarrosa	0.020	0.015	0.460	3.04	3.02	0.945	4.19	3.24	0.316
Melilotus officinalis	**0.091**	**0.031**	**0.005**	2.77	2.80	0.928	6.20	4.23	0.361
Solidago missouriensis	0.026	0.041	0.139	3.41	2.73	0.671	3.68	3.24	0.376
Verbena stricta	0.054	0.038	0.314	3.02	2.88	0.527	2.17	1.74	0.412
Gaillardia aristata	0.018	0.016	0.850	2.95	2.70	0.315	5.40	7.42	0.434
Tragopogon dubius	0.008	0.007	0.592	3.25	2.69	0.140	2.88	2.47	0.444
Oenothera biennis	0.236	0.117	0.197	2.98	2.66	0.099	1.95	1.69	0.669
Dicotyledonous Hemicryptophytes Late Succession									
Aster ericoides	**0.005**	**0.019**	**0.025**	**2.19**	**2.85**	**0.032**	1.82	2.31	0.476
Linum perenne	**0.007**	**0.017**	**0.025**	3.24	3.26	0.964	1.00	0.94	0.839
Chrysopsis villosa	**0.006**	**0.018**	**0.029**	2.44	2.69	0.181	4.53	2.39	0.175
Helianthus maximilliana	**0.005**	**0.016**	**0.032**	2.52	2.86	0.181	4.12	2.10	0.221
Geum triflorum	**0.034**	**0.007**	**0.037**	2.35	2.33	0.883	**3.06**	**2.27**	**0.044**
Vicia americana	**0.066**	**0.038**	**0.046**	**3.67**	**2.97**	**0.015**	**6.18**	**3.65**	**0.048**
Solidago rigida	0.033	0.016	0.185	2.80	2.56	0.423	4.03	2.79	0.069
Dalea purpurea	0.003	0.005	0.186	2.59	2.72	0.249	3.38	3.71	0.729
Helianthus rigidus	0.010	0.021	0.311	2.70	2.70	0.515	**3.73**	**2.13**	**0.029**
Heuchera richardsonii	0.033	0.046	0.320	2.15	1.81	0.120	**3.64**	**2.20**	**0.017**
Viola pedatifida	0.014	0.015	0.420	1.77	1.84	0.180	7.00	7.40	0.310
Psoralea esculenta	0.005	0.006	0.477	2.10	2.00	0.622	3.12	2.88	0.498
Liatris punctata	0.001	0.001	0.480	3.97	3.07	0.320	2.09	1.79	0.060
Lupinus perennis	0.043	0.030	0.491	3.23	2.95	0.114	4.23	4.14	0.845
Potentilla arguta	0.036	0.026	0.495	**2.60**	**2.71**	**0.003**	**3.50**	**2.66**	**0.050**
Anaphalis margantacea	0.006	0.007	0.560	**1.65**	**2.59**	**0.050**	**0.65**	**1.20**	**0.040**
Coreopsis lanceolata	0.019	0.022	0.582	3.00	2.72	0.217	3.49	3.27	0.693
Galium boreale	0.006	0.005	0.656	2.30	2.15	0.615	1.33	0.75	0.102
Astragalus canadensis	0.046	0.041	0.701	3.82	3.51	0.220	8.62	3.97	0.130
Oxytropis lambertii	0.008	0.007	0.769	**2.98**	**2.46**	**0.039**	6.73	5.96	0.610
Campanula rotundifolia	0.009	0.009	0.839	2.95	2.74	0.655	16.75	12.82	0.456
Sphaeralcea coccinea	0.017	0.017	0.917	3.04	2.85	0.458	3.68	4.20	0.521
Allium stellatum	0.004	0.004	0.949	2.86	2.84	0.946	1.33	1.02	0.112
Dicotyledonous Chamaephytes Late Succession									
Artemisia tridentata	**0.011**	**0.007**	**0.006**	2.36	2.43	0.644	1.50	1.71	0.673
Rosa arkansana	0.063	0.096	0.090	1.95	2.05	0.620	3.38	1.76	0.001
Amorpha canescens	0.019	0.012	0.159	**2.92**	**2.00**	**0.004**	3.04	2.70	0.606
Monocotyledonous Hemicryptophytes Mid Succession									
Hordeum jubatum	0.033	0.024	0.447	**3.17**	**2.77**	**0.009**	2.83	2.35	0.313
Sporobolus cryptandrus	0.043	0.033	0.688	**2.89**	**2.52**	**0.040**	12.31	10.28	0.604

Table 4. continued

Species	N Uptake (gN) for Even N & P Distribution	N Uptake (gN) for Patchy N & P Distribution	P-value	% N for Even N & P Distribution	% N for Patchy N & P Distribution	P-value	N Uptake per Root Surface Area ($gN.m^{-2}$) Even N & P Distribution	N Uptake per Root Surface Area ($gN.m^{-2}$) Patchy N & P Distribution	P-value
Agropyron cristatum	0.027	0.041	0.151	**3.00**	**2.72**	**0.042**	5.24	6.44	0.363
Bromus inermis	0.067	0.086	0.298	2.18	2.11	0.290	1.85	1.64	0.365
Monocotyledonous Hemicryptophytes									
Late Succession									
Agropyron spicatum	0.009	0.010	0.909	2.12	2.24	0.461	1.75	1.69	0.450
Andropogon gerardii	0.027	0.022	0.449	1.75	1.85	0.534	2.01	1.70	0.277
Bouteloua curtipendula	0.010	0.009	0.660	2.65	2.71	0.232	2.64	1.79	0.064
Bouteloua gracilis	0.003	0.006	0.209	2.14	2.19	0.681	1.23	1.10	0.719
Calamovilfa longifolia	0.010	0.013	0.661	2.21	1.97	0.319	2.28	2.39	0.626
Elymus canadensis	0.035	0.051	0.179	2.41	2.31	0.135	9.84	9.35	0.820
Koehlaria cristata	0.003	0.004	0.572	2.67	2.12	0.080	5.65	5.64	1.000
Panicum virgatum	0.012	0.019	0.183	2.10	2.22	0.431	3.91	4.65	0.516
Poa pratensis	0.008	0.004	0.450	2.41	2.45	0.871	3.76	4.09	0.681
Schizachyrium scoparium	0.023	0.013	0.389	2.16	2.14	0.914	10.28	12.67	0.373
Sorghastrum nutans	0.013	0.022	0.133	2.19	2.06	0.310	1.12	1.03	0.464
Stipa comata	0.006	0.005	0.628	2.28	2.27	0.969	3.20	3.75	0.612
Stipa viridula	0.011	0.009	0.722	2.56	2.49	0.681	5.36	4.99	0.708

we found in this study (Fig. 3A). Regarding forbs, Taub & Goldberg (1996), in a study of the root topology of 17 annual plant species, found a substantial degree of root plasticity on the part of dicotyledonous when subjected to various levels of N, P and potassium (K), but very little root plasticity on the part of grasses under the same experimental conditions. Robinson (1994) also found that 50% of the plant species reported in various studies had significant increases in R:S ratios in response to a non-uniform distribution of soil nutrients. Explanations for the observed increases in the R:S ratio fall into two categories. Drew & Saker (1975) and Bingham & Stevenson (1993) have suggested that the increases in R:S ratios are caused by a diversion of carbohydrates into the root system to support lateral root growth toward areas with high nutrient concentrations. The second hypothesis is based on the fact that a patchy supply of nutrients also generates a patchy pattern of osmotic pressures. Acevedo et al. (1971) found severe inhibitions in leaf extension when the root system of *Zea mays* was subjected to osmotic pressures of increasing strength. Robinson (1994) speculates that something similar may occur in localized nutrient experiments and that increases in R:S ratios, thus, are not driven by a reallocation of carbohydrates toward roots, but rather by a reduction in aboveground growth.

From an ecological perspective, the high levels of root plasticity we observed in forbs, and the propensity of grasses to increase their R:S ratio when subjected to a patchy with soil nutrient environment seem to fit, in broad terms, predictions from the "coarse" vs. "fine" scale foraging strategies hypothesis advanced by Campbell et al. (1991). Campbell et al. (1991) proposed that dominant plants capture and monopolize a large portion of soil resources through a coarse scale foraging strategy which consists of reallocating biomass toward roots and the development of extensive root systems. They argue, furthermore, that this strategy is mostly incompatible with the precise location of roots in local, undepleted soil nutrient patches. Subdominant species, on the other hand, capture soil resources through a fine scale foraging strategy which consists of a more precise allocation of RSA in the nutrient rich patches that are located between the depletion zones generated by the dominant species. With few exceptions, the vast majority of species that showed substantial root plasticity, are in fact subdominant in most of the vegetation types found within the Great Plains grasslands (Kuchler 1964). Conversely, a higher proportion of grasses than forbs showed increases in R:S in response to N and P patches (Fig. 3A) and some of these species, like *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*, and *Stipa viridula* are dominant components in many of the vegetation types that characterize the Great Plains grasslands (Biondini et al. 1999).

There is an area of root plasticity in which the species we tested fundamentally differed from some theoretical predictions and most of the results report-

ed in the literature. Gersani & Sachs (1992) hypothesized that there is a tight, negative correlation between root growth in a nutrient rich patch vs. root growth in a nutrient poor patch. More specifically, Gersani & Sachs (1992) predicted that if the rooting zone of a plant were to be split between a nutrient rich vs. nutrient poor side then: (**a**) increased root growth in the former should lead to an inhibition of root growth in the latter; and (**b**) the larger the difference in nutrient availability between the two sides the more one would be stimulated and the other inhibited. Robinson (1994) tried to establish whether this hypothesis could in fact be corroborated by empirical evidence. He collected data from the open literature on a variety of species and then ran linear regressions between two ratios of root biomass. The first one (denoted $\mathbf{R}^+$) represented the ratio between the root biomass in the nutrient rich patch of a treatment which consisted of a nutrient rich half and a nutrient poor half, and the root biomass (in the same side) of a control treatment in which both half of the experimental units where supplied with a nutrient rich solution. The second one (denoted $\mathbf{R}^-$) was the ratio between the root biomass in the nutrient poor patch of the experimental treatment and the corresponding root biomass in the control. If Gersani & Sachs (1992) predictions were to be true the correlation between $\mathbf{R}^+$ and $\mathbf{R}^-$ should be negative. Robinson (1994) found only a very weak negative correlation. A similar analysis for the species in this study that showed significant reallocation of RSA in response to N and P patchiness (Tab. 2) produced a drastically different result (Fig. 4). In our case $\mathbf{R}^+$ and $\mathbf{R}^-$ were actually positively correlated ($R^2 = 0.57$, $P < 0.05$). This positive correlation, suggests that for many species, in particular forbs, there is a synergistic effect by which an increases in RSA in the nutrient rich patches translate into increases in RSA in the nutrient poor patches. This synergist effect may partially explain why: (**a**) 9 of the species we studied had higher total RSA in the patchy soil nutrient treatment than in the even one; and (**b**) the average of the product $\mathbf{R}^+ \times \mathbf{R}^-$, which under the Gersani & Sachs (1992) hypothesis should be 1 (matching increases with decreases) was in fact significantly higher than 1: $\mathbf{R}^+ \times \mathbf{R}^- = 3.17$ ($P < 0.03$).

Its is interesting to note that even though more than 50% of all forbs reallocated their RSA to nutrient rich patches, that response was generally not equally matched by corresponding increases in total N uptake or plant growth (Figs. 3A–B). This weak coupling between root plasticity and plant performance have been widely reported in other studies, see for example literature reviews by Caldwell (1994) and Robinson (1994), and more recent studies by Larigauderie & Richards (1994), van Vuuren et al. (1996), Fransen et al. (1998), and Hodge et al. (2000). These results seem to suggest that while roots may rapidly respond to the presence of nutrient patches, that response may not translate itself immediately into plant performance. Along the same lines, we also found a strong positive relationship involving the ratio of N uptake between the patchy vs. even soil N and P treatments (denoted as N-uptake ratio) and the corresponding total plant biomass ratio (denoted as Biomass ratio) (Fig. 5). The slope of the regression was close to 1 (Fig. 5), indicating that increases in biomass as a result of a patchy distribution of soil nutrients were directly proportional to increases in N

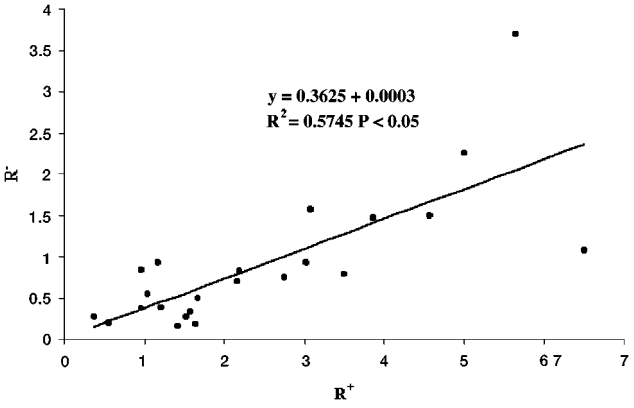

Fig. 4. Regression between R^+ and R^- for the species that showed significant reallocation of RSA in response of N and P patchiness (Tab. 2). R^+ is the ratio between the RSA in the nutrient rich patch of Treatment 2 (uneven distribution of soil N and P) and the RSA in the right side of Treatment 1 (even distribution of soil N and P). R^- is the ratio between the RSA in the nutrient poor patch of Treatment 2 and the RSA in the left side of Treatment 1. For treatment details see text.

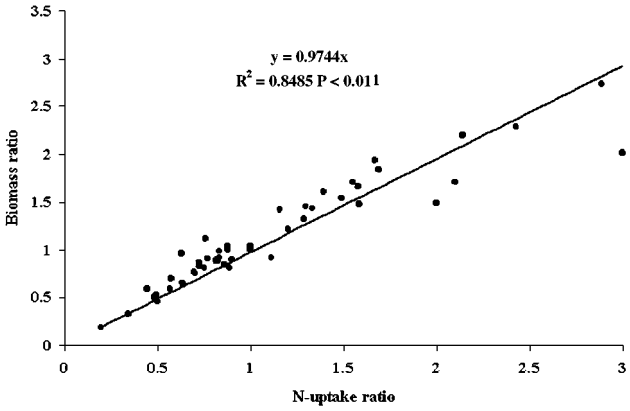

Fig. 5. Regression between N-uptake ratio and Biomass ratio for all species. N-uptake ratio is the ratio of N uptake between Treatment 2 (uneven distribution of soil N and P) and Treatment 1 (even distribution of soil N and P) while Biomass ratio is a similar ratio involving plant biomass. For treatment details see text.

uptake. However, since only 15% of the species under study (21% of forbs) showed increases in N uptake as a result of nutrient patchiness, this analysis tends to reinforce the proposition that, at least in the short term, soil nutrient patchiness may have a limited impact in plant performance. Robinson (1994) using published data also found a positive relationship between N-uptake ratio and Biomass ratio, but with a slope significantly higher than 1. Robinson (1994) explained the size of the slope by hypothesizing that when the supply of soil nutrients is restricted by location, nutrient uptake decreases faster than plant growth which causes declines in nutrient tissue concentration, and thus can lead in time to declines in plant growth. While for the species we studied, the slope between the Biomass ratio and N-uptake ratio was very close to 1 (Fig. 5), two other pieces of information tend to lend support to Robinson's hypothesis: (**a**) for the species that showed a significant treatment effect, all but 3 had higher %N in plant tissue in the even soil N and P treatment than in the patchy one (Tab. 4); and (**b**) when a treatment effect was detected, N uptake per unit of RSA was always higher in the even soil and N and P treatment than in the patchy one (Tab. 4).

Results from this study as well as supporting evidence from similar studies described above suggest that hypotheses advanced by Campbell et al. (1991), Biondini & Grygiel (1994), and Jackson & Caldwell (1996), among others, that have emphasized the critical role that small scale soil nutrient heterogeneity and root plasticity play in both nutrient acquisition and plant competition may have to be reevaluated. It may be that, as Hodge et al. (2000) have suggested: (**a**) most plants have sufficient plasticity in root system development to track the scale of soil nutrient heterogeneity and thus show similar performance regardless of the degree of nutrient patchiness; and (**b**) the benefits of root plasticity in terms of N capture are critical for plant competition in mixed communities regardless of the extent of soil nutrient heterogeneity. The latter proposition seems to be supported by the fact that late successional forbs had a higher proportion of species than either mid successional forbs or grasses that increase their total RSA, R:S ratio, or adjusted the spatial distribution of RSA in response to a patchy distribution of nutrients (Figs. 3B–C). As mentioned previously, the forbs we studied are mostly subdominant within the Great Plains grasslands (Kuchler 1964), and thus subjected to intense competition, a competition that is particularly severe for late successional forbs since they grow in highly diverse and crowded plant communities. The response pattern of roots to the spatial distribution of soil nutrients found among forbs, in particular late successional forbs (Figs. 2–3), may well be an adaptation developed by these species to compete for soil nutrients in general, rather than a specific one to deal with soil nutrient heterogeneity.

Like this one, the vast majority of studies in root plasticity have been conducted under controlled greenhouse conditions, using seedlings grown in individual pots for a relatively short period of time (see Robinson, 1994 for a review of published studies). The question that arises immediately, then, is whether these results can be used to make inferences about the behavior of larger plants, in mixed species communities, under field conditions. There are two lines of evidence that seem to suggest that, in principle, they can. Theoretical analyses conducted by Gleeson & Fry (1997) using an optimization model have suggested that plants grown in a patchy soil nutrient environment will spatially allocate their roots in such a way that the marginal gains from each nutrient patch are equilibrated, regardless of the size of the plant and the nature of the nutrient patch. Field studies conducted by Bilbrough & Caldwell (1995) and Caldwell et al. (1996) have produced data that are fairly consistent with results from greenhouse and pot experiments.

Conclusions

The analyses of 59 plant species common to the Great Plains grasslands showed the diversity of responses that plants can have to a non-uniform distribution of soil nutrients. There were, nevertheless, some important common patterns.

1. Root responses (defined by total RSA, RSA allocation, R:S ratio) were twice as prevalent as whole plant responses (defined by total N uptake, %N in plant tissue and plant biomass).
2. The percentage of species with the ability to allocate their RSA to nutrient rich patches was 9 times higher in forbs than in grasses. Conversely, there were proportionally more grasses than forbs that responded to a patchy distribution of soil nutrients by increasing their R:S ratios. These responses seem to be consistent with prediction from the theory of "coarse" vs. "fine" scale foraging strategies advanced by Campbell et al. (1991).
3. Within forbs (but not grasses), the proportions of late successional species that had either a root or an overall plant response to a patchy distribution of nutrients was higher than that of mid successional ones, while the size of the response was substantially larger in the latter. These result supports the general proposition that fast growing plants (in our case mid successional forbs) can more rapidly and thoroughly exploit nutrient patches than slow-

er growing ones (in our case late successional forbs).

4. We found a very weak coupling between root plasticity and plant performance. N uptake and biomass responses to variations in the spatial distribution of soil nutrients was limited in scope, restricted to forbs, and without a clear emerging pattern. There was however some level of support for the hypothesis that a localized nutrient supply restricts nutrient uptake more than plant growth which leads to declines in nutrient tissue concentration and potentially plant growth (Robinson 1994).
5. Data from this study seem to suggest that hypotheses that have emphasized the critical role that small scale soil nutrient heterogeneity and root plasticity play in both nutrient acquisition and plant competition may have to be reevaluated. Our results tend to suggest that: (**a**) most plants have sufficient plasticity in root system development to track the scale of soil nutrient heterogeneity and thus show similar performance regardless of the degree of nutrient patchiness; and (**b**) the benefits of root plasticity are more critical for subdominant species as a general adaptation to compete for soil nutrients in mixed plant communities regardless of the extent of soil nutrient heterogeneity.

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