New Phytologist

Research

# Linking leaf and root trait syndromes among 39 grassland and savannah species

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Received: *14 February 2005*
Accepted: *21 February 2005*

## Summary

• Here, we tested hypothesized relationships among leaf and fine root traits of grass, forb, legume, and woody plant species of a savannah community.

• $CO_2$ exchange rates, structural traits, chemistry, and longevity were measured in tissues of 39 species grown in long-term monocultures.

• Across species, respiration rates of leaves and fine roots exhibited a common regression relationship with tissue nitrogen (N) concentration, although legumes had lower rates at comparable N concentrations. Respiration rates and N concentration declined with increasing longevity of leaves and roots. Species rankings of leaf and fine-root N and longevity were correlated, but not specific leaf area and specific root length. The $C_3$ and $C_4$ grasses had lower N concentrations than forbs and legumes, but higher photosynthesis rates across a similar range of leaf N.

• Despite contrasting photosynthetic pathways and $N_2$-fixing ability among these species, concordance in above- and below-ground traits was evident in comparable rankings in leaf and root longevity, N and respiration rates, which is evidence of a common leaf and root trait syndrome linking traits to effects on plant and ecosystem processes.

**Key words:** functional groups, leaf lifespan, nitrogen-use efficiency, photosynthesis, respiration, root turnover, specific leaf area, specific root length.

*New Phytologist* (2005) **167**: 493–508

© *New Phytologist* (2005) **doi**: 10.1111/j.1469-8137.2005.01428.x

## Introduction

Despite considerable variation in leaf traits among plant species, common patterns of trait covariation are observed across diverse species and biomes (Diemer *et al.*, 1992; Reich *et al.*, 1997, 1998a, 1999; Niinemets, 1999; Craine & Lee, 2003; Wright *et al.*, 2004). High specific rates of $CO_2$ exchange are associated with high leaf nitrogen (N) concentrations, high specific leaf area (SLA, leaf area per unit leaf dry mass) and short leaf lifespan. Consistent correlations among leaf traits are thought to reflect fundamental trade-offs in leaf morphology, metabolic rates, and longevity and may be useful in categorizing species based on their ecological attributes and defining the linkages of traits to species effects on ecosystem functioning (Grime *et al.*, 1997; Lavorel & Garnier, 2002; Eviner & Chapin, 2003; Díaz *et al.*, 2004).

Compared with leaf traits, far less is known about interspecific variation in root traits or their correspondence with above-ground trait syndromes (Eissenstat & Yanai, 1997; Eissenstat *et al.*, 2000; Bouma *et al.*, 2001; Craine & Lee, 2003). Are there consistent correlations of leaf and fine root structure, function and longevity among species? For example, as in leaves, are high specific respiration rates in fine roots correlated with high N, high specific root length (SRL, root length per unit root dry mass) and short lifespan? There is evidence that fine roots of species differ widely in SRL and N concentration (Comas *et al.*, 2002; Pregitzer *et al.*, 2002) and that specific respiration rates of fine roots increase with higher

N concentration and SRL (Pregitzer *et al.*, 1998; Reich *et al.*, 1998b; Comas *et al.*, 2002), likely reflecting metabolic activity associated with nutrient uptake and assimilation, although species may differ in their specific costs of ion uptake (Scheurwater *et al.*, 1998). In some studies, root longevity among species is negatively correlated with N concentration, specific respiration rates, and SRL (Eissenstat *et al.*, 2000) or root tissue density (Ryser, 1996; Craine *et al.*, 2001), a pattern analogous to leaf trait correlations. Nitrogen concentration and tissue density of leaves were correlated with those of fine roots among 24 grass species sampled along an altitudinal transect (Craine & Lee, 2003). The correspondence of leaf and root traits raises the possibility that root traits may, in part, be predicted from more readily observed leaf traits. However, the generality of leaf and root trait syndromes, particularly in relation to physiological function remains largely untested.

The evidence to date suggests that a priori plant functional groups based on taxonomy (e.g. monocot, dicot) or functional categories ($N_2$-fixing, photosynthetic pathway) may be useful in categorizing species traits and their effects on ecosystem processes (Aerts & Chapin, 2000; Lavorel & Garnier, 2002). However, species effects on ecosystem function often arise from multiple, often continuously distributed traits and their potentially additive or interactive effects (Eviner & Chapin, 2003). Elucidating structural (tissue morphology and chemistry) and functional trait correlations (e.g. $CO_2$ exchange) and their correspondence in leaves and roots will aid in identifying underlying mechanisms and scaling relationships that link traits to plant and ecosystem function. Whether or not trait correlations differ among a priori plant functional groups in predictable ways is not well understood. For example, among grass species, high SLA, low tissue density leaves and corresponding low tissue density roots is associated with faster plant relative growth rates (van der Werf *et al.*, 1993; Ryser & Lambers, 1995; Wahl & Ryser, 2000), whereas among tree species, a faster growth rate is associated with higher SRL and smaller root diameters and not root tissue density (Comas *et al.*, 2002; Comas & Eissenstat, 2004). This suggests that grasses and trees may, in part, differ in trait correlations. In addition, woody and herbaceous plant growth forms may differ in traits underpinning leaf and plant-level nutrient-use efficiency (Aerts & Chapin, 2000).

The temperate grassland–savannah ecotone in the northern great plains of North America offers a diverse array of taxa with which to examine hypothesized trait correlations for above and below-ground traits and provide insight into the structure, N dynamics and productivity of communities in this region (Tilman, 1988; Tilman & Wedin, 1991; Reich *et al.*, 2001a; Craine *et al.*, 2002). Moreover, species in these grassland and savannah ecosystems differ in functional attributes in important ways, including photosynthetic pathway ($C_4$ vs $C_3$), $N_2$ fixation, and growth form (grasses, forbs and woody plants). In this study we examined leaf and fine root ecophysiological traits of a large number of sympatric species, including $C_4$ and $C_3$ grasses, nonlegume forbs (hereafter called forbs), herbaceous legumes (hereafter called legumes) and woody plant species. Replicate monoculture plots in a 5-yr-old common garden experiment enabled us to examine both leaf and root traits of 39 species grown individually under common field conditions. A concurrent study of multivariate trait correlations including productivity and N cycling is reported elsewhere (Craine *et al.*, 2002). Here we report an expanded set of bivariate trait relationships of leaves and fine roots, focusing on hypothesized structural–functional relationships.

In this study we sought to address several questions. To what extent do leaf and root traits exhibit structural and functional convergence among sympatric grassland–savannah species? We hypothesized that analogous trait correlations exist for leaves and fine roots in terms of morphology, longevity and rates of $CO_2$ exchange. Do species with leaves exhibiting high rates of $CO_2$ exchange and associated high SLA, N contents and short lifespan also exhibit a parallel syndrome of traits in fine roots? Do trait correlations differ among a priori functional groups (i.e. $C_3$ vs $C_4$ photosynthetic pathway)? Linking leaf and root trait relationships among species and functional groups may aid in predicting trait combinations and their ecological effects, including composition and productivity at regional scales (Paruelo *et al.*, 1998; Lavorel & Garnier, 2002), as well as species response to global change factors (Reich *et al.*, 2001b; Lee *et al.*, 2001; Poorter & Navas, 2003).

We tested several predictions of correlated leaf and fine root trait relationships among species and functional groups as follows: (1) rates of net photosynthesis and respiration of leaves and fine roots are correlated with tissue N (Ryan, 1991; Reich *et al.*, 1997, 1998a, 1999; Tjoelker *et al.*, 1999); (2) leaf and fine root N concentration increases with increasing SLA and SRL and N concentrations decrease with increasing tissue longevity; and (3) species exhibit similar rankings in leaf and fine root traits, namely, N concentration, SLA and SLR, longevity and specific respiration rates. Given hypothesized functional group contrasts, owing to differing photosynthetic pathways, we tested the predictions that: (4) $C_3$ vs $C_4$ groups differed in bivariate leaf trait-N relationships, reflecting expected higher leaf-level water- and photosynthetic N-use efficiencies for $C_4$ than for $C_3$ species (Sage & Pearcy, 1987; Ehleringer & Monson, 1993); and (5) that owing to higher N concentrations in legumes, leaf and root traits correlated with increased tissue N concentrations are higher in legumes compared with non-$N_2$-fixing forbs and grasses.

## Materials and Methods

### Site

The study site is at the Cedar Creek Natural History Area, a US National Science Foundation long-term ecological research site near Bethel, in east central Minnesota, USA (http://www.lter.umn.edu). The uplands at this site are

dominated by oak savannah, prairie, hardwood forest, pine forests and abandoned agricultural fields. The soils are entisols derived from a glacial outwash sand plain and are sandy and N-poor (Tilman, 1988). The region has a continental climate with cold winters, hot summers (mean January and July temperatures of −10°C and 25°C, respectively), and a mean annual precipitation of 660 mm.

The 39 species we examined in this long-term monoculture study include grasses, forbs, and woody plants common to remnant native oak savannah–prairie grasslands in the Midwestern USA. Species binomials are reported in the Appendices. Names and authorities follow those of Moore (1973) and B. C. Delaney (University of Minnesota, unpublished; http://www.lter.umn.edu). In the autumn of 1992, an old field was prepared by removing the topsoil, creating a sandy substrate (93%) low in organic matter. Replicated monoculture plots of the species were seeded in a fenced area and maintained by annual weeding. Plots were $2.2 \times 1.5$ m for most species, $1.1 \times 1.5$ m for the others. Sheet metal barriers that extended 25 cm below the ground separated the plots. We watered the plots weekly during the growing season in 1997 in the 5-yr-old plots as needed to ensure an equivalent of at least 2.5 cm of weekly precipitation to minimize water stress. Further details are provided in Craine *et al.* (2002).

## Leaf gas exchange

We determined light-saturated rates of leaf gas exchange of 36 species in the field sampled across four dates (25 June, and 7, 21 and 28 August, 1997). A portable photosynthesis system (CIRAS-1; PP Systems, Hitchin, UK) measured rates of net $CO_2$ and water vapor exchange. We conducted measurements on clear sunny days at light-saturating conditions between 10:30 and 14:00 hours Central Daylight Time (CDT). Mean photosynthetic photon flux density (PPFD, 400–700 nm) ranged from 1440 to 1560 μmol $m^{-2}$ $s^{-1}$ and mean air temperatures ranged from 26.3 to 29.3°C on the four dates. We measured two to four mature leaves from the top of the canopy in each of two to four replicate plots for a species. Following gas exchange measurement, we removed the sampled leaf and stored it in a cooler before measuring leaf area (one-sided, projected). Samples were oven dried at 65°C before determining dry mass. We calculated light-saturated photosynthesis rates on the basis of leaf area ($A_{area}$, μmol $m^{-2}$ $s^{-1}$) and dry mass ($A_{mass}$, nmol $g^{-1}$ $s^{-1}$).

## Leaf respiration

We harvested several intact shoot samples (two or three) from individual plots on the mornings (between 08:30 and 11:00 hours CDT) of 17 and 18 June, placed the samples in plastic bags in a cooler (*c.* 11°C), and transported them to the laboratory. Samples were immediately transferred to a controlled-environment chamber (Conviron E15; Controlled Environments, Inc., Winnipeg, Manitoba, Canada) to measure dark respiration at a standard temperature (26.1 ± 0.6°C SD) and $CO_2$ concentration (381 ± 15 μmol $mol^{-1}$ $CO_2$). We determined rates of net $CO_2$ efflux using infrared gas analysers and cuvettes (LCA-3 and PLC-C; Analytical Development Co. Ltd, Hoddesdon, UK), operated in an open configuration. Columns of magnesium perchlorate removed water vapor from the analyser air stream. Depending on leaf morphology and size, we measured either single leaves or multiple leaves with attached stems to provide adequate differential measurements, one per replicate plot. We dried the samples in an oven (65°C) and determined dry masses for calculation of respiration rates based on leaf mass ($R_{mass}$, nmol $g^{-1}$ $s^{-1}$) or area ($R_{area}$, μmol $m^{-2}$ $s^{-1}$).

## Fine root respiration

We collected aggregate root samples from soil cores (5 cm diameter, 20 cm deep) for each of up to four plots per species (minimum of two plots for three species) of 36 species on 18, 20, and 21 August. Roots were washed from soil cores with water over a 1.3 mm screen and separated into fine (< 2 mm diameter) and coarse fractions. Based on morphological measures described later, the mean diameter of the fine root sample among species was 0.30 mm with mean species values ranging from 0.13 to 0.44 mm. On average across species, 84% (± 0.08 SD) of the sampled root length was distributed in diameter classes < 0.5 mm and 92% (± 0.03 SD) was < 1.0 mm. An inspection of the diameter distributions and mean values suggested that we sampled only the finest two or three root orders, comparable to those reported for grass (Wahl & Ryser, 2000) and tree species (Pregitzer *et al.*, 2002; Comas & Eissenstat, 2004).

The root samples were kept moist at room temperature (*c.* 26°C) before measurement of respiration, typically within 2.5 h of harvest. We determined the net $CO_2$ efflux on each fine root sample of each plot at a standard temperature (25.7 ± 0.4)°C) and atmospheric $CO_2$ concentration (366 ± 13 SD μmol $mol^{-1}$ $CO_2$) using infrared gas analysers and cuvettes, as described above. Checks revealed no direct effect of measurement $CO_2$ concentration on rates of root respiration in agreement with recent findings (Amthor *et al.*, 2001; Tjoelker *et al.*, 2001; Burton & Pregitzer, 2002). Use of detached roots for measures of respiration followed standard protocols (Burton & Pregitzer, 2002; Comas *et al.*, 2002) and no correlation was observed between respiration rate and time of measurement for each of three sampling dates. Root length (see next section) and oven-dry mass measures were used to calculate respiration rates on the basis of root mass ($R_{mass}$, nmol $g^{-1}$ $s^{-1}$) and root length ($R_{length}$, nmol $m^{-1}$ $s^{-1}$).

## Tissue morphology, chemistry, and longevity

We measured leaf area (one-sided projected) using a video image analysis system (AgVision; Decagon Devices, Inc.,

Pullman, WA, USA). Root lengths and diameters were determined using a scanner-based, digital image analysis system (WinRhizo; Régent Instruments, Inc. Quebec City, Quebec, Canada). Following area or length determinations, the tissues were oven dried (65°C) and masses determined to calculate specific leaf areas (SLA, $cm^2$ leaf $g^{-1}$ leaf) and specific root lengths (SRL, m root $g^{-1}$ root). Nitrogen and carbon (C) concentrations of dried and ground leaf and root samples were measured using a CHN analyser (NA1500; Carlo Erba Instruments, Milan, Italy). Leaves sampled for the photosynthesis measures were pooled by plot before C and N analysis. Leaf N concentrations were used to calculate instantaneous photosynthetic nitrogen-use efficiency (PNUE, μmol $CO_2$ g $N^{-1}$ $s^{-1}$).

We obtained leaf longevity data of 14 species determined the same year in the same study (Craine *et al.*, 1999). Root longevity was estimated based on measured root turnover determined by in-growth and *in situ* root sampling in the plots. The standing crop of root biomass was determined in mid-August and root production estimated from ingrowth cores collected in July, August and October (Craine *et al.*, 2002). Root longevity was calculated as standing crop divided by total ingrowth, the inverse of root turnover. We assumed that annual root production and turnover approximated steady-state levels in these long-term (5-yr-old) monoculture plots, based on observed plant density and dry matter production values. With the exception of one annual and two biennial species, all species are perennial. Poorly stocked plots were excluded from the analysis of root turnover. Our estimates of root turnover were comparable to values in nearby grassy savannah openings (Reich *et al.*, 2001a) and other grasslands (Gill & Jackson, 2000).

### Data analysis

The experimental design was completely random with individual monoculture plots serving as replicates for each species ($n$ = 2–4). We calculated mean values for each species (see Appendices 1 and 2), since our objective was to examine variation in traits among species and species groups. Species means were log-transformed to satisfy assumptions of normality and homogeneity of variance. A priori, functional groups were $C_3$ grasses, $C_4$ grasses, forbs, legumes and woody plants. The woody plant group was comprised of only two species and consequently was excluded from functional group comparisons, but included in the rank correlation analysis of leaf vs root traits across all species. We tested hypothesized functional group effects using *F*-tests in analysis of variance in which fixed functional group effects (3 df) were tested against the effect of species nested within functional groups (experimental error). Preplanned comparisons among the four a priori groups included contrasts of $C_3$ vs $C_4$ photosynthetic pathways, grasses vs nongrasses, and $N_2$-fixing legumes vs nonlegumes. These comparisons were made using single-degree-of-freedom contrasts in the analysis of variance. Least squares means of log-transformed variables were back-transformed for reporting functional group means.

Bivariate trait relationships of log-transformed species means among the four a priori functional groups (excluding the woody plants) were examined using Type II linear regression. Unlike Type I regression, error is quantified in both variables and the linear regression fits are equivalent to the standard major axis or first principal component of the bivariate trait correlation. The slope of the Type II regression line between two log-transformed traits represents a proportional (scaling) relationship between the two variables. The intercept (or elevation) denotes the position of the regression line (scaling relationship) in bivariate trait space. The slopes and intercepts of the Type II major axes were compared among the four a priori groups using an approach analogous to testing the homogeneity of slopes and equality of intercepts in analysis of covariance (Wright *et al.*, 2001; Warton & Weber, 2002). Regression intercepts among the four functional groups were compared using *t*-tests (*post hoc* Tukey's HSD) after fitting same-slopes models (where appropriate) to variables transformed as $y - m(x)$, where $m$ is the common slope. We first tested for differences in slopes and intercepts among the four a priori functional groups ($C_3$ grasses, $C_4$ grasses, forbs and legumes) and those that did not differ statistically were subsequently grouped and separate Type II linear regressions fitted to illustrate the a posteriori group relationships. Incomplete sampling resulted in differing numbers of species in the various trait comparisons ($n$ = 31–36). Spearman's nonparametric rank correlation analysis was used to compare leaf vs root traits among species. All analyses were conducted using statistical analysis software (JMP 4.0; SAS Institute, Cary, NC, USA). Unless otherwise stated, $\alpha = 0.05$.

## Results

### Comparison of leaf traits among functional groups

The a priori functional groups differed in mean rates of leaf net photosynthesis whether expressed on the basis of leaf area ($A_{area}$, μmol $m^{-2}$ $s^{-1}$) or leaf dry mass ($A_{mass}$, nmol $g^{-1}$ $s^{-1}$). Overall, the $C_3$ and $C_4$ grasses had the highest mean rates of $A_{area}$ or $A_{mass}$ followed by the legumes and forbs (Table 1). Since specific leaf area (SLA, $cm^2$ $g^{-1}$) did not differ significantly among the functional groups (Table 1), group rankings of mean $A_{area}$ and $A_{mass}$ were comparable. Mean leaf longevity of a subset of the species ($n$ = 14) ranged from 29 to 94 d (Appendix 1; see also Craine *et al.*, 1999).

As predicted, light-saturated rates of net photosynthesis on mass and area bases were positively correlated with leaf $N_{mass}$ (%) and $N_{area}$ (g N $m^{-2}$ leaf area), respectively (Fig. 1a,b). $A_{area}$ was positively correlated with SLA ($r$ = 0.52, $P$ = 0.002, $n$ = 32, not shown). Mean leaf $N_{mass}$ ranged from 1.0 to 4.1% among species and differed among functional groups (Table 1),



 

**Table 1** Least squares mean (lower and upper 95% confidence intervals) leaf and fine root traits for functional groups of 39 grassland and savannah species grown in a common garden

| | $C_3$ grasses | | | $C_4$ grasses | | | Forbs | | | Legumes | | | ANOVA $P > F$ | Contrast $P > \|t\|$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | 95% CI | *n* | Mean | 95% CI | *n* | Mean | 95% CI | *n* | Mean | 95% CI | *n* | Functional group | $C_3$ vs $C_4$ | Grass vs rest | Legume vs rest |
| **Leaf traits** | | | | | | | | | | | | | | | | |
| $A_{area}$ ($\mu$mol $m^{-2}$ $s^{-1}$) | 29.2 | 23.0–37.1 | 5 | 27.4 | 22.0–34.1 | 7 | 16.9 | 14.6–19.5 | 16 | 19.7 | 15.5–25.1 | 6 | < 0.001 | 0.05 | < 0.001 | 0.16 |
| $A_{mass}$ (nmol $g^{-1}$ $s^{-1}$) | 283 | 207–386 | 5 | 263 | 202–342 | 7 | 177 | 148–210 | 16 | 232 | 174–308 | 6 | 0.02 | 0.32 | 0.03 | 0.91 |
| gs (mmol $m^{-2}$ $s^{-1}$) | 588 | 407–849 | 5 | 273 | 195–382 | 7 | 454 | 365–566 | 16 | 539 | 373–778 | 6 | 0.02 | 0.002 | 0.20 | 0.21 |
| SLA ($cm^2$ $g^{-1}$) | 99 | 78–127 | 5 | 102 | 82–128 | 7 | 103 | 89–119 | 16 | 118 | 92–151 | 6 | 0.74 | 0.75 | 0.42 | 0.27 |
| $N_{mass}$ (%) | 1.79 | 1.43–2.23 | 5 | 1.34 | 1.09–1.64 | 7 | 1.86 | 1.63–2.12 | 16 | 2.87 | 2.29–3.58 | 6 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| $N_{area}$ (g $m^{-2}$) | 1.90 | 1.47–2.45 | 5 | 1.38 | 1.09–1.74 | 7 | 1.83 | 1.57–2.13 | 16 | 2.47 | 1.91–3.18 | 6 | 0.02 | 0.005 | 0.02 | 0.01 |
| C:N | 25.1 | 19.9–31.6 | 5 | 33.3 | 26.9–41.1 | 7 | 23.2 | 20.2–26.6 | 16 | 15.7 | 12.5–19.8 | 6 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| WUE (mmol $CO_2$ $mol^{-1}$ $H_2O$) | 3.52 | 3.05–4.06 | 5 | 5.83 | 5.11–6.65 | 7 | 3.40 | 3.12–3.71 | 16 | 3.36 | 2.91–3.88 | 6 | < 0.001 | < 0.001 | < 0.001 | 0.01 |
| PNUE ($\mu$mol $CO_2$ $g^{-1}$ N $s^{-1}$) | 16.3 | 13.0–20.4 | 5 | 20.3 | 16.5–24.9 | 7 | 9.4 | 8.2–10.7 | 16 | 8.0 | 6.4–10.0 | 6 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| $R_{mass}$ (nmol $g^{-1}$ $s^{-1}$) | 17.5 | 13.7–22.3 | 5 | 13.0 | 10.4–16.2 | 6 | 16.2 | 14.0–18.7 | 14 | 18.0 | 14.1–22.9 | 5 | 0.18 | 0.03 | 0.26 | 0.26 |
| $R_{area}$ ($\mu$mol $m^{-2}$ $s^{-1}$) | 2.1 | 1.5–3.0 | 5 | 1.0 | 0.7–1.4 | 6 | 1.4 | 1.1–1.7 | 14 | 1.4 | 1.0–1.9 | 5 | 0.02 | 0.01 | 0.64 | 0.78 |
| A : R | 13.3 | 9.7–18.3 | 5 | 28.1 | 21.1–37.6 | 6 | 12.8 | 10.6–15.5 | 14 | 15.0 | 10.9–20.6 | 5 | < 0.001 | < 0.001 | 0.02 | 0.49 |
| Longevity (d) | 77 | 50–118 | 3 | 68 | 44–104 | 3 | 56 | 40–77 | 5 | 47 | 30–72 | 3 | 0.31 | 0.50 | 0.08 | 0.14 |
| **Fine root traits** | | | | | | | | | | | | | | | | |
| $R_{mass}$ (nmol $g^{-1}$ $s^{-1}$) | 11.4 | 7.7–16.6 | 5 | 5.7 | 4.0–8.1 | 6 | 12.4 | 9.8–15.7 | 17 | 13.2 | 9.0–19.3 | 6 | 0.005 | < 0.001 | 0.01 | 0.10 |
| $N_{mass}$ (%) | 1.08 | 0.81–1.44 | 5 | 0.52 | 0.40–0.67 | 6 | 1.13 | 0.95–1.35 | 15 | 1.99 | 1.49–2.64 | 6 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| $N_{length}$ (mg $m^{-1}$) | 0.32 | 0.10–1.03 | 5 | 0.18 | 0.06–0.52 | 6 | 0.41 | 0.20–0.83 | 15 | 0.76 | 0.24–2.43 | 6 | 0.32 | 0.12 | 0.11 | 0.13 |
| SRL (m $g^{-1}$) | 76.5 | 50.6–115.6 | 5 | 56.2 | 38.5–81.9 | 6 | 60.6 | 46.9–78.3 | 17 | 41.0 | 27.1–61.9 | 6 | 0.20 | 0.91 | 0.14 | 0.06 |
| C : N | 37.8 | 28.4–50.2 | 5 | 79.5 | 61.3–103.1 | 6 | 38.9 | 32.6–46.4 | 15 | 23.5 | 17.7–31.2 | 6 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| Longevity (d) | 504 | 243–1044 | 5 | 791 | 407–1540 | 6 | 182 | 118–281 | 15 | 136 | 65–281 | 5 | 0.001 | 0.003 | < 0.001 | 0.009 |

Means and 95% confidence intervals were back-transformed from $\log_{10}$; *n* is the number of species (see Appendices). $A_{area}$, area-based photosynthesis; $A_{mass}$, mass-based photosynthesis; gs, stomatal conductance; SLA, specific leaf area; $N_{mass}$, nitrogen concentration; $N_{area}$, area-based nitrogen concentration; C : N, carbon–nitrigen ratio; WUE, water use efficiency; PNUE, photosynthetic N-use efficiency; $R_{mass}$, mass-based respiration; $R_{area}$, area-based respiration; A : R, ratio of net photosynthesis to respiration; $N_{length}$, root length-based nitrogen concentration; SRL, specific root length.

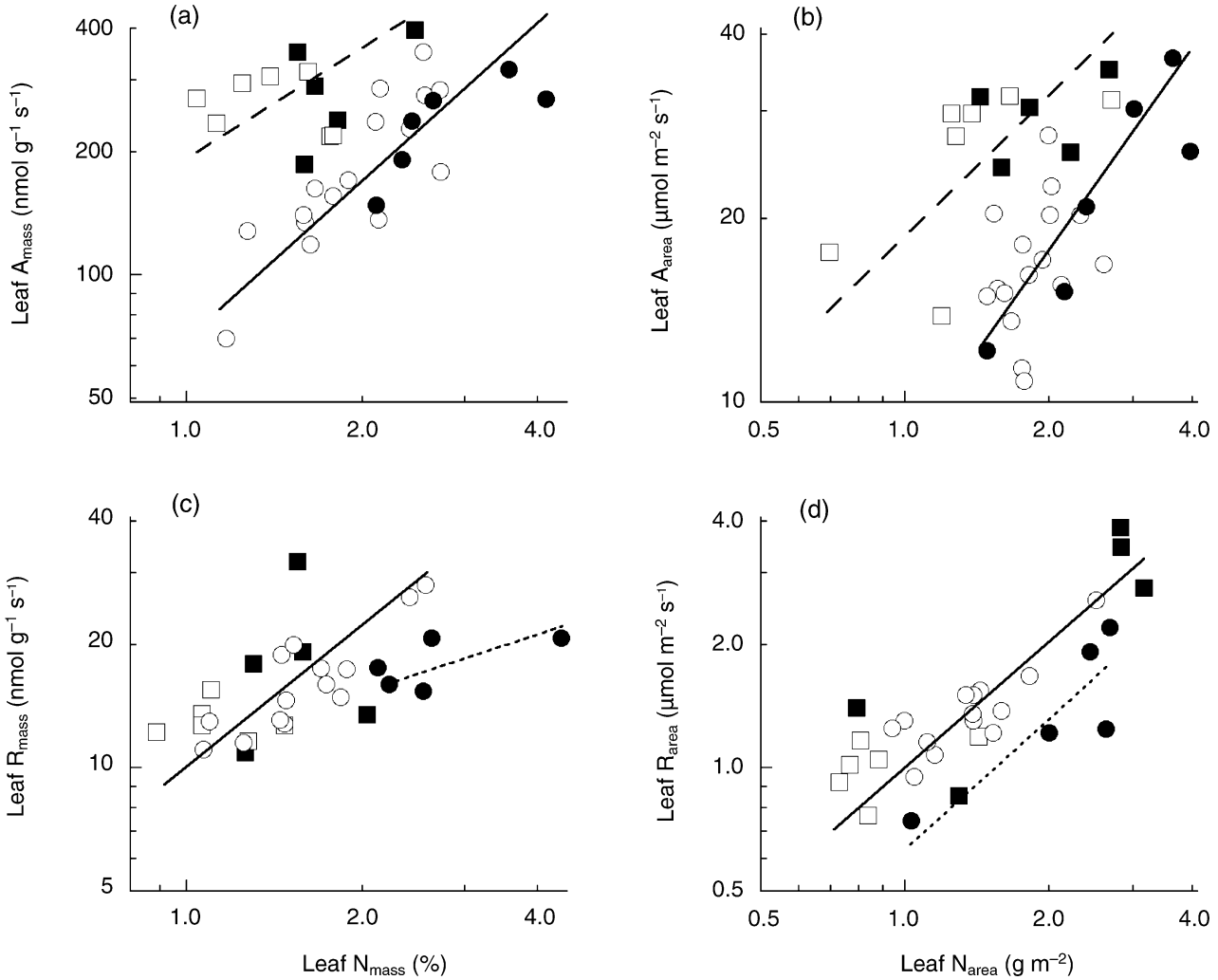


**Fig. 1** Leaf trait relationships among 39 savannah species. Species means are shown identified as forbs (○), legumes (●), $C_3$ grasses (■), and $C_4$ grasses (□). Note the $\log_{10}$ scale. Type II regression lines illustrate a posteriori group contrasts among species. (a) $A_{mass}$ – $N_{mass}$ correlations for the combined $C_3$ and $C_4$ grass groups ($r = 0.20$, $P = 0.52$, $n = 12$) and combined forb and legume groups ($r = 0.82$, $P < 0.001$, $n = 22$). (b) $A_{area}$ – $N_{area}$ correlations for the combined $C_3$ and $C_4$ grass groups ($r = 0.62$, $P = 0.03$, $n = 12$) and combined forb and legume groups ($r = 0.72$, $P < 0.001$, $n = 22$). (c) $R_{mass}$ – $N_{mass}$ correlations for the legume group ($r = 0.63$, $P = 0.26$, $n = 5$) and for the combined $C_3$ and $C_4$ grass and forb groups ($r = 0.64$, $P < 0.001$, $n = 25$). (d) $R_{area}$ – $N_{area}$ correlations for the legume group ($r = 0.85$, $P = 0.07$, $n = 5$) and for the combined $C_3$ and $C_4$ grass and forb groups ($r = 0.86$, $P < 0.001$, $n = 25$).

being greatest in legumes, followed in decreasing order by forbs, $C_3$ grasses, and $C_4$ grasses. However, for a given leaf $N_{mass}$ or $N_{area}$ the two grass groups (regardless of photosynthetic pathway) had higher $A_{mass}$ and $A_{area}$ compared with the forbs and legumes. Among the four a priori groups, the $C_3$ and $C_4$ grasses differed from forbs and legumes in terms of intercept ($P < 0.001$) but not slopes ($P \geq 0.32$) of the Type II regression between $A_{mass}$ and $N_{mass}$ as well as $A_{area}$ and $N_{area}$, providing evidence of separate trait correlations for the combined grass and combined forb and legume species (Fig. 1a,b).

Expressing rates of photosynthesis on a leaf nitrogen basis provided an estimate of leaf photosynthetic N-use efficiency (PNUE, µmol $CO_2$ $g^{-1}$ N $s^{-1}$). The two grass groups, regardless of photosynthetic pathway, had roughly double the PNUE of the legume and forb dicot groups (Table 1). The $C_4$ grasses also had higher PNUE than the $C_3$ grasses (Table 1), but this difference was modest compared with the monocot–dicot distinction. In addition, mean leaf conductance to water vapor (gs) was lower in the $C_4$ grasses than the remaining $C_3$ groups. Consequently, measures of instantaneous leaf WUE were about 60% higher among the $C_4$ grasses than in the other functional groups (Table 1).

Rates of leaf dark respiration differed three- to four-fold among species and increased with increasing leaf $N_{mass}$ and $N_{area}$ (Fig. 1c,d). Slopes of leaf respiration–N regression relationships did not differ from a common slope among the four functional groups on either a leaf mass ($P = 0.22$) or area basis ($P = 0.85$). However, legumes differed from the forb and two

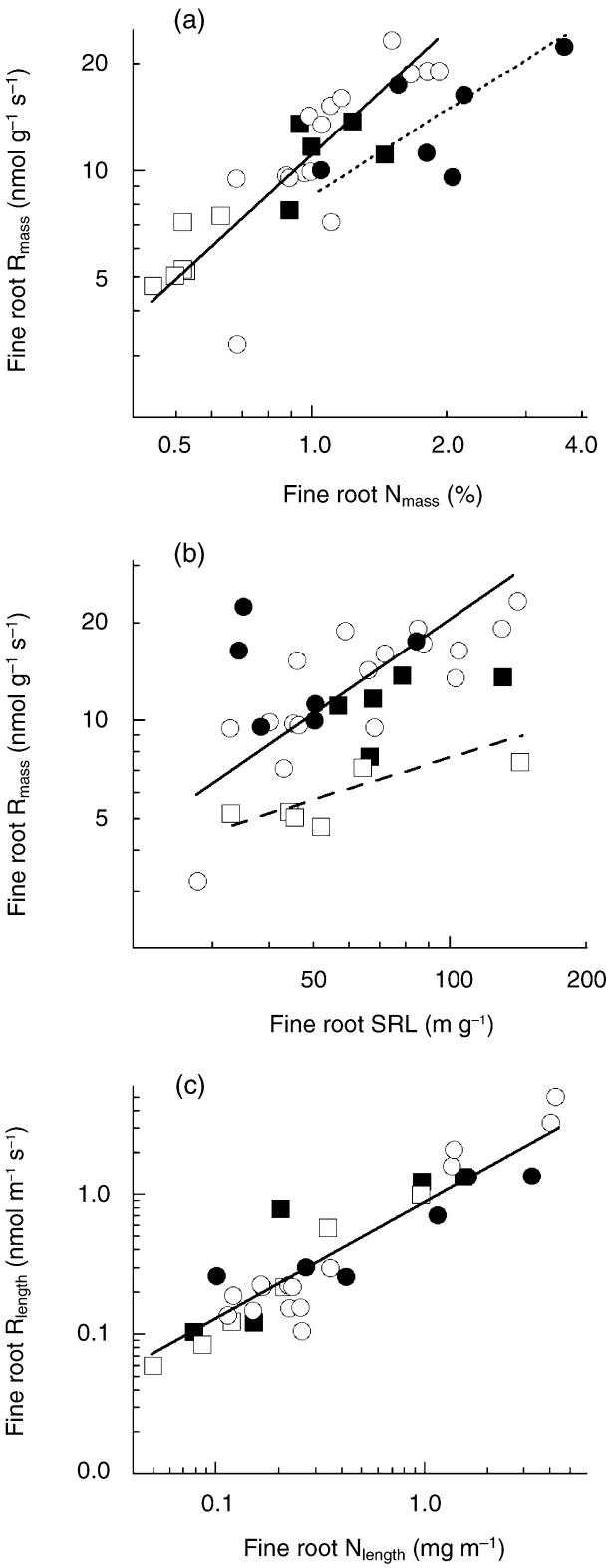


**Fig. 2** Rates of fine root respiration in relationship to root traits among functional groups of 39 savannah species (○, forbs; ●, legumes; ■, $C_3$ grasses; □, $C_4$ grasses). Type II regression lines illustrate a posteriori group contrasts among species. (a) $R_{mass}$ – $N_{mass}$ correlations for the legume ($r$ = 0.65, $P$ = 0.16, $n$ = 6) and the combined $C_3$ and $C_4$ grass and forb groups ($r$ = 0.85, $P$ < 0.001, $n$ = 26). (b) $R_{mass}$–specific root length (SRL) correlations for the $C_4$ grasses ($r$ = 0.79, $P$ = 0.06, $n$ = 6) and the combined $C_3$ grass, legume and forb groups ($r$ = 0.53, $P$ = 0.003, $n$ = 29). (c) $R_{mass}$ – $N_{length}$ correlation across all species ($r$ = 0.93, $P$ < 0.001, $n$ = 32).

grass groups by exhibiting lower elevations of the leaf $R_{mass}$ – $N_{mass}$ ($P$ = 0.002) and $R_{area}$ – $N_{area}$ ($P$ = 0.003) relationships, suggesting an a posteriori contrast between the legumes and the nonlegume species (Fig. 1c,d). As a group, the $C_4$ grasses had lower mean leaf $N_{area}$ and lower rates of leaf respiration than the $C_3$ grass, forb, and legume groups on a leaf area basis (Table 1). As a result of comparatively lower respiration and higher rates of net photosynthesis, $C_4$ grasses had roughly doubled ratios of net photosynthesis to respiration (A : R, C-use efficiency) compared with the $C_3$ grass, forb, and legume groups, which were similar in this regard (Table 1). Unlike the photosynthesis–leaf trait correlations in which $C_3$ and $C_4$ grasses differed from forbs and legumes, respiration-leaf trait correlations differed between legumes and the three nonlegume groups.

## Comparison of fine root traits among functional groups

Overall, fine root $R_{mass}$ was highest for the legume group and lowest for $C_4$ grasses compared with the other functional groups, largely paralleling functional group differences in fine root $N_{mass}$ (Table 1). Specific rates of fine root respiration ($R_{mass}$) increased with increasing fine root $N_{mass}$ (%) among the species (Fig. 2a). The regression slopes did not differ among the four functional groups ($P$ = 0.53), but legumes differed from the remaining three groups in terms of the intercept ($P$ < 0.001) of the relationships, providing evidence of differing correlations for legumes and nonlegume species (Fig. 2a). Legumes had a lower fine root $R_{mass}$ at a given $N_{mass}$ than the forb and two grass groups, similar to the leaf respiration–N relationships (Fig. 1c,d).

Specific root length (SRL, m root length $g^{-1}$ root dry mass) and $N_{length}$ (mg N $m^{-1}$ root length) of fine roots did not differ among the functional groups, although legumes had a lower SRL than the other groups (Table 1). Yet, fine root $R_{mass}$ was positively correlated with SRL among species, which were differentiated by Type II regression relationships of common slope ($P$ = 0.16) but lower elevation ($P$ < 0.001) for $C_4$ grasses compared with the $C_3$ grasses, forbs and legumes. For a given SRL, the $C_4$ grasses had lower fine root $R_{mass}$ (Fig. 2b). However, across species, fine root respiration rates expressed on the basis of root length ($R_{length}$, nmol $m^{-1}$ $s^{-1}$) were positively correlated with $N_{length}$. Neither regression slopes ($P$ = 0.32) nor intercepts ($P$ = 0.40) differed among the four a priori functional groups, providing evidence that all species groups exhibited the same regression relationship (Fig. 2c).

Estimated mean root longevity, based on root turnover calculations, ranged from 32 to 1409 d among the species and differed among species groups (Table 1). Mean root longevity ranged from 136 d in legumes to 791 d in $C_4$ grasses.

### Leaf and fine root longevity relationships

When comparing trait correlations with leaf and root longevity, $R_{mass}$ and $N_{mass}$ of leaves and fine roots declined with increased tissue longevity (Fig. 3a–d). Although Leaf $R_{mass}$ and longevity were weakly correlated for a subset of 14 species for which leaf longevity data were available (Fig. 3a), the trend follows well-established relationships. Neither the regression slopes of the fine root $R_{mass}$–root longevity relationship ($P = 0.21$) nor the intercepts ($P = 0.39$) differed among functional groups, suggesting a common relationship among species (Fig. 3b). Similarly, slopes of the fine root $N_{mass}$–root longevity relationship did not differ among the a priori functional groups ($P = 0.66$). The slope of the major axis for the $C_4$ grasses had a lower intercept compared with the legumes ($P = 0.009$); however, the individual group correlations were not statistically significant and thus the overall linear relationship is shown (Fig. 3d). Although SLA declined with increasing leaf longevity (Fig. 3e), root longevity was unrelated to SRL (Fig. 3f), $N_{length}$, or $R_{length}$ among species ($P \geq 0.28$, not shown). Leaf $N_{mass}$ and SLA were positively correlated among the species ($r = 0.38$, $P = 0.02$, $n = 36$, not shown). By contrast, fine root $N_{mass}$ was unrelated to SRL (not shown). Therefore, for leaves, and not for roots, an increased ratio of area or length per unit dry mass was associated with higher tissue $N_{mass}$.

### Comparing leaf and fine root trait syndromes

Rankings of leaf and fine root $N_{mass}$ were correlated among the species (Spearman rank correlation, Table 2), as was the bivariate trait correlation ($r = 0.77$, $P < 0.001$). Similarly, species rankings of leaf $R_{mass}$ and fine root $R_{mass}$ were positively correlated. Overall, specific rates of respiration of leaves and fine roots were positively correlated with tissue $N_{mass}$ and the regression slopes did not differ among the four a priori functional groups ($P = 0.21$, Fig. 4). However, the intercept was lower in the legumes compared with the other species groups ($P < 0.001$), suggesting differing correlations between legumes and nonlegume species (Fig. 4). By contrast, neither the rankings of SLA and SRL nor leaf $N_{area}$ and fine root $N_{length}$ were related among species (Table 2). Root and leaf longevity were positively correlated ($r = 0.67$, $P = 0.009$), as was the rank correlation (Table 2).

## Discussion

### Are there parallel leaf and root trait syndromes?

We tested several specific predictions of parallel leaf and fine root trait relationships among species and functional groups of the grassland savannah taxa. First, rates of $CO_2$ exchange of leaves and fine roots were positively correlated with tissue N, as expected (prediction 1) based on well-documented leaf trait relationships (Evans, 1989; Ryan, 1991; Reich *et al.*, 1997, 1998a). However, our findings suggest that these relationships also hold among sympatric taxa within a regional flora. A striking pattern was that specific respiration rates of both leaves and fine roots shared a common regression relationship with N, with the exception of the legumes which exhibited somewhat lower respiration rates for a given N concentration. Thus, species not only exhibited concordant rankings in leaf and fine root N concentrations and leaf and fine root specific respiration rates, but also exhibited a common respiration–N regression relationship across combined roots and leaves of $C_3$ and $C_4$ grasses and forbs. By contrast, for young seedlings of nine woody plant species during a rapid growth phase, both leaf and fine root specific respiration rates were linearly related to leaf and fine root $N_{mass}$, respectively, but fine roots had much higher respiration rates than leaves at any given tissue N concentration (Reich *et al.*, 1998b). The relative contribution of growth vs maintenance respiration was likely much higher in the study of young woody plant seedlings than in our current study of older field-grown plants late in the growing season. We are unaware of other direct comparisons of leaf and root respiration–N relationships. Our findings suggest that the respiration–N relationship may be robust across species and tissue type and thus a useful predictor in linking species traits to their effects on ecosystem function (Lavorel & Garnier, 2002; Eviner & Chapin, 2003). In this regard, tissue N contents may be used to model autotrophic respiration (Ryan, 1991), a critical component of net ecosystem exchange and production.

Second, we tested predicted leaf and root trait correlations linking structural traits to tissue longevity (prediction 2). Although root longevity (estimated as the inverse of root turnover) was much greater than that of leaves, species rankings in leaf and root longevity were correlated, suggesting that tissue longevity constitutes a consistent leaf and root trait syndrome among these species. In leaves, respiration rates, N concentration, and SLA decreased with increasing longevity in agreement with well-documented leaf trait syndromes in plants (Reich *et al.*, 1997, 1998a,b, 1999; Garnier *et al.*, 1999; Wright *et al.*, 2001, 2004). Similarly in roots, N concentration and respiration rates declined with increasing longevity, as noted in other studies (Eissenstat *et al.*, 2000), but demonstrated here among a large set of species. We are unaware of other studies that directly compare leaf and root longevity among species grown in a common environment as there are few datasets available to compare leaf and root traits on the same sets of plants. Nitrogen concentration and tissue density of leaves are correlated with those of fine roots among 24 grass species along an altitudinal transect (Craine & Lee, 2003). Our findings suggest that tissue longevity, N concentration and metabolic activity (respiration) traits are linked above and below ground, constituting a consistent leaf–root trait syndrome among this set of sympatric grassland and savannah species, and potentially linking above- and below-ground processes.

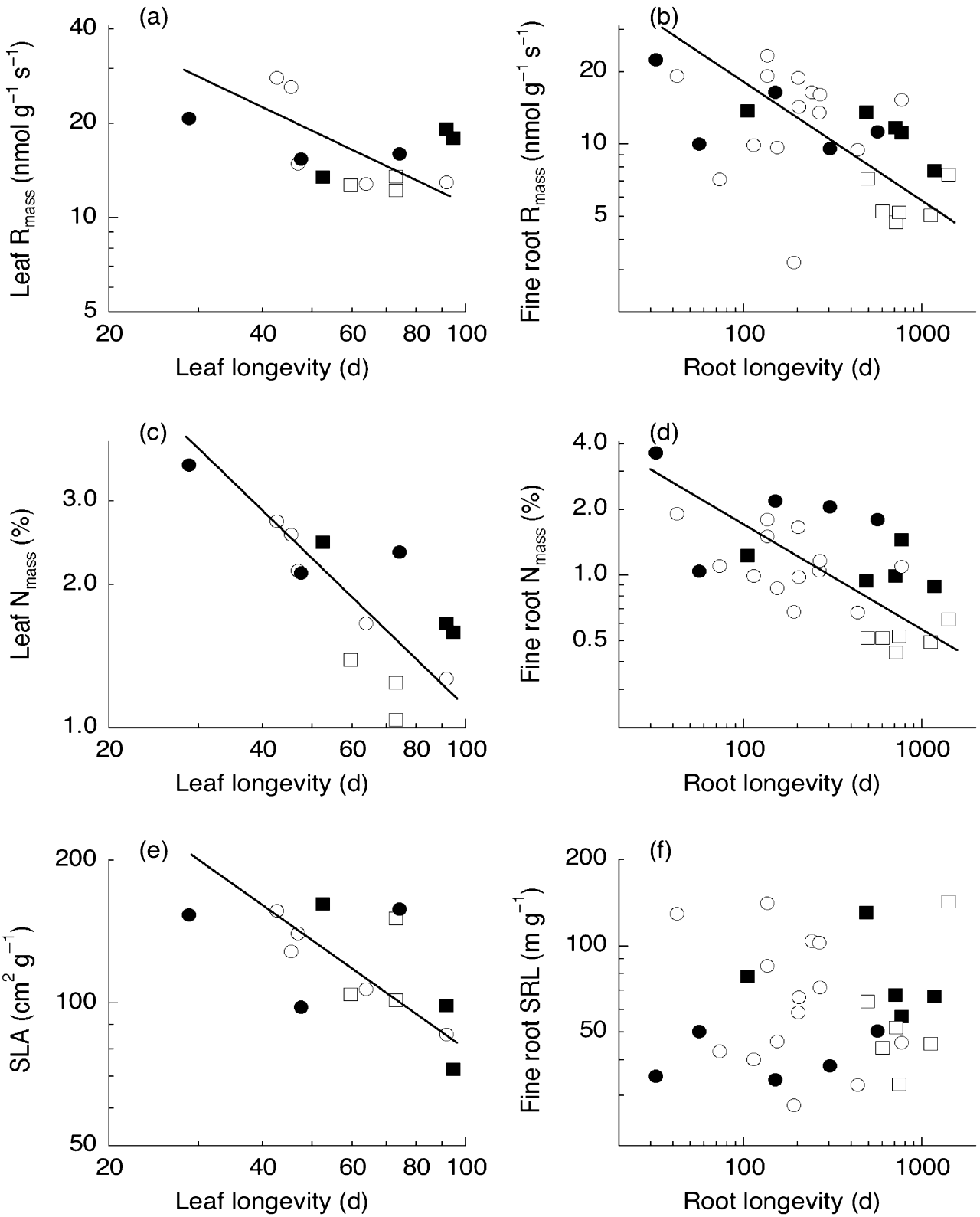


**Fig. 3** Comparison of leaf and fine root traits of savannah species in relation to tissue longevity (○, forbs; ●, legumes; ■, $C_3$ grasses; □, $C_4$ grasses). Type II regression lines illustrate a posteriori group contrasts among species. Leaf longevity was determined on a subset of the species (Appendix 1; see also Craine *et al*., 1999). (a) Leaf $R_{mass}$–leaf longevity ($r$ = –0.43, $P$ = 0.12, $n$ = 14); (b) fine root $R_{mass}$–root longevity ($r$ = –0.48, $P$ = 0.0076, $n$ = 30); (c) leaf $N_{mass}$–leaf longevity ($r$ = –0.77, $P$ = 0.0012, $n$ = 14); (d) fine root $N_{mass}$–root longevity ($r$ = –0.60, $P$ < 0.001, $n$ = 29); (e) specific leaf area (SLA)–leaf longevity ($r$ = –0.61, $P$ = 0.02, $n$ = 14); (f) fine root SRL–root longevity ($r$ = 0.03, $P$ = 0.89, $n$ = 30).

**Table 2** Nonparametric rank correlation coefficients for leaf and fine root traits among grassland and savannah species

| Leaf–root trait | *n* | Spearman's ρ | $P > \lvert \rho \rvert$ |
|---|---|---|---|
| Leaf $N_{area}$–fine root $N_{length}$ | 31 | −0.13 | 0.48 |
| Leaf $N_{mass}$–fine root $N_{mass}$ | 31 | 0.69 | < 0.001 |
| Leaf C : N–fine root C : N | 31 | 0.70 | < 0.001 |
| Leaf SLA–fine root SRL | 33 | 0.12 | 0.50 |
| Leaf $R_{mass}$–fine root $R_{mass}$ | 31 | 0.53 | 0.002 |
| Leaf $R_{area}$–fine root $R_{length}$ | 31 | −0.02 | 0.90 |
| Leaf longevity–root longevity | 14 | 0.50 | 0.067 |

*n* is number of species; SLA, specific leaf area; SRL, specific root length.

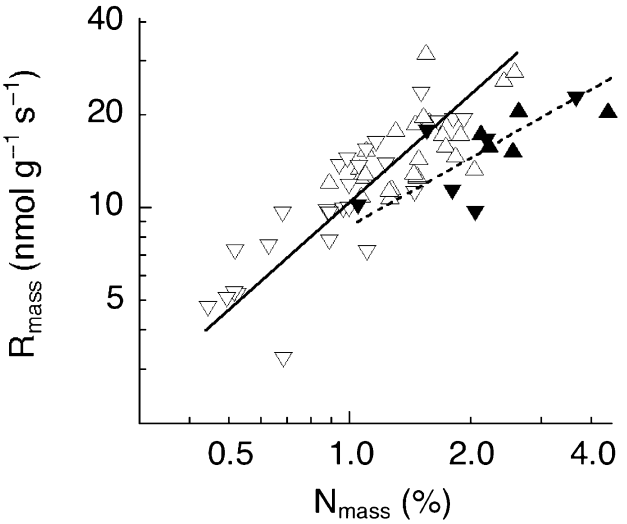


**Fig. 4** Specific respiration rates ($R_{mass}$, nmol $g^{-1}$ $s^{-1}$) of leaves (△, ▲) and fine roots (▽, ▼) in relation to nitrogen concentration ($N_{mass}$) for legumes (closed symbols) and the combined $C_3$ and $C_4$ grass and forb groups (open symbols). Type II regression lines are shown for pooled leaf and fine root data for legumes ($r = 0.71$, $P = 0.01$, $n = 11$) and nonlegume species ($r = 0.85$, $P < 0.001$, $n = 51$).

Although our root samples reflect the architecture of the finest root orders of all species, potentially important variation in longevity within root systems (Wells & Eissenstat, 2001; Anderson *et al.*, 2003) may be averaged across when using sequential soil coring to estimate root turnover, and longevity estimates may differ among methods (Matamala *et al.*, 2003). Within a species, the finest roots and lowest root orders tend to have higher N concentrations, higher specific respiration rates, higher SRL and shorter lifespans than higher-order roots (Pregitzer *et al.*, 1997, 1998; Eissenstat *et al.*, 2000; Wells & Eissenstat, 2001; Anderson *et al.*, 2003) and exhibit declining metabolic activity with age (Volder *et al.*, 2005). These within species patterns largely parallel the broad interspecific patterns described in the present study.

Unlike the concordant rankings observed in leaf and root N, rates of respiration, and longevity among species, SLA and SRL were unrelated, representing a contrast between leaf and root trait syndromes among these grassland and savannah species. In addition, both SRL and SLA failed to differ among the a priori functional groups in agreement with Craine *et al.* (2001) and Díaz *et al.* (2004). Moreover, unlike leaves, SRL was unrelated to root longevity or N concentration. Among grasses, leaf and root tissue density (dry mass to volume ratio) is positively correlated with tissue longevity (Ryser, 1996); however, leaf thickness and not leaf density is related to $A_{area}$ in 14 grass species (Garnier *et al.*, 1999) and among woody plants (Niinemets, 1999). Among species in the present study, SRL and mean fine root diameter were uncorrelated ($r = -0.19$, $P = 0.25$, $n = 36$, not shown), suggesting that differences in SRL among these savannah and grassland species may be related more to differences in tissue density than diameter (Wahl & Ryser, 2000; Craine *et al.*, 2001).

Overall, our findings demonstrate a common leaf and root trait syndrome of N concentration, respiration rate and longevity among a diverse array of sympatric grassland taxa when grown in a common garden. These findings support the concept of key trait syndromes that arise from trade-offs in plant traits and function (Lambers & Poorter, 1992; Aerts & Chapin, 2000; Lavorel & Garnier, 2002; Westoby *et al.*, 2002; Eviner & Chapin, 2003; Díaz *et al.*, 2004). In both leaves and roots, increasing tissue N concentrations were associated with increased rates of metabolic activity and declining tissue longevity, reflecting a tradeoff between rapid acquisition of resources and conservation of resources within protected tissues (Díaz *et al.*, 2004). The strong leaf and root trait relationship with tissue N shown in the present study perhaps reflects the low N availability in this grassland ecosystem (Tilman, 1988; Craine *et al.*, 2002). Low tissue nutrient concentrations and turnover rates are key determinants of high nutrient retention in nutrient-poor environments (Aerts & Chapin, 2000). Finding consistent trait differences among species is one objective in assembling comparative datasets of plant functional types across wide-ranging sites and timescales (Wilson *et al.*, 1999; Garnier *et al.*, 2001). Although mean values of many of the traits differed among the a priori functional groups in this study, the trait values were largely continuously distributed among the species. Thus, our findings demonstrate that trait differences among species may be represented in terms of their bivariate trait relationships that link structural traits to function and, in turn, provide insight into the mechanisms governing species effects on ecosystem processes.

## Do a priori functional groups differ in trait scaling relationships?

The regression analysis of trait relationships permitted examination of functional group effects in terms of the slope (scaling relationship) and its elevation. The $C_3$ and $C_4$ grass species groups together differed from forbs and legumes in the elevation of the slopes of the leaf photosynthesis–N

relationships but not respiration. As expected (prediction 4) based on well-documented differences between photosynthetic pathways (Sage & Pearcy, 1987; Ehleringer & Monson, 1993), $C_4$ grasses exhibited higher instantaneous efficiencies of N use (PNUE), water use (WUE) and carbon use (A : R) compared with the $C_3$ grasses, forbs and legumes. Somewhat unexpected was the increased PNUE of the $C_3$ grasses relative to the forbs and legumes, the similarity of PNUE of $C_3$ and $C_4$ grasses and the comparable slope of the leaf photosynthesis–N relationship for $C_3$ and $C_4$ grasses despite their different photosynthetic pathways. Thus, for $C_3$ and $C_4$ grass species together, the increased efficiencies were manifested in shifts in elevation but not slopes of the regression relationships that, in effect, resulted in greater $A_{mass}$ or $A_{area}$ for a given $N_{mass}$ or $N_{area}$. In addition, the grasses and $C_4$ grasses in particular had the lowest leaf N concentrations compared with the other functional groups. These findings suggest that compared with forbs and legumes, the $C_3$ and $C_4$ grasses exhibit increased leaf-level resource-use efficiencies, which are reflected in a shift in elevation of the leaf-trait regression slopes.

In a greenhouse study of seedlings of many of the same species, $C_4$ grasses did have a different elevation of the photosynthesis–N relationship than the $C_3$ grasses, which followed the same relationship as all other $C_3$ plants (Reich *et al.*, 2003). Moreover, the young seedlings of the $C_3$ grasses had similar tissue $N_{mass}$ (%) and lower photosynthetic rates than the $C_4$ grasses. Perhaps plant maturation under field conditions leads these species in different ontogenetic pathways, with the $C_4$ grasses exhibiting progressively lower N concentrations and concomitantly, having slightly lowered photosynthetic rates relative to the $C_3$ grasses. Among woody plant species, trait correlations may differ between juvenile and mature plants (Cornelissen *et al.*, 2003).

The photosynthesis–N relationships for legumes were shifted upward along a common slope that included the forb species (supporting prediction 5). Consequently, legumes had higher leaf and fine root N concentrations, increased $CO_2$ exchange rates and reduced tissue longevity than forbs. These structural and functional traits in large part contributed to the more rapid N cycling in legumes in monoculture compared with the other functional groups among these grassland species (Craine *et al.*, 2002). By contrast to the common photosynthesis–N relationship among legumes and forbs, both leaf and fine root respiration–tissue N relationships exhibited a lower elevation in legumes compared with the forb or grass species groups. The legumes had lower rates of respiration for a given tissue N concentration compared with the other functional groups. This was somewhat surprising, especially in roots, given the expectation that respiratory carbon costs are higher for roots that support $N_2$ fixation compared with nitrate assimilation. Maintenance respiration is thought to scale generally with the adenylate demand associated with turnover of protein, maintenance of ion gradients and nutrient assimilation (Amthor, 2000). The respiration–N relationship in legumes may, in effect, be altered through increased concentrations of organic nitrogen in roots and leaves, reflected in the substantially lower root C : N ratio in legumes compared with the other functional groups (24 vs ≥ 38). Production, storage and transport of organic forms of N in legumes would also presumably differ in underlying respiratory carbon costs on a per unit N basis compared with non-$N_2$-fixing forbs. For a given root N concentration, a comparatively lower net $CO_2$ efflux from roots of legumes may, in part, result from re-fixation of respired $CO_2$ in roots and root nodules (Atkins *et al.*, 2001).

## Conclusions

Concordance in above- and below-ground traits was evident in similar rankings in leaf and root tissue N, respiration rate and longevity among this set of sympatric grassland species. Moreover, the relationships between tissue N and respiration rate exhibited a common regression relationship for leaves and fine roots. Although trait values were continuously distributed among species, a priori functional group differences were manifested in differing elevations of regression slopes of certain gas exchange and structural trait relationships. In this regard, $C_3$ and $C_4$ grasses had lower leaf N concentrations but higher photosynthesis rates across a similar range of leaf N compared with forbs and legumes. Similarly, legumes had lower respiration rates for a given tissue N concentration compared with grasses and forbs. Functional shifts in ecophysiological traits reflect key trade-offs in tissue structure and function that resulted in greater tissue level resource-use efficiency among $C_3$ and $C_4$ grasses compared with forbs and legumes. Tissue-level traits are associated with competitive abilities and species effects on ecosystem-scale processes in grasslands (Tilman & Wedin, 1991; Craine *et al.*, 2001) and other ecosystems (Grime *et al.*, 1997; Aerts & Chapin, 2000; Lavorel & Garnier, 2002; Westoby *et al.*, 2002; Eviner & Chapin, 2003; Díaz *et al.*, 2004). Understanding leaf and root function in the context of integrated above- and below-ground trait syndromes will aid in predicting plant and ecosystem response to global change factors (Reich *et al.*, 2001b).

## Acknowledgements

We thank Rebekah Root, Cindy Buschena, Chris Lusk and Paul Fine for assistance in the field and laboratory. We acknowledge the National Science Foundation LTER program and the US Department of Energy PER program for funding.

## References

**Aerts R, Chapin FS III. 2000.** The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* **30**: 1–67.

**Amthor JS. 2000.** The McCree–de Wit–Penning de Vries–Thornley respiration paradigms: 30 years later. *Annals of Botany* **86**: 1–20.

**Amthor JS, Koch GW, Willms JR, Layzell DB. 2001.** Leaf $O_2$ uptake in the dark is independent of coincident $CO_2$ partial pressure. *Journal of Experimental Botany* **52**: 2235–2238.

**Anderson LJ, Comas LH, Lakso AN, Eissenstat DM. 2003.** Multiple risk factors in root survivorship: a 4-yr study in Concord grape. *New Phytologist* **158**: 489–501.

**Atkins C, Smith P, Mann A, Thumfort P. 2001.** Localization of carbonic anhydrase in legume nodules. *Plant, Cell & Environment* **24**: 317–326.

**Bouma TJ, Yanai RD, Elkin AD, Hartmond U, Flores-Alva DE, Eissenstat DM. 2001.** Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. *New Phytologist* **150**: 685–695.

**Burton AJ, Pregitzer KS. 2002.** Measurement carbon dioxide concentration does not affect root respiration of nine tree species in the field. *Tree Physiology* **22**: 67–72.

**Comas LH, Eissenstat DM. 2004.** Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology* **18**: 388–397.

**Comas LH, Bouma TJ, Eissenstat DM. 2002.** Linking root traits to potential growth rate in six temperate tree species. *Oecologia* **132**: 34–43.

**Cornelissen JHC, Cerabolini B, Castro-Díez P, Villar-Salvador P, Montserrat-Martí G, Puyravaud JP, Maestro M, Werger MJA, Aerts R. 2003.** Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science* **14**: 311–322.

**Craine JM, Lee WG. 2003.** Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. *Oecologia* **134**: 471–478.

**Craine JM, Berin DM, Reich PB, Tilman DG, Knops JMH. 1999.** Measurement of leaf longevity of 14 species of grasses and forbs using a novel approach. *New Phytologist* **142**: 475–481.

**Craine JM, Froehle J, Tilman DG, Wedin DA, Chapin FS III. 2001.** The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos* **93**: 274–285.

**Craine JM, Tilman D, Wedin D, Reich P, Tjoelker M, Knops J. 2002.** Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology* **16**: 563–574.

**Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Díez P, Funes G, Hamzehee B, Khoshnevi M, Pérez-Harguindeguy N, Pérez-Rontomé MC, Shirvany FA, Vendramini F, Yazdani S, Abbas-Azimi R, Bogaard A, Boustani S, Charles M, Dehghan M, de Torres-Espuny L, Falczuk V, Guerrero-Campo J, Hynd A, Jones G, Kowsary E, Kazemi-Saeed F, Maestro-Martínez M, Romo-Díez A, Shaw S, Siavash B, Villar-Salvador P, Zak MR. 2004.** The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.

**Diemer M, Körner C, Prock S. 1992.** Leaf life spans in wild perennial herbaceous plants: a survey and attempts at a functional interpretation. *Oecologia* **89**: 10–16.

**Ehleringer JR, Monson RK. 1993.** Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* **24**: 411–439.

**Eissenstat DM, Yanai RD. 1997.** The ecology of root lifespan. *Advances in Ecological Research* **27**: 1–60.

**Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL. 2000.** Building roots in a changing environment: implications for root longevity. *New Phytologist* **147**: 33–42.

**Evans JR. 1989.** Photosynthesis and nitrogen relationships in leaves of $C_3$ plants. *Oecologia* **78**: 9–19.

**Eviner VT, Chapin FS III. 2003.** Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution and Systematics* **34**: 455–485.

**Garnier E, Salager J-L, Laurent G, Sonié L. 1999.** Relationships between photosynthesis, nitrogen and leaf structure in 14 grass species and their dependence on the basis of expression. *New Phytologist* **143**: 119–129.

**Garnier E, Laurent G, Bellmann A, Debain S, Berthelier P, Ducout B, Roumet C, Navas M-L. 2001.** Consistency of species ranking based on functional leaf traits. *New Phytologist* **152**: 69–83.

**Gill RA, Jackson RB. 2000.** Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**: 13–31.

**Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, RossFraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J. 1997.** Integrated screening validates primary axes of specialization in plants. *Oikos* **79**: 259–281.

**Lambers H, Poorter H. 1992.** Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* **23**: 187–261.

**Lavorel S, Garnier E. 2002.** Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**: 545–556.

**Lee TD, Tjoelker MG, Ellsworth DS, Reich PB. 2001.** Leaf gas exchange responses of 13 prairie grassland species to elevated $CO_2$ and increased nitrogen supply. *New Phytologist* **150**: 405–418.

**Matamala R, Gonzàlez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH. 2003.** Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* **302**: 1385–1387.

**Moore JW. 1973.** *A catalog of the flora of Cedar Creek natural history area, Anoka and Isanti Counties, Minnesota.* Minneapolis, MN, USA: Bell Museum of Natural History/University of Minnesota.

**Niinemets Ü. 1999.** Components of leaf dry mass per area – thickness and density – alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist* **144**: 35–47.

**Paruelo JM, Jobbagy EG, Sala OE, Lauenroth WK, Burke IC. 1998.** Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecological Applications* **8**: 194–206.

**Poorter H, Navas M-L. 2003.** Plant growth and competition at elevated $CO_2$: on winners, losers and functional groups. *New Phytologist* **157**: 175–198.

**Pregitzer KS, Kubiske ME, Yu CK, Hendrick RL. 1997.** Relationships among root branch order, carbon, and nitrogen in four temperate species. *Oecologia* **111**: 302–308.

**Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR. 1998.** Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* **18**: 665–670.

**Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL. 2002.** Fine root architecture of nine North American trees. *Ecological Monographs* **72**: 293–309.

**Reich PB, Walters MB, Ellsworth DS. 1997.** From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* **94**: 13730–13734.

**Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman WD. 1998a.** Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia* **114**: 471–482.

**Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C. 1998b.** Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology* **12**: 395–405.

**Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999.** Generality of leaf trait relationships: a test across six biomes. *Ecology* **80**: 1955–1969.

**Reich PB, Peterson DW, Wedin DA, Wrage K. 2001a.** Fire and vegetation effects on productivity and nitrogen cycling across a forest–grassland continuum. *Ecology* **82**: 1703–1719.

 

**Reich PB, Tilman D, Craine J, Ellsworth D, Tjoelker MG, Knops J, Wedin D, Naeem S, Bahauddin D, Goth J, Bengston W, Lee TD. 2001b.** Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric $CO_2$ and N availability regimes? A field test with 16 grassland species. *New Phytologist* **150**: 435–448.

**Reich PB, Buschena C, Tjoelker MG, Wrage K, Knops J, Tilman D, Machado JL. 2003.** Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. *New Phytologist* **157**: 617–631.

**Ryan MG. 1991.** Effects of climate change on plant respiration. *Ecological Applications* **1**: 157–167.

**Ryser P. 1996.** The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology* **10**: 717–723.

**Ryser P, Lambers H. 1995.** Root and leaf attributes accounting for the performance of fast-growing and slow-growing grasses at different nutrient supply. *Plant and Soil* **170**: 251–265.

**Sage RF, Pearcy RW. 1987.** The nitrogen use efficiency of $C_3$ and $C_4$ plants. II. Leaf nitrogen effects on the gas exchange characteristics of *Chenopodium album* (L.) and *Amaranthus retroflexus*. *Plant Physiology* **84**: 959–963.

**Scheurwater I, Cornelissen C, Dictus F, Welschen R, Lambers H. 1998.** Why do fast- and slow-growing grass species differ so little in their rate of root respiration, considering the large differences in rate of growth and ion uptake? *Plant, Cell & Environment* **21**: 995–1005.

**Tilman D. 1988.** *Plant strategies and the dynamics and structure of plant communities*. Princeton, NJ, USA: Princeton University Press.

**Tilman D, Wedin D. 1991.** Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* **72**: 685–700.

**Tjoelker MG, Reich PB, Oleksyn J. 1999.** Changes in leaf nitrogen and carbohydrates underlie temperature and $CO_2$ acclimation of dark respiration in five boreal tree species. *Plant, Cell & Environment* **22**: 767–778.

**Tjoelker MG, Oleksyn J, Lee TD, Reich PB. 2001.** Direct inhibition of leaf dark respiration by elevated $CO_2$ is minor in 12 grassland species. *New Phytologist* **150**: 419–424.

**van der Werf A, van Nuenen M, Visser AJ, Lambers H. 1993.** Effects of N-supply on the rates of photosynthesis and shoot and root respiration of inherently fast- and slow-growing monocotyledonous species. *Physiologia Plantarum* **89**: 563–569.

**Volder A, Smart DR, Bloom AJ, Eissenstat DM. 2005.** Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. *New Phytologist* **165**: 493–502.

**Wahl S, Ryser P. 2000.** Root tissue structure is linked to ecological strategies of grasses. *New Phytologist* **148**: 459–471.

**Warton DI, Weber NC. 2002.** Common slope tests for bivariate errors-in-variables models. *Biometrical Journal* **44**: 161–174.

**Wells CE, Eissenstat DM. 2001.** Marked differences in survivorship among apple roots of different diameters. *Ecology* **82**: 882–892.

**Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002.** Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**: 125–159.

**Wilson PJ, Thompson K, Hodgson JG. 1999.** Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* **143**: 155–162.

**Wright IJ, Reich PB, Westoby M. 2001.** Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology* **15**: 423–434.

**Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot H, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. 2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

## Appendix 1

Mean leaf traits (± 1 SE) of North American grassland savannah species

| Species | *n* | $A_{area}$ | SE | $A_{mass}$ | SE | *gs* | SE | WUE | SE | PNUE | SE | SLA | SE | $N_{mass}$ | SE | C : N | SE | $N_{area}$ | SE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **$C_3$ grasses** | | | | | | | | | | | | | | | | | | | |
| *Agropyron repens* | 4 | 24.3 | 2.5 | 396 | 65 | 455 | 98 | 3.97 | 0.58 | 16.3 | 3.1 | 162 | 20 | 2.46 | 0.16 | 18.9 | 1.3 | 1.59 | 0.21 |
| *Agrostis scabra* | 2 | 31.7 | 2.5 | 351 | 66 | 513 | 43 | 4.49 | 0.71 | 25.3 | 10.5 | 118 | 4 | 1.55 | 0.38 | 29.4 | 5.5 | 1.43 | 0.48 |
| *Koeleria cristata* | 4 | 25.7 | 3.1 | 186 | 23 | 536 | 99 | 3.42 | 0.35 | 11.8 | 1.3 | 73 | 2 | 1.59 | 0.10 | 27.6 | 1.5 | 2.22 | 0.15 |
| *Poa pratensis* | 3 | 30.4 | 4.2 | 289 | 66 | 747 | 127 | 2.52 | 0.54 | 17.9 | 4.9 | 99 | 16 | 1.66 | 0.07 | 25.9 | 1.3 | 1.82 | 0.29 |
| *Stipa spartea* | 4 | 35.1 | 3.0 | 240 | 10 | 753 | 129 | 3.49 | 0.36 | 13.3 | 0.3 | 71 | 7 | 1.81 | 0.10 | 25.0 | 1.2 | 2.67 | 0.30 |
| **$C_4$ grasses** | | | | | | | | | | | | | | | | | | | |
| *Andropogon gerardii* | 4 | 29.7 | 3.5 | 295 | 32 | 271 | 33 | 6.71 | 0.56 | 23.6 | 0.5 | 102 | 8 | 1.24 | 0.12 | 36.3 | 3.1 | 1.25 | 0.13 |
| *Bouteloua curtipendula* | 4 | 27.3 | 3.2 | 235 | 12 | 312 | 46 | 5.22 | 0.45 | 21.0 | 0.7 | 95 | 7 | 1.12 | 0.06 | 38.6 | 1.4 | 1.28 | 0.10 |
| *Calamovilfa longifolia* | 4 | 31.3 | 4.3 | 218 | 34 | 387 | 136 | 5.68 | 0.25 | 12.7 | 2.4 | 73 | 9 | 1.76 | 0.11 | 25.8 | 1.6 | 2.71 | 0.52 |
| *Panicum capillare* | 2 | 13.9 | 4.1 | 220 | 99 | 308 | 165 | 3.07 | 0.16 | 11.7 | 3.7 | 151 | 27 | 1.78 | 0.28 | 24.9 | 3.4 | 1.19 | 0.03 |
| *Panicum virgatum* | 3 | 31.7 | 3.1 | 314 | 20 | 304 | 31 | 5.75 | 0.49 | 19.5 | 1.8 | 103 | 8 | 1.61 | 0.04 | 27.8 | 0.0 | 1.65 | 0.21 |
| *Schizachyrium scoparium* | 4 | 17.6 | 2.1 | 270 | 45 | 165 | 20 | 5.07 | 0.30 | 25.8 | 3.0 | 151 | 6 | 1.04 | 0.07 | 42.1 | 2.6 | 0.69 | 0.04 |
| *Sorghastrum nutans* | 4 | 29.8 | 1.5 | 307 | 20 | 251 | 28 | 6.75 | 0.57 | 22.1 | 1.2 | 104 | 6 | 1.39 | 0.08 | 32.1 | 1.7 | 1.38 | 0.11 |
| **Forbs** | | | | | | | | | | | | | | | | | | | |
| *Achillea millefolium* | 2 | 20.3 | 3.2 | 276 | 50 | 542 | 52 | 3.76 | 0.36 | 10.7 | 0.4 | 130 | 10 | 2.56 | 0.36 | 17.2 | 2.7 | 2.01 | 0.11 |
| *Agastache foeniculum* | 2 | 16.8 | 2.5 | 179 | 8 | 449 | 53 | 3.42 | 0.62 | 6.6 | 0.6 | 108 | 12 | 2.73 | 0.37 | 18.0 | 2.8 | 2.61 | 0.64 |
| *Ambrosia artemisiifolia* | 4 | 27.4 | 4.3 | 351 | 54 | 1035 | 326 | 3.63 | 0.42 | 13.9 | 0.8 | 129 | 2 | 2.55 | 0.44 | 18.2 | 3.0 | 1.99 | 0.35 |
| *Anemone cylindrica* | 4 | 15.4 | 0.8 | 163 | 7 | 390 | 27 | 3.30 | 0.10 | 9.9 | 0.4 | 107 | 4 | 1.66 | 0.06 | 27.1 | 0.7 | 1.56 | 0.05 |
| *Asclepias syriaca* | 3 | 18.1 | 2.0 | 284 | 35 | 455 | 115 | 4.39 | 0.54 | 10.5 | 1.5 | 157 | 2 | 2.72 | 0.09 | 14.8 | 0.9 | 1.76 | 0.08 |
| *Asclepias tuberosa* | 3 | 11.3 | 1.4 | 137 | 12 | 188 | 29 | 3.32 | 0.24 | 6.6 | 0.9 | 121 | 4 | 2.13 | 0.25 | 21.9 | 2.3 | 1.76 | 0.19 |
| *Asclepias verticillata* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Aster azureus* | 4 | 13.6 | 1.5 | 135 | 21 | 460 | 69 | 3.16 | 0.14 | 8.4 | 1.1 | 98 | 6 | 1.60 | 0.11 | 25.1 | 1.3 | 1.67 | 0.12 |
| *Aster ericoides* | 3 | 20.3 | 1.3 | 156 | 10 | 355 | 87 | 4.16 | 0.31 | 8.7 | 0.4 | 78 | 8 | 1.78 | 0.06 | 23.5 | 0.9 | 2.33 | 0.15 |
| *Aster novae-angliae* | 3 | 15.1 | 1.4 | 228 | 12 | 314 | 27 | 3.19 | 0.18 | 9.5 | 0.4 | 152 | 6 | 2.41 | 0.21 | 17.7 | 1.5 | 1.61 | 0.20 |
| *Coreopsis palmata* | 4 | 10.8 | 2.3 | 70 | 13 | 255 | 27 | 2.32 | 0.33 | 6.0 | 1.0 | 66 | 3 | 1.17 | 0.07 | 37.2 | 2.3 | 1.77 | 0.14 |
| *Liatris aspera* | 4 | 15.6 | 1.9 | 119 | 13 | 460 | 97 | 2.81 | 0.11 | 7.5 | 0.4 | 78 | 3 | 1.63 | 0.25 | 28.1 | 4.2 | 2.12 | 0.35 |
| *Penstemon grandiflorus* | 4 | 22.6 | 1.0 | 237 | 15 | 720 | 71 | 3.87 | 0.15 | 11.3 | 0.7 | 105 | 5 | 2.11 | 0.11 | 22.2 | 1.2 | 2.03 | 0.09 |
| *Potentilla arguta* | 4 | 16.2 | 1.1 | 170 | 17 | 409 | 34 | 3.42 | 0.17 | 9.0 | 0.4 | 105 | 11 | 1.89 | 0.18 | 22.3 | 1.2 | 1.82 | 0.08 |
| *Rudbeckia serotina* | 3 | 20.4 | 0.4 | 287 | 5 | 619 | 43 | 3.54 | 0.11 | 13.5 | 1.0 | 140 | 5 | 2.14 | 0.16 | 17.0 | 1.4 | 1.53 | 0.12 |
| *Solidago nemoralis* | 4 | 17.1 | 1.2 | 141 | 12 | 480 | 78 | 3.37 | 0.19 | 8.9 | 0.5 | 82 | 2 | 1.58 | 0.11 | 26.2 | 2.4 | 1.94 | 0.13 |
| *Solidago rigida* | 3 | 14.9 | 0.9 | 128 | 12 | 511 | 66 | 3.12 | 0.31 | 10.1 | 0.7 | 86 | 3 | 1.27 | 0.05 | 34.8 | 1.4 | 1.49 | 0.03 |
| *Solidago speciosa* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| **Legumes** | | | | | | | | | | | | | | | | | | | |
| *Astragalus canadensis* | 3 | 25.8 | 5.1 | 269 | 49 | 734 | 191 | 3.68 | 0.27 | 6.4 | 0.9 | 106 | 7 | 4.13 | 0.25 | 10.5 | 0.6 | 3.95 | 0.40 |
| *Desmodium canadense* | 4 | 12.1 | 1.2 | 191 | 21 | 257 | 40 | 2.82 | 0.15 | 8.1 | 0.7 | 158 | 2 | 2.34 | 0.07 | 20.7 | 0.8 | 1.49 | 0.04 |
| *Lespedeza capitata* | 4 | 15.2 | 1.5 | 149 | 15 | 333 | 27 | 3.41 | 0.36 | 7.0 | 0.5 | 98 | 1 | 2.11 | 0.10 | 21.8 | 1.0 | 2.16 | 0.09 |
| *Lupinus perennis* | 4 | 20.9 | 1.7 | 318 | 28 | 834 | 146 | 3.51 | 0.17 | 8.9 | 0.7 | 154 | 10 | 3.57 | 0.14 | 12.0 | 0.4 | 2.39 | 0.22 |
| *Petalostemon candidum* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Petalostemon purpureum* | 4 | 36.6 | 7.8 | 238 | 23 | 1209 | 364 | 3.30 | 0.17 | 9.8 | 0.8 | 75 | 16 | 2.43 | 0.03 | 18.2 | 0.2 | 3.63 | 0.58 |
| *Petalostemon villosum* | 4 | 30.3 | 3.5 | 267 | 20 | 866 | 118 | 3.44 | 0.05 | 10.2 | 0.9 | 90 | 6 | 2.64 | 0.08 | 16.8 | 0.6 | 3.02 | 0.25 |
| **Woody plants** | | | | | | | | | | | | | | | | | | | |
| *Corylus americana* | 4 | 15.6 | 0.6 | 149 | 12 | 458 | 37 | 3.22 | 0.17 | 7.5 | 0.8 | 95 | 6 | 2.01 | 0.09 | 23.3 | 1.0 | 2.17 | 0.16 |
| *Quercus macrocarpa* | 3 | 15.9 | 0.9 | 167 | 8 | 286 | 6 | 3.66 | 0.33 | 7.1 | 0.4 | 106 | 6 | 2.36 | 0.08 | 20.3 | 0.8 | 2.26 | 0.20 |

**Appendix 1** *continued*

| Species | *n* | $R_{area}$ | SE | $N_{area}$ | SE | $R_{mass}$ | SE | $N_{mass}$ | SE | *n* | Longevity | SE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **$C_3$ grasses** | | | | | | | | | | | | |
| *Agropyron repens* | 3 | 0.86 | 0.05 | 1.29 | 0.12 | 13.5 | 0.6 | 2.04 | 0.12 | 4 | 52 | 1 |
| *Agrostis scabra* | 3 | 1.40 | 0.11 | 0.79* | 0.08 | 32.0 | 7.7 | 1.55* | 0.38 | | – | – |
| *Koeleria cristata* | 4 | 3.87 | 0.22 | 2.83 | 0.22 | 18.0 | 0.9 | 1.30 | 0.02 | 4 | 94 | 6 |
| *Poa pratensis* | 3 | 3.47 | 0.44 | 2.84 | 0.28 | 19.2 | 0.7 | 1.58 | 0.05 | 4 | 92 | 3 |
| *Stipa spartea* | 4 | 2.75 | 0.45 | 3.16 | 0.49 | 10.9 | 0.6 | 1.26 | 0.07 | – | – | – |
| **$C_4$ grasses** | | | | | | | | | | | | |
| *Andropogon gerardii* | 4 | 0.92 | 0.05 | 0.73 | 0.07 | 13.6 | 0.8 | 1.06 | 0.07 | 4 | 73 | 1 |
| *Bouteloua curtipendula* | 4 | 1.17 | 0.15 | 0.81 | 0.02 | 15.5 | 1.1 | 1.10 | 0.07 | – | – | – |
| *Calamovilfa longifolia* | 4 | 1.19 | 0.11 | 1.43 | 0.18 | 12.7 | 2.1 | 1.47 | 0.13 | – | – | – |
| *Panicum capillare* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Panicum virgatum* | 4 | 0.76 | 0.02 | 0.84 | 0.03 | 11.6 | 0.3 | 1.27 | 0.05 | – | – | – |
| *Schizachyrium scoparium* | 4 | 1.02 | 0.16 | 0.77 | 0.19 | 12.2 | 0.9 | 0.89 | 0.08 | 4 | 73 | 8 |
| *Sorghastrum nutans* | 4 | 1.05 | 0.05 | 0.88 | 0.07 | 12.7 | 0.3 | 1.06 | 0.05 | 4 | 60 | 4 |
| **Forbs** | | | | | | | | | | | | |
| *Achillea millefolium* | 4 | 2.57 | 0.29 | 2.51 | 0.09 | 17.5 | 2.2 | 1.70 | 0.01 | – | – | – |
| *Agastache foeniculum* | | – | – | – | – | – | – | – | – | – | – | – |
| *Ambrosia artemisiifolia* | 4 | 1.55 | 0.10 | 1.44 | 0.15 | 26.1 | 2.9 | 2.41 | 0.24 | 4 | 46 | 2 |
| *Anemone cylindrica* | 4 | 1.38 | 0.15 | 1.59 | 0.06 | 12.8 | 1.6 | 1.47 | 0.03 | 4 | 64 | 4 |
| *Asclepias syriaca* | 4 | 1.51 | 0.15 | 1.39 | 0.18 | 28.1 | 3.2 | 2.57 | 0.33 | 4 | 43 | 2 |
| *Asclepias tuberosa* | 4 | 1.31 | 0.09 | 1.00 | 0.11 | 18.9 | 2.0 | 1.45 | 0.20 | – | – | – |
| *Asclepias verticillata* | | – | – | – | – | – | – | – | – | – | – | – |
| *Aster azureus* | 4 | 1.31 | 0.22 | 1.39 | 0.14 | 17.4 | 2.1 | 1.88 | 0.14 | – | – | – |
| *Aster ericoides* | 4 | 1.25 | 0.25 | 0.94 | 0.07 | 20.0 | 3.3 | 1.52 | 0.05 | – | – | – |
| *Aster novae-angliae* | | – | – | – | – | – | – | – | – | – | – | – |
| *Coreopsis palmata* | 4 | 1.08 | 0.15 | 1.15 | 0.22 | 11.5 | 1.4 | 1.25 | 0.25 | | – | – |
| *Liatris aspera* | 4 | 1.16 | 0.17 | 1.11 | 0.21 | 11.1 | 1.7 | 1.07 | 0.20 | | – | – |
| *Penstemon grandiflorus* | 4 | 1.68 | 0.14 | 1.82 | 0.16 | 16.0 | 0.9 | 1.73 | 0.07 | – | – | – |
| *Potentilla arguta* | 4 | 0.95 | 0.04 | 1.05 | 0.05 | 13.1 | 0.5 | 1.44 | 0.06 | – | – | – |
| *Rudbeckia serotina* | 3 | 1.22 | 0.12 | 1.53 | 0.16 | 14.9 | 2.0 | 1.83 | 0.13 | 3 | 47 | 3 |
| *Solidago nemoralis* | 4 | 1.35 | 0.11 | 1.39 | 0.14 | 14.6 | 1.1 | 1.48 | 0.04 | – | – | – |
| *Solidago rigida* | 4 | 1.51 | 0.21 | 1.34 | 0.33 | 13.0 | 1.1 | 1.09 | 0.07 | 4 | 92 | 2 |
| *Solidago speciosa* | – | – | – | – | – | – | – | – | – | – | – | – |
| **Legumes** | | | | | | | | | | | | |
| *Astragalus canadensis* | 4 | 1.24 | 0.19 | 2.64 | 0.41 | 20.8 | 2.1 | 4.39 | 0.38 | – | – | – |
| *Desmodium canadense* | 4 | 0.74 | 0.11 | 1.03 | 0.17 | 16.0 | 1.2 | 2.22 | 0.19 | 4 | 74 | 4 |
| *Lespedeza capitata* | 4 | 1.22 | 0.11 | 2.00 | 0.12 | 15.4 | 1.2 | 2.55 | 0.13 | 4 | 48 | 1 |
| *Lupinus perennis* | 4 | 1.92 | 0.20 | 2.44 | 0.23 | 20.8 | 1.8 | 2.63 | 0.11 | 3 | 29 | 6 |
| *Petalostemon candidum* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Petalostemon purpureum* | – | – | – | – | – | – | – | – | – | – | – | – |
| *Petalostemon villosum* | 4 | 2.20 | 0.16 | 2.68 | 0.30 | 17.6 | 1.8 | 2.12 | 0.22 | – | – | – |
| **Woody plants** | | | | | | | | | | | | |
| *Corylus americana* | 4 | 0.81 | 0.07 | 1.12 | 0.14 | 10.1 | 0.8 | 1.36 | 0.05 | – | – | – |
| *Quercus macrocarpa* | 3 | 1.68 | 0.09 | 2.24 | 0.20 | 17.7 | 1.1 | 2.36 | 0.08 | – | – | – |

The number of samples (*n*) indicated for each species applies to all photosynthesis and respiration traits, except where indicated (*$n$ = 2). No data are indicated as dashes. Units for traits are: $A_{area}$, area-based photosynthesis, μmol $m^{-2}$ $s^{-1}$; $A_{mass}$, mass-based photosynthesis, nmol $g^{-1}$ $s^{-1}$; gs, stomatal conductance, mmol $m^{-2}$ $s^{-1}$; WUE, water-use efficiency, mmol $CO_2$ $mol^{-1}$ $H_2O$; PNUE, photosynthetic N-use efficiency, μmol $CO_2$ $g^{-1}$ N $s^{-1}$; SLA, specific leaf area, $cm^2$ $g^{-1}$; $N_{mass}$, %; C : N, carbon–nitrogen ratio; $N_{area}$, g $m^{-2}$; $R_{area}$, area-based respiration, μmol $m^{-2}$ $s^{-1}$; $R_{mass}$, mass-based respiration, nmol $g^{-1}$ $s^{-1}$; leaf longevity, d. Note that leaf N-values are shown separately for both photosynthesis and respiration samples. Leaf longevity data are from Craine *et al*. (1999).

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## Appendix 2

Mean root traits (± 1 SE) of North American grassland savannah species

| Species | *n* | $R_{mass}$ | SE | $N_{mass}$ | SE | $R_{length}$ | SE | $N_{length}$ | SE | SRL | SE | C:N | SE | *n* | Longevity | SE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **$C_3$ grasses** | | | | | | | | | | | | | | | | |
| *Agropyron repens* | 4 | 11.1 | 1.1 | 1.45 | 0.18 | 0.79 | 0.63 | 0.20 | 0.05 | 57 | 19 | 31.4 | 4.4 | 4 | 761 | 538 |
| *Agrostis scabra* | 4 | 13.7 | 2.0 | 1.23 | 0.16 | 1.35 | 1.23 | 1.53 | 1.43 | 78 | 37 | 36.0 | 4.7 | 2 | 105 | 20 |
| *Koeleria cristata* | 4 | 13.6 | 2.3 | 0.94 | 0.01 | 0.10 | 0.01 | 0.08 | 0.01 | 131 | 22 | 46.6 | 2.7 | 4 | 484 | 83 |
| *Poa pratensis* | 3 | 11.7 | 1.1 | 1.00 | 0.15 | 1.24 | 0.84 | 0.97 | 0.59 | 68 | 57 | 35.0 | 2.8 | 3 | 709 | 148 |
| *Stipa spartea* | 4 | 7.7 | 0.8 | 0.89 | 0.05 | 0.12 | 0.01 | 0.15 | 0.04 | 67 | 11 | 44.7 | 1.0 | 4 | 1173 | 696 |
| **$C_4$ grasses** | | | | | | | | | | | | | | | | |
| *Andropogon gerardii* | 4 | 4.7 | 0.6 | 0.44 | 0.02 | 0.08 | 0.02 | 0.09 | 0.02 | 52 | 5 | 85.1 | 11.1 | 4 | 710 | 107 |
| *Bouteloua curtipendula* | 4 | 7.2 | 1.2 | 0.52 | 0.05 | 0.58 | 0.51 | 0.34 | 0.29 | 64 | 21 | 85.4 | 9.3 | 4 | 494 | 108 |
| *Calamovilfa longifolia* | 4 | 5.2 | 0.7 | 0.52 | 0.03 | 0.22 | 0.10 | 0.21 | 0.07 | 33 | 9 | 89.8 | 7.4 | 4 | 740 | 584 |
| *Panicum capillare* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Panicum virgatum* | 3 | 5.3 | 0.8 | 0.52 | 0.06 | 0.12 | 0.03 | 0.12 | 0.01 | 44 | 5 | 85.3 | 17.4 | 4 | 600 | 140 |
| *Schizachyrium scoparium* | 4 | 5.0 | 0.6 | 0.49 | 0.05 | 1.00 | 0.55 | 0.95 | 0.52 | 45 | 25 | 83.0 | 10.1 | 4 | 1118 | 518 |
| *Sorghastrum nutans* | 3 | 7.4 | 0.4 | 0.63 | 0.02 | 0.06 | 0.02 | 0.05 | 0.01 | 143 | 33 | 61.0 | 7.6 | 4 | 1409 | 492 |
| **Forbs** | | | | | | | | | | | | | | | | |
| *Achillea millefolium* | 4 | 16.5 | 1.3 | – | – | 0.19 | 0.05 | – | – | 104 | 23 | – | – | 2 | 241 | 45 |
| *Agastache foeniculum* | 3 | 17.2 | 0.4 | – | – | 0.20 | 0.01 | – | – | 87 | 5 | – | – | – | – | – |
| *Ambrosia artemisiifolia* | 4 | 23.3 | 3.1 | 1.51 | 0.15 | 0.19 | 0.06 | 0.12 | 0.03 | 141 | 26 | 30.9 | 2.9 | 4 | 135 | 80 |
| *Anemone cylindrica* | 4 | 15.3 | 1.1 | 1.10 | 0.14 | 1.60 | 1.34 | 1.34 | 1.17 | 46 | 15 | 39.3 | 6.7 | 4 | 768 | 481 |
| *Asclepias syriaca* | 3 | 19.2 | 1.1 | 1.80 | 0.11 | 0.30 | 0.10 | 0.35 | 0.05 | 85 | 33 | 25.3 | 2.0 | 4 | 135 | 61 |
| *Asclepias tuberosa* | 4 | 18.9 | 1.1 | 1.66 | 0.11 | 5.03 | 4.79 | 4.25 | 4.03 | 59 | 20 | 28.2 | 1.8 | 4 | 201 | 39 |
| *Asclepias verticillata* | 2 | 9.8 | 2.1 | 0.96 | 0.18 | 0.22 | 0.02 | 0.22 | 0.03 | 45 | 14 | 47.1 | 7.6 | – | – | – |
| *Aster azureus* | 4 | 14.3 | 2.1 | 0.98 | 0.07 | 0.22 | 0.03 | 0.17 | 0.01 | 66 | 5 | 43.1 | 3.4 | 3 | 203 | 41 |
| *Aster ericoides* | 2 | 7.1 | 4.5 | 1.10 | * | 0.15 | 0.08 | 0.22 | * | 43 | 6 | 40.0 | * | 2 | 73 | 8 |
| *Aster novae-angliae* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Coreopsis palmata* | 4 | 9.9 | 1.9 | 0.99 | 0.14 | 3.27 | 3.10 | 4.01 | 3.82 | 40 | 20 | 47.1 | 7.4 | 4 | 113 | 28 |
| *Liatris aspera* | 4 | 13.5 | 0.9 | 1.05 | * | 0.14 | 0.02 | 0.11 | * | 103 | 10 | 40.1 | * | 2 | 265 | 126 |
| *Penstemon grandiflorus* | 4 | 9.7 | 2.3 | 0.88 | 0.11 | 0.22 | 0.03 | 0.23 | 0.06 | 46 | 12 | 51.6 | 8.1 | 4 | 153 | 66 |
| *Potentilla arguta* | 2 | 3.2 | 2.1 | 0.68 | 0.02 | 0.11 | 0.05 | 0.26 | 0.06 | 28 | 5 | 69.6 | 2.5 | 2 | 191 | 72 |
| *Rudbeckia serotina* | 3 | 19.2 | 6.1 | 1.92 | 0.24 | 0.15 | 0.05 | 0.15 | 0.03 | 130 | 7 | 23.3 | 2.6 | 3 | 42 | 9 |
| *Solidago nemoralis* | 4 | 16.1 | 0.4 | 1.16 | 0.08 | 0.23 | 0.01 | 0.16 | 0.01 | 72 | 5 | 40.3 | 2.9 | 4 | 267 | 69 |
| *Solidago rigida* | 4 | 9.5 | 1.1 | 0.68 | 0.09 | 2.11 | 1.13 | 1.38 | 0.77 | 33 | 18 | 66.4 | 5.9 | 4 | 433 | 74 |
| *Solidago speciosa* | 3 | 9.5 | 1.7 | 0.89 | * | 0.16 | 0.04 | 0.25 | * | 68 | 17 | 53.0 | * | – | – | – |
| **Legumes** | | | | | | | | | | | | | | | | |
| *Astragalus canadensis* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Desmodium canadense* | 4 | 16.4 | 1.8 | 2.19 | 0.08 | 1.34 | 0.75 | 1.61 | 0.82 | 34 | 15 | 20.7 | 0.5 | 4 | 150 | 37 |
| *Lespedeza capitata* | 4 | 9.6 | 1.4 | 2.05 | 0.19 | 1.36 | 1.08 | 3.28 | 2.66 | 38 | 21 | 24.1 | 2.2 | 4 | 302 | 111 |
| *Lupinus perennis* | 3 | 22.4 | 3.5 | 3.65 | 0.74 | 0.72 | 0.23 | 1.15 | 0.38 | 35 | 6 | 14.1 | 3.8 | 3 | 32 | 14 |
| *Petalostemon candidum* | 3 | 17.6 | 3.8 | 1.55 | 0.02 | 0.30 | 0.11 | 0.27 | 0.15 | 84 | 48 | 31.7 | 2.3 | – | – | – |
| *Petalostemon purpureum* | 4 | 11.3 | 2.6 | 1.80 | 0.14 | 0.26 | 0.05 | 0.42 | 0.12 | 51 | 20 | 27.1 | 2.1 | 4 | 562 | 133 |
| *Petalostemon villosum* | 3 | 10.0 | 3.2 | 1.05 | * | 0.26 | 0.07 | 0.10 | * | 50 | 27 | 44.0 | * | 2 | 56 | 0 |
| **Woody plants** | | | | | | | | | | | | | | | | |
| *Corylus americana* | 4 | 6.8 | 0.8 | 1.12 | 0.13 | 0.61 | 0.49 | 0.88 | 0.67 | 40 | 12 | 39.1 | 6.9 | 4 | 430 | 179 |
| *Quercus macrocarpa* | 4 | 6.7 | 0.2 | 0.99 | 0.04 | 0.13 | 0.02 | 0.20 | 0.02 | 52 | 7 | 43.7 | 3.2 | 4 | 360 | 153 |

The number of individual plots (*n*) applies to all traits of each species, except where indicated (*$n$ = 1). No data are indicated by dashes. Units for traits are: $R_{mass}$, mass-based respiration, nmol $g^{-1}$ $s^{-1}$; $N_{mass}$, %; $R_{length}$, length-based respiration, nmol $m^{-1}$ $s^{-1}$; $N_{length}$, mg $m^{-1}$; SRL, specific root length, m $g^{-1}$; C : N, carbon–nitrogen ratio; longevity, d.

 