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Growth rate, root development and nutrient uptake of 55 plant species from the Great Plains Grasslands, USA

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Abstract

Empirical and theoretical studies have highlighted that plant competition and species diversity are substantially affected by interactions among plant growth and nutrient uptake rates, root lateral spread, root plasticity, and small scale soil nutrient heterogeneity. This study was designed to **(a)** experimentally estimate parameters regarding root scaling patterns, root biomass allocation, growth rates, nutrient productivity, and root nutrient influx rates of 55 plant species common to Great Plains grasslands; and **(b)** determine if grasses and forbs can be classified into statistically distinct groups based on these characteristics. We found that: **(1)** In all species root lateral spread, root length, and root surface area had significant allometric scaling relationships with root biomass, but that the relationships were unaffected by N availability. **(2)** Reductions in the supply of N increased the root-:shoot ratio in 62% of the species. **(3)** The frequency distribution and mean values of maximum relative growth rates were very similar for grasses and forbs/shrubs, but mid successional grasses had a higher relative growth rate than late successional ones. **(4)** In 78% of the species tested, N productivity was increased by reductions in the N supply. **(5)** When subjected to a high N supply, the N and P productivity of grasses was, on average, higher than that of forbs/shrubs, and the N and P productivity of C_4 grasses was, on average, higher than that of C_3 grasses. No differences were found under a low N supply. **(6)** No differences on the average maximum N and P influx rates per unit of root surface area were found between grasses and forbs or between C_3 and C_4 grasses, but both were correlated with maximum relative growth rate. **(7)** The set of parameters we measured were able to separate grasses and forbs/shrubs into statistically distinct groups that tend to follow in broad terms the "coarse" vs. "fine" scale foraging strategies hypothesis.

Introduction

The links among plant community composition, competition for below-ground resources, and differences in the timing of resource use among plants have been extensively reported in the literature (e.g. Bazzaz and Sultan (1987) and Turner and Knapp (1996), Casper and Jackson (1997), Hooper (1998)). Empirical and theoretical studies by Biondini and Grygiel (1994) and Jackson and Caldwell (1996), among others, have further highlighted that plant competition and plant diversity is also substantially affected by interactions among plant growth and nutrient uptake rates, root lateral spread, root plasticity, and small scale soil nutrient heterogeneity. Consequently, any theory designed to investigate connections among plant diversity, plant production, plant community stability, and the spatial distribution and supply rate of soil nutrients needs to incorporate these mechanisms.

There is a growing number of ecological theories and plant models, in particular in the field of prairie restoration, designed to investigate and predict relationships between plant diversity and plant community production that require for their implementation species specific information in plant parameters like maximum relative growth rate, root nutrient uptake rates, root biomass allocation patterns, nutrient productivity, and at least some set of measurements that

describe the spatial distribution patterns of roots, like root lateral spread, root depth, root length, and root surface area (see for example Rengel (1993) and Smethurst and Comeford (1993), Biondini and Grygiel (1994), Buysee et al. (1996), Jackson and Caldwell (1996), Leadley et al. (1997), Grant (1998), Somma et al. (1998)). Some of the data in question is currently available for some crop species as well as for a number of native species common to the UK and to wetlands of southeastern Canada (see for example Grime and Hunt (1975) and Grime et al. (1988), Poorter and Remkes (1990), Shipley and Peters (1990), Hunt and Cornelissen (1997), for data on relative growth rate, root biomass allocation patterns, and root lateral spread; and Poorter and Remkes (1990) for nitrogen productivity). A series of review articles published in recent years have also summarized available data on rooting depth and root to shoot ratios for plant species from a variety of biomes (Canadell et al. 1996; Jackson et al. 1996; Schulze et al. 1996). Unfortunately, there are significantly less data available for many of the plant physiological and morphological parameters required to accurately estimate nutrient uptake in an heterogeneous soil environment, included among them are details about how plants scale root biomass to root lateral spread, root length and root surface area, and about the kinetics of root nutrient uptake (Boot and Mensink 1990; Bassirirad et al. 1993; Jackson and Caldwell 1996). Regarding most of the species that are common to the Great Plains grasslands, however, there is almost a complete dearth of data for the vast majority of the parameters just discussed. In fact, only recently has there been any efforts to extract quantitative information about root depth and total root length from Weaver's (Weaver 1968) extensive root line drawings of several Great Plains' grassland species (Sun et al. 1997).

The objective of this study was to experimentally estimate parameters regarding root scaling patterns, root biomass allocation, growth rates, nutrient productivity, and root nutrient influx rates of 55 plant species common to Great Plains grasslands. The availability of these data from such a broad number of species will provide applied ecologists, in particular prairie restoration ecologists, with part of the information needed to identify plant morphological and physiological parameters that can lead to the coexistence of various species combinations under different soil nutrient environments. It will also help theoretical ecologists investigate the connections between plant diversity, plant production, and plant community stability, by providing the data needed to develop individual based and spatially explicit plant models that simulate plant growth and competition in heterogeneous soil environments. The specific objectives we addressed were:

1. Determine how soil nitrogen (N) availability affects plant biomass allocation to aboveground (stem and leaves) and belowground components (roots).
2. Determine how plants scale root biomass to root lateral spread, root length, and root surface area, and how these scaling patterns are affected by N availability. In particular we wanted to test the Biondini and Grygiel (1994) hypothesis that root lateral spread, root length, and root surface can be described by allometric scaling functions of root biomass ($Y = a^{*}RB^{b}$), with scaling parameters (*a* and *b*) that are independent of N availability.
3. Determine how the availability of soil N affects the N and phosphorus (P) productivity of plants (defined as plant growth per unit of N or P).
4. Determine maximum relative growth rates.
5. Determine maximum N and P influx rates per unit of root surface area.
6. Determine if grasses and forbs can be classified into statistically distinct groups based on the root scaling, root biomass allocation, growth rate, nutrient productivity, and root nutrient influx rate parameters described above.

Materials and methods

Design of experiment 1

This experiment was conducted in the greenhouse and was designed to address objectives 1–3: **(a)** determine how soil N availability affects plant biomass allocation to aboveground (stem and leaves) and belowground components (roots); **(b)** determine how plants scale root biomass to root lateral spread (rls in m, defined as the furthest linear separation between roots through the center of the plant), total root length (RL in m), and root surface area (RSA in m^2); and **(c)** determine how the availability of soil N affects the N and P productivity of plants. The experiment was organized as a completely randomized design with 55 species (Table 1) and two treatments: a low N supply treatment (1 ppm N), and a high N supply treatment (32 ppm N). Each treatment was replicated 10 times

Table 1. List of species used in experiments 1 and 2. Nomenclature and authorities follows the Great Plains Flora Association (1986). The C and S symbols shown in brackets indicates seeds that were subjected to a cold and/or scarification treatments.

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

for a total of 1100 plants. The seed for this experiment was provided by Prairie Restoration, Inc (Hawley, Minnesota, USA).

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 with sand to a depth of 19 cm. 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 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 dura-

tion of the study, with the light being supplied by Son Agro 430 W High Pressure Sodium lamps configured to produce 5000 lux at plant height.

Seedlings were germinated in flat trays and then transplanted (after 1 to 2 weeks depending on the species) to the experimental pots. Some of the species used in this experiment required stratification and/or scarification of seeds for germination (see Table 1 for the species in question). Stratification 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 was done by slightly abrading the seed coats with sandpaper prior to placement of the seed in the flat trays.

Nutrient application to each plant commenced between 3 and 4 days after transplanting by means of one trickle irrigation emitter placed in each pot. The emitters were connected to 2 Dosatron® injectors. One of the injectors dripped N (in the form of $Ca(NO_3)_2$) at the required treatment concentrations of 1 or 32 ppm. The other injector supplied the rest of the macro- and micronutrients via a Rorison solution with the same concentration for all plants and treatments: 80 ppm Ca^{2+} ($Ca(NO_3)_2$), 24 ppm Mg^{2+} ($MgSO_4$), 78 ppm K^+ (K_2HPO_4), 31 ppm P^{3-} (K_2HPO_4), 3 ppm Fe^{2-} (Fe EDTA), 0.5 ppm Mn^{2+} ($MnSO_4$), 0.5 ppm B^{3+} (H_3BO_3), 0.1 ppm Mo^{6+} ($(NH_4)_6Mo_7O_{24}$), 0.1 ppm Zn^{2+} ($ZnSO_4$), and 0.1 ppm Cu^{2+} ($CuSO_4$). The pH of the solution was maintained between 5.5 and 6.0. Nutrients were supplied daily for 20 minutes to completely replace the soil solution. The entire system was regulated by a programmable Rain Bird Controller®.

Plants were harvested after 60–90 days of growth (depending on the plant species). Growth length for each species was timed so as to prevent roots from reaching the edge of the pots, since that would have invalidated estimates of root lateral spread. Prior to implementing this experiment we conducted extensive trials to determine, for each of the species in question, the maximum length of growth that would be compatible with roots not reaching the edge of the pot. We established that the maximum growth length should ranged from 60 to 90 days, depending on the species, and thus the selected harvest intervals. The accuracy of this estimate can be gauged by the fact that the maximum root lateral spread we measured among all 1100 plants used in the experiment was 19.8 cm, with no species reaching the edge of the pot.

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. Root lateral spread was determined by measuring the furthest linear separation (through the center of the plant) between roots embedded in the grids. After these measurements were completed the aboveground (stems and leaves) and belowground (roots) components were clipped. Roots were digitized with a high resolution Hewlett Packard® scanner, and the images analyzed for total root length, average diameter, and total surface area with the use of a Delta-T Scan® imaging system (Delta-T Devices Ltd). Aboveground biomass and roots were then dried for 72 hrs at 60 °C and weighed. Nitrogen and P content for aboveground and root biomass were determined with the Kjeldahl (Nelson and Sommers 1980) and photometric (Windham 1997) methods.

Design of experiment 2

This experiment was also conducted in the greenhouse and was designed to address objectives 4–5: **(a)** determine maximum relative growth rate ($g\,g^{-1}\,d^{-1}$); and **(b)** estimate the maximum N and P influx rates per unit of root surface area ($g\,m^{-2}\,d^{-1}$) for the species of interest.

We adapted for this experiment protocols developed by Grime and Hunt (1975). The experiment was repeated 2 times. The species studied were the same as in experiment 1 (Table 1). Seedlings for each species were germinated in flat trays (subjected to the required stratification and/or scarification as described in experiment 1), and 5 days after germination transplanted to individual pots (1 plant per pot) filled with pure silica sand to guarantee total control over the nutrient supply. The experimental pots were 5 cm in diameter and 20 cm in height. We used a total of 30 plants per species per replication for a total of 3300 experimental pots. Plants were watered every day with a full strength Rorison solution (56 ppm of N plus concentrations for Ca, Mg, K, P, Fe, Mn, B, Mo, Zn, and Cu as described in experiment 1) to completely replace the nutrient solution in the pot. Temperature, lighting, solution ph, and the arrangement of the pots in the greenhouse bench were as described in experiment 1.

For each replication the experiment was run for 42 days, with 5 plants harvested at weekly intervals. At harvest time, the sand was carefully removed from the pots by washing it out through slits cut into the sides of the pots. Each plant was dried 72 hrs at 60 °C. After drying the roots and aboveground plant bio-

mass were separated and weighed. In addition to this sequential harvesting, 5 seedlings were also dried and weighed as shown above prior to planting to determine initial plant weights. The combined material of 6 weeks of growth and 30 plants per replication was pooled into roots and aboveground biomass and analyzed for total N and P using the Kjeldahl (Nelson and Sommers 1980), and photometric (Windham 1997) methods. The pooling of plant biomass was necessary to generate enough material for the N and P analyses.

Parameter calculations

The scaling relationship between root biomass (BGB in g) and root lateral spread (rls), root length (RL), and root surface area (RSA) were analyzed using an allometric model of the form: $Y = A^{*}BGB^{B}$, where Y was rls (m), RL (m), or RSA (m^2). The scaling parameters (A and B) were estimated with the use of a linear regression on the logarithmic transformation of the allometric equation: $\log_e(Y) = \log(A) + B^{*}\log_e(BGB)$ (Zar 1999). The nomenclature we use for the rls, RL, and RSA scaling parameters are: α, γ, and η for A and β, δ, ρ for B.

Maximum relative growth rate, defined as:

$$RGR_{\max} = \frac{1}{TPB}\frac{dTPB}{dt} \quad (1)$$

was calculated using a linear regressing of the natural logarithm of total plant biomass (TPB in g) against time (t) in days: $\log_e(TB) = a + RGR_{max} \times t$. Maximum relative growth rate in terms of above ground biomass defined as:

$$RGR_{\max} - AGB = \frac{1}{AGB}\frac{dTPB}{dt} \quad (2)$$

was calculated as follows:

1. Total plant biomass was partitioned into its BGB and aboveground (stem plus leaves) biomass (AGB) components: TPB = AGB + BGB.
2. The maximum growth rate of AGB defined as:

$$AGB_{\max gr} = \frac{1}{AGB}\frac{dAGB}{dt} \quad (3)$$

was estimated using a linear regressing of the natural logarithm of AGB (g) against time (t) in days: $\log_e(AGB) = a + AGB_{max\ gr} \times t$.

3. We then calculated the scaling constant for root-shoot development (RSD) by regressing BGB against AGB and using the slope of this regression as an estimate of RSD (Hunt and Cornelissen 1997): $BGB \cong RSD^{*}AGB$
4. By combining steps 1 and 3 we have that $TPB = AGB^{*}(1 + RSD)$. If we take the time derivative of both sides of this equation and then divide by AGB we have:

$$\frac{1}{AGB}\frac{dTPB}{dt} = \frac{1}{AGB}\frac{dAGB}{dt}(1 + RSD) \quad (4)$$

and thus from Equations (2) and (3)

$$RGR_{\max} - AGB = AGB_{\max gr}{}^{*}(1 + RSD) \quad (5)$$

RGR_{max}-AGB was calculated because it is a useful indicator of a plant species ability to regrow after defoliation, since it relates RGR_{max} to available photosynthetic material (stem and leaves). The plant biomass values (TPB, AGB, and BGB) per time period used in these calculations were the averages of the 5 plants harvested at each sampling period (see experiment 2 for details). The RGR_{max} and RGR_{max}-AGB data reported in the results section are the average and standard error for the 2 replications.

Nitrogen productivity (NP in $g\,gN^{-1}$) was estimated using data from both the high and low N treatments of experiment 1. Phosphorus productivity (PP in $g\,gP^{-1}$) was only calculated for the high N treatment, because the low N treatment unfortunately did not produce enough material to analyze both N and P. We calculated NP and PP using the equation suggested by Vazquez de Aldana and Berendse (1997) adapted to our to experimental design. According to Vazquez de Aldana and Berendse (1997) nutrient productivity during a given time period (A[t]) is equal to:

$$A(t) = \frac{TPB_t - TPB_{t-1}}{\frac{Nutr_t + Nutr_{t-1}}{2}} \quad (6)$$

In our case, since we only harvested once (at the end

of the experiment), this equation reduces to:

$$A = \frac{TPB_{end} - TPB_0}{\frac{Nutr_{end} + Nutr_0}{2}} \quad (7)$$

The term A in this equation is NP or PP, TPB_0 and TPB_{end} are total plant biomass (g) at the beginning of the experiment and at harvest time, $Nutr_0$ and $Nutr_{end}$ are total N or P content (gN or gP) in plant biomass at the beginning of the experiment and at harvest time. However, since TPB_0 was always several orders of magnitude lower than TPB_{end} the equation can be further reduced to:

$$A \cong \frac{TPB_{end}}{Nutr_{end}} \quad (8)$$

which is the one we used for calculations.

Nitrogen and P maximum influx rates per unit of root surface area (Imax-N and Imax-P in $g\,m^{-2}\,d^{-1}$) were estimated with data from experiment 2 using the flux equations from the Barber and Cushman model (Barber 1984). In this model nutrient flux at the root surface follows Michaelis-Menten kinetics of the form:

$$J_r = \frac{Imax^*(C_l - C_{\min})}{K_m + (C_l - C_{\min})} \quad (9)$$

where J_r is nutrient flux to the root ($g\,m^{-2}\,d^{-1}$), Imax is the maximum influx per unit of root surface area, C_l and C_{min} are the actual nutrient concentrations in soil solution, and the minimum nutrient concentrations in solution required for root uptake ($g\,g^{-1}$), and K_m is the half saturation constant for nutrient uptake ($g\,g^{-1}$). Since in experiment 2 plants were watered every day with a full strength Rorison solution that completely replaced the nutrient solution in the pot, it is safe to say that there were minimum limitations for N or P uptake and thus the following approximations can be made:

$$\frac{C_l - C_{\min}}{K_m + (C_l - C_{\min})} \cong 1 \text{ and therefore} \quad (10)$$

and therefore

$$J_r \cong \mathrm{Im}ax \quad (11)$$

With this in mind, according to Barber (1984) the plant cumulative N or P uptake (Tuptake in g of N or P) at time *te* (end of experiment) would be equal to:

$$Tuptake_{te} = \int_0^{te} \mathrm{Im}ax^*RSA_0 ds + \int_0^{te} \mathrm{Im}ax \frac{d\,RSA_{te-t}}{dt} \int_0^{} \mathrm{Im}ax\, ds\, dt \quad (12)$$

where RSA_0 is the plant initial root surface area, $\frac{d\,RSA}{dt}$ and is the rate of change of RSA with time. Using the allometric equations for RSA developed from experiment 1 and the growth rate equations from experiment 2 we can estimate root surface area at time t an its derivative as:

$$\begin{aligned} RSA_t &= \eta^*BGB_t^{\rho} \\ &= \eta^*BGB_0^{\rho}{}^*e^{\rho^*BGB_{\max gr}{}^*t} \text{ since } BGB_t \\ &= BGB_0{}^*e^{BGB_{\max gr}{}^*t} \end{aligned} \quad (13)$$

and

$$\frac{d\,RSA}{dt} = \eta^*BGB_0^{\rho}{}^*\rho^*BGB_{\max gr}{}^*e^{\rho^*BGB_{\max gr}{}^*t} \quad (14)$$

where η and ρ are the allometric constants that relate BGB to RSA, BGB_0 is the initial root biomass, and BGB_{maxgr} is the maximum growth rate for root biomass. BGB_{maxgr} was estimated with data from experiment 2 by regressing the natural logarithm of BGB with time: $\log_e(BGB) = a + BGB_{maxgr} \times t$. By Replacing RSA_0 and $\frac{d\,RSA}{dt}$ in Equation (12) with Equation (13) and Equation (14) and solving the integrals we can estimate Imax as follows:

$$Tuptake_{te} = \mathrm{Im}ax^*\frac{\eta^*BGB_0^{\rho}}{\rho^*BGB_{\max gr}}{}^*(e^{\rho^*BGB_{\max gr}{}^*te} - 1) \quad (15)$$

thus

$$\mathrm{Im}ax = \frac{Tuptake_{te}{}^*\rho^*BGB_{\max gr}}{\eta^*BGB_0^{\rho}{}^*(e^{\rho^*BGB_{\max gr}{}^*te} - 1)} \quad (16)$$

where

$$Tuptake_{te} = \frac{AGB_{te}*\%N - AGB_{te}\{\text{or } \%P\} + BGB_{te}*\%N - BGB_{te}\{\text{or } \%P\}}{100} \quad (17)$$

where AGB_{te}, BBG_{te}, %N-AGB_{te} {or %P}, and %N-BGB_{te} {or %P} are the aboveground and root biomass (g), and their corresponding %N or %P at harvest time (*te* = 42 days). All the data used in these calculations came from experiment 2.

Statistical analysis

Statistical comparisons between high and low N treatments (experiment 1) for root:shoot (R:S) ratios, average root diameter, and nitrogen productivity were conducted using an unequal variance t-test (Zar (1999), p 122). Differences among treatments were considered significant for a Bonferroni adjusted $P < 0.05$ (Zar (1999), p 209). Linear regressions to estimate the scaling parameters for the allometric relationships between root biomass and root lateral spread, root length, and root surface area were first calculated for both the high and low N treatments. We then determined if the slopes and intercepts of these regressions where statistically different ($P < 0.05$), if they were not we proceeded to calculate a common slope and intercept. Testing for differences in and calculations of common values for slopes and intercepts were done using methods outlined by Zar (1999), p 360).

One of the objectives of this study (Objective 6) was to investigate if the root scaling, root biomass allocation, growth rate, nutrient productivity, and root nutrient influx rate parameters could be used to separate both grasses and forbs/shrubs into statistically distinct groups. To address this objective we used cluster analysis employing the hierarchical linkage method (Ward's method) with a cut-off point of 50% of the maximum Euclidian group distance (Ludwig and Reynolds 1988). The variables we used in the cluster analysis were: **(a)** the rls, RL, and RSA allometric scaling constants α, β, γ, δ, η, and ρ **(b)** the R:S ratios for the high and low N treatments; **(c)** the growth rate parameters RGR_{max} and RGR_{max}-AGB; **(d)** NP for the high and low N treatments; **(e)** PP for the high N treatment; and **(f)** Imax-N and Imax-P. To account for their differences in units, all the variables were standardized to the 0–1 range using the maximum value for each variable. Statistical differences ($P < 0.001$) among the clusters were tested, using all the variables as a multivariate vector, with a multi response permutation procedure (MRPP, Biondini et al. (1991)). Statistical differences among clusters for single variables ($P < 0.05$) were tested using analysis of variance (Zar (1999), p 177) and the Tukey test (Zar (1999), p 210).

Results

Biomass allocation and root scaling parameters

Root lateral spread, root length, and root surface area had significant allometric relationships with root biomass, but there were no statistical differences between the regressions for the high and low N treatments, thus the results reported are for the common regression (Figures 1, 2 and 3)(Appendices 1 and 2). A note, it cannot be totally disregarded that the lack of treatment effect on the allometric equations is partially an artifact of the relatively small number of replications (10 replications per treatment, thus 8 degrees of freedom per regression). In addition to these species level allometric relationships (Appendices 1 and 2), we also found common allometric scaling pattern at a different hierarchical level, this one involving statistically distinct group of species (Figures 1, 2 and 3) derived from the cluster analyses discussed latter (Table 2). These results indicate that the allometric relationship of root biomass with root lateral spread, root length, and root surface area is composed of 2 distinct hierarchical components: **(a)** a species group component defined by the common allometric scaling patterns shown in Figures 1, 2 and 3; and **(b)** a species specific component defined by the allometric scaling patterns shown in (Appendices 1 and 2). The only exception to this hierarchical structure involved the allometric relationship of root biomass with root surface area for 6 grasses: *Bouteloua curtipendula*, *Bouteloua gracilis*, *Koeleria cristata*, *Poa pratensis*, *Stipa comata*, and *Stipa viridula* (Figure 3A), (Table 2), (Appendix 2). At the individual species level these plants showed significant allometric relationships between root biomass and root surface area (Appendix 2) but there was no common allometric pattern for the group of species as a whole (Figure 3A), even though they comprise a statistically distinct cluster (Table 2).

The lack of treatment effect on the allometric relationship between root biomass and root surface area

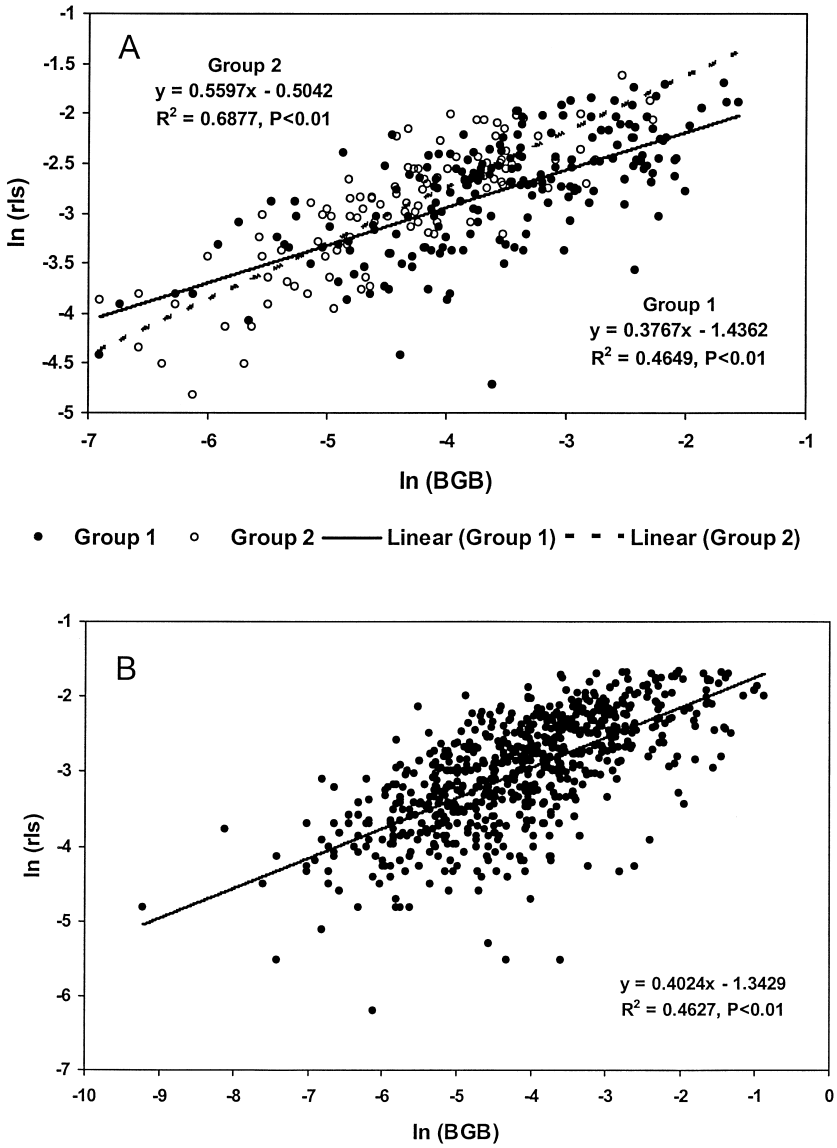

Figure 1. Relationship between the log of root lateral spread (rls in m) and the log of root biomass (BGB in g). **(A)** Relationship for grasses. Group 1: *Agropyron cristatum*, *Agropyron spicatum*, *Andropogon gerardii*, *Bromus inermis*, *Calamovilfa longifolia*, *Elymus canadensis*, *Hordeum jubatum*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorgastrum nutans*, and *Sporobolus cryptandrus*. Group 2: *Bouteloua curtipendula*, *Bouteloua gracilis*, *Koeleria cristata*, *Poa pratensis*, *Stipa comata*, and *Stipa viridula*. The slope of regressions for Group 1 and 2 are statistically different ($P < 0.05$). A note Group 1 correspond to Clusters 1 and 3 in (Table 2), while Group 2 correspond to Cluster 2 in the same table. **(B)** Relationship for all forbs combined.

was further supported by the response of the average root diameter to the N supply, and thus root biomass. There was no overall relationship between root biomass and average root diameter (Figure 4), and only 13 of the 55 species studied showed any response to the N treatments, with high root diameters evenly split between them (Appendix 2): 7 species (4 grasses and 3 forbs) had larger average root diameters under the high N treatment than under the low one, while for 6 species (3 grasses and 3 forbs) the reverse was the case.

The N supply had a significant effect on how plants partition biomass between roots and aboveground compartments (R:S ratio). A total of 34 of the 55 species studied (62%) showed a significant treatment effect, with the R:S ratio higher under the low

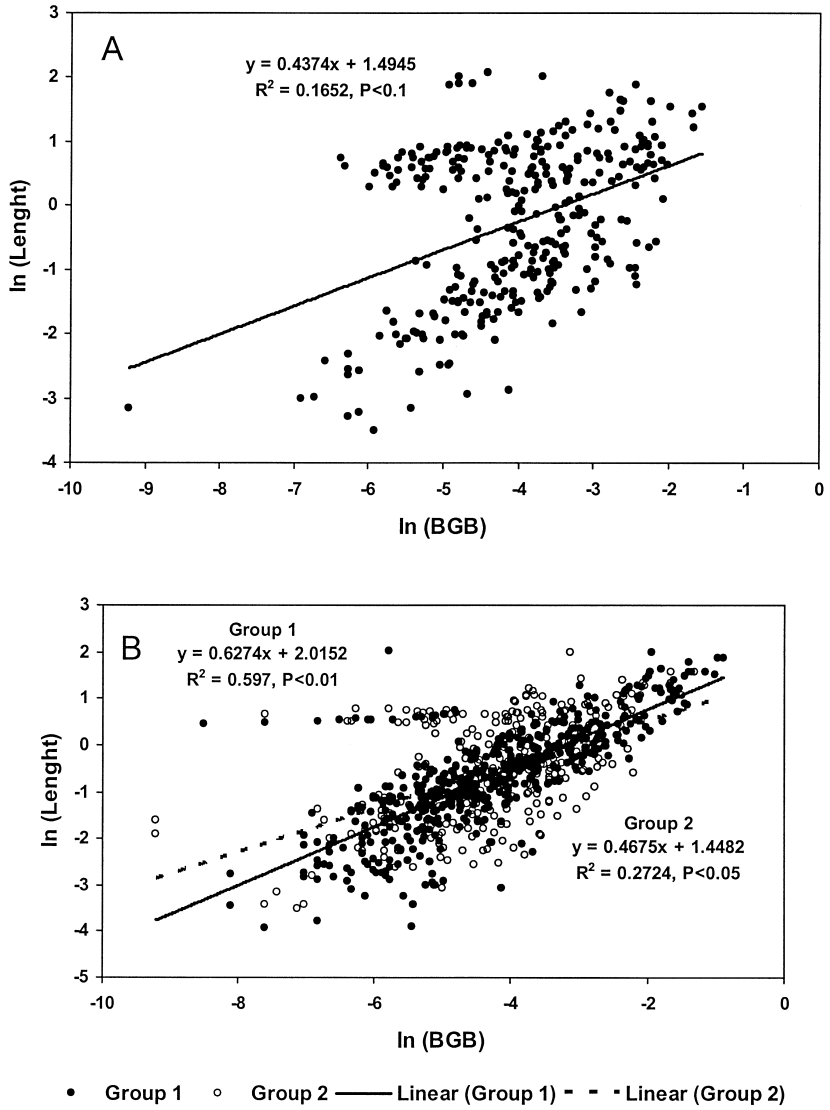

Figure 2. Relationship between the log of root length (in m) and the log of root biomass (BGB in g). **(A)** Relationship for all grasses. **(B)** Relationship for forbs. Group 1: *Achillea millefolium*, *Anaphalis margaritacea*, *Artemisia dracunculus*, *Artemisia tridentate*, *Asclepias verticillata*, *Chrysopsis villosa*, *Cirsium arvense*, *Coreopsis lanceolata*, *Gaillardia aristata*, *Geum triflorum*, *Lupinus perennis*, *Melilotus officinalis*, *Potentilla arguta*, *Ratibida columnifera*, *Rudbeckia hirta*, *Solidago missouriensis*, *Solidago rigida*, *Taraxacum officinale*, *Tragopogon dubius*, *Verbena stricta*, and *Vicia americana*. Group 2: *Allium stellatum*, *Aster ericoides*, *Astragalus canadensis*, *Chenopodium album*, *Conyza canadensis*, *Dalea purpurea*, *Galium boreale*, *Grindelia squarrosa*, *Hedeoma hispidum*, *Helianthus maximilianii*, *Liatris punctata*, *Linum perenne*, *Oenothera biennis*, *Oxytropis lambertii*, *Psoralea esculenta*, *Rosa arkansana*, and *Sphaeralcea coccine*. The slope of regressions for Group 1 and 2 are statistically different ($P < 0.05$). A note Group 1 correspond to Clusters 1 in (Table 3), while Group 2 correspond to Clusters 2 and 3 in the same table.

N treatment than under the high one: an average of 1.3 in the low N treatment vs. 0.73 in the high one (Appendix 3).

Growth rates, nutrient productivity, and nutrient influx

Maximum relative growth rate expressed in terms of both total plant biomass (RGR_{max}) and aboveground biomass (RGR_{max}-AGB) for all the species are shown in (Appendix 3). As expected there was a significant

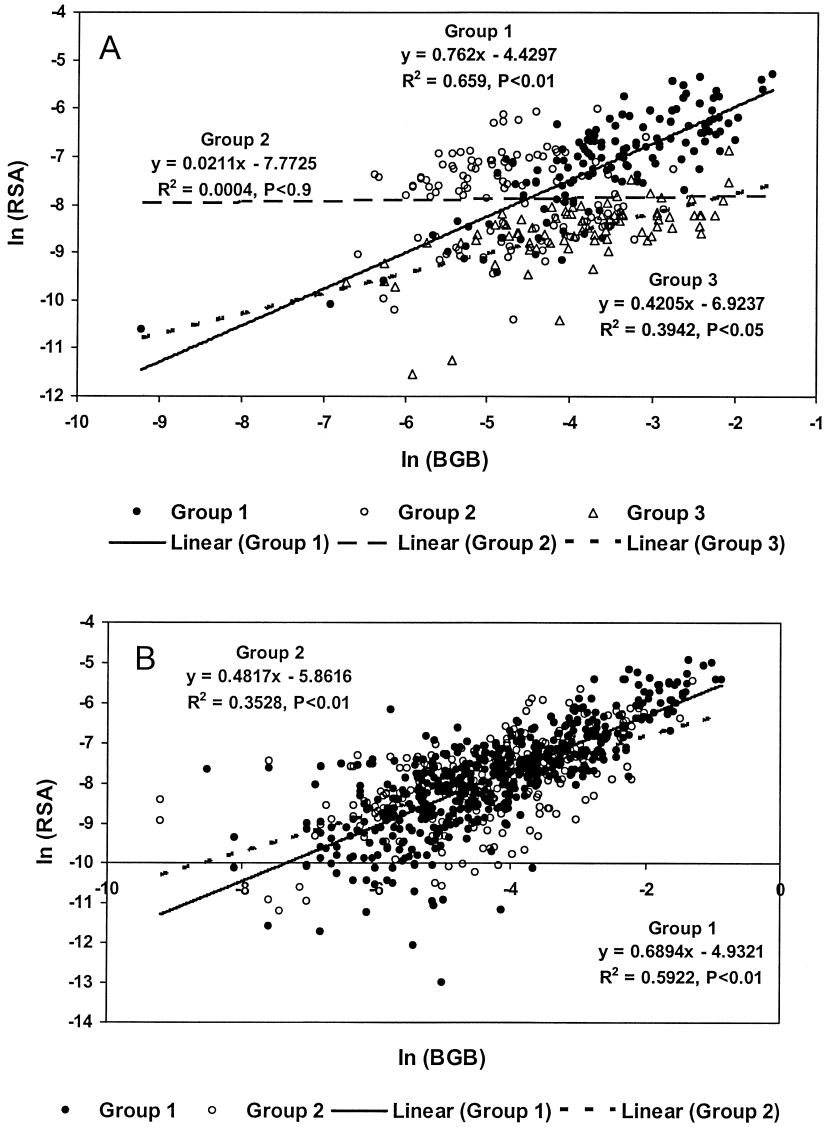

Figure 3. Relationship between the log of root surface area (RSA in m^2) and the log of root biomass (BGB in g). **(A)** Relationship for grasses. Group 1: *Agropyron cristatum*, *Andropogon gerardii*, *Bromus inermis*, *Hordeum jubatum*, *Panicum virgatum*, *Schizachyrium scoparium*, and *Sorgastrum nutans*. Group 2: *Bouteloua curtipendula*, *Bouteloua gracilis*, *Koeleria cristata*, *Poa pratensis*, *Stipa comata*, and *Stipa viridula*. Group 3: *Agropyron spicatum*, *Calamovilfa longifolia*, *Elymus canadensis*, and *Sporobolus cryptandrus*. The slope of regressions for Group 1, 2 and 3 are statistically different ($P < 0.05$). A note Groups 1, 2 and 3 correspond to Clusters 1, 2, and 3 in (Table 2). **(B)** Relationship for forbs. Groups 1 and 2 are as defined in (Figure 2). The slope of regressions for Group 1 and 2 are statistically different ($P < 0.05$).

relationship between RGR_{max} and RGR_{max}-AGB but it fell well below a perfect fit ($R^2 = 0.64$, Figure 5B). Both the frequency distribution and mean values for grasses and forbs/shrubs were very similar: mean and standard error (SE) for grasses were 0.11 (± 0.005) for RGR_{max} and 0.18 (± 0.014) for RGR_{max}-AGB; for forbs the corresponding values were 0.11 (± 0.005) and 0.17 (± 0.008). Within grasses, however, mid successional species have consistently higher relative growth rates than late successional ones (Figure 5A): 0.13 $g\,g^{-1}\,d^{-1}$ (± 0.005) vs. 0.10 $g\,g^{-1}\,d^{-1}$ (± 0.001) ($P = 0.017$) for RGR_{max}, and 0.23 $g\,g^{-1}\,d^{-1}$ (± 0.022) vs. 0.17 $g\,g^{-1}\,d^{-1}$ (± 0.002) ($P = 0.016$) for RGR_{max}-AGB.

Plants N productivity was significantly affected by the N treatments. A total of 42 of the 55 species stud-

Table 2. Result from the cluster analysis of grasses. Clusters were tested for overall statistical significance at $P < 0.001$. Mean values within a row with different letters are different at the $P < 0.05$ (P-value column). For definition of the parameters see text (only parameters that differ among clusters are shown).

	Cluster 1	Cluster 2	Cluster 3	
	Agropyron cristatum			
	Andropogon gerardii	*Bouteloua curtipendula*		
	Bromus inermis	*Bouteloua gracilis*		
	Hordeum jubatum	*Koeleria cristata*	*Agropyron spicatum*	
	Panicum virgatum	*Poa pratensis*	*Calamovilfa longifolia*	
	Schizachyrium scoparium	*Stipa comata*	*Elymus canadensis*	
Parameters	*Sorgastrum nutans*	*Stipa viridula*	*Sporobolus cryptandrus*	**P-value**
α	0.29[a]	**0.68**[b]	0.34[a]	0.002
β	0.40[a]	**0.58**[b]	0.44[a]	0.050
η	**0.015**[a]	0.004[b]	0.001[b]	0.038
ρ	**0.75**[a]	0.40[b]	0.45[b]	0.002
R:S High N	0.56[a]	0.56[a]	**0.78**[b]	0.051
R:S Low N	**1.36**[a]	0.73[b]	1.13[b]	0.028
Imax-N ($gN\,m^{-2}\,d^{-1}$)	0.2865[a]	0.3488[a]	**0.9445**[b]	0.016
Imax-P ($gP\,m^{-2}\,d^{-1}$)	0.08259[a]	0.07935[a]	**0.2490**[b]	0.007

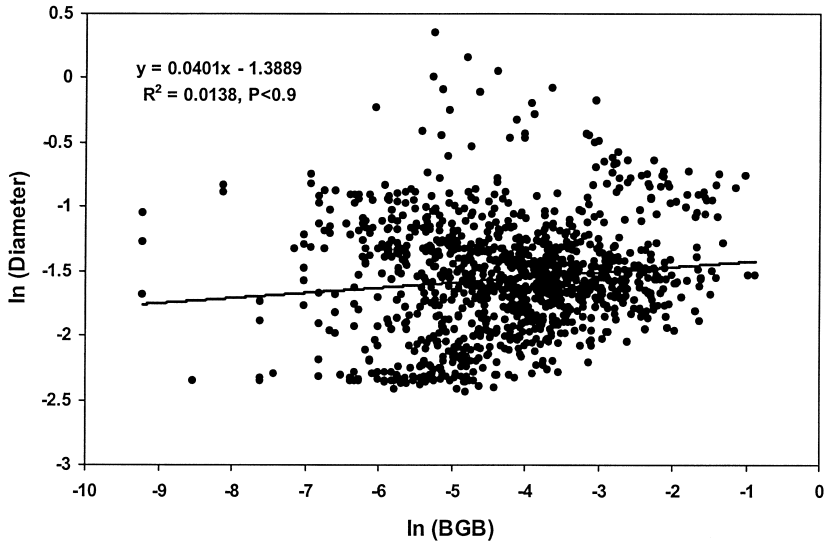

Figure 4. Relationship between average the log of root diameter (in mm) and the log of root biomass (BGB in g) for all the species.

ied (78%) showed a significant treatment effect, with NP being higher under the low N treatment than under the high one in 41 of these species, the only exception being *Aster ericoides* where the reverse was the case (Figure 6)(Appendix 4). Under the high N treatment both N and P productivity were significantly higher in grasses than in forbs/shrubs (Figure 6): for NP the mean and SE values were 43 (± 1.88) for grasses vs. 37 (± 0.99) for forbs/shrubs ($P = 0.008$), while for PP the corresponding values were 191 (± 10.4) vs. 131 (± 9.6) ($P < 0.0002$). Furthermore, the NP and PP of C_4 grasses was, on average, higher than that of C_3 grasses but only in the high N supply treatment (Figure 6): 48 (± 3.16) vs. 39 (± 1.01) for NP ($P = 0.029$) and 210 (± 17.5) vs. 171 (± 10.4) for NP ($P = 0.07$). No differences in NP were found between grasses and forbs or between C_3 and C_4 grasses under the low N treatment where it averaged 63 (± 2.76). Overall, the NP in the high and low N treatment were correlated, although very weakly (Figure 7A). A stronger correlation was found between PP and NP in the high N treatment (Figure 7B).

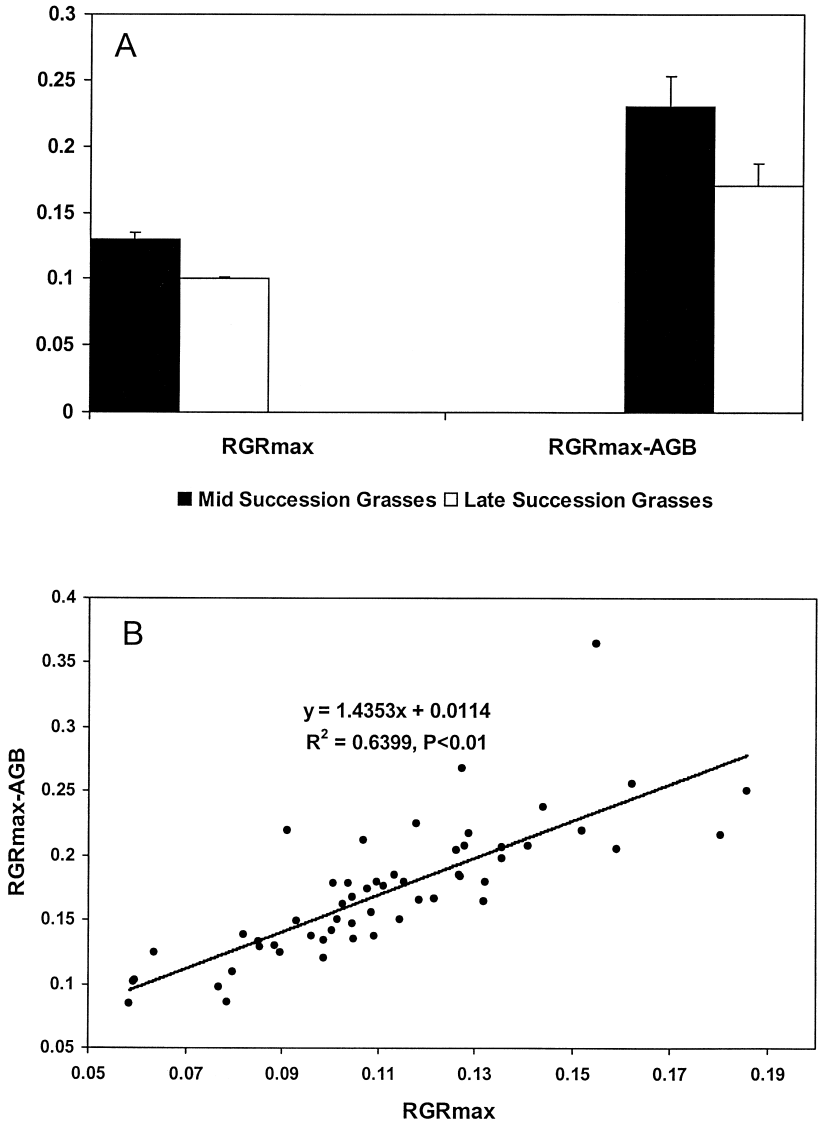

Figure 5. **(A)** Average maximum relative growth rate (RGR_{max} in $g\,g^{-1}\,d^{-1}$) and maximum relative growth rate in terms of above ground biomass (RGR_{max}-AGB in $g\,g^{-1}\,d^{-1}$) for mid and late succession grasses. Vertical bars are the SE of the mean. Within each measurement means are statically significant at $P < 0.05$. **(B)** Relationship between RGR_{max} and RGR_{max}-AGB for all species.

Maximum N and P influx rates per unit of root surface area (Imax-N and Imax-P in $g\,m^{-2}\,d^{-1}$) for all species are shown in (Appendix 5). No differences in Imax-N or Imax-P were found between grasses and forbs or between C_3 and C_4 grasses. There was, however, a significant, although weak, relationships across all species among Imax-N, Imax-P, and RGR_{max} (Figure 8)

Grass and forb groups

We used cluster analysis to determine if grasses and forbs/shrubs could be classified into distinct groups on the bases of the root scaling, root biomass allocation, growth rates, root nutrient productivity, and nutrient influx rate parameters described in Appendices 1, 2, 3, 4 and 5. Both grasses and forbs/shrubs did in fact separate into 3 statistically distinct ($P < 0.001$) clusters (Tables 2 and 3).

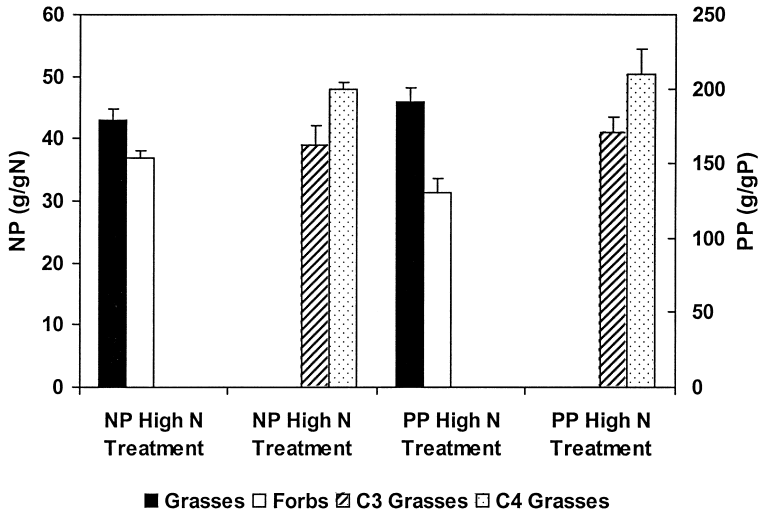

Figure 6. Comparisons in N and P productivity (NP and PP in $g\,gN^{-1}$ and $g\,gP^{-1}$) between grasses and forbs and between C_3 and C_4 grasses. Vertical bars are the SE of the mean. Within each comparison mean are statically significant at $P < 0.05$.

For grasses the parameters that statistically ($P < 0.05$) differentiated the clusters were: **(a)** the scaling constants for root lateral spread (α and β) and root surface area (η and ρ); **(b)** the R:S ratios for both the high and low N treatments; and **(c)** Imax-N and Imax-P rates. The first cluster is composed of 7 grasses that have on average large scaling constants for root surface area and a high R:S ratio under a low N supply (Table 2). The main characteristic of the 6 grasses in the second cluster (Table 2) is their large scaling constants for root lateral spread. Finally, the 4 grasses in the third cluster (Table 2) have high R:S ratio under a high N supply and Imax-N and Imax-P rates that are, on average, 3 times higher than the ones for grasses in the 2 other clusters.

The parameters that statistically differentiated the clusters of forbs/shrubs were: **(a)** the scaling parameters for root length (γ and δ) and root surface area; **(b)** the R:S ratios for the high N treatments; **(c)** RGR_{max} and RGR_{max}-AGB; **(d)** the N productivity in the high N treatment; and **(e)** the Imax-N and Imax-P rates. The first cluster is composed of 20 forbs and 1 shrub (Table 3) with its main characteristic being large scaling constants for root length and root surface area. The second cluster is composed of 6 forbs (Table 3) that have, on average, larger NP and R:S ratios than the forbs and shrubs in the other 2 clusters. The third cluster is composed of 10 forbs and 1 shrub (Table 3) whose main characteristics are: **(a)** a statistically higher RGR_{max} and RGR_{max}-AGB vis a vis the other 2 clusters; and **(b)** Imax-N and Imax-P rates that are, on average, 2 times larger than the equivalent ones in the other 2 clusters (Table 3).

Discussion

There is a substantial body of both empirical and theoretical data that suggests that there are trade-offs in the way plants allocate biomass to roots: under low nutrient conditions plants increase their biomass allocation to roots at the expense of leaves and shoots to increase nutrient uptake, thus increasing their R:S ratio (Boot and Mensink 1990; Aerts et al. 1991; Ryser and Lambers 1995; Reynolds and D'Antonio 1996; Fransen et al. 1998; McConnaughay and Coleman 1999). Drew and Saker (1975) and Bingham and Stevenson (1993) have suggested that the increases in R:S ratios in response to a low N supply are caused by a diversion of carbohydrates into the root system to support increased lateral root growth toward soil pockets within the plants rooting area that have high nutrient concentrations. Our results are very consistent with the hypothesized trade-offs: two thirds of the 55 species used in our experiment had significant increases in their R:S ratio in response to declines in the N supply. It is also interesting to note that while R:S ratios increased with reductions in the N supply, the species patterns of R:S ratios themselves did not change as shown by the positive correlations between the R:S ratios for the high and low N treatments (Figure 9).

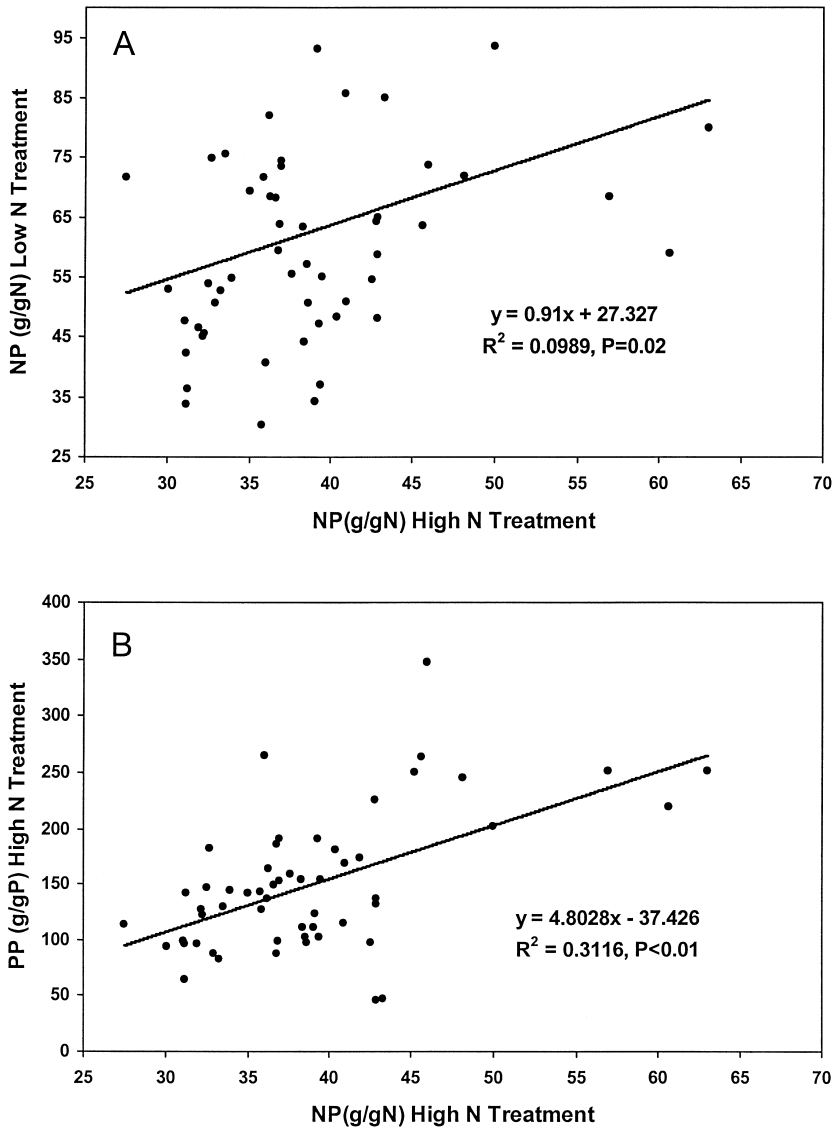

Figure 7. **(A)** Relationship between the N productivity (NP in g gN^{-1}) in the high vs. the low N treatment. **(B)** Relationship between the N and P productivity (PP in g gP^{-1}) in the high N treatment.

Tilman (1990) advanced the proposition that there should be a negative relationship between the allocation of plant biomass to roots and RGR (the higher the R:S ratio the lower the RGR). Shipley and Peters (1990), however, after analyzing 68 species (mostly from southeastern Canada), argued that Tilman's proposition was not supported by the evidence. A similar conclusion using a different set of species was reached by Aerts et al. (1991). Likewise, we did not find any correlation between RGR_{max} and R:S ratios. The lack of relationship between the R:S ratio and RGR, however, may have resulted from the fact that we did not differentiate between stem and leaf biomass. Tilman (1991), in a response to Shipley and Peters (1990), made precisely this argument. More extensive studies by Poorter and Remkes (1990) and Hunt and Cornelissen (1997) have supported Tilman's argument. In these studies the RGR was found to be highly correlated not with total above ground biomass but with leaf area. Hunt and Cornelissen (1997) have emphasized, that on a evolutionary scale, many plant species have been able to increase RGR, without increasing their leaf biomass, by changing their specific leaf area (leaf area per unit of leaf biomass). While

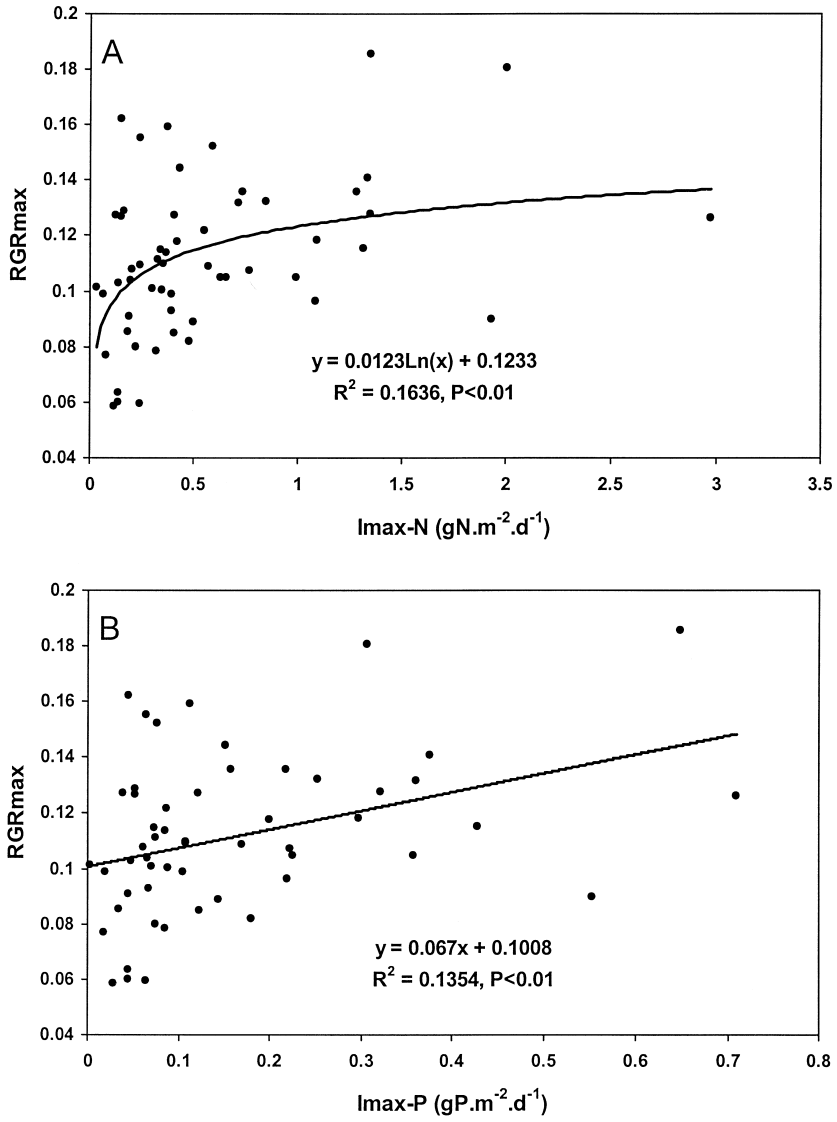

Figure 8. Relationship (all species) between maximum relative growth rate (RGR_{max} in $g\,g^{-1}\,d^{-1}$) and the maximum influx rates per unit of root surface area for: **(A)** N (Imax-N in $gN\,m^2\,d^{-1}$); **(B)** P (Imax-P in $gP.m^2\,d^{-1}$).

we did not find a direct relationship between R:S ratio and RGR with did find positive correlations within grasses among R:S, Imax-N, and Imax-P (Figure 10), and within all plants among RGR, Imax-N, and Imax-P (Figure 8). These results tend to lend further support, at least for the case of grasses, to another side of Tilman's proposition regarding plant biomass allocation trade-offs: while reductions in biomass allocation to photosynthetic tissue depresses RGR, they lead to increases in the plant's ability to compete for soil resources.

Our results confirmed data from other studies that have shown a higher N productivity (NP) in the part of C_4 grasses when compared with C_3 grasses (see for example (Brown 1978)). This higher NP is believed to be an adaptation to growth in low N sites, even though the advantage may also extend to high N sites, since C_4 grasses have been shown to be aggressive invaders in cultivated and highly fertilized crop fields (Brown 1978). The NP of C_3 grasses, however, was negatively correlated to RGR_{max} (Figure 11) a result that is in conflict with similar data for C_3 grasses reported by Poorter et al. (1990) and

Table 3. Result from the cluster analysis of forbs and shrubs. Clusters were tested for overall statistical significance at $P < 0.001$. Mean values within a row with different letters are different at the $P < 0.05$ (P-value column). For definition of the parameters see text (only parameters that differ among clusters are shown).

	Cluster 1	Cluster 2	Cluster 3	
	Achillea millefolium			
	Anaphalis margaritacea			
	Artemisia dracunculus			
	Artemisia tridentata			
	Asclepias verticillata			
	Chrysopsis villosa			
	Cirsium arvense			
	Coreopsis lanceolata			
	Gaillardia aristata			
	Geum triflorum			
	Lupinus perennis		*Aster ericoides*	
	Melilotus officinalis		*Astragalus canadensis*	
	Potentilla arguta		*Conyza canadensis*	
	Ratibida columnifera		*Dalea purpurea*	
	Rudbeckia hirta		*Grindelia squarrosa*	
	Solidago missouriensis	*Allium stellatum*	*Hedeoma hispidum*	
	Solidago rigida	*Chenopodium album*	*Helianthus maximilianii*	
	Taraxacum officinale	*Galium boreale*	*Linum perenne*	
	Tragopogon dubius	*Liatris punctata*	*Oenothera biennis*	
	Verbena stricta	*Oxytropis lambertii*	*Rosa arkansana*	
Parameters	*Vicia americana*	*Psoralea esculenta*	*Sphaeralcea coccinea*	**P-value**
γ	**18.57**[a]	7.10[b]	10.69[b]	0.0001
δ	**0.81**[a]	0.43[b]	0.54[b]	0.0001
η	**0.0172**[a]	0.0043[b]	0.0033[b]	0.0017
ρ	**0.80**[a]	0.45[b]	0.51[b]	0.0006
R:S High N	0.65[a]	**1.04**[b]	0.90[b]	0.0194
RGR_{max} ($g\,g^{-1}\,d^{-1}$)	0.11[a]	0.08[b]	**0.14**[c]	0.0004
RGR_{max}- AGB ($g\,g^{-1}\,d^{-1}$)	0.16[a]	0.13[a]	**0.21**[b]	0.0005
NP High N ($g\,gN^{-1}$)	35.78[a]	**44.95**[b]	35.19[a]	0.0007
Imax-N ($gN.m^{-2}d^{-1}$)	0.5269[a]	0.1507[a]	**1.10517**[b]	0.0026
Imax-P ($gP.m^{-2}d^{-1}$)	0.14664[a]	0.0411[a]	**0.3230**[b]	0.0009

Vazquez de Aldana and Berendse (1997) that showed a positive correlation between NP and RGR. It is interestingly to note, however, that for the C_3 grasses we studied, there was a positive correlation between the scaling constant (δ) that relates root biomass to root length and NP (Figure 11): the larger the root length a plant was able to generate per unit of root biomass the higher its NP. We suggest, thus, that **(a)** NP is probably more related to N uptake, and thus root length, than RGR; and **(b)** it is possible that for the species used in the Poorter et al. (1990) and Vazquez de Aldana and Berendse (1997) studies, RGR may have acted as a proxy for N uptake, and thus root length.

In addition to the differences we found in NP productivity between C_3 and C_4 grasses, we also found differences among these grasses as a function of their successional status. Mid successional grasses had lower NP than late successional ones under a high N supply (Appendix 4): 38 $g\,gN^{-1}$ vs. 45 $g\,gN^{-1}$ ($P < 0.05$). Conversely, mid successional grasses had higher RGR_{max} than late successional ones: 0.13 $g\,g^{-1}\,d^{-1}$ vs. 0.10 $g\,g^{-1}\,d^{-1}$ ($P < 0.05$, Figure 5A). The picture that emerges from these analyses is that mid successional grasses have faster growth rates and thus can establish themselves more aggressively in the early stages of succession, but are not very efficient in the use of N. Late successional grasses have slower

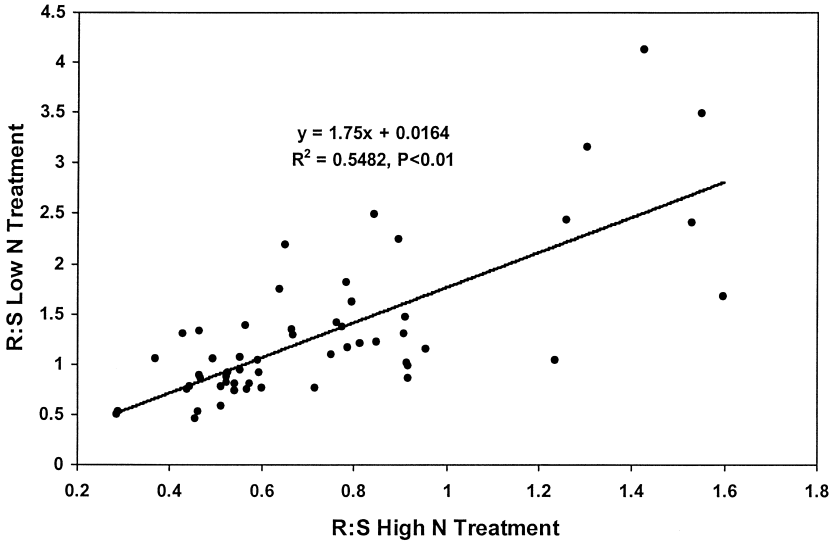

Figure 9. Relationship between the root:shoot ratio (R:S) of plants grown in the high N treatment vs. the low N treatment.

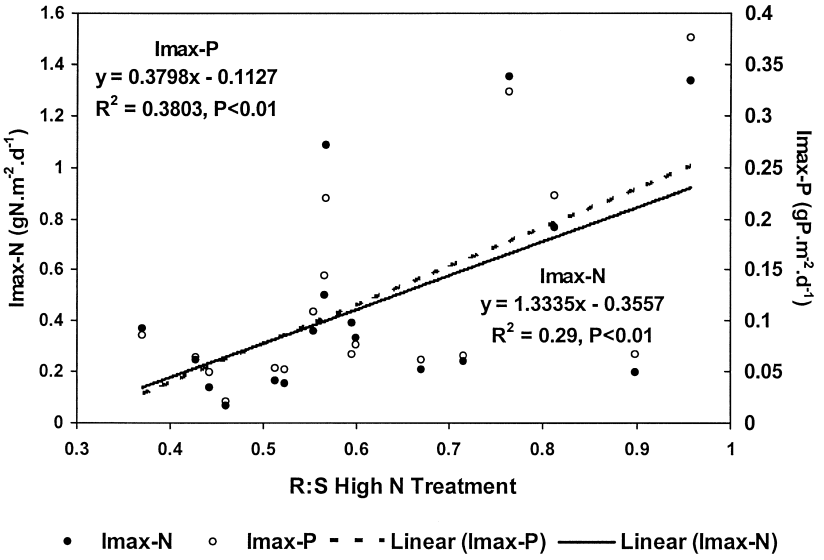

Figure 10. Relationship between the root:shoot ratio (R:S) of grasses and their N and P maximum influx rates per unit of root surface area (Imax-N and Imax-P in $g\,m^2\,d^{-1}$).

growth rates but are very efficient in the use of N, a trait that becomes very useful under the conditions of intense competition for soil resources that characterize diverse late successional communities.

Available data on the spatial distribution of soil resources is limited but shows variability that ranges from within the root zone (0.1 m or less) to the landscape level (Palmer and Dixon 1990; Jackson and Caldwell 1993; Mahmoudjafari et al. 1997; Robertson et al. 1997). Since plants acquire nutrients through their root system by integrating over a given volume of soil, root lateral spread, root length, and root surface area are critical to their ability to compete for limited resources. Root lateral spread, by controlling the area covered by the root system, can directly affect the resource environment to which a plant is actually exposed (Biondini and Grygiel 1994; Mordelet et al. 1996). In an analysis of the literature Casper and Jackson (1997) concluded that large root systems should have a disproportionate advantage in patchy soil environments because they are more likely to encounter a high nutrient patch within their

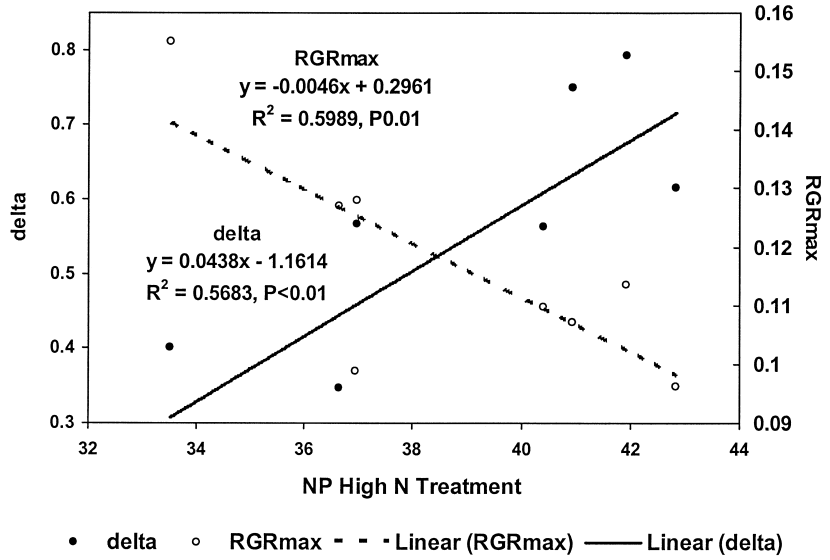

Figure 11. Relationship within C_3 grasses among the N productivity (NP in $gN.g^{-1}$) in the high N treatment, maximum relative growth rate (RGR_{max} in $g\,g^{-1}\,d^{-1}$) and the root length scaling constant δ (delta).

nutrient zone. In addition van Vuuren et al. (1996) and Einsmann et al. (1999), Hodge et al. (2000) have shown that the total root length, root surface area, and root uptake rates within the plant's rooting volume can also influence how successful plants are in competing for nutrients in an heterogeneous soil environment. As hypothesized by Biondini and Grygiel (1994) all the 55 plants we studied showed significant allometric relationships between root biomass and root lateral spread, root length and root surface area (Figure 1, 2, 3 and Appendix 1, 2, 3), and the parameters that characterized these equations were unaffected by the N supply. Furthermore, the variability in the allometric scaling parameters was large enough and sufficiently structured to allow for the clustering of grasses and forbs into statistically distinct groups (Tables 2 and 3).

Evaluations of the root scaling, root biomass allocation, growth rates, nutrient productivity, and nutrient influx rate parameters that characterize the species we studied can provide some insights regarding the life-history strategies and tradeoffs that plants may make in adapting to different soil nutrient environments. Of particular interest for us is the "coarse" vs. "fine" scale root 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 argued, 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 an increase in root length and root surface area, or root uptake rates, or both in the nutrient rich patches that are located between the depletion zones generated by the dominant species. While the grass and forb groups in our study did not break down totally along the "coarse" vs. "fine" scale root foraging strategies proposed by Campbell et al. (1991), they nevertheless showed some interesting patterns that can play an important role in nutrient acquisition.

In the case of grasses the major clustering patterns involved root surface area, root lateral spread and the associated Imax-N and Imax-P (Table 2). Plants that generated the largest surface area per root biomass (large η and ρ) produced the lowest root lateral spread per root biomass (low α and β), and had relatively low Imax-N and Imax-P rates (Cluster 2, Table 2). The inverse relationship we observed between root surface area and root lateral spread may result from the fact that large root lateral spread is often associated with long, thickened root systems, which tend to have a small root surface area, while smaller and finer root systems tend to have the opposite pattern, a small root lateral spread and a large root surface area (Campbell et al. 1991). The large root surface area per

root biomass that characterizes the grasses in the first cluster may involve a compensation for the low Imax-N and Imax-P rates associated with these species (Table 2). Plants in the third cluster compensated for low root lateral spread and root surface area with high Imax-N and Imax-P rates.

The same inverse relationship between root surface area and Imax-N and Imax-P rates found in grasses were also found in the forbs/shrubs clusters (Table 3). Root lateral spread however did not play any role in differentiating among the forbs/shrubs cluster, but RGR_{max} and RGR_{max}-AGB did (Table 3), primarily because they were positively correlated with Imax-N and Imax-P rates (Figure 8). With few exceptions, the forbs and shrubs we studied are subdominant in most of the vegetation types found within the Great Plains grasslands (Kuchler 1964), so it is important to point out that the major dichotomy between high root surface area and length vs. high RGR, Imax-N and Imax-P rates that we found among these species (Table 3) is very much consistent with the "fine" scale foraging strategy that, according to Campbell et al. (1991) should characterize subdominant species.

Like this one, the vast majority of studies involving roots and relative growth rates have been conducted under controlled greenhouse conditions, using seedlings grown in individual pots for a relatively short period of time (see (Grime and Hunt 1975; 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. In the area of roots, there are two lines of evidence that seem to suggest that, in principle, they can. Theoretical analyses conducted by Gleeson and Fry (1997) using an optimization model have suggested that plants grown in a patchy soil nutrient environment will develop their root systems in such a way that the marginal gains from the various nutrient patches within their rooting zone are equilibrated, regardless of the size of the plant and the nature of the nutrient patch. Field studies conducted by Bilbrough and Caldwell (1995) and Caldwell et al. (1996) have produced data that are fairly consistent with results from greenhouse and pot experiments. Regarding relative growth and nutrient uptake rates, we agree with Grime and Hunt (1975) that it would be naïve to believe that they one can directly extrapolate pot results to larger plants. Nevertheless these values do provide a useful index of the maximum potential growth and uptake rates that one can expect from the species in question.

In summary, some important patterns emerged from the analyses of the root scaling, root biomass allocation, growth rates, nutrient productivity, and root nutrient influx rate parameters that characterized the 55 plant species we studied.

1. In all species, root lateral spread, root length, and root surface area had significant allometric scaling relationships with root biomass, but the relationships were unaffected by N availability.
2. There is strong support for the existence of a tradeoff in the way plants allocate biomass to roots: under low nutrient conditions plants increase their biomass allocation to roots at the expense of leaves and shoots, while under high nutrient conditions the reverse is the case.
3. We did not find an overall negative relationship between the R:S ratios and RGR_{max}, but we did find positive relationships within grasses between R:S and Imax-N, and for all species among RGR_{max}, Imax-N, and Imax-P.
4. We found that C_3 as well as mid successional grasses have a lower N and P productivity than C_4 and late successional grasses.
5. The RGR_{max} of mid successional grasses is on average 25% higher than that of late successional ones.
6. The root scaling, root biomass allocation, growth rates, nutrient productivity, and root nutrient influx rate parameters we measured in this study separated grasses and forbs into statistically distinct groups that tend to follow, in broad terms, the "coarse" vs. "fine" scale foraging strategies hypothesis advanced by Campbell et al. (1991).
7. A note of caution should be made regarding the species groups generated by this study. While the parameters we measured were able to classify plant species into statistically discrete groups, the impression should not be left that there is a discrete universe of these parameters. What we have is a continuum of root scaling, root biomass allocation, growth rates, nutrient productivity, and nutrient influx rate parameters from which "statistically different" populations can be identified. A species performance, thus, will depend on its location within the hypervolume (space of n dimensions) defined by the parameters in question and how effective this location is for exploiting another hypervolume, this one defined by the supply

rate and spatial distribution pattern of a set of limiting soil nutrients.

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Appendix 1

Table A1. Root parameter values for the allometric constants α, β, γ, and δ that relate root biomass (RB[g]) to root lateral spread (rls[m] = $\alpha^{*}RB^{\beta}$) and root length (RL[m] = $\gamma\ ^{*}RB^{\delta}$). The P-values are the statistical fit of the allometric models (for details see text).

Species	α	β	R^2	P-value	γ	δ	R^2	P-value
Forbs/Shrubs: Mid Succession								
Achillea millefolium	0.315	0.411	0.84	< 0.0001	10.86	0.793	0.77	< 0.0001
Artemisia dracunculus	0.839	0.588	0.71	0.0083	16.14	0.910	0.32	0.1895
Asclepias verticillata	0.204	0.338	0.72	< 0.0001	9.29	0.744	0.91	< 0.0001
Chenopodium album	0.418	0.458	0.83	< 0.0001	4.99	0.208	0.79	< 0.0001
Cirsium arvense	0.560	0.584	0.87	< 0.0001	15.81	0.769	0.95	< 0.0001
Conyza canadensis	0.705	0.487	0.65	0.0029	7.77	0.282	0.39	0.0411
Gaillardia aristata	0.109	0.170	0.92	< 0.0001	13.14	0.929	0.68	0.0003
Hedeoma hispidum	0.244	0.336	0.92	< 0.0001	8.64	0.728	0.92	< 0.0001
Helianthus maximilianii	0.669	0.590	0.73	0.0001	4.16	0.479	0.87	< 0.0001
Melilotus officinalis	0.622	0.559	0.61	0.0001	9.35	0.877	0.63	0.0008
Oenothera biennis	0.356	0.355	0.87	< 0.0001	0.84	0.304	0.43	0.0114
Ratibida columnifera	0.473	0.411	0.77	< 0.0001	12.93	0.803	0.83	< 0.0001
Rudbeckia hirta	0.670	0.647	0.83	0.0003	9.68	0.723	0.93	< 0.0001
Solidago missouriensis	0.540	0.526	0.62	0.0005	70.88	0.729	0.95	< 0.0001
Tragopogon dubius	0.590	0.578	0.60	0.0005	24.55	0.968	0.81	< 0.0001
Verbena stricta	0.204	0.283	0.88	< 0.0001	18.1	0.718	0.89	< 0.0001
Vicia americana	0.256	0.356	0.69	< 0.0001	7.21	0.635	0.75	0.0001
Forbs/Shrubs: Late Succession								
Allium stellatum	0.457	0.532	0.43	0.0018	13.88	0.617	0.25	0.0219
Anaphalis margaritacea	0.421	0.485	0.77	0.0009	23.00	0.955	0.45	0.0091
Artemisia tridentata	0.387	0.538	0.81	< 0.0001	31.67	0.965	0.68	0.0003
Aster ericoides	0.476	0.488	0.87	< 0.0001	59.48	0.693	0.53	0.0033
Astragalus canadensis	0.788	0.726	0.76	0.0005	1.70	0.476	0.79	< 0.0001
Chrysopsis villosa	0.437	0.478	0.77	0.0004	7.94	0.596	0.69	0.0003
Coreopsis lanceolata	0.241	0.317	0.48	0.0087	9.77	0.621	0.52	0.0038
Dalea purpurea	2.382	0.932	0.54	0.0006	4.96	0.849	0.61	0.0009
Galium boreale	0.216	0.368	0.84	< 0.0001	17.44	0.596	0.79	< 0.0001
Geum triflorum	0.206	0.41	0.52	0.0003	11.34	0.646	0.70	< 0.0001
Grindelia squarrosa	0.274	0.449	0.78	< 0.0001	10.24	0.700	0.89	< 0.0001
Liatris punctata	0.602	0.881	0.34	0.011	2.03	0.408	0.24	0.0754
Linum perenne	0.108	0.113	0.84	< 0.0001	6.56	0.378	0.49	0.0056
Lupinus perennis	0.596	1.260	0.65	< 0.0001	13.6	1.027	0.79	< 0.0001
Oxytropis lambertii	0.485	0.71	0.61	0.008	3.01	0.557	0.74	0.0001
Potentilla arguta	0.217	0.358	0.94	0.0003	14.63	0.783	0.91	< 0.0001

Table A1. Continued.

Species	α	β	R^2	P-value	γ	δ	R^2	P-value
Psoralea esculenta	0.754	0.839	0.71	0.0001	1.28	0.198	0.08	0.3404
Rosa arkansana	0.286	0.455	0.70	< 0.0001	5.47	0.579	0.75	0.0001
Solidago rigida	0.100	0.245	0.66	< 0.0001	35.72	0.890	0.77	< 0.0001
Sphaeralcea coccinea	0.171	0.105	0.96	< 0.0001	7.78	0.464	0.60	0.0011
Taraxacum officinale	0.219	0.348	0.38	0.0065	24.28	0.912	0.79	< 0.0001
Grasses Mid Succession- C_3								
Agropyron cristatum	0.053	0.007	0.76	< 0.0001	9.73	0.562	0.59	0.0013
Bromus inermis	0.367	0.496	0.64	0.0001	13.77	0.793	0.85	< 0.0001
Hordeum jubatum	0.603	0.667	0.58	0.0025	13.56	0.401	0.86	< 0.0001
Grasses Mid Succession- C_4								
Sporobolus cryptandrus	0.364	0.443	0.91	< 0.0001	1.82	0.508	0.61	0.001
Grasses Late Succession- C_3								
Agropyron spicatum	0.509	0.527	0.43	0.0024	5.04	0.749	0.52	0.0034
Elymus canadensis	0.233	0.439	0.67	< 0.0001	2.03	0.567	0.50	0.0045
Koeleria cristata	0.414	0.476	0.69	0.0005	10.64	0.267	0.19	0.3334
Poa pratensis	0.575	0.544	0.54	0.0002	8.48	0.347	0.81	< 0.0001
Stipa comata	0.795	0.668	0.49	0.0006	5.3	0.619	0.26	0.0654
Stipa viridula	0.693	0.602	0.74	< 0.0001	2.53	0.615	0.63	0.0007
Grasses Late Succession- C_4								
Andropogon gerardii	0.297	0.515	0.37	0.0021	6.85	0.472	0.53	0.0032
Bouteloua curtipendula	0.892	0.631	0.73	< 0.0001	59.48	0.693	0.53	0.0033
Bouteloua gracilis	0.708	0.584	0.74	< 0.0001	2.66	0.57	0.8	< 0.0001
Calamovilfa longifolia	0.254	0.372	0.56	0.0008	1.35	0.298	0.3	0.0417
Panicum virgatum	0.16	0.202	0.58	0.001	13.14	0.474	0.3	0.0413
Schizachyrium scoparium	0.338	0.534	0.56	0.0001	15.67	0.685	0.71	0.0002
Sorgastrum nutans	0.214	0.348	0.52	0.0003	2.62	0.522	0.8	< 0.0001

Appendix 2

Table A2. Data for: (a) average root diameter (RD in mm) and standard error for the high (32 ppm) and low (1 ppm) N treatments; and (b) allometric scaling constants η and ρ that relate root biomass (RB[g]) to root surface area ($RSA[m^2] = \eta\ {}^{*}RB^{\rho}$). The P-value for root diameter are the statistical comparisons between the high vs. low N treatments (numbers in bold are statistically different at the $P < 0.05$). The P-values for root surface area are the statistical fit of the allometric model (for details see text).

Species	RD High N Treatment	SE	RD Low N Treatment	SE	P-value	η	ρ	R^2	P-value
Forbs/Shrubs: Mid Succession									
Achillea millefolium	**0.604**	0.087	**0.250**	0.022	**0.0019**	0.0278	0.968	0.77	< 0.0001
Artemisia dracunculus	0.126	0.009	0.129	0.001	0.8387	0.0032	0.703	0.25	0.0338
Asclepias verticillata	0.257	0.029	0.318	0.031	0.1664	0.0038	0.595	0.80	< 0.0001
Chenopodium album	0.126	0.011	0.095	0.009	0.5009	0.0023	0.278	0.78	< 0.0001
Cirsium arvense	0.560	0.047	0.614	0.074	0.5318	0.0218	0.718	0.86	< 0.0001
Conyza canadensis	0.118	0.009	0.105	0.007	0.2561	0.0023	0.236	0.48	0.001
Gaillardia aristata	0.723	0.144	0.643	0.224	0.7627	0.0346	0.969	0.46	0.0227
Hedeoma hispidum	0.195	0.004	0.247	0.027	0.0677	0.0041	0.646	0.88	< 0.0001
Helianthus maximilianii	0.221	0.014	0.245	0.032	0.4918	0.0015	0.325	0.91	< 0.0001
Melilotus officinalis	0.488	0.030	0.470	0.074	0.8375	0.0273	1.076	0.46	0.001
Oenothera biennis	0.224	0.014	0.247	0.030	0.4437	0.0005	0.258	0.53	0.0031

Table A2. Continued.

Species	RD High N Treatment	SE	RD Low N Treatment	SE	P-value	η	ρ	R^2	P-value
Ratibida columnifera	**0.160**	0.004	**0.139**	0.005	**0.0049**	0.0063	0.802	0.85	< 0.0001
Rudbeckia hirta	0.150	0.004	0.147	0.005	0.6372	0.0049	0.703	0.88	< 0.0001
Solidago missouriensis	0.113	0.004	0.117	0.003	0.7775	0.0012	0.121	0.76	< 0.0001
Tragopogon dubius	0.218	0.01	0.236	0.035	0.5462	0.0137	0.920	0.61	< 0.0001
Verbena stricta	**0.200**	0.004	**0.174**	0.005	**0.0004**	0.0125	0.766	0.87	< 0.0001
Vicia americana	0.196	0.005	0.201	0.009	0.6417	0.0034	0.545	0.72	< 0.0001
Forbs/Shrubs: Late Succession									
Allium stellatum	0.164	0.006	0.166	0.010	0.8977	0.0058	0.569	0.24	0.0277
Anaphalis margaritacea	0.100	0.031	0.141	0.023	0.3363	0.0499	1.246	0.53	0.0003
Artemisia tridentata	0.220	0.011	0.274	0.029	0.0708	0.0392	1.033	0.63	0.0007
Aster ericoides	0.239	0.034	0.179	0.035	0.3188	0.0017	0.623	0.72	0.0001
Astragalus canadensis	0.216	0.015	0.227	0.027	0.7124	0.0009	0.401	0.70	0.005
Chrysopsis villosa	0.166	0.010	0.203	0.015	0.1260	0.0023	0.461	0.46	0.0218
Coreopsis lanceolata	0.240	0.014	0.229	0.018	0.6475	0.0066	0.618	0.64	0.0002
Dalea purpurea	0.227	0.026	0.170	0.013	0.1365	0.0030	0.853	0.57	0.0003
Galium boreale	0.249	0.009	0.26	0.017	0.5836	0.0118	0.567	0.74	< 0.0001
Geum triflorum	0.301	0.014	0.288	0.014	0.4372	0.0135	0.703	0.72	< 0.0001
Grindelia squarrosa	0.217	0.012	0.266	0.035	0.1858	0.0044	0.58	0.84	< 0.0001
Liatris punctata	0.281	0.014	0.267	0.018	0.5498	0.0026	0.515	0.49	0.0006
Linum perenne	0.207	0.024	0.220	0.014	0.6146	0.0083	0.618	0.75	< 0.0001
Lupinus perennis	0.400	0.011	0.428	0.016	0.1651	0.0168	1.000	0.78	< 0.0001
Oxytropis lambertii	0.276	0.027	0.339	0.064	0.3362	0.0011	0.344	0.63	0.0061
Potentilla arguta	**0.208**	0.011	**0.248**	0.017	**0.0010**	0.0251	1.001	0.93	0.0001
Psoralea esculenta	**0.254**	0.009	**0.292**	0.012	**0.0224**	0.0024	0.448	0.31	0.0325
Rosa arkansana	0.268	0.018	0.263	0.019	0.8525	0.0027	0.456	0.65	< 0.0001
Solidago rigida	0.253	0.014	0.260	0.015	0.7304	0.0169	0.790	0.69	< 0.0001
Sphaeralcea coccinea	**0.175**	0.011	**0.133**	0.011	**0.0224**	0.0062	0.584	0.56	0.0004
Taraxacum officinale	0.221	0.010	0.205	0.020	0.5340	0.0306	1.073	0.79	< 0.0001
Grasses Mid Succession- C_3									
Agropyron cristatum	0.202	0.012	0.177	0.012	0.1764	0.0059	0.589	0.55	0.0005
Bromus inermis	**0.343**	0.015	**0.202**	0.013	**0.0001**	0.0232	1.066	0.80	< 0.0001
Hordeum jubatum	**0.206**	0.012	**0.130**	0.014	**0.0023**	0.0196	0.719	0.91	< 0.0001
Grasses Mid Succession- C_4									
Sporobolus cryptandrus	0.229	0.022	0.249	0.038	0.6525	0.0009	0.434	0.38	0.0053
Grasses Late Succession- C_3									
Agropyron spicatum	0.170	0.013	0.183	0.017	0.5613	0.0016	0.593	0.37	0.0046
Elymus canadensis	**0.193**	0.010	**0.240**	0.015	**0.0170**	0.0011	0.473	0.56	0.0001
Koeleria cristata	0.115	0.007	0.094	0.003	0.1155	0.0144	0.556	0.43	0.0018
Poa pratensis	**0.126**	0.003	**0.095**	0.001	**0.0007**	0.0023	0.296	0.46	0.0011
Stipa comata	0.166	0.009	0.186	0.010	0.1501	0.0017	0.479	0.24	0.0295
Stipa viridula	**0.239**	0.016	**0.358**	0.018	**0.0002**	0.0007	0.358	0.28	0.0297
Grasses Late Succession- C_4									
Andropogon gerardii	0.215	0.006	0.207	0.008	0.418	0.0086	0.746	0.64	0.0001
Bouteloua curtipendula	0.125	0.006	0.119	0.004	0.5562	0.0047	0.326	0.36	0.0051
Bouteloua gracilis	**0.232**	0.017	**0.32**	0.019	**0.0026**	0.0009	0.368	0.56	0.0003
Calamovilfa longifolia	0.195	0.015	0.222	0.011	0.1477	0.0009	0.289	0.50	0.0015
Panicum virgatum	**0.223**	0.011	**0.192**	0.008	**0.0353**	0.0358	0.884	0.62	< 0.0001
Schizachyrium scoparium	0.156	0.004	0.153	0.005	0.6283	0.0079	0.697	0.77	< 0.0001
Sorgastrum nutans	0.250	0.024	0.265	0.024	0.6711	0.002	0.514	0.77	< 0.0001

Appendix 3

Table A3. Mean and standard error values for: (a) root to shoot ratio (R:S) for the high (32 ppm) and low (1 ppm) N treatment; and (b) maximum relative growth rate (g g^{-1} d^{-1}) expressed in terms of total biomass $\left(RGR_{\max} = \frac{1}{Total\ Biomass}\ \frac{d\ Total\ Biomass}{dt}\right)$, and in terms of above ground biomass $\left(RGR_{\max} - AGB = \frac{1}{AGB}\ \frac{d\ Total\ Biomass}{dt}\right)$. The P-value represents statistical comparisons in R:S between the high vs. low N treatments (numbers in bold are statistically different at the $P < 0.05$).

Species	R:S High N Treatment	SE	R:S Low N Treatment	SE	P-value	RGR_{max}	SE	RGR_{max}-AGB	SE
Forbs/Shrubs: Mid Succession									
Achillea millefolium	**0.84**	0.156	**2.50**	0.544	**0.01**	0.14	0.021	0.24	0.053
Artemisia dracunculus	**0.29**	0.039	**0.50**	0.112	**0.01**	0.13	0.011	0.18	0.005
Asclepias verticillata	**0.78**	0.080	**1.37**	0.267	**0.05**	0.09	0.001	0.13	0.016
Chenopodium album	**0.64**	0.039	**1.75**	0.050	**0.01**	0.13	0.005	0.18	0.016
Cirsium arvense	0.79	0.059	1.17	0.180	0.30	0.11	0.015	0.14	0.041
Conyza canadensis	**0.59**	0.068	**1.04**	0.124	**0.01**	0.16	0.014	0.26	0.04
Gaillardia aristata	0.92	0.126	0.98	0.138	0.58	0.08	0.007	0.11	0.014
Hedeoma hispidum	**1.30**	0.080	**3.16**	0.497	**0.01**	0.13	0.004	0.27	0.035
Helianthus maximilianii	0.75	0.161	1.09	0.337	0.53	0.13	0.033	0.16	0.039
Melilotus officinalis	**1.43**	0.252	**4.13**	0.582	**0.01**	0.14	0.017	0.20	0.007
Oenothera biennis	0.91	0.102	1.30	0.298	0.40	0.19	0.016	0.25	0.001
Ratibida columnifera	**0.29**	0.02	**0.53**	0.076	**0.01**	0.10	0.015	0.14	0.020
Rudbeckia hirta	0.54	0.066	0.74	0.238	0.26	0.12	0.003	0.17	0.007
Solidago missouriensis	0.57	0.120	0.80	0.089	0.34	0.10	0.036	0.15	0.068
Tragopogon dubius	**0.49**	0.073	**1.05**	0.146	**0.01**	0.10	0.012	0.17	0.024
Verbena stricta	**0.44**	0.063	**0.75**	0.123	**0.04**	0.11	0.007	0.16	0.016
Vicia americana	**0.67**	0.081	**1.35**	0.133	**0.01**	0.08	0.018	0.14	0.035
Forbs/Shrubs: Late Succession									
Allium stellatum	**1.26**	0.201	**2.43**	0.208	**< 0.01**	0.06	0.005	0.08	0.015
Anaphalis margaritacea	0.54	0.108	0.81	0.150	0.41	0.15	0.015	0.22	0.023
Artemisia tridentata	**0.78**	0.116	**1.81**	0.256	**0.01**	0.12	0.000	0.22	0.033
Aster ericoides	0.92	0.071	1.01	0.266	0.46	0.12	0.005	0.18	0.013
Astragalus canadensis	1.53	0.299	2.41	0.642	0.35	0.13	0.003	0.20	0.018
Chrysopsis villosa	0.55	0.096	0.95	0.404	0.44	0.09	0.001	0.13	0.010
Coreopsis lanceolata	**0.47**	0.060	**0.88**	0.088	**0.01**	0.11	0.017	0.15	0.025
Dalea purpurea	**0.47**	0.056	**1.33**	0.127	**0.01**	0.09	0.000	0.12	0.002
Galium boreale	0.65	0.198	2.19	1.121	0.14	0.08	0.020	0.10	0.029
Geum triflorum	**0.52**	0.053	**0.82**	0.061	**< 0.01**	0.08	0.005	0.09	0.009
Grindelia squarrosa	0.92	0.171	0.86	0.163	0.29	0.14	0.007	0.21	0.019
Liatris punctata	1.60	0.175	1.67	0.113	0.15	0.06	0.003	0.12	0.019
Linum perenne	**1.55**	0.216	**3.49**	0.458	**0.01**	0.09	0.011	0.22	0.067
Lupinus perennis	**0.91**	0.087	**1.47**	0.157	**0.01**	0.10	0.007	0.15	0.020
Oxytropis lambertii	1.24	0.226	1.03	0.386	0.59	0.10	0.005	0.18	0.011
Potentilla arguta	0.46	0.062	0.46	0.119	0.18	0.10	0.001	0.12	0.009
Psoralea esculenta	**0.85**	0.120	**1.22**	0.133	**0.01**	0.06	0.000	0.10	0.001
Rosa arkansana	**0.51**	0.062	**0.77**	0.063	**0.01**	0.18	0.024	0.22	0.058
Solidago rigida	**0.80**	0.074	**1.62**	0.214	**< 0.01**	0.10	0.004	0.14	0.015
Sphaeralcea coccinea	**0.47**	0.066	**0.86**	0.153	**0.01**	0.16	0.031	0.20	0.061
Taraxacum officinale	**0.53**	0.051	**0.91**	0.090	**0.01**	0.12	0.037	0.17	0.049

Table A3. Continued.

Species	R:S High N Treatment	SE	R:S Low N Treatment	SE	P-value	RGR_{max}	SE	RGR_{max}-AGB	SE
Grasses Mid Succession- C_3									
Agropyron cristatum	**0.55**	0.037	**1.07**	0.163	**0.01**	0.11	0.002	0.18	0.017
Bromus inermis	**0.37**	0.027	**1.06**	0.104	**0.01**	0.11	0.016	0.18	0.045
Hordeum jubatum	**0.43**	0.041	**1.31**	0.166	**0.01**	0.15	0.015	0.36	0.042
Grasses Mid Succession- C_4									
Sporobolus cryptandrus	0.96	0.172	1.15	0.174	0.58	0.14	0.006	0.21	0.025
Grasses Late Succession- C_3									
Agropyron spicatum	**0.81**	0.131	**1.20**	0.111	**0.01**	0.11	0.006	0.21	0.035
Elymus canadensis	**0.77**	0.146	**1.41**	0.146	**0.01**	0.13	0.008	0.21	0.018
Koeleria cristata	0.46	0.070	0.52	0.157	0.18	0.1	0.001	0.13	0.004
Poa pratensis	**0.52**	0.052	**0.88**	0.105	**0.01**	0.13	0.004	0.18	0.002
Stipa comata	0.72	0.061	0.76	0.049	0.46	0.06	0.004	0.10	0.003
Stipa viridula	0.57	0.050	0.74	0.096	0.56	0.10	0.009	0.14	0.017
Grasses Late Succession- C_4									
Andropogon gerardii	**0.90**	0.056	**2.25**	0.231	**0.01**	0.10	0.007	0.18	0.003
Bouteloua curtipendula	0.51	0.070	0.58	0.024	0.42	0.13	0.008	0.22	0.003
Bouteloua gracilis	**0.60**	0.043	**0.91**	0.123	**0.01**	0.09	0.022	0.15	0.034
Calamovilfa longifolia	0.60	0.074	0.76	0.141	0.24	0.11	0.023	0.18	0.049
Panicum virgatum	**0.44**	0.051	**0.78**	0.124	**0.01**	0.10	0.003	0.16	0.020
Schizachyrium scoparium	**0.67**	0.054	**1.29**	0.173	**0.01**	0.11	0.008	0.17	0.002
Sorgastrum nutans	**0.57**	0.102	**1.38**	0.205	**< 0.01**	0.09	0.006	0.13	0.013

Appendix 4

Table A4. Mean and standard error values for (a) N productivity (NP in g gN^{-1}) under the high (32 ppm) and low (1 ppm) N treatment; and (b) P productivity (PP in g gP^{-1}) under the high N treatment. The P-value represent statistical comparisons in NP between the high vs. low N treatments (numbers in bold are statistically different at the $P < 0.05$).

Species	NP for the High N Treatment	SE	NP for the Low N Treatment	SE	P-value	PP for the High N Treatment	SE
Forbs/Shrubs: Mid Succession							
Achillea millefolium	**31.13**	3.26	**47.70**	4.53	**0.0141**	98.14	11.05
Artemisia dracunculus	**32.54**	2.61	**53.86**	4.63	**0.0025**	146.88	12.90
Asclepias verticillata	**39.12**	1.94	**93.16**	5.16	**0.0001**	123.01	5.85
Chenopodium album	60.62	4.26	58.96	4.07	0.7850	219.62	14.04
Cirsium arvense	**40.90**	9.61	**85.71**	18.26	**0.0500**	114.99	23.91
Conyza canadensis	**30.12**	1.47	**52.98**	2.64	**0.0001**	94.04	5.24
Gaillardia aristata	**31.19**	0.68	**33.69**	0.76	**0.0334**	96.28	2.38
Hedeoma hispidum	31.30	2.79	36.32	3.38	0.2795	141.07	11.73
Helianthus maximilianii	**38.61**	3.35	**50.70**	4.12	**0.0460**	97.03	7.05
Melilotus officinalis	33.26	6.63	52.61	11.45	0.1744	82.54	17.48
Oenothera biennis	**36.75**	0.48	**125.24**	1.76	**0.0001**	87.14	1.30
Ratibida columnifera	**32.97**	2.78	**50.54**	4.11	**0.0054**	87.56	7.87
Rudbeckia hirta	**27.52**	1.87	**71.66**	4.71	**0.0001**	113.3	8.75
Solidago missouriensis	**36.05**	0.21	**40.61**	0.23	**0.0001**	264.75	1.35
Tragopogon dubius	**38.40**	0.29	**44.26**	0.37	**0.0001**	110.82	0.79

Table A4. Continued.

Species	NP for the High N Treatment	SE	NP for the Low N Treatment	SE	P-value	PP for the High N Treatment	SE
Verbena stricta	39.09	6.41	34.30	5.87	0.5933	110.46	15.61
Vicia americana	39.42	6.04	36.93	5.96	0.7748	102.65	12.69
Forbs/Shrubs: Late Succession							
Allium stellatum	**35.04**	1.66	**69.36**	2.92	**< 0.0001**	141.27	7.63
Anaphalis margaritacea	38.55	4.48	56.97	7.34	0.0579	101.65	14.11
Artemisia tridentata	31.23	5.03	42.40	6.09	0.1874	64.14	10.45
Aster ericoides	**35.75**	1.22	**30.41**	1.09	**0.0085**	142.82	4.50
Astragalus canadensis	**33.91**	0.61	**54.81**	0.91	**0.0001**	144.55	2.45
Chrysopsis villosa	**32.20**	0.59	**45.00**	0.89	**0.0001**	127.01	2.71
Coreopsis lanceolata	**36.33**	3.56	**68.36**	6.72	**0.0018**	163.83	13.15
Dalea purpurea	**32.32**	0.59	**45.54**	0.76	**0.0001**	121.61	2.16
Galium boreale	**45.24**	11.36	**129.32**	32.82	**0.0360**	249.76	52.90
Geum triflorum	**35.88**	2.19	**71.72**	4.07	**0.0001**	127.38	7.50
Grindelia squarrosa	**31.97**	3.53	**46.55**	5.30	**0.0450**	95.99	10.57
Liatris punctata	**43.32**	1.56	**84.91**	3.27	**0.0001**	46.79	1.94
Linum perenne	**37.63**	2.03	**55.54**	3.28	**0.0009**	158.57	8.86
Lupinus perennis	**36.91**	1.66	**63.81**	2.86	**0.0001**	98.67	4.30
Oxytropis lambertii	42.91	2.50	47.98	2.48	0.1806	45.95	3.00
Potentilla arguta	**39.46**	1.87	**54.94**	2.69	**0.0008**	153.39	7.96
Psoralea esculenta	**42.56**	1.16	**54.54**	1.43	**0.0001**	97.75	3.10
Rosa arkansana	46.01	7.10	73.64	11.68	0.0708	346.72	61.42
Solidago rigida	**36.19**	1.42	**82.05**	3.52	**0.0001**	137.05	4.82
Sphaeralcea coccinea	**32.67**	2.04	**74.89**	5.00	**0.0001**	182.16	9.27
Taraxacum officinale	**42.94**	4.89	**64.82**	7.16	**0.0303**	136.76	17.58
Grasses Mid Succession- C_3							
Agropyron cristatum	40.42	4.14	48.39	5.16	0.2559	181.03	20.95
Bromus inermis	**41.93**	1.38	**102.00**	3.33	**0.0001**	173.48	4.87
Hordeum jubatum	**33.51**	0.55	**75.64**	1.12	**0.0001**	129.28	2.38
Grasses Mid Succession- C_4							
Sporobolus cryptandrus	36.8	7.27	59.49	11.6	0.1284	185.95	38.51
Grasses Late Succession- C_3							
Agropyron spicatum	40.94	5.31	50.77	6.89	0.2846	168.5	19.87
Elymus canadensis	**36.97**	3.64	**73.39**	7.21	**0.0011**	190.45	18.54
Koeleria cristata	**36.95**	2.47	**74.44**	4.93	**0.0001**	152.26	8.99
Poa pratensis	**36.64**	2.14	**68.22**	3.96	**0.0001**	149.07	8.77
Stipa comata	**39.34**	0.19	**47.09**	0.25	**0.0001**	190.16	0.91
Stipa viridula	**42.84**	3.01	**64.26**	4.79	**0.0036**	225.76	17.67
Grasses Late Succession- C_4							
Andropogon gerardii	**62.94**	1.19	**79.99**	1.62	**0.0001**	251.04	5.30
Bouteloua curtipendula	**48.21**	3.78	**71.84**	5.54	**0.0055**	244.34	19.63
Bouteloua gracilis	**38.26**	0.16	**63.24**	0.27	**0.0001**	153.60	0.66
Calamovilfa longifolia	**45.69**	4.72	**63.64**	6.42	**0.0480**	262.83	24.77
Panicum virgatum	**42.94**	0.05	**58.65**	0.07	**0.0001**	131.91	0.17
Schizachyrium scoparium	56.93	11.34	68.44	12.27	0.5068	250.78	50.77
Sorgastrum nutans	**49.98**	2.57	**93.54**	5.17	**0.0001**	201.86	9.01

Appendix 5

Table A5. Mean and standard errors for the estimated maximum influx rate per unit of root surface area ($g\,m^{-2}\,d^{-1}$) for N (Imax-N) and P (Imax-P) at high N and P concentrations (32 ppm of N and 31 ppm of P).

Species	Imax-N	SE	Imax-P	SE
Forbs/Shrubs: Mid Succession				
Achillea millefolium	0.4363	0.0036	0.1517	0.0014
Artemisia dracunculus	0.8507	0.2062	0.2529	0.0590
Asclepias verticillata	0.4105	0.1253	0.1241	0.0435
Chenopodium album	0.1278	0.0001	0.0393	0.0001
Cirsium arvense	0.2466	0.0212	0.1083	0.0109
Conyza canadensis	0.1488	0.0451	0.0457	0.0154
Gaillardia aristata	0.2267	0.1625	0.0750	0.0487
Hedeoma hispidum	0.4096	0.0063	0.1214	0.0020
Helianthus maximilianii	0.7170	0.0223	0.3607	0.0133
Melilotus officinalis	1.2851	0.4287	0.1579	0.0553
Oenothera biennis	1.3504	0.9583	0.6483	0.3870
Ratibida columnifera	0.9931	0.0174	0.3586	0.0059
Rudbeckia hirta	1.0892	0.0936	0.2979	0.0227
Solidago missouriensis	0.0297	0.0200	0.0025	0.0020
Tragopogon dubius	0.6571	0.3002	0.2260	0.1174
Verbena stricta	0.5721	0.0900	0.1693	0.0311
Vicia americana	0.4790	0.0702	0.1797	0.0291
Forbs/Shrubs: Late Succession				
Allium stellatum	0.1190	0.0160	0.0281	0.0033
Anaphalis margaritacea	0.5927	0.0020	0.0761	0.0003
Artemisia tridentata	0.4220	0.0667	0.1996	0.0270
Aster ericoides	1.3150	0.4601	0.4292	0.1250
Astragalus canadensis	2.9724	0.1657	0.7098	0.0441
Chrysopsis villosa	0.1858	0.0522	0.0345	0.0102
Coreopsis lanceolata	0.3450	0.0423	0.0737	0.0091
Dalea purpurea	1.9311	0.0732	0.5538	0.0226
Galium boreale	0.0817	0.0113	0.0185	0.0025
Geum triflorum	0.3213	0.0800	0.0850	0.0177
Grindelia squarrosa	0.7372	0.0002	0.2184	0.0001
Liatris punctata	0.1400	0.0259	0.0457	0.0074
Linum perenne	0.1931	0.0420	0.0456	0.0112
Lupinus perennis	0.6303	0.0108	0.2251	0.0035
Oxytropis lambertii	0.2994	0.2071	0.0703	0.0439
Potentilla arguta	0.3926	0.0502	0.1058	0.0110
Psoralea esculenta	0.1367	0.0112	0.0445	0.0044
Rosa arkansana	2.0071	0.1149	0.3075	0.0142
Solidago rigida	0.3477	0.0112	0.0882	0.0033
Sphaeralcea coccinea	0.3753	0.0295	0.1125	0.0087
Taraxacum officinale	0.5504	0.0684	0.0875	0.0111
Grasses Mid Succession- C_3				
Agropyron cristatum	0.3576	0.0819	0.1082	0.0278
Bromus inermis	0.3695	0.0271	0.0855	0.0059
Hordeum jubatum	0.2433	0.1172	0.0641	0.0325
Grasses Mid Succession- C_4				
Sporobolus cryptandrus	1.3337	0.0895	0.3761	0.0299
Grasses Late Succession- C_3				
Agropyron spicatum	0.7674	0.0422	0.2222	0.0109
Elymus canadensis	1.3480	0.1750	0.3221	0.0369
Koeleria cristata	0.0635	0.0120	0.0202	0.0038
Poa pratensis	0.1501	0.0129	0.0521	0.0052
Stipa comata	0.2413	0.2531	0.0646	0.0677
Stipa viridula	1.0824	0.0693	0.2198	0.0110
Grasses Late Succession- C_4				
Andropogon gerardii	0.1961	0.0658	0.0669	0.0199
Bouteloua curtipendula	0.1628	0.0826	0.0522	0.0253
Bouteloua gracilis	0.3927	0.1222	0.0671	0.0217
Calamovilfa longifolia	0.3289	0.0655	0.0756	0.0159
Panicum virgatum	0.1359	0.0119	0.0485	0.0049
Schizachyrium scoparium	0.2043	0.0591	0.0611	0.0180
Sorgastrum nutans	0.4986	0.1809	0.1439	0.0463

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