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ENVIRONMENTAL CONSTRAINTS ON A GLOBAL RELATIONSHIP AMONG LEAF AND ROOT TRAITS OF GRASSES

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Abstract. Uncertainties regarding the relationships between leaf and root traits have impeded an integrated understanding of plant evolution and the efficient parameterization of ecosystem models. We measured key root and leaf traits of grasses from 77 sites in four grassland regions of the world (New Zealand, Australia, South Africa, North America). Within each region, the relationships among leaf traits paralleled those among root traits. Plants with low root or leaf N concentrations had roots or leaves with high tissue density, high lignin concentrations, low amount of mass that was soluble in a neutral detergent solution, large diameter/thickness, and were less enriched in ¹⁵N. Yet, whether comparing plants within a region or among all four regions, there was little relationship between root traits and leaf traits, except for a positive relationship between root and leaf N concentration and between root and leaf $\delta^{15}\text{N}$. At the global scale, factors such as soil freezing and the type of nutrient limitation appear to determine relationships among leaves and roots. *C*₄ grasses not only had lower leaf N concentrations than *C*₃ grasses but also lower root N concentrations. When compared at the same root N concentration, *C*₄ grasses had greater leaf N concentrations than *C*₃ grasses.

Key words: grass; leaf; nitrogen cycling; plant functional traits; root.

INTRODUCTION

Understanding the evolution and expression of plant traits, the controls over resource acquisition and species abundance in ecosystems, and how plant species respond to anthropogenic changes requires comprehensive studies of how leaves and roots are constructed across broad geographic and taxonomic contrasts (e.g., Chapin 1991). Moreover, the ability to predict root traits from environmental parameters or leaf traits would greatly improve our models of global ecosystem functioning (Norby and Jackson 2000). For example, root longevity might be able to be predicted from simple measurements of leaf traits, and consequently belowground net primary production could be estimated better.

Recent research into the geographic and taxonomic patterns of leaf traits has provided evidence of integrated suites of leaf traits that represent evolutionary

and/or biophysical constraints on form and function (Reich et al. 2003). Though relationships for roots are less well developed than for leaves, phenotypic and genotypic patterns of root and leaf traits appear similar along nutrient supply gradients and among species. At low N supply, leaves and roots have low specific rates of activity and low N concentrations, along with high structural investment and long lifespan (Yin and Perry 1991, Reich et al. 1997, Hendricks et al. 2000). Moreover, it has been shown that there is congruence among species at a given site for root and leaf traits. Plants that have the low-N suite of leaf traits also have the low-N suite of root traits (Ryser and Lambers 1995, Craine et al. 2002). Although a few studies show relationships between root and leaf traits, it is unknown if there is one global set of relationships among root and leaf traits, or whether climate, resource availability, stress, or disturbance alter them.

Environmental factors might constrain or alter the evolution and/or expression of the relationships among leaves and roots. For example, environmental extremes such as freezing soils (Majdi et al. 1992) or droughts (Hayes and Seastedt 1987) might differentially limit

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root longevity and select for lower structural investment in roots if the cost of extra investment does not substantially increase root longevity and net resource acquisition. Alternatively, whether N or P is most limiting might alter root construction based on acquisition strategies with little effect on leaf construction.

Photosynthetic pathway (C_3 vs. C_4) is likely to alter the relationship between root and leaf nitrogen concentrations. C_4 photosynthesis is thought to confer lower leaf N concentrations than species with C_3 photosynthesis via higher photosynthetic nitrogen use efficiency (PNUE; Long 1999), but would not necessarily alter root N concentrations. As such, C_3 grasses would have lower leaf N concentrations than C_4 grasses when compared at the same root N concentration. Alternatively, if the extra C is allocated belowground, the greater C supply per unit leaf N for C_4 species could lead to lower root N concentrations than C_3 species when compared at a common leaf N concentration. C_4 species could also have lower leaf and root N concentrations than C_3 species, but the relationship between leaf and root N concentrations would be the same.

To examine relationships between leaf traits, root traits, and climate across grassland regions that differ in their evolutionary history and environmental characteristics, roots and leaves were collected from 293 plants (all grasses) in four grassland regions of the world: the temperate South Island of New Zealand (Craine and Lee 2003), the tropical Northern Territory of Australia, subtropical eastern South Africa, and the temperate central grassland region of North America. Grasses were chosen for this study in part because of the wide range of climate, soils, and disturbance regimes they occupy, the low incidence of secondary compounds, the contrast in photosynthetic pathway among species, and the similarity in root and leaf morphology among species.

For both fine roots (<1 mm) and leaves, we measured six sets of corresponding traits that relate to resource acquisition and ecosystem carbon and nitrogen dynamics: root diameter/leaf thickness, tissue density (dry mass per unit volume), N concentrations, $\delta^{15}\text{N}$, soluble cell content fraction, and lignin concentrations. Ecosystems with more open N cycling are characterized by more losses due to volatilization or denitrification, nitrification, and/or uptake of ammonium by plants. Since each process enriches the N pool that plants acquire (Högberg 1997), we assume that greater $\delta^{15}\text{N}$ represents more open ecosystem N cycling.

We used multivariate and bivariate analyses to determine the relationships among leaf and root functional traits and their relationships to climatic parameters. We test whether there is a general relationship among the above-mentioned leaf and root traits. We hypothesized that plants that had the low-N suite of leaf traits would also have the low-N set of root traits. We also test whether there are differences in the relationship between and within regions, and interpret

this with respect to climate, N-cycling characteristics (implied by ^{15}N data and measurements of N cycling in New Zealand), and photosynthetic pathway. For example, we expected sites with freezing soils to have roots that reflected high turnover rates and were more like high-N plants.

METHODS

Plant material was collected from 90 species at 67 sites in four grassland regions (New Zealand, Australia, South Africa, and North America). Thirty sites in New Zealand were arrayed along an east–west transect on the South Island from the coastal area of Dunedin to the alpine area of the Southern Alps and ranged from fertilized, improved pastures to xeric rangeland (~400 mm mean annual precipitation [MAP]) to high-precipitation, native, alpine tussock grasslands (>1200 m, >1500 mm MAP). Root and leaf trait data on these plants have already been published (Craine and Lee 2003). The 15 Australian sites were arrayed along a north–south transect that began near Darwin (~1500 mm MAP) and continued south into the drier interior (~550 mm MAP) with a few additional sites around Kakadu National Park. The 14 South African sites were selected in Ithala and Hluhluwe-Umfolozi National Parks and ranged in elevation from 150 m to 1400 m. Eight North American sites were composed of sand prairies arrayed along a transect from Colorado (420 mm MAP) to Illinois (820 mm MAP). Plants from New Zealand all had the C_3 photosynthetic pathway, while those from South Africa and Australia were all C_4 . Both C_3 and C_4 plants were obtained from North America.

At each of the sites, mature green leaves and fine roots were obtained from generally four or five of the most abundant grass species. For each species, a patch of grass 10–20 cm diameter was excavated to a depth of 10–20 cm. For each species at a site, three representative sections of leaves were analyzed for mass and volumetric dimensions. Volume was assumed to be the product of leaf thickness, length, and mid-length width with thickness measured with digital calipers. Roots were washed free of soil and fine root diameter and density were calculated by scanning representative subsamples of the root system that were less than 1 mm in diameter. Roots were scanned at 1200 dots per inch (dpi) and analyzed with WinRhizo (Régent Instruments, Quebec, Canada).

C and N concentrations and $\delta^{15}\text{N}$ were determined on a Europa Scientific Integra Mass Spectrometer (PDZ Europa, Rudheath, UK) at the University of California, Davis, Stable Isotope Facility, except for the North American sites, which were determined on a ThermoFinnigan Delta Plus (Thermo Electron Corporation, Bremen, Germany) at Kansas State University. Ash-free neutral detergent soluble fraction and acid-resistant lignin were determined from serial chemical extractions (Van Soest 1982) for 100 root and leaf samples using an ANKOM fiber analyzer system (ANKOM

TABLE 1. Coefficients for eigenvectors for main axes of PCAs of root and leaf traits.

Parameter	Australia	New Zealand	North America	South Africa	All sites, leaves or roots	All sites, leaves and roots, axis 1	All sites, leaves and roots, axis 2
[N _L]	-0.54	-0.47	-0.54	-0.49	-0.46	-0.45	-0.14
Leaf density	0.41	0.24	0.31	0.33	0.28	0.22	-0.09
Leaf thickness	0.09	0.33	0.17	0.12	0.30	0.27	-0.10
Leaf soluble	-0.45	-0.49	-0.59	-0.51	-0.51	-0.44	0.05
Leaf lignin	0.48	0.46	0.20	0.47	0.46	0.40	-0.14
Leaf δ ¹⁵ N	-0.31	-0.40	-0.43	-0.41	-0.38	-0.35	0.31
[N _R]	-0.62	-0.59	-0.59	-0.41	-0.56	-0.26	-0.45
Root density	0.41	0.20	0.27	0.48	0.37	0.04	0.35
Root thickness	0.10	0.24	0.44	-0.14	0.43	0.12	0.38
Root soluble	0.18	-0.17	-0.31	-0.52	-0.26	0.01	-0.27
Root lignin	0.08	0.45	0.43	0.46	0.55	0.14	0.49
Root δ ¹⁵ N	-0.63	-0.56	-0.31	-0.32	0.00	-0.32	0.23

Notes: PCAs were run independently for leaves and roots for each region and then all regions combined. Then a PCA was run for all regions with roots and leaves combined. The first two axes are reported. Nitrogen concentrations of leaves and roots, respectively, are indicated by [N_L] and [N_R].

Technology, Macedon, New York, USA) and neutral detergent, acid detergent, and 72% sulfuric acid. The results of these 100 samples were used to calibrate measurements on a FOSS near-infrared spectrometer (FOSS NIRSystems, Silver Spring, Maryland, USA) ($r^2 > 0.8$ for both fractions) that were used in statistical analyses of soluble and lignin fractions. Climate data (mean annual temperature, mean temperature of hottest and coldest months, mean annual precipitation) for each site was obtained from regional databases or local weather stations (no climate data were available for five sites in South Africa).

Although we were unable to measure nutrient supply in all sites, annual N supplies were measured for the New Zealand sites. Nylon bags containing 5 g anion-exchange resin were installed in November 2001 for 22 New Zealand sites, collected 12 mo later and then extracted with 2 mol/L KCl before determining N concentrations in the extractant.

All statistical analyses were performed in JMP 5.0.1 (SAS Institute, Cary, North Carolina, USA). Pairwise relationships between selected traits were determined with a model II regression, which is required when there is no clearly defined independent variable and/or there exists measurement error for both variables (Sokal and Rohlf 1994). With so many traits and correlations, a multivariate analysis (PCA) was used to examine the general patterns in traits within and among regions without any preconceptions of how the data are structured. Five sets of PCAs were run in order to determine the relationships among leaf traits for each region, root traits for each region, leaf traits for all regions, root traits for all regions, and leaf and root traits for all regions.

RESULTS

The single-region PCAs for leaf traits revealed that, within each region, there were consistent correlations among leaf traits. Plants with low leaf N concentration had high leaf tissue density, thick leaves, low soluble

mass, and high lignin (Table 1). The negative relationships between lignin and soluble fractions are unlikely to represent a tradeoff that results from analyzing fractions that sum to 1. The average sum of the soluble and lignin fractions for leaves was only 33% of the total mass (37% for roots). The eigenvector coefficients of the first axes of each regional PCA were well correlated ($r > 0.94$ for all pairwise comparisons), indicating similar patterns among regions. The multiregional PCA of the leaf traits showed the same pattern as the regional PCAs (Table 1), indicating that differences among regions in trait relationships were similar to the relationships within regions. Both within and among regions, plants with the low-N set of leaf traits also had lower leaf δ¹⁵N (Table 1), consistent with the idea that the N supply for species with low leaf N was less open.

Within each region, there were consistent correlations among root traits that paralleled the pattern seen among leaf traits (Table 1). Plants with low root N concentrations had high root tissue density and generally had thicker roots with less soluble mass and more lignin. The coefficients of the eigenvectors of the first axes for root traits of each regional PCA again were strongly correlated (average $r = 0.77$ for all pairwise comparisons). The multiregional PCA of root traits showed a similar pattern as the regional PCAs, except for root δ¹⁵N (Table 1). Plants with the low-N set of root traits in each region were less enriched in ¹⁵N, but this did not hold across regions.

Although there are consistent, parallel patterns among leaf traits and among root traits, plants that have the low-N set of leaf traits do not necessarily have the full low-N set of root traits. When comparing the pairwise correlations between analogous leaf and root traits among all plant samples, only one of five correlations was significant. Root N concentrations ([N_R]) increase with increasing leaf N concentration ([N_L]), with [N_R] about half of [N_L] ([N_R] = 0.55 × [N_L] - 0.7 mg N/g;

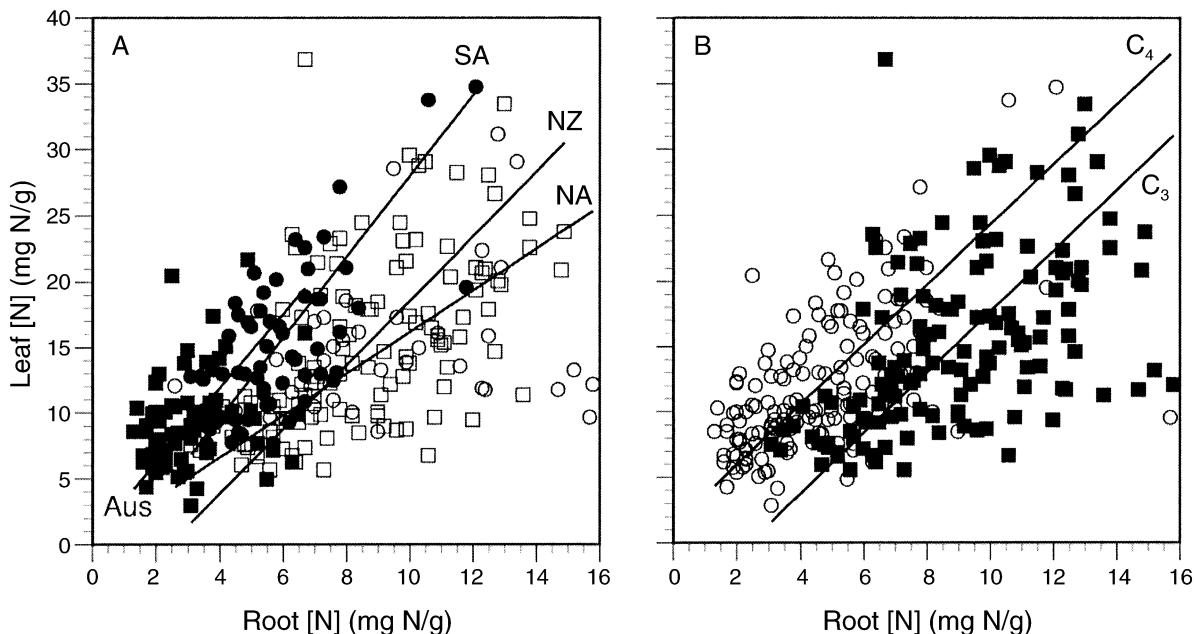


FIG. 1. Relationships between leaf N concentration and root N concentration for (A) Australian (Aus; solid squares), South African (SA; solid circles), New Zealand (NZ; open circles), and North American (NA; open squares) sites and (B) C_3 grasses (solid squares) and C_4 grasses (open circles) (B). Lines represent model II regression.

model II, $r^2 = 0.32$, $P < 0.001$). There was no overall relationship between leaves and roots in thickness/diameter ($P = 0.97$), tissue density ($P = 0.49$), lignin concentrations ($P = 0.65$), or soluble fraction ($P = 0.97$). Including grassland region as a categorical factor in the regression model of $[N_R]$ by $[N_L]$ doubled explanatory power ($r^2 = 0.63$, $P < 0.001$). Leaves from Australia and South Africa had a greater $[N_L]$ at a given $[N_R]$ when compared to New Zealand and North America (Fig. 1A). $\delta^{15}N$ of leaves increased with $\delta^{15}N$ of roots ($\delta^{15}N_L = 1.35 \times \delta^{15}N_R - 0.10\text{‰}$; model II, $r^2 = 0.58$, $P < 0.001$) with roots having a $\delta^{15}N$ 0.34‰ greater than leaves ($-0.69 \pm 0.14\text{‰}$ vs. $-1.03 \pm 0.19\text{‰}$ [all error measurements reported are ± 1 SE]).

On a global scale, knowing the characteristics of leaves provides little predictive power of root traits. In the multiregional PCA of leaf and root traits, the positive relationship between leaf N and root N concentrations is the only consistent root-leaf linkage (axis 1, Table 1). The lack of correspondence between leaf and root traits across regions is also evident when comparing the multiregional PCAs that were restricted to leaf traits or root traits. We calculated the scores of plants on the main axis of the multiregional PCA of root traits and compared them with the scores of the plants on the main axis of the multiregional PCA of leaf traits. Scores of plants based on their leaf traits were poorly correlated with their scores based on root traits ($r = 0.17$, $P = 0.004$). Similar analyses with regional patterns led to similar conclusions (data not shown).

These consistent patterns of leaf traits and root concentrations within regions likely reflect variation in N supply and/or N limitation. Plants that have low leaf N concentrations are less enriched in ^{15}N , which most likely reflects greater N limitation (Fig. 2). This is corroborated with data from the resin bags installed in the New Zealand sites. Total extracted N (NH_4^+-N and $NO_3^- - N$) was positively correlated with $\delta^{15}N$ and $[N]$ for leaves ($r^2 = 0.28$, $P = 0.01$; $r^2 = 0.42$, $P < 0.001$) and roots ($r^2 = 0.18$, $P < 0.05$; $r^2 = 0.33$, $P < 0.01$). Across all sites, mean annual precipitation predicted 32% of the variation in axis 1 ($P < 0.001$; Fig. 3), and more-humid grasslands have the suite of traits associated with lower leaf N concentrations and a less open N cycle. There were no significant relationships between axis 1 and mean annual temperature, mean temperature of the hottest month, or mean temperature of the coldest month ($P > 0.52$).

The second axis from the multiregional PCA of leaf and root traits reveals a separate set of correlations that mirrors the patterns seen among root traits in each of the regions. Plants with low root N concentrations have high root tissue density, are thick, have low soluble mass, high lignin, and have greater $\delta^{15}N$ (Table 1). Yet, 70% of the variation in axis 2 is accounted for by regional identity. Plants from New Zealand and North America had markedly lower scores on axis 2 (-1.47 ± 0.14 , -1.09 ± 0.08 , respectively) than those from Australia and South Africa (1.57 ± 0.10 , 1.14 ± 0.11 ; Fig. 3). This indicates that plants from New Zealand and North America had higher root N concentrations,

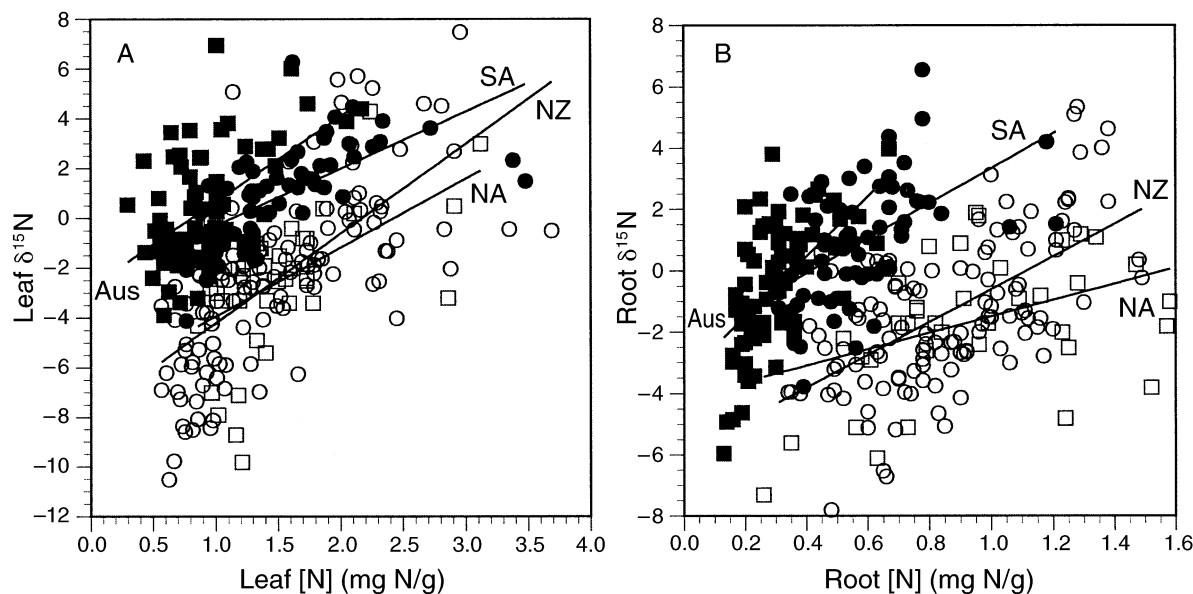


FIG. 2. Relationships between $\delta^{15}\text{N}$ and N concentrations for (A) leaves and (B) roots for all plants samples (model II regression). Australian (Aus; solid squares) and South African (SA; solid circles) samples had greater $\delta^{15}\text{N}$ at mean N concentrations than New Zealand (NZ; open circles) and North American (NA; open squares) samples (Tukey's hsd, $P < 0.05$).

lower root tissue density, more soluble mass, and less lignin than plants of South Africa or Australia. Roots from New Zealand and North America also were thinner and had lower root and leaf $\delta^{15}\text{N}$.

One factor that differentiates the two pairs of regions is temperature. The mean temperature of the coldest month was the best predictor of mean axis 2 scores for each site (Fig. 4), and colder sites (New Zealand and North America) had lower axis 2 scores (e.g., higher root N concentration, lower root lignin, etc.) than warmer sites. When comparing regions at a common leaf or root N concentration, the average $\delta^{15}\text{N}$ of leaves and roots from the presumably more P-limited sites of South Africa and Australia was greater (Fig. 2).

Across all plants, the leaf N concentrations were greater for C_3 species than C_4 species (15.3 ± 0.5 mg N/g vs. 12.0 ± 0.5 mg N/g, respectively), but C_3 - C_4 classification explained only 7.3% of the variation in $[\text{N}_L]$ ($P < 0.001$, Fig. 1B). For roots, C_3 - C_4 classification explained 42% of the total variation in N concentrations ($P < 0.001$), with root N concentrations greater for C_3 species than C_4 species (9.0 ± 0.2 mg N/g vs. 4.6 ± 0.2 mg N/g, respectively).

In a least-squares regression model, both root N concentration and C_3 - C_4 classification are significant predictors of leaf N concentration ($r^2 = 0.34$; $ss = 29.9$, $P < 0.001$; $ss = 1.88$, $P < 0.01$, respectively) with no significant interaction between the two ($P = 0.38$; Fig. 1B). Contrary to hypotheses regarding C_4 species having lower leaf N concentration, when compared at a common root N concentration, C_4 grasses have higher leaf N concentrations than C_3 grasses (least squares

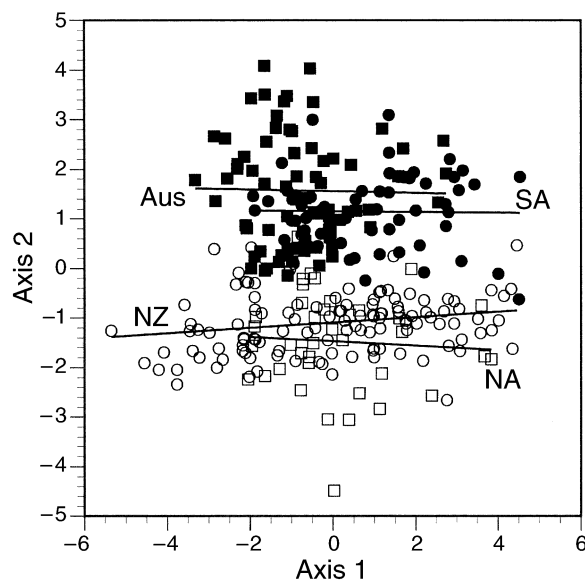


FIG. 3. Relationships between axis 2 and axis 1 of the multiregional PCA for all plant samples. South African (SA; solid circles) samples scored higher on axis 1 than Australian (Aus; solid squares) or New Zealand (NZ; open circles) samples (Tukey's hsd, $P < 0.05$; 0.86 ± 0.21 [mean ± 1 SE] vs. -0.74 ± 0.15 or -0.02 ± 0.21 ; North America [NA; open squares] score = 0.09 ± 0.25), although there was high overlap among all regions. Australian and South African plants scored significantly higher on axis 2 (Tukey's hsd, $P < 0.05$) than North American and New Zealand plants (1.57 ± 0.13 and 1.15 ± 0.09 vs. -1.09 ± 0.06 and -1.47 ± 0.17 , respectively).

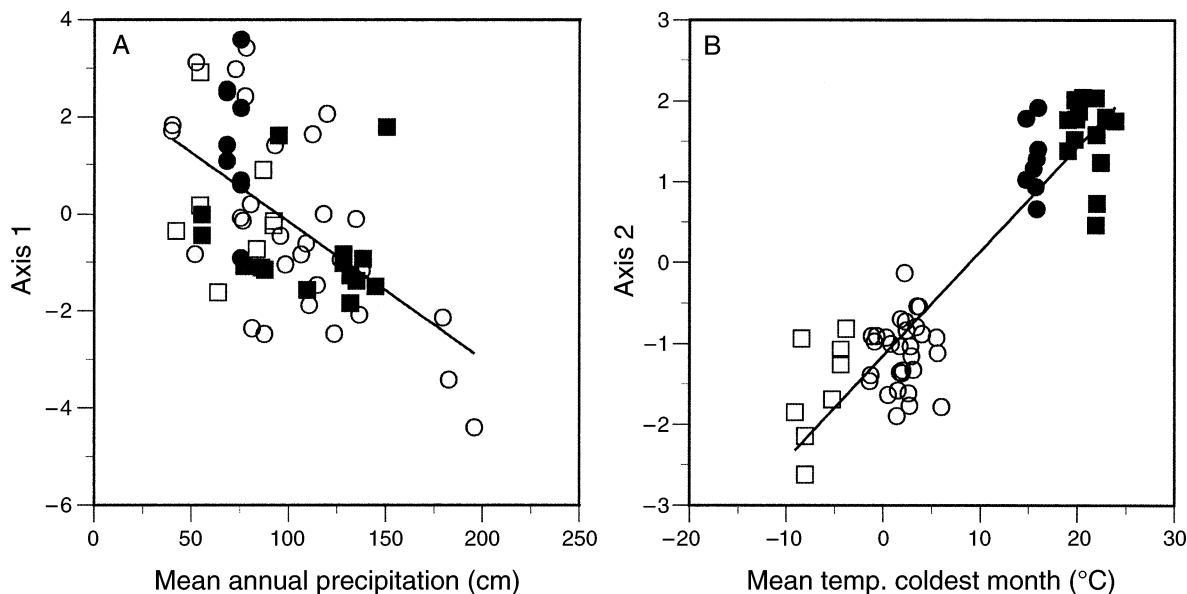


FIG. 4. Linear regressions between (A) mean annual precipitation and site-averaged scores for axis 1 of the multiregional PCA for leaves and roots ($y = 2.68 - 2.84x$; $P < 0.001$, $r^2 = 0.32$) and (B) mean temperature of the coldest month of the year and site-averaged scores for axis 2 ($y = -1.16 + 1.29x$; $P < 0.001$, $r^2 = 0.84$). Axis 2 was also strongly positively associated with mean annual temperature ($r^2 = 0.81$, $P < 0.001$). Symbols are as in Fig. 3.

means of leaf N concentrations = 1.27 ± 0.05 mg N/g for C₃ grasses, 1.48 ± 0.05 mg N/g for C₄ grasses across all sites). When comparing C₃ and C₄ grasses in North America, C₄ grasses have a greater axis 2 score of the multiregional PCA for all traits than C₃ grasses (-0.98 ± 0.21 vs. -1.91 ± 0.20 , respectively).

DISCUSSION

Based on our sampling of 90 grass species from 67 sites in four grassland regions, a single, uniform, global relationship among major leaf and root traits that is consistent among environments appears unlikely. Within each region, there were consistent patterns among leaf traits and consistent patterns among root traits that were similar to those previously published (Ryser and Lambers 1995, Reich et al. 1997, Craine et al. 2002). Yet, only N concentrations were correlated between leaves and roots. Both within and among regions, leaf and root traits were divorced in their patterns.

Although there might not be a single global relationship among root and leaf traits, there was a strong general positive relationship between leaf and root N concentrations. It is uncertain whether the low N concentrations of roots and leaves are a result of natural selection. For example, in an ecosystem with low N supply, herbivory aboveground and belowground could be intense for plants with high N concentrations. Alternatively, the low N concentrations may not be species traits and could be a direct consequence of growing in an ecosystem with low N supply.

Photosynthetic pathway affected the relationship between leaf and root N concentrations, but C₃ species

and C₄ species were more differentiated by root N concentrations than leaf N concentrations. Although C₄ species had lower leaf N concentrations on average than C₃ species, C₃ species and C₄ species overlapped broadly in the range of leaf N concentrations and photosynthetic pathway explained little in the variation in leaf N. When standardized for root N concentrations, C₄ grasses have higher leaf N concentrations than C₃ grasses. Yet, if C₄ photosynthesis provides higher PNUE that allows leaves to be produced with lower N concentrations, if anything, C₄ leaf N concentration should be lower than that of C₃ species, not higher. It is currently unknown how much of the variation that has been observed in N concentrations between C₃ species and C₄ species is due to differences in N supply (Craine et al. 2003) or a result of differences in relative allocation of C and/or N between leaves and roots.

Although there were limited relationships between leaf and root traits, there were consistent patterns among root traits within and among regions. Plants with low root N concentrations had high root tissue density, low root soluble mass, and high root lignin concentrations. It seems unlikely that these relationships represent biophysical constraints. For example, plants with low root tissue density could have low N concentrations. The patterns of root traits follow the "evergreen" hypotheses (Monk 1966, Chapin 1980, Aerts 1995, Reich et al. 1997) that have been developed for leaves. Presumably, net resource gain is greater in low N-supply ecosystems for roots that have low N concentrations and high structural fractions (Yanai et al. 1995), but the basis for this has yet to be shown

definitively. The relationship between $\delta^{15}\text{N}$ and these traits within regions suggests that the major patterns in root traits may follow soil N supply. Like with leaves, if the evergreen hypothesis is responsible for the observed patterns of root traits, future research will have to focus on the disadvantage of given trait sets in an environment, such as high root N concentration in sites with low N supply.

Regarding differences among regions, New Zealand and North American sites had lower mean minimum monthly temperatures that were near or below freezing. Soil freezing can be associated with extreme physical stress for plant roots as ice expands and soils shift. High root N concentrations, low lignin, and low tissue density are likely to be associated with shorter root longevity and if so, freezing soils and the physical stress they impart may constrain the longevity of roots and the advantages of physically tough roots and/or roots that are built to overwinter. Previous syntheses of root longevity based primarily on repeated harvests (Gill and Jackson 2000) suggested that root longevity decreased with mean annual temperature in grasslands. This seems inconsistent with the results here that show warmer sites have root traits that should be associated with longer, not shorter, root longevity.

If soil freezing is an important determinant of root life history, the importance of disturbance might help explain patterns of root and leaf longevity in different ecosystems. For example, black spruce (*Picea mariana*), which grows in nutrient-limited, high-latitude ecosystems in the northern hemisphere, has long leaf longevity, but short root longevity (Ruess et al. 1998). This might not be because there is an inverse relationship between root longevity and leaf longevity, but because freezing soils impose constraints on root longevity, but not leaf longevity.

In addition to the lack of soil freezing, South Africa and Australia have older and presumably more P-deficient soils. The greater ^{15}N signatures of plants from these sites may reflect a more open N cycle where, as a result of greater P limitation, N is more likely to be lost via denitrification or volatilization that enriches the ^{15}N signature of the remaining N. Plants that are N or P limited are likely to have leaves that are built similarly (Chapin 1991). In either case, N and P concentrations are likely to be low since the ratio of N:P is relatively constrained (Grime et al. 1997, Elser et al. 2000) and leaves should live a long time (Craine et al. 1999, Ryser and Urbas 2000). Yet, since N and P have different dynamics in the soil, there are likely to be differences in how roots are built to best acquire the different nutrients. The thicker roots of Australian and South African grass roots could represent greater dependence on mycorrhizae (Fitter 1996) and genuinely reflect greater P limitation there.

More research is necessary to extend these correlations to other grassland regions and other vegetation types. Yet, together with a better understanding of the

relationship between root construction and function, these global relationships among leaf and root traits have the potential to serve as a key in understanding the evolution of integrated suites of plant traits and more efficiently parameterize ecosystem models for parameters that are difficult to obtain, such as root longevity.

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