The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients

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For 76 annual, biennial, and perennial species common in the grasslands of central Minnesota, USA, we determined the patterns of correlations among seven organ-level traits (specific leaf area, leaf thickness, leaf tissue density, leaf angle, specific root length, average fine root diameter, and fine root tissue density) and their relationships with two traits relating to growth form (whether species existed for part of the growing season in basal, non-caulescent form and whether species were rhizomatous or not). The first correlation of traits showed that grasses had thin, dense leaves and thin roots while forbs had thick, low-density leaves and thick roots without any significant differences in growth form or life history. The second correlation of traits showed a gradient of species from those with high-density roots and high-density erect leaves to species with low-density roots and low-density leaves that were held parallel to the ground. High tissue density species were more likely to exist as a basal rosette for part of the season, were less likely to be rhizomatous, and less likely to be annuals. We examined the relationships between the two axes that represent the correlations of traits and previously collected data on the relative abundance of species across gradients of nitrogen addition and disturbance. Grasses were generally more abundant than forbs and the relative abundance of grasses and forbs did not change with increasing nitrogen addition or soil disturbance. High tissue density species became less common as fertility and disturbance increased.

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Plant strategies are sets of correlations that describe relationships among functional traits (e.g. Grime 1977, Chapin 1980). Consequently, plant strategies describe the patterns of trait variation that should be responsible for differential performance among species and have been used in attempts to help understand issues such as the relationship between biodiversity and ecosystem function (Tilman et al. 1997), exotic species invasions (Rejmánek and Richardson 1996) and vegetational response to global climate change (Allen-Diaz et al. 1996, Woodward et al. 1997).

Since plant strategies represent correlations of many traits across taxa, small sets of traits should be able to serve as surrogates for the larger plant strategies. If these traits are easily measured, this would facilitate the examination of large numbers of species and the relationship between plant strategies and ecological performance. For leaves, specific leaf area (SLA), its

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components (leaf thickness and leaf tissue density) and leaf angle are relatively easy to measure and represent the principal traits that relate biomass investment in leaves and light interception (Ehleringer 1989, Witkowski and Lamont 1991, Ryser 1996, Reich et al. 1997, 1998a, b). Under low N availability, root length is the functional unit of root biomass that determines N uptake (Tinker and Nye 1977). Specific root length (SRL) and its components (root diameter and root tissue density) are easy to measure and represent the quantity of biomass invested per unit of standing root length (Aerts et al. 1991, Eissenstat 1991, Reich et al. 1998a, b).

Although these seven traits may be of great utility in explaining ecological patterns, the relationships of these traits among species have not been determined no less their predictive capacity. Whole-plant growth form is also important ecologically and easily measured, yet the relationships between growth form and organlevel traits are poorly understood. For example, the degree of vegetative reproduction and the presence of a non-caulescent stage are important for plant growth, reproduction, competitive ability, and ecological distributions (Raunkiær 1934, McIntyre et al. 1995, Bazzaz 1996).

In general, although plant strategies have the potential to help predict the differential performance of species in different environments, there is a lack of data with which to examine the relationships of important functional traits that have been quantified independent of the gradients on which species performance will be examined (MacGillivray et al. 1995). Therefore, the first goal of this study was to examine the relationship among seven potentially ecologically important organlevel functional traits (SLA, leaf thickness, leaf tissue density, leaf angle, SRL, root diameter, and root tissue density) over a broad range of species grown in the field under similar conditions of low nitrogen (N) availability. Species were selected so as to differ in their life history (annuals, biennials, perennials), current functional classifications (C3 grass, C4 grass, C3 forb, legume) and to include species that are common in high-fertility environments and species that are common in low-fertility environments. For our second goal, we examined the relationship between these organ-level traits and traits relating to growth form, specifically whether species were rhizomatous or not and whether species grew as basal rosettes for part of their life cycle.

Third, we tested the ability of the expanded set of trait relationships to predict relative abundance of species along experimental gradients of N supply and disturbance. These represent some of the primary gradients along which ecologists have sought to explain the pattern of species abundance (Grime 1979, Chapin 1980, Oksanen et al. 1981, Tilman 1988). Although we did not know the relationship among the seven traits we examined, we hypothesized that species that have

the strategy associated with denser tissues aboveground and belowground would decrease in relative abundance as N supply increased (Craine et al. 1999). With respect to disturbance, sites where the soil has recently been disturbed often have higher nutrient availability (Fox and Fox 1986, Crawley 1987, Robinson et al. 1995) in part due to decreased nutrient uptake by plants, increased transfers from live biomass to dead organic matter, increased soil aeration, and/or soil warming. We hypothesized that high-density species will decrease in relative abundance with increasing soil disturbance.

For these purposes, we measured a series of root and leaf traits as well as aspects of whole-plant growth form on 76 species from sites that had relatively low N availability. The relationships of the seven organ-level traits among species were determined with a principal components analysis and the predictive power of resultant principal component axes were tested with previously acquired data on species composition from established Cedar Creek Long-Term Ecological Research (LTER) studies of fertility and disturbance.

Methods

Sample collection and trait measurement

Plant samples from 76 species were taken from monoculture plots or isolated individuals growing in one of three locations at Cedar Creek or seed production fields at Prairie Restorations, Inc. (Princeton, MN) (Appendix 1). All sites are located on the Anoka sandplain of central Minnesota and are considered or known to have low N supplies. Sites at Cedar Creek included 1) Cedar Creek LTER Experiment 111 (E111), a longterm monoculture garden (Craine et al. 1999), 2) an invasive species garden and surrounding unmanipulated area, adjacent to LTER experiments E120 and E123, and 3) 3-month-old seedlings established adjacent to E120 in 1-L pots with soil from areas adjacent to E120. These sites are described in more detail in the Cedar Creek web site (www.lter.umn.edu). The remaining samples were collected from seed production plots at Prairie Restorations, Inc. (Princeton, MN). None of the Cedar Creek sites are actively fertilized, while none of the sites at Prairie Restorations, Inc. receive more than 4 g N m⁻² yr⁻¹ (Jim Rittenauer, Prairie Restorations, Inc.). An ANOVA detected no differences in the PCA scores (see below) of species collected from different sites (data not shown).

Only one plant or clone was sampled per species. Although this minimizes our confidence in the value for a parameter of any one species, for a given amount of sampling effort, this approach maximizes the confidence in the overall relationship among all species. To determine SLA, fully expanded leaves in the fully lit portion of the canopy were removed from the plant and kept moist until measurement. Generally enough leaves were collected to provide at least 10 cm^2 of leaf area. Within 8 h of sampling, the area of the leaves were determined using a Li-Cor LI-3000 Leaf Area Meter (Li-Cor Inc., Lincoln, NE). Petioles of leaves were not included in this measurement. Leaf samples were dried at 85°C for at least 24 h and weighed to the nearest milligram. SLA was calculated as the ratio of leaf area to leaf mass. To determine leaf thickness, in the field, calipers were placed on a leaf at a representative point off of the midrib, closed until the leaf was securely grasped by the calipers and the calipers slowly opened until the leaf would slide out when pulled gently. This distance, measured to the nearest 0.01 mm, was considered the leaf's thickness. Leaf tissue density was calculated as the ratio of leaf mass to leaf volume, where leaf volume is the product of leaf thickness and leaf area.

Leaf angle was measured using a protractor and determined relative to the ground surface (Norman and Campbell 1989), with leaves parallel to the ground defined as having an angle of zero degrees. For each plant, only fully expanded leaves at the top of the canopy were used. If there was a range in leaf angle along fully lit portions of a stem, the modal leaf was chosen. Root samples were obtained by either removing a 7.5-cm-diameter, 20-cm-deep core around a chosen plant or by digging up an equivalent volume of soil with a trowel. Roots were washed over a 2-mm screen until they were free of soil. A representative subsample of the fine root mass (<1 mm) was scanned on a Hewlett Packard 6100 scanner at 600 dpi (0.04 mm resolution). Average diameter, total root length and root volume of the subsample were determined with WinRhizo (Régent Instruments, Quebec, Canada). Afterwards, subsamples were dried and weighed as described for leaves. Specific root length (SRL) was calculated as the ratio of total root length and subsample mass. Root tissue density was calculated as the ratio of subsample mass and total root volume.

For growth form traits, at the time of sampling we determined whether species reproduced vegetatively by rhizomes. A species was classified as rhizomatous if its rhizomes were longer than 2 cm. If no rhizome was present or rhizomes were less than 2 cm long, (a.k.a. root offshoots), multiple individuals were excavated to insure the non-rhizomatous status of the plant. Also, multiple individuals were observed in order to determine if any leaves were produced from a basal meristem or if all leaves were produced on elongated stems. Species that were geophytes, flat or versatile rosettes, erect rosettes, or partial rosettes (sensu McIntyre et al. 1995) were considered "basal" species. Species that had no basal stage (proto-hemicryptophytes and chamephytes, sensu McIntyre et al. 1995) were classified as "non-basal".

Plant strategies analysis

All statistical analyses were performed in JMP 3.2 (SAS Institute). A principal components analysis (PCA) was performed with the correlation matrix of the following seven variables: leaf angle, leaf thickness, leaf tissue density, SLA, average root diameter, root tissue density, and SRL. PCA produces uncorrelated multivariate axes that can be interpreted to represent a given plant strategy. Use of the correlation matrix standardizes differences among variables due to measurement scale. The importance of different traits in a given axis is indicated by the relative loading of the trait in the eigenvector. The relative importance of a given axis in explaining variation among species is represented by the eigenvalue of the axis, the variation among species in component variables that is explained by that axis relative to the variation that would be explained by chance. The first two axes had eigenvalues of 2.5 and 1.7 and the third axis had an eigenvalue of less than one, indicating that it explained less variation than would be expected by chance.

To understand the relationships between currently used functional classifications and the PCA axes, ANOVAs or *t*-tests were computed with data from Axis 1 and Axis 2. Categories were based on 1) the most common functional group classifications used at Cedar Creek: C₃ grasses and sedges, C₄ grasses, C₃ forbs, and legumes, 2) life history classification (annual, biennial, perennial), 3) whether species were basal or not, and 4) whether species were rhizomatous or not. Data on life history were taken from McGregor et al. (1986), Fernald (1987), Britton and Brown (1970) and the USDA-NRCS PLANTS database (USDA and NRCS 1999). Significance of differences between groups was computed using a Tukey-Kramer HSD test. For a few species, we were unable to collect data on the presence of a basal stage or the presence of rhizomes. These species were not included in the comparisons.

Predictive capacity of plant strategies

To test the predictive and explanatory power of each PCA axis, the scores of species on each PCA axis were used in regression models that predicted plant species composition in two previously established Cedar Creek LTER experiments relating to N addition and disturbance at the Cedar Creek Natural History Area.

The first experiment with which we tested the utility of the PCA axes was the long-term fertilization gradient (LTER experiment E001) (Tilman 1987). This experiment consists of 54 plots in each of three fields and 45 plots in a fourth field. Since 1982, there have been eight different NH_4NO_3 fertilizer addition rates (0–27.2 g N m⁻² yr⁻¹) with other nutrients (P, K, Ca, Mg, S, and micronutrients) added to ensure that N is the limiting nutrient, along with a control which receives no nutrients. This experiment was repeated in four fields each of different successional age.

In E001, between 7 July 1997 and 28 August 1997, the proportional aboveground biomass of each species was determined from a 0.1-m² strip of vegetation that was clipped to the soil level and sorted to species (Tilman 1987). 38 species that were used in the construction of the PCA had been sampled in E001. The proportion of biomass of each species in a plot was modeled with a linear regression model that included field identity, the score of the species on Axis 1, the score of the species on Axis 2, the rate of N addition (coded as continuous), and the six pairwise interactions of these four variables. Data points where species were not present in a plot (zeros) were not included in the model. Since some species that had biomass in plots were not among the 76 species that we sampled and could not be included in the model, the relative biomass of each individual species was standardized such that the total relative biomass for a plot equaled 1. A total of 833 plot-level species abundances from the 207 plots were used in this model, of which 439 were of three species (Agropyron repens, Poa pratensis, and Schizachyrium scoparium).

Since the sum of the proportional biomass must always be one, if field, N addition rate, or the interaction between these two variables were significant, this would be due to a change in richness of the plot, since with increasing richness, the average relative biomass of a species would decline. If across all fields and treatments, species high or low on Axis 1 had proportionally more biomass, Axis 1 would be significant. A significant interaction between Axis 1 and field identity indicates that species at one end of Axis 1 had proportionally more biomass in at least one of the fields than in the other fields. The specific estimates of these coefficients represent the differences among fields in the relative dominance of species on Axis 1. A significant interaction between Axis 1 and N addition rate indicates that with increasing N addition rate, species high on Axis 1 would tend to have increasingly higher or lower proportional biomass, depending on the sign of the parameter for the interaction. Interpretation of results for parameters including Axis 2 is similar. Based on the results of the PCA, we consider the significance of the interaction between Axis 2 and N addition rate to represent a test of our hypothesis on the relationship between N strategies and site fertility.

We also examined data on the relative abundances of species in an experiment that tests the interactive effects of disturbance and fertility (LTER experiment E052, Wilson and Tilman 1991). In this experiment, there were three disturbance treatments and an undisturbed control. These treatments had been applied for 11 yr before the percent cover of different species was sampled. For the disturbance treatments, plots were rototilled annually in April to a depth of 25 cm to produce approximately 25%, 50% and 100% bare ground. There were four different NH_4NO_3 addition rates (0, 2, 5.4, 17 g N m⁻² yr⁻¹) with other nutrients added to ensure that N is the limiting nutrient except in the control which receives no additional nutrients. Plot-level treatments were a factorial combination of the four fertilization treatments and the four disturbance treatments, for a total of 16 treatments. Each treatment was replicated four times except for the four extreme ends of the treatment combinations (lowest N, lowest disturbance; highest N, lowest disturbance, etc.) which were replicated 14 times. Treatments were applied in a completely randomized design. Each of the 104 plots were 5 m × 5 m.

On 20 and 21 August 1998, the percent cover of each species was determined relative to total plant cover in two 0.5-m² quadrats. 28 species that were used in the construction of the PCA were present in E052. As with E001, all cover estimates were standardized so that the total cover in a plot would be equal to one. No data points where species cover was equal to zero were included in the model. The percent cover of each species was modeled with a linear regression model as a function of N addition rate (continuous), level of disturbance (1-4, continuous), the score of the species on Axis 1, the score of the species on Axis 2, and all pairwise interactions. As in the previous experiments, we consider the interactions between Axis 2 and the rates of disturbance or N addition to represent tests of our hypotheses regarding plant strategies. Interpretation for the rest of the variables is similar to E001 as described above. A total of 849 species abundances from the 104 plots were used in this model, of which 401 were of four species (Panicum capillare, Polygonum convolvulus, Schizachyrium scoparium, and Setaria glauca).

Results

The correlations of traits associated with plant strategies

The principal components analysis revealed two independent sets of correlations. The first set of correlations, Axis 1 (Table 1), explained 36.1% of the variation explained by PCA (14.5% expected). Axis 1 represents a continuous distribution of species from species that have thin, high-density leaves and thin roots (high Axis 1) to those that have thick, low-density leaves and thick roots (low Axis 1), with no pattern for life history (Table 2, Fig. 1). Although species distributions along this axis were continuous and there were many forb species that were more "grassy" than "forby", for ease of discussion we use the convention of describing species differences associated with this axis as differences

Table 1. Results of the principal components analysis of seven functional traits for 76 species. The eigenvalue for Axis 1 was 2.5, and Axis 1 explained 36.1% of the variation explained by PCA (14.5% expected). The eigenvalue for Axis 2 was 1.7, explaining 24.6% of the variation explained by PCA (14.5% expected).

Eigenvectors	Axis 1	Axis 2	
Leaf thickness	-0.46	-0.06	
Leaf angle	0.26	0.45	
Leaf tissue density	0.43	0.45	
Specific leaf area	0.04	-0.49	
Root diameter	-0.51	0.13	
Specific root length	0.49	-0.33	
Root tissue density	-0.19	0.48	

between grasses and forbs. Grasses generally had thinner, denser leaves and thinner roots than forbs, which had thicker, lower-density leaves and thicker roots (Table 1). There was no general pattern along Axis 1 with regards to the likelihood of having a basal growth stage or being rhizomatous (Table 2).

The second set of correlations (Axis 2) explained 24.6% of the variation explained by PCA (14.5% expected). Axis 2 represents a gradient of species from those that had erect, high tissue density leaves and high tissue density roots to species that had flatly held, low-density leaves and low-density roots (Table 1, Fig. 2). Species with erect, dense leaves and dense roots were more likely to have a basal morphology and less likely to be rhizomatous (Table 2). There was no strong pattern along Axis 2 for leaf thickness or root diameter. Although C_4 grasses scored consistently higher on Axis 2, there was no other general pattern for functional

groups with forbs, legumes, and C_3 grasses distributed evenly across this axis (Table 2, Fig. 2). Annuals had significantly lower scores on Axis 2 (Table 2), although there were also many perennials that scored low on Axis 2 (Fig. 2). Among legumes, there was clear separation of legumes associated with their phenological patterns. Cool-season legumes such as *Baptisia leucantha*, *Vicia villosum*, and *Lupinus perennis*, all scored low on Axis 2 while warm-season species such as *Astragalus canadensis*, *Petalostemum purpureum*, and *Lespedeza capitata*, scored high (Fig. 2). In a similar manner to Axis 1, for ease of discussion we refer to Axis 2 as representing a gradient of species from "low-density" to "high-density" species.

Species performance

In the long-term fertilization gradient (E001), 23% of the total variation in species composition was explained with the model of field identity, Axis 1, Axis 2, N addition rate, and their interactions (Table 3). Little of the variation was explained by field identity or interactions with field identity (Table 3). On average, across the entire experiment, grasses had greater proportional cover than forbs. Likewise, high-density species had greater proportional cover than low-density species. With increasing N addition the average proportional cover of a species was greater, i.e. richness decreases with increasing N addition. Individual forb species held a statistically significant greater proportion of the cover with increasing rates of N addition, but only 2% of all of the explained variation was explained by this factor.

Table 2. Results of ANOVAs and *t*-tests for functional classifications of plant species and the scores of the species on Axis 1 and Axis 2. Functional classifications tested include the functional classification currently used at Cedar Creek (C_3 grass, C_4 grass, forb, legume), a life-history classification (annual, biennial, perennial), whether species have a basal rosette stage (basal, non-basal), and whether species have conspicuous rhizomes or not (Rhizome, Non-rhiz.). The number of replicates for each classification is shown in parentheses. Means and standard errors reported. Superscript letters refer to comparisons within a row.

	r^2	$\operatorname{Prob} > F$	C ₃ grass (12)	C ₄ grass (9)	Forb (45)	Legume (10)
Axis 1 Axis 2	0.43 0.22	<0.001 <0.001	$\begin{array}{c} 2.15 \pm 0.35^{a} \\ 0.16 \pm 0.33^{b} \end{array}$	$\begin{array}{c} 0.74 \pm 0.41^{b} \\ 1.55 \pm 0.38^{a} \end{array}$	$\begin{array}{c} -0.65 \pm 0.18^{\rm bc} \\ -0.20 \pm 0.17^{\rm b} \end{array}$	$\begin{array}{c} -0.23 \pm 0.38^{\rm c} \\ 0.51 \pm 0.36^{\rm b} \end{array}$
			Annual (10)	Biennial (5)	Perennial (61)	
Axis 1 Axis 2	0.05 0.15	0.14 <0.01		$ \begin{array}{c} -1.14 \pm 0.70^{a} \\ 0.06 \pm 0.53^{ab} \end{array} $	$\begin{array}{c} 0.02 \pm 0.20^{\rm a} \\ 0.23 \pm 0.15^{\rm b} \end{array}$	
			Basal (37)	Non-Basal (34)		
Axis 1 Axis 2	0.03 0.24	0.18 < 0.001	$\begin{array}{c} 0.26 \pm 0.27^{\rm a} \\ 0.70 \pm 0.18^{\rm a} \end{array}$	$-0.26 \pm 0.28^{\rm a} \\ -0.53 \pm 0.19^{\rm b}$		
			Rhizome (23)	Non-rhiz. (49)		
Axis 1 Axis 2	$\begin{array}{c} 0.004\\ 0.04\end{array}$	0.60 0.11	$-0.12 \pm 0.34^{\rm a} \\ -0.29 \pm 0.27^{\rm a}$			
			Rhizome (23)*	Non-rhiz.(34)*		
Axis 1 Axis 2	$\begin{array}{c} 0.006\\ 0.14\end{array}$	0.58 <0.01	$-0.12 \pm 0.35^{\rm a} \\ -0.29 \pm 0.25^{\rm b}$	$\begin{array}{c} 0.14 \pm 0.29^{a} \\ 0.69 \pm 0.20^{a} \end{array}$		

* Only includes non-legumes that are perennials.

Fig. 1. Scores of individual species on Axis 1 grouped by their current functional classification (C_3 grass, C_4 grass, forb, legume). White, gray, and black bars designate annuals, biennials, and perennials, respectively.



With increasing rates of N addition, species with lower tissue density held a higher proportion of total cover, supporting the hypothesis that the differences in tissue density strategies are related to abundance along fertility gradients.

In the experiment that examined the interaction between fertility and disturbance (E052), 27% of the total variation in species composition was explained (Table 4). Axis 2 and the interactions between Axis 2 and both disturbance and N addition rate explained 80% of this variation. On average for the entire experiment, highdensity species held a greater proportion of the cover. The percent cover of low-density species increased with both increasing rates of N addition and disturbance. Little of the variance was explained by interactions between Axis 1 and disturbance or fertility, i.e. the proportional cover of the average grass or forb species did not change greatly with increasing disturbance or fertilization.

Discussion

Grasses and forbs

Axis 1 mainly represented a distribution of species from "forby" species to "grassy" species, although some grasses, such as *Panicum virgatum* or *Calamovilfa longifolia*, were measured to be more like forbs than grasses in their functional traits. Similarly, some forbs were more like grasses in their functional traits. For example, *Berteroa incana*, *Hedeoma hispida*, and *Gentiana andrewsii* had leaves and roots that were similar to grasses in their patterns of tissue density and thickness. Although our confidence in the placement of any single species along these axes is low because we analyzed only one individual per species, the pattern of distribution of grasses and forbs along this "grass-forb" axis clearly reveals that grasses and forbs consistently differ in the traits that compose this axis and that some species may be more like species of the other functional classification than its own.

In all, it is not clear whether or when grasses and forbs should be considered separate functional groups. Functional classification of species that are determined both a priori and post hoc reflect real distinctions between grasses and forbs (Kindscher and Wells 1995, Lauenroth et al. 1997, Tilman et al. 1997). The separation of grasses and forbs in a priori classifications is most common when the traits used for the delineations rely heavily on morphological traits or phylogeny. Yet, there is often little difference between grasses and forbs in functional traits, such as SLA, leaf longevity, relative growth rate, or growth on low-nutrient media (Cornelissen and Thompson 1997, Grime et al. 1997, Craine et al. 1999). Similarly, Axis 1 and Axis 2 reveal that the same patterns of organ-level functional traits, growth forms, and life history exist within both grasses and forbs from low-N to high-N species (Fig. 3).

Although many functional traits that are considered important in the growth of species do not differ consistently between grasses and forbs, examining the distribution and abundances of grasses often shows strong differences in ecological performance between the two classes of species (Weaver 1958). In both E001 and E052, individual grass species held a larger proportion of biomass or cover than forbs regardless of disturbance frequency or N addition rate (also see). This was not due to greater richness of forbs than grasses (19 forbs vs 9 grasses in E052; 28 forbs vs 10 grasses in E001) as on average, grasses held 3.6 times the total cover than forbs in E052 and had 8.1 times the total biomass of forbs in E001 (data not shown). In general, as N addition rate or disturbance increased, community composition shifts from one set of grass species to another. If grasses generally only differ from forbs in a few traits, such as root diameter, leaf thickness, leaf tissue density, or root foraging (Grime et al. 1997), the manner in which these traits confer competitive superiority is unknown.

It is important to examine the components of SLA and SRL, as well as the measures themselves (Witkowski and Lamont 1991, Craine et al. 1999). SLA did not differ among grasses and forbs, though the components of SLA did. Similarly, it often has been assumed that species differences in SRL reflect differences in average diameter of roots (Boot 1990). This was true for differences in SRL between grasses and forbs. Yet, SRL was greater for low-density species, but mainly due to having lower tissue density, not thinner roots.

"Tissue density" strategies

The tissue density axis parallels a general strategy seen by others in many other floras (Leishman and Westoby 1992, Diaz and Cabido 1997, Grime et al. 1997). Herbaceous species that occupy infrequently disturbed, low-N environments are more likely to have roots and leaves with high tissue density. Greater tissue density leads to greater tensile strength of tissues and in other studies is correlated with greater leaf longevity, greater herbivore resistance, resistance to physical damage, and greater nutrient use efficiency which are thought to be important in minimizing nutrient losses, allowing plants to grow large at low nutrient supply rates (Weaver 1958, Berendse and Aerts 1987, Dijkstra and Lambers 1989, Grime et al. 1997, Reich et al. 1997, Aerts and Chapin 2000, Craine et al. 1999).

Herbaceous species that occupy frequently disturbed, high-N environments have roots and leaves that have low tissue density. Low leaf tissue density has been associated with rapid turnover of leaves in an ascending canopy as older leaves are shaded out by new leaves higher in the canopy. Since leaves are turned over quickly, there is no advantage to producing carbon-expensive, high-density leaves that are resistant to physical injury (Dijkstra and Lambers 1989). Although less work has been done on roots, many functional relationships involving root traits parallel relationships involving leaf traits, such as the positive correlation between tissue density and root longevity (Craine et al. 1999). Although it remains to be quantified, high root tissue density should also be important in resistance to mechanical stresses of root systems, such as the stresses associated with frost heaving, and may be directly linked to other important traits including herbivory deterrence and decomposition.

High-density species held their leaves at a higher angle than low-density species. Previous research on leaf angle has shown that variation in leaf angle within





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Table 3. Results of the regression model that predicts the proportional biomass of species in LTER E001, a long-term fertilization experiment. Parameters included the species' scores on Axis 1, the species' scores on Axis 2, the categorical identity of the field in which the plots were located (Field), the rate of N addition (NAdd), and the pairwise interactions between these four parameters. For each of the four fields, A–D, the estimates of the coefficients for the specific interactions with Axis 1, Axis 2, and N addition rate. The r^2 of the model was 0.23.

Parameter	Estimate	F ratio	$\operatorname{Prob} > F$
Axis 1	0.054	53.6	< 0.001
Axis 2	0.060	30.3	< 0.001
Axis 1×Axis 2	-0.045	36.8	< 0.001
Field		4.2	< 0.01
А	0.073		
В	0.0013		
С	-0.025		
D	-0.049		
Axis $1 \times \text{Field}$		1.5	ns
Axis $1 \times A$	0.0024		
Axis $1 \times B$	-0.0087		
Axis $1 \times C$	0.014		
Axis $1 \times D$	-0.0077		
Axis $2 \times \text{Field}$		2.9	< 0.05
Axis $2 \times A$	0.019		
Axis $2 \times B$	0.032		
Axis $2 \times C$	-0.024		
Axis $2 \times D$	-0.027		
NAdd	0.031	41.0	< 0.001
Axis $1 \times NAdd$	-0.00050	4.8	< 0.05
Axis $2 \times NAdd$	-0.0025	39.4	< 0.001
Field × NAdd		8.0	< 0.001
$NAdd \times A$	-0.0021		
$NAdd \times B$	0.0030		
$NAdd \times C$	-0.00024		
$NAdd \times D$	-0.00066		

a canopy serves to decrease ratio of incident light to leaf N at the top of the canopy (Terashima and Hikosaka 1995). Diurnal and seasonal variation in average leaf angle is also associated with the variation in the availability of resources (Ehleringer and Forseth 1980, Comstock and Mahall 1985). In high-N sites,

Table 4. Results of the regression model that predicts the proportional biomass of LTER E052, a disturbance by fertility gradient. Parameters included the rate of N addition (NAdd), the disturbance frequency (Dist), the species' score on Axis 1, the species' score on Axis 2, and the pairwise interactions between these four parameters. The r^2 of the model was 0.27.

Parameter	Estimate	F ratio	$\operatorname{Prob} > F$
Nadd	0.0054	28.4	< 0.001
Dist	0.030	7.7	< 0.01
Nadd \times Dist	-0.0017	23.5	< 0.001
Axis 1	0.036	5.2	< 0.05
Nadd \times Axis 1	-0.00028	1.0	ns
$Dist \times Axis 1$	-0.0034	0.4	ns
Axis 2	0.23	144.8	< 0.001
Nadd \times Axis 2	-0.0023	53.6	< 0.001
$Dist \times Axis 2$	-0.05	87.7	< 0.001
Axis 1×Axis 2	0.013	5.0	< 0.05

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Fig. 3. Diagram of the parallel patterns of growth form for grasses and forbs. Grasses and forbs of low-fertility sites tend to have a basal rosette stage, erect high-density leaves, high-density roots and have short rhizomes if any. Grasses and forbs of high-fertility sites have no basal rosette stage, tend to have low-density leaves held at an angle that is closer to being parallel to the ground, low-density roots and are more likely to be rhizomatous.

ratios of light availability to leaf N are lower so that flatly held leaves maximize light acquisition per unit leaf N. As long as water is not limiting, high-N plants are less likely to suffer from photoinhibition because transpiration is sufficient to reduce heat load. Having flat leaves in high-N habitats also maximizes light acquisition at the top of a plant's canopy and contributes to the competitive success of these species. In low-N sites, flat leaves would cause photoinhibition of photosynthesis and excess heat load during midday. As an index of the range of leaf angle among species in this study, the 25% to 75% quartiles of the data set on leaf angle ranged from 70° to 23.75°, corresponding to 63% reduction in radiation load midday.

High-density species often delay stem production until the flowering stage and exist in a basal stage early in the growing season. Competition for light is not as important in structuring communities in the undisturbed low-N habitats as in undisturbed high-N habitats (Tilman 1988). Consequently, high-density species do not produce stems for better light acquisition, but rather to raise reproductive parts, presumably to increase dispersal distance of propagules or to better attract pollinators or come in contact with airborne pollen. In herbaceous communities in high-N habitats, light levels near the ground are low (Wilson and Tilman 1991). Consequently, low-density species produce stems at the time of emergence to raise leaves high in the canopy as well as to raise reproductive parts.

The perennial plants that occupy low-N habitats are also less rhizomatous than perennial herbaceous plants of high-N areas, a pattern previously noted (Grime 1979, McGraw and Chapin 1989, Bazzaz 1996). Evolutionarily, lower allocation to rhizomes may be associated with either 1) low-N areas having a higher proportion of bare ground, increasing the likelihood that seeds can come in contact with bare ground and germinate unshaded by vegetation (Kitajima and Tilman 1996), or 2) the lack of need for plants to expand laterally to gather light in low-N habitats. Many of the species that are not rhizomatous still reproduce vegetatively, with new individuals arising directly from the caudex (a.k.a. root offshoots) or the rhizomes being relatively short, both resulting in a "bunch" or tussock morphology. Consequently, new individuals are produced relatively close to parent plants. In high-N habitats, rhizomes provide an effective means of short distance reproduction, as new individuals are provided with a carbon subsidy (Hartnett and Bazzaz 1983) that allows them to emerge through existing canopies or litter layers under which seedlings are likely to perish.

The gradient of tissue density strategies was important in determining the relative success of species across both fertility and soil disturbance gradients. Species that occupy frequently disturbed areas of ecosystems should experience relatively higher N availability than undisturbed areas. Consequently, species that are common in frequently disturbed areas would have leaves and roots that were built similarly to the leaves and roots of species that are successful in high-N, undisturbed habitats. MacGillivray et al. (1995) showed that in 21 species common in Britain, species that had traits equivalent to those that scored high on Axis 2, had greater "resistance" to imposed frost, drought, and fire treatments. Species that scored low on the "toughness" axis had low resistance to these disturbances, but high "resilience", i.e. increased quickly following disturbance. Soil disturbances such as gopher mounds, which are simulated in E052, are generally beyond the capacity of most individuals to survive. Consequently, species that are prominent in the disturbed plots are ones that are most "resilient" and can grow quickly from seed following disturbance of the soil. Some species, such as Asclepias syriaca, may have been abundant at high disturbance due to the presence of deep rhizomes. Although disturbance leads to greater nutrient availability, the growth forms of early successional annuals vary with the timing of disturbance. Fall-germinating annuals are generally basal while spring-germinating annuals are generally caulescent (Wilson and Tilman 1991).

Summary

In all, there were two independent sets of correlations among the organ-level and growth form traits that we examined. Grasses held greater cover regardless of the disturbance frequency or the N addition rate. With increasing rates of N addition or disturbance, high-density species became less abundant and low-density species became more abundant. More mechanistic research is necessary to understand the bases of the differential performances associated with the plant strategies. In addition, the predictive capacity of plant strategies may be improved by examining plasticity of traits across environmental gradients as well as between young and more mature plants. Future work should also expand the traits that are incorporated in plant strategies and test plant strategies in different environments. Future work that examines plant strategies in ecosystems that differ in the relative limitation of water and N may reveal important differences that relate to success in these ecosystems.

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and root tissue density (Root den	is.) (g cm ⁻¹	3).	() m a)	na aurade), urviuge				and a support of the		5 m 9 (1
Species	Rhiz.	Basal	Fxnl	ABP	Leaf thick.	Leaf angle	Leaf dens.	SLA	Root diam.	SRL	Root dens.	Axis 1	Axis 2
Achillea millefolium ¹	>	>	Ц	٩	0.31	40	0.35	03	0.030	75	0 11	0.45	0.44
A onstache foeniculum ¹	->	-Z	, ſĽ	- A	0.41	۶¢	0.16	157 89	0.040	04	0.18	-0.40	-0.66
A gronvron renews ¹	· >	zz	. Ú	, d	0.22	55	0.32	141.29	0.030	133	0.11	1.06	-0.39
Agrostis alba ²	Y	X	ິບໍ	, d	0.21	20	0.31	151.88	0.025	169	0.12	1.75	-0.46
Agrostis scabra ¹	Z	Y	ĵ	Ч	0.16	80	0.46	135	0.021	140	0.2	2.4	1.21
Ambrosia artemisiifolia elatior ¹	Z	Z	Ъ	A	0.19	0	0.37	141.2	0.036	129	0.08	0.47	-1.23
Andropogon gerardii ¹	Z	Y	C₄	Ь	0.14	70	0.52	137.5	0.031	56	0.24	1.25	2.09
Anemone cylindrica ¹	Z	Y	۲	Ь	0.3	15	0.34	99.36	0.036	52	0.19	-0.88	0.52
Artemisia ludoviciana ²	Y	Z	Ĺ	Ь	0.3	10	0.24	138	0.034	107	0.11	-0.44	-1.3
Asclepias incarnata ⁴	Y	Z	ĹĻ	Ь	0.34	20	0.16	185.93	0.036	70	0.14	-1.33	-1.58
Asclepias syriaca ¹	Y	Z	Ц	Ь	0.48	48	0.13	158.28	0.043	48	0.14	-2.38	-0.71
Asclepias tuber osa^{1}	Z	Z	ц	Ь	0.32	16	0.23	133.81	0.050	23	0.22	-2.54	0.31
Aster azureus ¹	Z	Y	۲ <u>ـ</u>	4	0.5	09	0.2	98.19	0.035	87	0.12	-1.24	-0.02
Aster ericoides ¹	Y	Y	Ĺц	<u>с</u> ,	0.32	09	0.25	122.75	0.040	52	0.15	-0.96	0.51
Aster laevis ⁴	č. Z	ċ	ĹЦ	ር ነ	0.26	35	0.3	127.14	0.030	89	0.16	0.11	-0.08
Aster lanceolatus ⁴	?: Z ;	Y	ц,	<u>н</u> ,	0.22	40 0 0	0.34	132.33	0.036	68	0.15	0.01	0.23
Aster novae-angliae ¹	Y	z	Гц (<u>а</u> (0.37	30	0.18	148.64	0.046	52	0.12	- 5 - 7	-0.77
Aster puniceus ⁻	NZ Z	ŻŻ	ц,	בי כ	0.26	07	0.31	123.43	0.028	147	0.12	/9.0	-0.85
Astragalus canadensis	ZŻ	ZŻ	-, -	ב, נ	0.24	<u>ر</u> د	4.0 16.0	103.33	0.042	2 5 4 0	0.22	-0.3/	21.2
Baptista leucanina ⁻ Rerteroa incana ¹	ΖZ	Z >	니다	ב ה	0.00	0 02	10.0 10.4	90.60 170	0.019	916 737	0.07	1.09 787	-2.10
Bouteloua curtinendula ¹	z	·≻	ď	, d	0.19	72.5	0.48	108.96	0.032	-22	0.19	1.02	1.92
Calamagrostis canadensis ³	Υ	Y	ťŰ	Ь	0.15	09	0.52	128.31	0.022	249	0.11	3.5	-0.04
Calamovilfa longifolia ¹	Y	Y?	°.	Ь	0.22	60	0.53	86.42	0.048	33	0.18	-0.32	2.49
Carex lasiocarpa ¹	Z	Y	ۍ	Р	0.21	50	0.65	73.12	0.023	252	0.09	3.55	0.81
Cassia fasciculata ²	Z	Z;	L,	٩	0.14	55 25	0.33	215.45	0.034	10	0.16	0.62	-0.44
Chenopodium album ²	Z	ZŻ	цĹ	A d	0.46	0 8	0.17	130	0.025	144 44 :	0.14	$\frac{0}{1000}$	-1.65
Coreopsis paimata	×Z	Z>	r (r	ч <	0.21	000	0.78	177	0.024	011	0.00	0.61	1.18
Desmodium canadense ¹	zz	-Z	- <u>-</u>	t ط	032	20	0.18	180.19	0.034	176	0.0	-0.48	-2.0
Elvmus canadensis ³	Z	Z	ıű	- d	0.17	65	0.43	136.08	0.023	288	0.09	3.44	-0.74
Eragrostis trichodes ²	Z	Y	ິບັ	Ь	0.17	75	0.43	136.33	0.021	73	0.39	1.14	2.73
Erigeron canadensis ¹	z	Z	т Ц	A	0.2	80	0.26	188.85	0.035	119	0.09	0.83	-0.73
$Festuca ovina^2$	Z	Y	ပိ	Ь	0.26	70	0.32	120.55	0.020	170	0.18	1.69	0.27
Festuca rubra ²	Υ	Z	Ű	Ь	0.28	80	0.23	153.61	0.022	158	0.17	1.27	-0.32
Gentiana andrewsii ⁴	Z?	Z	ц	Ь	0.15	35	0.29	231.63	0.031	129	0.11	1.03	-1.88
Hedeoma hispida ²	Z;	Z;	ц,	V (0.3	30	0.38	88.18	0.022	166	0.15	1.24	0.02
Helianthus giganteus	ž	ZZ	r þ	ב, כ	0.0	01	0.14	140.05	0.040	10	0.13	/ 7 - 7 - 7	- 1.4
Heliantinus rigiaus Heliansis helianthaidas4	1 V9	ZZ	цĹ	ן מ	0.04	}	0.16 0.16	164 27	0.020	77	0.17	00.7-	0.4.0 1 61
Itenopsis neuannouces Iris persiralar ⁴	Z	2>	L L	ц Ф	0.57	080	0.10	75.01	00.00 800.0	119	0.14	-1.79	-1.01
Koeleria cristata ¹	zz	- >	. Ú	- d	0.36	20	0.35	50.28	0.026	99	0.29	-0.09	2.59
Lespedeza capitata ¹	z	Z	, L	Р	0.23	35	0.4	108.96	0.037	73	0.13	0.1	0.5

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Species	Rhiz.	Basal	Fxnl	ABP	Leaf thick.	Leaf angle	Leaf dens.	SLA	Root diam.	SRL	Root dens.	Axis 1	Axis 2
Liatris aspera ¹	z	Y	ц	Ь	0.39	65	0.33	78.6	0.045	80	0.08	-0.86	0.74
Lupinus perennis ¹	Z	Y	L	Ь	0.61	10	0.1	167.43	0.034	117	0.32	-2.83	-0.84
Melilotus alba ²	Z	Z	L	в	0.23	45	0.25	170.88	0.029	100	0.15	0.39	-0.7
Monarda fistulosa ⁴	Y	Z	Ц	Ь	0.25	0	0.25	158.35	0.031	121	0.11	-0.01	-1.72
Oenethera biennis ¹	Z	Y	Ц	в	0.38	70	0.27	96.27	0.032	95	0.13	-0.16	0.49
Panicum capillare ¹	Z	Z	ڻ	A	0.2	55	0.23	216.67	0.020	218	0.14	2.02	-1.96
Panicum virgatum ¹	Y	Y	°,	Ь	0.25	65	0.3	131.71	0.044	36	0.19	-0.89	1.11
Penstemon grandiflorus ¹	Z	Υ	L	в	0.5	30	0.22	91.62	0.041	51	0.15	-2.21	0.1
Petalostemon purpureum ¹	Z	Z	L	Ь	0.335	25	0.42	72.13	0.042	40	0.24	-1.25	1.83
Phleum prateñse ²	Z	Y	ؾ	Ь	0.23	75	0.28	155.77	0.022	142	0.19	1.42	0.02
Physalis [¯] virginiana ¹	Y	Z	Ц	Ь	0.31	40	0.26	123.43	0.030	54	0.27	-0.73	0.85
Poa pratensis ¹	Y	Y	ڻ	Ь	0.24	75	0.6	69.1	0.021	284	0.1	3.84	0.91
Polygonum convolvulus ²	Z	>	, г	A	0.34	0	0.18	159.66	0.025	201	0.1	0.38	-2.61
Potentilla arguta ¹	Z	Y	ц	Ь	0.34	25	0.25	126	0.043	21	0.32	-2.33	1.27
Pycnanthemum virginianum ⁴	Z?	Z	ц	Ь	0.21	20	0.38	126	0.034	84	0.13	0.23	-0.12
Ratibida pinnata ⁴	°.Z	Z	Ц	Ь	0.4	0	0.25	99.3	0.044	56	0.12	-2.03	-0.51
Rudbeckia serotina ¹	Z	Y	ц	в	0.38	70	0.19	139.16	0.041	35	0.22	-1.72	0.77
Rumex acetosella ¹	Υ	Y	Ц	Ь	0.45	45	0.16	138.31	0.034	127	0.09	-0.82	-1.33
Schizachyrium scoparium ¹	z	Y	C₄	Ь	0.13	70	0.54	142	0.032	58	0.22	1.39	1.99
Setaria glauca ²	Z	Y	C4	A	0.27	75	0.19	197.01	0.022	148	0.18	1.01	-0.96
Solidago nemoralis ¹	Z	Υ	Ĩ	Ь	0.38	70	0.3	87.8	0.042	42	0.17	-1.25	1.46
Solidago ptarmicoides ⁴	Z?	\dot{Y} ?	ц	Ь	0.33	50	0.39	76.73	0.039	34	0.24	-0.96	2.14
Solidago rigida ¹	Z	Y	Ц	Ь	0.435	81.5	0.25	92.07	0.039	43	0.21	-1.39	1.58
Solidago speciosa ¹	z	Z	Ц	Ь	0.38	40	0.3	88.34	0.038	46	0.19	-1.29	0.98
Sorghastrum nutans ¹	Z	Y	C₄	Ь	0.16	80	0.48	130.6	0.027	107	0.17	1.97	1.32
Sporobolus heterolepis ¹	z	Y	C4	Ь	0.21	50	0.4	119.27	0.035	52	0.2	0.09	1.25
$Trifolium \ pratense^2$	Z	Y	L	Ь	0.16	35	0.29	217.73	0.029	112	0.14	0.87	-1.45
Verbascum thapsus ¹	Z	Υ	Ц	в	0.53	45	0.14	136.11	0.033	60	0.19	-2	-0.35
Verbena hastata ⁴	Y	Z	Ц	Ь	0.3	10	0.23	143.9	0.032	92	0.13	-0.58	-1.16
Vernonia fasciculata ⁴	Z?	۶	Ц	Ь	0.27	65	0.31	120.08	0.031	123	0.11	0.74	0.03
Veronicastrum virginicum ⁴	č.Z	Z	Ц	Ь	0.28	10	0.4	90.4	0.030	131	0.11	0.56	-0.31
Vicia villosa ¹	Z	Z	L	A	0.22	35	0.18	254.17	0.043	60	0.12	-0.99	-1.94
Zizia aurea ³	N;	Υ?	ц	Р	0.24	45	0.29	144.76	0.031	100	0.13	0.37	-0.38
Source of plants = ${}^{1}E111$, ${}^{2}area$ ad	ljacent to E	3123, ³ seedli	ings with s	soil from a	rea adjacer	nt to E120,	⁴ Prairie R	estorations,	Inc.				

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Appendix 1 (Continued)

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