

A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora

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Summary

1. Westoby's [*Plant and Soil* (1998), **199**, 213] Leaf-Height-Seed (LHS) plant strategy scheme quantifies the strategy of a plant based on its location in a three-dimensional space defined by three functional traits: specific leaf area (SLA), height, and seed mass. This scheme is based on aboveground traits and may neglect strategies of belowground resource capture if root functioning is not mirrored in any of the axes. How then do fine roots fit into the LHS scheme?

2. We measured 10 functional traits on 133 plant species in a ponderosa pine forest in northern Arizona, USA. This data set was used to evaluate how well the LHS scheme accounts for the variation in above and belowground traits.

3. The three most important plant strategies were composed of multiple correlated traits, but SLA, seed mass, and height loaded on separate principle components. The first axis reflected the widely observed 'leaf economics spectrum'. Species at the high end of this spectrum had high SLA, high leaf and fine root nitrogen (N) concentration, and low leaf dry matter content. The second axis reflected variation in seed mass and fine root morphology. Plants at the positive end of this spectrum were plants with large seeds and low specific root length (SRL). The third axis reflected variation in height and phenology. Plants at the positive end of this spectrum were tall species that flower late in the growing season.

4. Leaf N concentration was positively correlated with fine root N concentration. SRL was weakly positively correlated with SLA. SRL was not correlated with fine root N concentration. Leaf litter decomposition rate was positively correlated with the leaf economics spectrum and was negatively correlated with the height and phenology spectrum.

5. Leaf traits, seed mass, and height appear to be integrating properties of species that reflect much of the variation in plant function, including root function. Fine root N concentration was positively mirrored by the leaf economics spectrum, and SRL was inversely mirrored by seed mass. The leaf and height axes play a role in controlling leaf litter decomposability, indicating that these strategy axes have important consequences for ecosystem functioning.

Key-words: comparative ecology, functional traits, leaf economics spectrum, litter decomposition, nitrogen, seed mass, specific leaf area, specific root length

Introduction

Plants are multifaceted organisms that have evolved ecological strategies for sustaining populations in resource-limited environments (Grime 1979; Craine 2009). Plant strategies can be quantified by measuring functional traits (Grime *et al.* 1997; Reich *et al.* 2003), which are the properties of plants that impact plant fitness (Violle *et al.* 2008) and

ecosystem processes (Lavorel & Garnier 2002). Comparisons of functional traits across taxa have provided insight into the primary functional gradients among plants (e.g. Grime *et al.* 1997; Reich *et al.* 1999; Craine *et al.* 2001; Díaz *et al.* 2004). One important gradient describes differences in resource acquisition (Reich, Walters & Ellsworth 1997), known as the 'leaf economics spectrum' (*sensu* Wright *et al.* 2004a), which runs from plants with quick returns on investment in nutrients and dry matter [i.e. plants with leaves that have high photosynthetic rates, short life spans,

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high SLA, and high leaf nitrogen (N) concentrations] to plants with slower returns on their investments. This multi-trait spectrum (or strategy axis) is only one out of potentially many spectra important to plant growth, reproduction, and survival (Reich *et al.* 2003; Craine 2009).

Westoby (1998) proposed a simple 'Leaf-Height-Seed' (LHS) scheme that operationally quantifies the strategy of a plant species by its location in a three-dimensional space defined by three functional traits: specific leaf area, height, and seed mass. Specific leaf area (SLA, leaf area per unit dry mass) represents variation along the leaf economics spectrum and is indicative of a species' ability to respond to opportunities for rapid growth (Reich *et al.* 1999). Plant height at maturity has been related to competitive ability and fecundity (Keddy & Shipley 1989; Aarssen & Jordan 2001). Seed mass reflects variation in dispersal capability and cotyledon-stage seedling survivorship (Westoby, Leishman & Lord 1996; Jakobsson & Eriksson 2000). This LHS plant ecology strategy scheme is potentially useful since it requires the measurement of only three easy-to-measure traits. However, plant strategies are thought to be gradients in multiple correlated traits rather than gradients in single traits (Reich *et al.* 2003). Moreover, any plant strategy scheme based entirely on aboveground traits may neglect strategies of belowground resource capture if root functioning is not mirrored in any of the three axes. How then do fine roots fit into the LHS scheme?

Root traits are harder to measure and have received far less attention than aboveground traits, despite the fact that most of the biomass and production in perennial-dominated ecosystems is belowground, and that many important ecosystem processes are tightly coupled with plant roots and rhizospheres (Aerts & Chapin 2000). There is some evidence for a 'root economics spectrum' analogous to tradeoffs seen in leaves (Eissenstat & Yanai 1997). For example, fine root N concentration scales positively with leaf N concentration (Craine & Lee 2003; Tjoelker *et al.* 2005; Kerkhoff *et al.* 2006). A recent analysis by Kembel *et al.* (2008) indicates that there are at least two gradients of root function. The strongest gradient suggests that species with fast relative growth rates have high leaf and root N concentrations, shorter-lived roots, and high SLA, indicating that roots and leaves are functionally coordinated. The weaker orthogonal axis described variation in specific root length. Specific root length (SRL, root length per unit root dry mass) of fine absorptive roots has been suggested to be the belowground analogue to SLA (Cornelissen *et al.* 2003). SRL is indicative of the potential rate of water and nutrient uptake and is considered to be a morphological index of belowground competitive ability (Lambers, Chapin & Pons 1998). SLA and fine root SRL were uncorrelated among a set of grassland species despite the positive association between leaf and fine root tissue chemistry (Tjoelker *et al.* 2005). Some studies have illustrated positive relationships between relative growth rate (which scales positively with SLA; Lambers & Poorter 1992) and SRL (Reich *et al.* 1998; Wright & Westoby 1999), whereas others have reported opposite

trends (Boot 1989; Lambers & Poorter 1992) or even no relationship (Poorter & Remkes 1990; Huante, Rincon & Gavito 1992). If an independent root economics spectrum exists, then the LHS scheme may need additional dimensions (Westoby *et al.* 2002; Westoby & Wright 2006), but if leaf and root traits are functionally coordinated, then the LHS scheme will be supported because variation in root traits will be mirrored by aboveground traits.

Functional traits not only define plant strategies for survival, they are thought to influence important ecosystem processes (Chapin *et al.* 2000). Decomposition of leaf litter is one critical step in the internal recycling of limiting nutrients. Decomposition rates are partly controlled by tissue nutrient concentration and the density of structural material in the leaf (Cornwell *et al.* 2008), suggesting that the leaf axis in the LHS scheme controls leaf litter decomposition rates.

We quantified 10 functional traits on 133 plant species that commonly occur in southwestern USA *Pinus ponderosa* var. *scopulorum* P. & C. Lawson (ponderosa pine) forests. In addition to SLA, height, seed mass, SRL, leaf N and fine root N, we measured four additional traits that can influence plant fitness: leaf phosphorus concentration, which has been shown to be an important component of the leaf economics spectrum (Wright *et al.* 2004a); flowering date and duration, which summarize phenological aspects of a species' life history (Grime *et al.* 1997); and leaf dry matter content (LDMC, ratio of leaf dry mass to fresh mass), which is indicative of the amount of structural material in a leaf (Garnier *et al.* 2001; Kazakou *et al.* 2006). We asked the following questions: (1) Is the LHS scheme supported when multiple traits, including root traits, are assessed simultaneously in a multivariate framework? (2) Are root traits correlated with leaf traits? (3) Do the LHS axes explain variation in leaf litter decomposition rates?

Materials and methods

STUDY SYSTEM

This is the first study to document functional traits for the common plant species found in the widespread semi-arid ponderosa pine forest ecosystem in the southwestern USA. Water and nitrogen are the primary limiting resources in this ecosystem. Frequent low-intensity surface fire was historically the most important disturbance agent (Moore, Covington & Fulé 1999). These fires maintained a savanna-like system where clumps of large trees persisted amidst a matrix of a grassy understory, but fire suppression over the last century has caused tree densities to increase dramatically. In dense forest stands, the ponderosa pine overstory suppresses understory production and diversity (Laughlin *et al.* 2008). In open stands, the understory is dominated by both C₃ and C₄ bunchgrasses and forbs, which comprise the majority of the species pool.

This study was conducted on a ~12 000 ha landscape in the Coconino National Forest near Flagstaff, Arizona, USA. The mean annual precipitation of Flagstaff is 56 cm and the mean annual temperature is 7.7 °C (Kohn & Welker 2005). Southwestern USA ponderosa pine forests occur across a broad edaphic gradient and therefore have a large species pool (Laughlin & Abella 2007). We

chose to study 133 species that were detected either historically or currently on a set of long-term permanent plots. These species span 33 taxonomic families and 95 genera, and includes 88 C₃ forbs, 13C₃ grasses, nine C₃ legumes, three C₃ shrubs, two C₃ trees, 14 C₄ grasses, and four CAM forbs. All nomenclature follows the USDA NRCS Plants Database (<http://plants.usda.gov/>) accessed in 2009.

FUNCTIONAL TRAITS

Plants were sampled from the same study sites from which the species list was generated. In cases where species occurred at more than one site, traits were measured at multiple sites. Following the recommendations of Cornelissen *et al.* (2003), we measured traits on robust, ungrazed plants grown in well-lit environments. When measuring traits on species that are adapted to shady conditions (e.g. *Carex geophila*, *Thalictrum fendleri*), we tried to sample individuals in canopy openings. Sampling began in May 2008 and ended in September 2008. The Flagstaff region received *c.* 47 cm of precipitation during the water year of 2008 (<http://www.wrcc.dri.edu>) and the Palmer Drought Severity Index for the same time period was *c.* 0.7 (<http://www.ncdc.noaa.gov>), each indicating that plants were sampled during a climatically average year.

We measured a core set of functional traits that reflect aspects of each species' ability to disperse, establish, acquire water and nutrients, and photosynthesize (Weiher *et al.* 1999; Cornelissen *et al.* 2003). For all 133 species we measured SLA, height, seed mass, SRL, leaf N concentration, fine root N concentration, leaf phosphorus concentration, and LDMC. Julian flowering date and flowering duration were also obtained for each species. We measured leaf litter decomposition rates on 103 species. See Table S1 in electronic Supporting Information for mean trait values for every trait on all species in the study.

SLA is the ratio of leaf area to dry weight expressed as mm² mg⁻¹. SLA was measured on ten to twenty individuals when the species was flowering. We non-randomly selected one fully expanded, healthy leaf from each individual for this measurement. One-sided leaf area was measured using the Agvis Imaging System (Decagon Devices, Pullman, WA, USA) within 5 h of harvesting. The leaf petiole and rachis on compound leaves were retained for this measurement. Leaves were oven-dried for 72 h at 55 °C prior to obtaining dry weights.

Canopy height is the height of the foliage (not the height of the inflorescence) of a species measured in cm. Height was measured on robust flowering individuals and therefore reflects an average maximum height for each species.

Seed mass is the oven-dry mass of an average seed expressed in mg. When possible, seeds were harvested from several individuals of each species. Seeds housed inside fleshy fruits (e.g., *Rosa woodsii*) were removed from the fruiting structures, and if a pappus was present it was removed (Weiher *et al.* 1999). Mean seed mass was determined by weighing the total mass of between 20 and 100 individual seeds (depending on the species), then dividing the total dry weight by the number of seeds in the sample.

Leaf dry matter content (LDMC) is the ratio of leaf dry mass to fresh mass expressed as mg mg⁻¹. LDMC was not measured on the same leaves that were used to measure SLA. LDMC was measured on leaves harvested from two individuals of each species, and variance of this trait within each species was very low (see also Weiher *et al.* 1999). Following Garnier *et al.* (2001), the shoots were harvested and placed in humid plastic bags in the field. Within 5 h, we re-cut each stem under water, and keeping the cut ends submerged, stored them in a refrigerator for 24 h to fully rehydrate the leaves. This procedure is necessary because LDMC is sensitive to hourly fluctuations in leaf

water status (Garnier *et al.* 2001). After bringing the leaves back to room temperature, we weighed the rehydrated leaves to obtain 'fresh weights'. Leaves were then oven-dried for 72 h at 55 °C prior to obtaining dry weights.

Foliar concentrations of nitrogen (N_{mass}) and phosphorus (P_{mass}) were determined on at least three (often five) individual replicates per species. Fully expanded, healthy leaves were harvested from the entire axis of a plant when it was flowering. Samples were oven-dried for 72 h at 55 °C, then ground to <0.5 mm using a Wiley Mill (Thompson Scientific, Swedesboro, NJ, USA). Foliar N_{mass} was analyzed on a Flash EA 1112 Elemental Analyzer (CE Elantech Inc., Lakewood, NJ, USA) at the United States Department of Agriculture (USDA) Forest Service Rocky Mountain Research Station (RMRS) Analytical Lab in Flagstaff, Arizona, USA. To determine P_{mass}, we digested ground leaf matter with sulfuric acid, potassium sulphate and copper sulphate in a block digester to convert the phosphorus in the samples to orthophosphate. These samples were analyzed on a Lachat Quikchem 8000 (Lachat Instruments, Inc., Milwaukee, WI, USA) at the USDA Forest Service RMRS in Flagstaff, Arizona, USA.

Specific root length is the ratio of fine root length to dry mass expressed as m g⁻¹. Specific root length was measured on three individuals of each species during the latter part of the growing season. We excavated entire root systems from the soil with shovels and trowels, and gently washed soil from the roots in the laboratory with clean water rinses. Following the standardized protocol of Cornelissen *et al.* (2003), we used the fine (<2 mm) absorptive roots (i.e. unsuberized, often with evidence of root tips or hairs) in our determination of SRL. Only a subsample of fine roots from each individual was used in the measurement. This method yields a measure that better mirrors its aboveground analogue SLA (Cornelissen *et al.* 2003). The vast majority of the fine roots that we harvested were <0.5 mm. Root length was measured using the software WINRHIZO V. 2003a (Regent Instruments, Nepean, Ontario, Canada). Roots were then oven-dried for 72 h at 55 °C prior to obtaining dry weights.

Fine root N_{mass} was measured on the same roots used in the determination of SRL. After drying for 72 h at 55 °C, fine roots were ground to <0.5 mm in a Wiley Mill and were analyzed on a Flash EA 1112 Elemental Analyzer at the USDA Forest Service RMRS in Flagstaff, Arizona, USA.

Mean Julian flowering dates and flowering duration for each species were determined using regional floras that describe the first and last months that a species is in flower. For example, *Artemisia carruthii* flowers from August through October, which corresponds to the Julian days 213 through 304. Therefore, the mean Julian flowering day = (213 + 304)/2 = 259, and the flowering duration = 304–213 = 91 days. Data primarily came from McDougall (1973), but for some species we used data from the Intermountain Flora (Cronquist *et al.* 1986+) or the Flora of North America (Flora of North America Editorial Committee 1993+).

Species-specific leaf litter decomposition rates were quantified using litterbags (Harmon, Nadelhoffer & Blair 1999) inside an experimental enclosure at the G. A. Pearson Natural Area (located 10 km northwest of Flagstaff, Arizona, USA) from October 2007 to September 2008. Green (i.e. non-senesced) leaves were collected from living plants from 103 species. Litterbags had an inside area of 20 × 20 cm constructed with window screen material (1 × 2 mm mesh). Approximately 2 g of leaf dry mass were placed in these bags. Decomposition rates were determined for 103 of the 133 species in the study. The most dominant species (*n* = 53) had two independent replicates, and the remainder of the species (*n* = 50)

were not replicated. Litterbags were placed on the surface of the forest floor in an open, well-lit environment. After the harvest, we removed any soil particles from the decomposed litter with brushes prior to drying at 55 °C for 72 h to obtain oven-dry weights. The decomposition rates reported here reflect the proportional mass loss over a 1-year period.

DATA ANALYSES

We evaluated Westoby's (1998) LHS scheme by subjecting the large species-trait matrix that included root traits to a principal components analysis (PCA). If the LHS model is robust, then SLA, height, and seed mass will each load highly on the first three components, respectively, and root traits will either load on the first three axes, or they will contribute to additional dimensions. Following Westoby (1998), all variables were \log_{10} -transformed because trait values can vary by orders of magnitude, and because traits are often lognormally distributed between species. We calculated the eigenvalues and eigenvectors of the correlation matrix (see Table S2 in electronic Supporting Information) using SAS-JMP version 8.0. Decomposition rate was not included as a variable in the matrix because rates were determined for only 103 species. We used ANOVA and Tukey's HSD (Honestly Significant Difference) post-hoc tests to determine how plant functional types (C_3 forbs, C_3 legumes, C_3 woody plants, C_3 graminoids, C_4 graminoids, and CAM forbs) differed in each of the three major axis scores.

We evaluated the relationship between leaf and fine root traits. The results of the PCA informed our evaluation, but we also used regression analysis to determine the strength and sign of the relationship between: SLA and SRL; leaf N_{mass} and fine root N_{mass} ; and fine root N_{mass} and the leaf economics spectrum (quantified by the axis scores of the first principal component, see Results). We also evaluated the relationship between SRL and fine root N_{mass} .

We used simple linear and backward multiple regression analyses to evaluate the relationships between leaf litter decomposition rate and four leaf traits (SLA, LDMC, leaf N_{mass} , leaf P_{mass}) to determine which trait or combination of traits were the best predictors of decomposition rate. In addition, we used linear and multiple regression to determine whether any of the first three principal components (i.e. plant strategy axes) were correlated with leaf litter decomposition rate.

Results

THE LEAF-HEIGHT-SEED STRATEGY SCHEME

The 133 plant species exhibited broad ranges in each of the 10 functional traits (see Table S3 in electronic Supporting Information). Three principal components accounted for 58% of the total variance of the species-trait correlation matrix (Table 1).

The first principal component (PC1) accounted for 25% of the total variance and represented an axis of resource acquisition and turnover consistent with the leaf economics spectrum. Species found at the positive end of this spectrum exhibited high SLA, leaf N_{mass} , and fine root N_{mass} , and low LDMC (Fig. 1, Table 1). SLA exhibited the highest loading on PC1.

The second principal component (PC2) accounted for an additional 20% of the total variance and represented varia-

Table 1. Results of the principal components analysis of the species-trait correlation matrix. All variables were \log_{10} -transformed. Eigenvectors $>|0.30|$ are highlighted in bold. Percents reflect the percent of total variance (i.e. the sum of the diagonal elements in the correlation matrix) accounted for by each principal component

	PC1	PC2	PC3
Eigenvalues	2.54	1.98	1.32
Percent	25.4	19.8	13.2
Cumulative percent	25.4	45.2	58.4
Eigenvectors			
SLA	0.50	0.03	-0.03
LDMC	-0.47	0.03	0.05
Leaf N_{mass}	0.42	0.40	0.11
Fine root N_{mass}	0.35	0.27	0.13
Leaf P_{mass}	0.25	0.17	-0.05
Seed mass	-0.16	0.55	0.13
SRL	0.25	-0.49	0.20
Height	-0.19	0.30	0.63
Flowering date	0.18	-0.29	0.54
Flowering duration	0.11	0.17	-0.47

tion in seed mass, root morphology, and leaf N_{mass} . Species found at the positive end of PC2 had large seeds, low SRL and high leaf N_{mass} (Fig. 1, Table 1). Seed mass exhibited the highest loading on PC2 (Table 1).

The third principal component (PC3) accounted for an additional 13% of the total variance and represented variation in height, flowering date and flowering duration. Species found at the positive end of PC3 were tall species that flowered late in the season for only a short duration (Fig. 1, Table 1). Height exhibited the highest loading on PC3 (Table 1).

Plant functional types accounted for some of the variation in axis scores (Fig. 2). C_3 forbs, C_3 legumes, and CAM forbs were located at the high end of the leaf economics spectrum (PC1), whereas C_3 woody plants and both C_3 and C_4 graminoids were located at the low end (Fig. 2a). Plant functional types accounted for 31% of the variation of PC1. C_3 legumes and C_3 woody plants were located at the high end of the seed mass spectrum (Fig. 2b). C_3 graminoids had larger seeds and lower SRL than C_4 graminoids (Fig. 2b). Plant functional types accounted for 40% of the variation in PC2. Other than C_3 woody plants being taller than most other species in the flora, plant functional types accounted for only 11% of the variance in PC3 (Fig. 2c).

LEAF AND FINE ROOT TRAITS

Leaf N_{mass} was positively correlated with fine root N_{mass} (Fig. 3a). Similarly, the leaf economics spectrum, as represented by the first principal component, was positively correlated with fine root N_{mass} (Fig. 3b). Fine root N_{mass} loaded most strongly on PC1 (Table 1).

Specific root length was not correlated with fine root N_{mass} (Fig. 3c, $P = 0.65$), and SRL was only weakly positively correlated with SLA (Fig. 3d). Specific root length loaded most strongly on PC2 (Table 1).

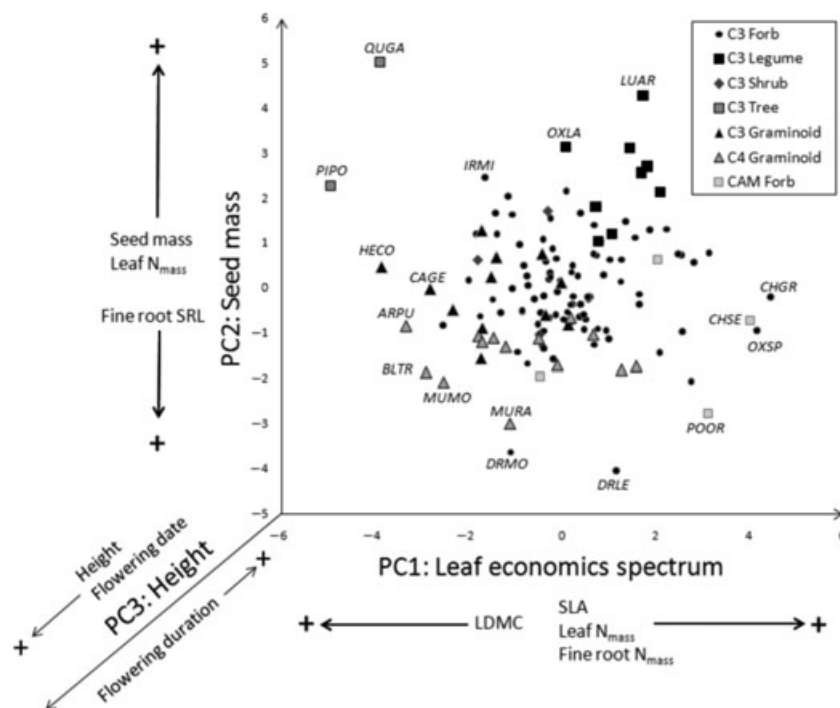


Fig. 1. The Leaf-Height-Seed plant ecology strategy scheme is supported by a principal components analysis of 10 functional traits of 133 plant species that occur in southwestern USA ponderosa pine forests. Only the first two principal component scores are plotted here explicitly. Labels and arrows show the variables that exhibited eigenvector scores $> |0.3|$ (see Table 1). Species symbols are coded by plant functional types. Species codes: ARPU, *Aristida purpurea*; BLTR, *Blepharoneuron tricholepis*; CAGE, *Carex geophila*; CHSE, *Chamaesyce serpyllifolia*; CHGR, *Chenopodium graveolens*; DRMO, *Drymaria molluginea*; DRLE, *Drymaria leptophylla*; HECO, *Hesperostipa comata*; IRMI, *Iris missouriensis*; LUAR, *Lupinus argenteus*; MUMO, *Muhlenbergia montana*; MURA, *Muhlenbergia ramulosa*; OXSP, *Oxalis* sp.; OXLA, *Oxytropis lambertii*; PIPO, *Pinus ponderosa*; POOR, *Portulaca oleracea*; QUGA, *Quercus gambelii*.

PLANT STRATEGIES AND LEAF LITTER DECOMPOSITION

Using data measured on 103 species, leaf litter decomposition rate was positively correlated with SLA ($R^2 = 0.07$, $P = 0.0078$), leaf N_{mass} (Fig. 4a, $R^2 = 0.18$, $P < 0.0001$), and leaf P_{mass} ($R^2 = 0.04$, $P = 0.0339$), and was negatively correlated with LDMC (Fig. 4b, $R^2 = 0.22$, $P < 0.0001$). A multiple regression model with LDMC (partial $r^2 = 0.10$, $P < 0.0001$) and leaf N_{mass} (partial $r^2 = 0.07$, $P = 0.0026$) as predictors explained 27% of the variance in decomposition rate (proportion mass loss = $0.34 + \log \text{LeafN} \times 0.29 - \log \text{LDMC} \times 0.31$).

The leaf economics spectrum (i.e. PC1) was significantly positively correlated with decomposition rate (Fig. 4c). The seed mass and root morphology spectrum (i.e. PC2) was not significantly correlated with decomposition rate ($R^2 = 0.04$, $P = 0.053$). The height and phenology spectrum (i.e. PC3) was weakly negatively correlated with litter mass loss (Fig. 4d). A multiple regression model with PC1 (partial $r^2 = 0.18$, $P < 0.0001$) and PC3 (partial $r^2 = 0.08$, $P = 0.0020$) as predictors explained 26% of the variance in leaf litter decomposition rate (proportion mass loss = $0.64 + \text{PC1} \times 0.04 - \text{PC3} \times 0.04$).

Discussion

Westoby's (1998) Leaf-Height-Seed plant ecology strategy scheme was well supported in this multi-trait analysis of 133

species. The three principle strategies were composed of multiple correlated traits, but SLA, seed mass, and height loaded on separate axes. The LHS scheme also accounts for belowground plant function since root traits were correlated with aboveground traits.

The leaf economics spectrum is one important axis of specialization in this flora, and it likely plays a role in controlling productivity, litter decomposition, and N cycling. The leaf economics spectrum represents a fundamental tradeoff between species with traits that confer rapid acquisition of resources and rapid turnover of biomass vs. species that efficiently conserve their slowly acquired resources. This axis reflects a gradient in litter decomposition rate because species with high SLA, low LDMC and high leaf N_{mass} (e.g. *Chenopodium graveolens*, *Oxalis* sp., *Chamaesyce serpyllifolia*) decompose more rapidly than species at the opposite end of the spectrum (e.g., trees, such as *Pinus ponderosa* and *Quercus gambelii*).

Leaf N_{mass} is well known as a predictor of litter decomposition rate (Cornwell *et al.* 2008), but the ability to predict decomposition rates from LDMC is relatively new. Quested *et al.* (2007) found that community-aggregated LDMC was the best predictor of community litter decomposition rates. Our results show that LDMC was negatively correlated with decomposition rate, and that LDMC is an important component of the leaf economics spectrum (Wilson, Thompson & Hodgson 1999). LDMC is likely a good predictor of

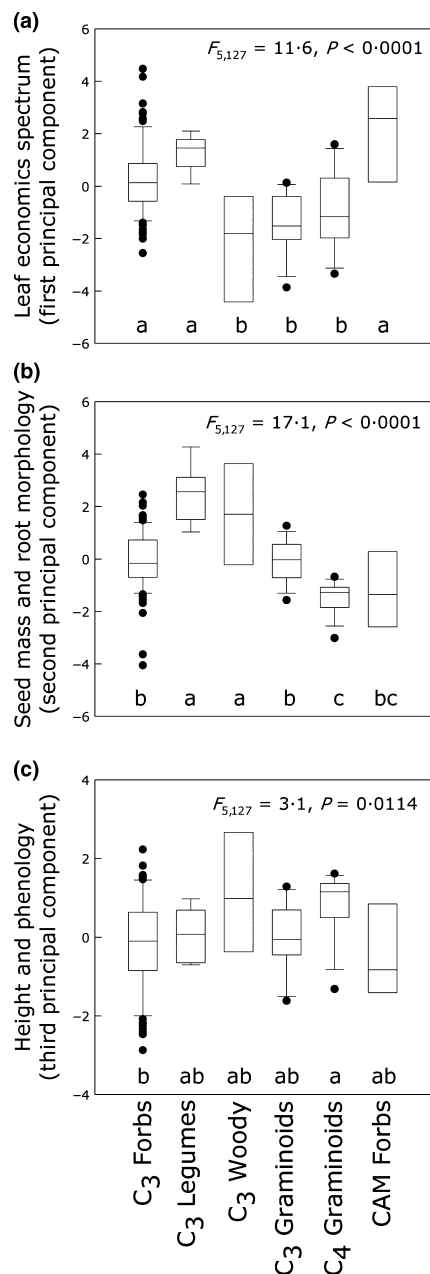


Fig. 2. Box and whisker plots illustrate plant functional type variation along the (a) leaf economics spectrum (PC1), (b) seed mass and SRL spectrum (PC2), and (c) height and phenology spectrum (PC3). The three shrubs and two trees were combined into a 'C₃ woody plants' group for simplicity. Each of the three ANOVA tests were significant ($P < 0.05$), and significantly different pairwise contrasts (Tukey's HSD) are indicated by different lowercase letters.

decomposition rate because it has been shown to be positively correlated with lignin concentration (Kazakou *et al.* 2006), which is slow to break down. Predicting decomposition rate from LDMC alone may be especially useful since LDMC is simpler to measure and less expensive than measuring leaf nutrient concentrations. These results suggest that plant strategies, such as the leaf economics spectrum, can have significant consequences for ecosystem processes, such as carbon and nutrient cycling (Cornwell *et al.* 2008).

There was a clear positive link between leaf N_{mass} and fine root N_{mass} . The positive relationship is one of the few consistent linkages between leaf and root traits (Craine & Lee 2003). Because leaf N_{mass} is known to influence decomposition rates (Cornwell *et al.* 2008), species with rapidly decomposing leaf litter will likely also have rapidly decomposing fine roots. Species with high fine root N_{mass} also have short root lifespans (Kembel *et al.* 2008), and species with high root tissue density also have high LDMC (Wahl & Ryser 2000). These results imply that there is functional coordination between roots and shoots (Grime 1979), but SRL does not reflect this coordination.

The second axis of specialization in this flora reflects a gradient in seed mass and SRL. Variation in seed mass reflects the fundamental tradeoff between seed output and seed size (Henery & Westoby 2001) and between seed size and persistence in the seed bank (Thompson, Band & Hodgson 1993). Annual plants, such as the two *Drymaria* spp., are examples of small-seeded species that produce many seeds that emerge from the soil seed bank each year during the wet season. This axis also represents a gradient from species with high SRL and low seed mass to low SRL and high seed mass. Reich *et al.* (1998) found that seed mass and SRL were also inversely correlated among nine boreal tree species, but the relationship was less pronounced in other studies (Gross, Maruca & Pregitzer 1992; Huante, Rincon & Gavito 1992). Perhaps small-seeded species require high SRL in order to rapidly obtain water and mineral nutrients in the absence of endosperm reserves. Seedlings may have different SRL than adult plants, so this interpretation is somewhat confounded by ontogeny. Several studies have suggested a negative relationship between seed mass and relative growth rate (Hunt & Cornelissen 1997; Reich *et al.* 1998; Wright & Westoby 1999), but the pattern is not universal (Shipley & Peters 1990). Species with high SRL exhibit a root morphology that is conducive to more rapid acquisition of water and mineral nutrients (Lambers, Chapin & Pons 1998), which should allow the species to grow faster in productive environments (Grime *et al.* 1997). If this interpretation is correct, then SRL should have been positively correlated with the leaf economics spectrum. Other studies have shown strong correlations between SRL and SLA (Reich *et al.* 1998; Wright & Westoby 1999) for seedlings grown in pots. However, SRL and tissue N_{mass} were uncorrelated in this study and in another comparative analysis (Tjoelker *et al.* 2005).

What can explain the lack of covariance between SRL and the leaf economics spectrum? SRL is a composite metric of both fine root diameter and tissue density. Species with identical SRL may have different diameters and tissue density, indicating different functional responses to gradients in resources. Unfortunately, data on tissue density is not available for comparison in this study. Furthermore, SRL is but one simple aspect of belowground resource capture and does not take into account total root mass, root-to-shoot ratio, root turnover, distribution of fine roots throughout the soil profile, root architecture, or foraging

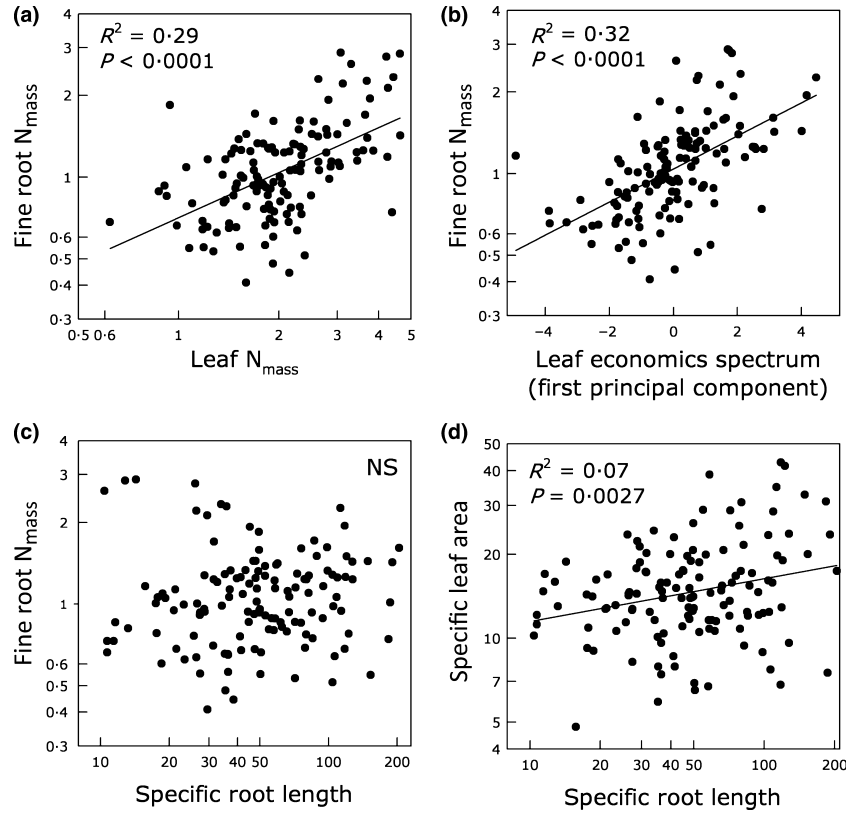


Fig. 3. Simple linear relationships between fine root N_{mass} (%) and (a) leaf N_{mass} (%), (b) the leaf economics spectrum (represented by the first principal component), and (c) specific root length (g m^{-2}), and between (d) specific leaf area ($\text{mm}^2 \text{mg}^{-1}$) and specific root length.

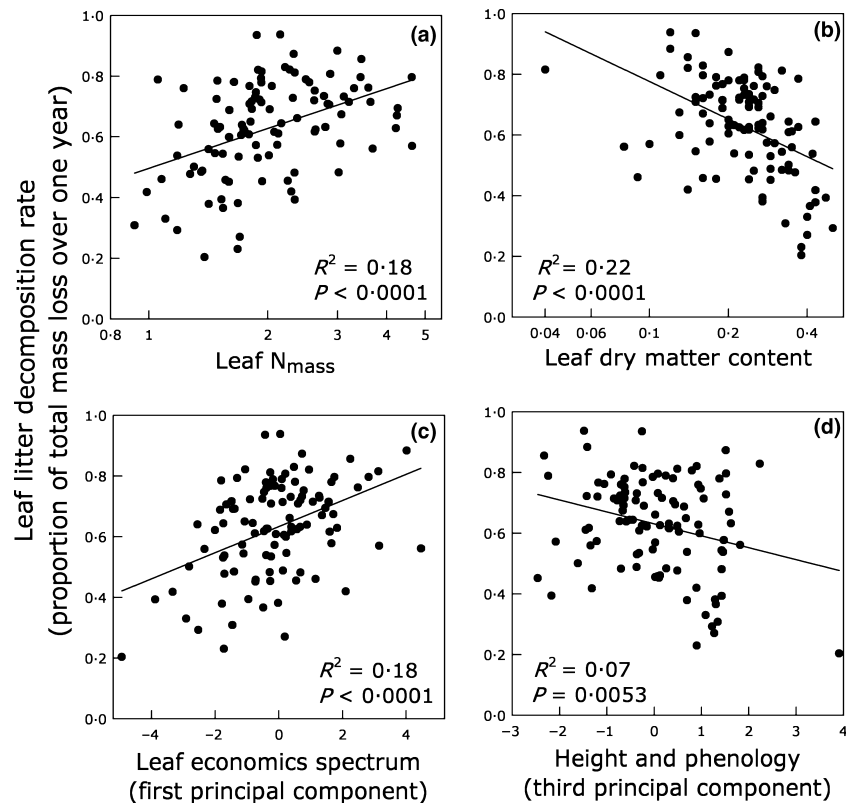


Fig. 4. Simple linear relationships between litter decomposition rate (measured as the proportion of litter mass loss after decomposing in the forest for 1 year) and (a) leaf N_{mass} (%), (b) leaf dry matter content (mg mg^{-1}), (c) the leaf economics spectrum (represented by the first principal component), and (d) the height and phenology spectrum (represented by the third principal component). The outlier in panels b and d represents ponderosa pine, and both relationships were still significant if this species was removed from the regression analysis.

ability into resource-rich soil patches, all of which are important determinants of belowground resource capture (Kembel *et al.* 2008; Hodge 2009). The lack of covariance between SRL and leaf traits does not necessarily mean that

root and leaf function are uncoordinated. Given the methodological problems with measuring SRL (Ryser 2006), other metrics may be better indicators of root function. Root tissue density and nutrient concentration, for exam-

ple, scale positively with leaf traits (Wahl & Ryser 2000; Craine *et al.* 2001).

The third axis represented a gradient from tall plants that flower late in the growing season to short plants that flower early in the growing season. *Pinus ponderosa* is the tallest species in the forest and suppresses understory diversity and productivity (Laughlin *et al.* 2008). Tall herbs, such as *Bahia dissecta*, require the full growing season to attain their maximum height, whereas species like *Noccaea montana* and *Antennaria rosulata* flower early in the season and are short in stature. Height was not completely independent of seed mass because tall species generally had large seeds (Díaz *et al.* 2004). The height axis was negatively correlated with leaf litter decomposition rate perhaps because tall species require more structural material and may have higher leaf lignin content (not measured in this study) than short species.

Plant functional types are important categories used by ecologists to determine how plants respond to perturbations and environmental gradients. Plant functional types accounted for much less than half of the variance in each of the major axes of specialization, and although the mean values within types can differ from each other, there is large overlap in trait ranges. Given this considerable overlap, we concur with Wright *et al.* (2004b), and urge caution when assigning mean trait values to plant functional type categories in vegetation models. Given recent advances in our ability to model continuous trait variation among species (e.g., Garnier *et al.* 2004), future research should evaluate how the functional composition of communities, especially with respect to the leaf-height-seed spectrums, influences ecosystem function.

Plant strategy axes are gradients of multiple correlated traits (Craine 2009). However, leaf traits, seed mass, and height at maturity appear to be fundamental and integrating properties of species that reflect much of the total variation in plant function, including root function (Westoby 1998; Westoby & Wright 2006). Though root morphology could not adequately be predicted from leaf morphology, root tissue chemistry aligned with the leaf economics spectrum (Wahl & Ryser 2000; Kembel *et al.* 2008). The leaf and height axes can be used to predict leaf litter decomposition rate, indicating that plant strategies have important consequences for ecosystem functioning.

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References

Aarssen, L.W. & Jordan, C.Y. (2001) Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Ecoscience*, **8**, 471–477.

- Aerts, R. & Chapin, F.S. III (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**, 1–67.
- Boot, R.G.A. (1989) The significance of size and morphology of root systems for nutrient acquisition and competition. *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants* (eds H. Lambers, M.L. Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Queded, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V. & Westoby, M. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.
- Craine, J.M. (2009) *Resource Strategies of Wild Plants*. Princeton University Press, Princeton, New Jersey, USA.
- Craine, J.M. & Lee, W.G. (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, J.M., Froehle, J., Tilman, D.G., Wedin, D.A. & Chapin, F.S. III (2001) The relationships among leaf and root traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos*, **93**, 274–285.
- Cronquist, A., Holmgren, A.H., Holmgren, N.H., Reveal, J.L. *et al.* (1986+) *Intermountain Flora: Vascular Plants of the Intermountain West, USA*. The New York Botanical Garden, Bronx, New York.
- Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Koshinevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendrmini, 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., Maestromartínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M.R. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.
- Eissenstat, D.M. & Yanai, R.D. (1997) The ecology of root lifespan. *Advances in Ecological Research*, **27**, 1–60.
- Flora of North America Editorial Committee, eds. (1993+) *Flora of North America North of Mexico*. 12 + vols. New York and Oxford.
- Garnier, E., Shipley, B., Roumet, C. & Laurent, G. (2001) A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology*, **15**, 688–695.
- Garnier, E., Cortez, J., Billès, G., Navas, M., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, Chichester.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davidson, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodgkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C. & Whitehouse, J. (1997) Integrated screening validates primary axes of specialization in plants. *Oikos*, **79**, 259–281.
- Gross, K.L., Maruca, D. & Pregitzer, K.S. (1992) Seedling growth and root morphology of plants with different life histories. *New Phytologist*, **120**, 535–542, New York, NY, USA.
- Harmon, M.E., Nadelhoffer, K.J. & Blair, J.M. (1999) Measuring decomposition, nutrient turnover, and stores in plant litter. *Standard Soil Methods for Long-Term Ecological Research* (eds G.P. Robertson, D.C. Coleman,

- C.S. Bledsoe & P. Sollins). pp. 202–240, Oxford University Press, Inc., New York, NY, USA.
- Henery, M.L. & Westoby, M. (2001) Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos*, **92**, 479–490.
- Hodge, A. (2009) Root decisions. *Plant, Cell, and Environment*, **32**, 628–640.
- Huante, P., Rincon, E. & Gavito, M. (1992) Root system analysis of seedlings of seven tree species from a tropical dry forest in Mexico. *Trees*, **6**, 77–82.
- Hunt, R. & Cornelissen, J.H.C. (1997) Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist*, **135**, 395–417.
- Jakobsson, A. & Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, **88**, 494–502.
- Kazakou, E., Vile, D., Shipley, B., Gallet, C. & Garnier, E. (2006) Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old field succession. *Functional Ecology*, **20**, 21–30.
- Keddy, P. & Shipley, B. (1989) Competitive hierarchies in herbaceous plant communities. *Oikos*, **54**, 234–241.
- Kemmel, S.W., de Kroon, H., Cahill, J.F. & Mommer, L. (2008) Improving the scale and precision of hypotheses to explain root foraging ability. *Annals of Botany*, **101**, 1295–1301.
- Kerckhoff, A., Fagan, W.F., Elser, J.J. & Enquist, B.J. (2006) Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *American Naturalist*, **168**, 103–122.
- Kohn, M.J. & Welker, J.M. (2005) On the temperature correlation of $\delta^{18}\text{O}$ in modern precipitation. *Earth and Planetary Science Letters*, **231**, 87–96.
- Lambers, H., Chapin, F.S. III & Pons, T.L. (1998) *Plant Physiological Ecology*. Springer-Verlag New York Inc., New York, NY, USA.
- 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.
- Laughlin, D.C. & Abella, S.R. (2007) Abiotic and biotic factors explain independent gradients of community composition in ponderosa pine forests. *Ecological Modelling*, **205**, 231–240.
- Laughlin, D.C., Bakker, J.D., Daniels, M.L., Moore, M.M., Casey, C.A. & Springer, J.D. (2008) Restoring plant species diversity and community composition in a ponderosa pine-bunchgrass ecosystem. *Plant Ecology*, **197**, 139–151.
- 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.
- McDougall, W.B. (1973) *Seed Plants of Northern Arizona*. Museum of Northern Arizona, Flagstaff, Arizona.
- Moore, M.M., Covington, W.W. & Fulé, P.Z. (1999) Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications*, **9**, 1266–1277.
- Poorter, H. & Remkes, C. (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia*, **83**, 553–559.
- Quested, H., Eriksson, O., Fortunel, C. & Garnier, E. (2007) Plant traits relate to whole-community litter quality and decomposition following land use change. *Functional Ecology*, **21**, 1016–1026.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences*, **94**, 13730–13734.
- Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D.W. & Buschena, C. (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology*, **12**, 327–338.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.
- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleskyn, J., Westoby, M. & Walters, M.B. (2003) The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Science*, **164**(Suppl 3), S143–S164.
- Ryser, P. (2006) The mysterious root length. *Plant and Soil*, **286**, 1–6.
- Shipley, B. & Peters, R.H. (1990) The allometry of seed size and seedling relative growth rate. *Functional Ecology*, **4**, 523–529.
- Thompson, K., Band, S.R. & Hodgson, J.G. (1993) Seed size and shape predict persistence in soil. *Functional Ecology*, **7**, 236–241.
- Tjoelker, M.G., Craine, J.M., Wedin, D., Reich, P.B. & Tilman, D. (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist*, **167**, 493–508.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2008) Let the concept of trait be functional! *Oikos*, **116**, 882–892.
- Wahl, S. & Ryser, P. (2000) Root tissue structure is linked to ecological strategies of grasses. *New Phytologist*, **148**, 459–471.
- Weier, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science*, **10**, 609–620.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby, M., Leishman, M.R. & Lord, J.M. (1996) Comparative ecology of seed size and seed dispersal. *Philosophical Transactions of the Royal Society B*, **351**, 1309–1318.
- Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**, 261–268.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation among species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Wilson, P.J., Thompson, K. & Hodgson, J.G. (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, **143**, 155–162.
- Wright, I.J. & Westoby, M. (1999) Differences in seedling growth behavior among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology*, **87**, 85–97.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.A., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lusk, C., Midgley, J.J., Navas, M., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004a) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I. & Westoby, M. (2004b) Assessing the generality of global leaf trait relationships. *New Phytologist*, **166**, 485–496.

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Supporting Information

Additional Supporting information may be found in the online version of this article.

Table S1. Mean trait values for every trait on all species in the study.

Table S2. Correlation matrix of 10 functional traits used in the PCA.

Table S3. Summary of moments for each trait distribution.

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