

Evidence of the ‘plant economics spectrum’ in a subarctic flora

Grégoire T. Freschet*, Johannes H. C. Cornelissen, Richard S. P. van Logtestijn and Rien Aerts

Department of Systems Ecology, Institute of Ecological Science, Faculty of Earth and Life Sciences, VU University, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

Summary

1. A fundamental trade-off among vascular plants between traits inferring rapid resource acquisition and those leading to conservation of resources has now been accepted broadly, but is based on empirical data with a strong bias towards leaf traits. Here, we test whether interspecific variation in traits of different plant organs obeys this same trade-off and whether within-plant trade-offs are consistent between organs.

2. Thereto, we measured suites of the same chemical and structural traits from the main vegetative organs for a species set representing aquatic, riparian and terrestrial environments including the main vascular higher taxa and growth forms of a subarctic flora. The traits were chosen to have consistent relevance for plant defence and growth across organs and environments: carbon, nitrogen, phosphorus, lignin, dry matter content, pH.

3. Our analysis shows several new trait correlations across leaves, stems and roots and a striking pattern of whole-plant integrative resource economy, leading to tight correspondence between the local leaf economics spectrum and the root ($r = 0.64$), stem ($r = 0.78$) and whole-plant ($r = 0.93$) economics spectra.

4. *Synthesis.* Our findings strongly suggest that plant resource economics is consistent across species’ organs in a subarctic flora. We provide thus the first evidence for a ‘plant economics spectrum’ closely related to the local subarctic ‘leaf economics spectrum’. Extending that concept to other biomes is, however, necessary before any generalization might be made. In a world facing rapid vegetation change, these results nevertheless bear considerable prospects of predicting below-ground plant functions from the above-ground components alone.

Key-words: dry matter content, growth form, nutrient content, phylogeny, plant trait, specific leaf area, terrestrial and aquatic environments, trade-off, vegetative organs

Introduction

Functional traits of plants are nowadays widely accepted as potentially powerful indicators of the ecology of species. They are indeed a consistent tool to determine plant strategies world-wide and allow the synthesis of various empirical data from contrasting areas and environments. Plant ecological strategy schemes (e.g. Grime 1977; Westoby 1998; Díaz *et al.* 2004) classify plants according to meaningful axes of plant specialization. Each of these axes represents a trade-off that limits possible investments of resources to different parts of cells, different tissues and different plant organs. Recent syntheses and reviews have emphasized the existence of one of these axes, which describes a fundamental trade-off among vascular

plants between rapid acquisition and conservation of resources (Grime *et al.* 1997; Reich, Walters & Ellsworth 1997; Díaz *et al.* 2004; Wright *et al.* 2004). Sets of plant functional traits are widely recognized as powerful proxies for this trade-off. Thus, for instance, rapid acquisition of resources is generally correlated with high specific leaf area (SLA), leaf nitrogen (N) and phosphorus (P) content or pH of foliar extracts (a proxy for cation content; see Cornelissen *et al.* 2006), while high leaf dry matter content (DMC), lignin content or carbon (C) to N ratio reflect the resource conservation strategy.

This trade-off, described as the ‘world-wide leaf economics spectrum’ (Wright *et al.* 2004), has so far not been extended to the entire plant. This is due partly to the difficulty of measuring attributes of other plant parts, especially below-ground. Consequently, it is still highly uncertain whether or where traits of other plant components such as stems or roots will fit on this

*Correspondence author. E-mail: gregoire.freschet@falw.vu.nl

axis of specialization. In other words, do all organs of a plant species support either a more resource conservative or acquisitive strategy (e.g. Grime 2001), or is it common to find organs supporting resource conservation and organs supporting acquisition within the same plant species (e.g. Tilman 1982)? To understand how the different plant parts are coordinated along this gradient of traits related to the acquisition or conservation of resources is a high research priority, because variation not only in leaf traits but also in stem and root traits may determine important effects of plant species composition on ecosystem processes and services (De Deyn, Cornelissen & Bardgett 2008; Suding *et al.* 2008). To know whether interspecific variation in leaf traits alone reliably reflects trait variation of other plant organs would thus be a major advance in plant ecology.

To understand the resource economics trade-off at the whole-plant level, several steps still need to be taken. Despite promising advances for stems alone (e.g. Castro-Díez *et al.* 1998; Wright *et al.* 2006; Chave *et al.* 2009) and roots alone (e.g. Ryser & Lambers 1995; Reich *et al.* 1998; Roumet, Urceley & Díaz 2006), the role of integrated interspecific variation in leaf, stem and root traits still needs to be tested comprehensively (Westoby & Wright 2006). So far, few studies have investigated trait covariation between above- and below-ground organs. These have revealed promising, if partly inconsistent, relationships (see Table 1, for an overview). Leaf, stem and root N content were found consistently correlated world-wide (Kerkhoff *et al.* 2006). Mass-based respiration was also correlated between leaves and roots (Tjoelker *et al.* 2005), which is supported by data by Reich *et al.* (2008) who showed a strong link between N and respiration within each vegetative organ. SLA and specific root length were strongly correlated for woody species (Reich *et al.* 1998; Wright & Westoby 1999; Withington *et al.* 2006) but decoupled when the species pools comprised both woody and herbaceous species (correlations derived from Craine *et al.* 2001 and Reich *et al.* 2003a; Tjoelker *et al.* 2005). According to Ryser (2006), the decoupling between specific root length of herbaceous and woody plants may be a consequence of plant size differences, as taller plants need stronger anchorage and more transport capacity. Specific root length might thus not carry precisely the same meaning across plant types and clades in term of resource economics. More generally, tissue density, organ thickness, lignin content or life span were found either poorly or non-correlated between leaves and roots (Table 1; Craine & Lee 2003; Craine *et al.* 2005). These relationships need to be synthesized and extended to traits of plant stems. Exploring the differences in resource allocation between organs is another challenge. Consistency in trait relationships and differential investments between organs should also be tested across different environments, and wider ranges of plant functional types and clades.

While ultimately the application of large world-wide data sets on roots and stems (e.g. Reich *et al.* 2008; Chave *et al.* 2009) is essential for testing this approach, we analyse here a local data set to bring together a wide range of plant species and traits for different plant organs into one theoretical framework. The choice of the local scale, where the resource

economics trade-off is likely to operate most strongly (Wright *et al.* 2004), is appropriate to test for plant organ coordination of interspecific trait patterns. Furthermore, the reasons for the great variation in species traits occurring at local scale are still poorly understood (Ackerly & Cornwell 2007). In world-wide meta-analyses or large-scale studies, disentangling local environmental variations is generally out of reach and only between-site, macro-climatic variations are thus taken into account. Nevertheless, great differences in soil characteristics, microclimate, successional phase and biotic interactions exist at local scales, the link of which to plant functional trait diversity needs to be tested further (Wright *et al.* 2005).

Focusing on plant traits representative of the acquisition–conservation trade-off across species, we here test the hypotheses that (i) interspecific trait variation of non-leaf plant organs is correlated with that of leaf traits across environments, clades and plant types; (ii) trait values for leaves, stems and roots of the same species generally occupy the same position on the acquisition–conservation trade-off axis; (iii) local environmental features explain a significant part of the variance in plant functional trait variations; and that (iv) the 'leaf economics spectrum' is an adequate predictor of the 'plant economics spectrum' as defined by whole-plant trait coordination.

We addressed these hypotheses by measuring suites of similar plant traits from the main vegetative organs, i.e. leaves, stems and roots, for a subarctic flora representing the key species from aquatic, riparian and terrestrial environments and covering the main vascular higher taxa and growth forms in this region.

Materials and methods

STUDY AREA, SPECIES TYPES AND SAMPLING

The study was carried out around the Abisko Research Station, North Sweden (68°21' N, 18°49' E), at low altitude (350–400 m a.s.l.), below the tree line. Climatic data from the recent decade (1999–2008) showed a mean annual rainfall of 352 mm and mean January and July temperatures of –9.7 and 12.3 °C, respectively, with temperatures ranging from –39.0 to 21.3 °C (meteorological data, Abisko Research Station). The forested area, which was the focus of this study, features Podsol soils (Sjögersten & Wookey 2002) and covers most of the landscape below 700–800 m a.s.l. except for occasional swamps and peatlands. The three most distinct ecosystem types within the chosen forested sites were: upland dry birch forest, riparian birch forest and forested freshwater systems (ponds and streams). Seven sampling sites (*c.* 20-m transects) each including all three ecosystem types were used to identify the dominant species (roughly 80–90% of total vascular plant biomass) of each of the ecosystems (see Cornelissen *et al.* 2003). These included 15 species from the dry forest, 18 from the riparian forest and 7 from aquatic systems (see Table S1 in Supporting Information for the species list and characteristics; or the TRY online data base <http://www.try-db.org> for trait data). When present in two or more ecosystem types, species were sampled only from the ecosystem where they occurred most abundantly. Within each ecosystem type, species were collected from the sampling site where they were the most abundant. Species were identified according to Mossberg, Stenberg & Ericsson (1992). Among these species, seven groups of plant types (woody evergreens (4),

Table 1. Overview of multi-species studies investigating similar plant traits across leaves, stems and roots

Source	Trait	Leaves versus stems			Leaves versus roots			Stems versus roots			Clades	Plant types
		<i>r</i>	<i>P</i> -value	No. species	<i>R</i> , <i>r</i> or ρ^*	<i>P</i> -value	No. species	<i>r</i>	<i>P</i> -value	No. species		
Correlations explicitly inquired in previous studies												
Reich <i>et al.</i> (1998)	SLA versus SRL			202	0.78	< 0.05	9				Core eudicot Gymnosperm Core eudicot Monocot	Woody deciduous Woody evergreen Woody deciduous Graminoid
Wright & Westoby (1999)	SLA versus SRL			33	0.73	< 0.001	33					
Craine & Lee (2003)	Nitrogen			24	0.55	< 0.001	24					
	Tissue density			24	0.29	< 0.001	24					
Craine <i>et al.</i> (2005)	Nitrogen			90	0.57	< 0.001	90					
	Thickness			90	NA	NS (0.97)	90					
	Tissue density			90	NA	NS (0.49)	90					
	Lignin			90	NA	NS (0.65)	90					
	Soluble fraction			90	NA	NS (0.97)	90					
Tjoelker <i>et al.</i> (2005)	Nitrogen			31	0.77	< 0.001	31				Monocot	Graminoid
	C/N			31	0.70*	< 0.001	31					
	SLA versus SRL			33	0.12*	NS (0.50)	33				Monocot Core eudicot	Graminoid Forb Woody deciduous
	R _{mass}			31	0.53*	0.002	31					
	Life span			14	0.50*	NS (0.07)	14					
Kerkhoff <i>et al.</i> (2006)	Nitrogen	0.69	< 0.05	202	0.62	< 0.05	173	0.84	< 0.05	146	Monocot	Graminoid Forb
	Phosphorus	0.62	< 0.05	176	0.69	< 0.05	123	0.72	< 0.05	96	Basal eudicot	Woody deciduous
	N/P	0.66	< 0.05	149	0.59	< 0.05	117	0.61	< 0.05	91	Gymnosperm Magnoliid	Woody evergreen
Withington <i>et al.</i> (2006)	SLA versus SRL			11	0.77	< 0.05	11				Core eudicot	Woody deciduous
	Life span			11	-0.12	NS (0.73)	11				Gymnosperm	Woody evergreen
Correlations derived from published studies with available data sets												
Craine <i>et al.</i> (2001)	SLA versus SRL			76	0.15	NS (0.21)	76				Monocot	Graminoid
	Tissue density			76	0.02	NS (0.86)	76				Core eudicot	Forb
Reich <i>et al.</i> (2003a)	SLA versus SRL			30	-0.11	NS (0.56)	30				Monocot Core eudicot	Graminoid Forb Woody deciduous

SLA, specific leaf area; SRL, specific root length; R_{mass}, mass-based respirator; NA, non-available data.

The goodness of relationships were found in the literature either as linear regression coefficient (*R*), Pearson's correlation coefficient (*r*), or Spearman's correlation coefficient (ρ), the latter being notified by an asterisk. *P* is significance of the relationship.

woody deciduous (12), fern allies (3), club mosses (1), graminoids (4), terrestrial forbs (12) and aquatic forbs (4)) and six clades (core eudicots (26), basal eudicots (2), monocots (6), gymnosperms (2), pteridophytes (3) and lycophytes (1)) were identified following the APG II (2003) classification. Each species was sampled for living leaves, fine stems (< 3 mm diameter) and fine roots (< 2 mm diameter). To ensure a fair comparison of root types in terms of structure and function, only the finest root branch order visible to the naked eye was considered for each species. Similarly, twigs of woody species (< 3 mm diameter) were thought more closely related to stems of forbs and herbs in terms of function and physiological activity. In total, 40 species were sampled for leaves, 39 for stems and 36 for fine roots. Leaves, stems and roots were sampled from distinct individuals. A minimum of 10 different plant individuals (up to 50 for some species) were used for each species and organ to ensure the representativeness of the pool collected. For each organ, one part of the collection was placed in a paper bag and air-dried for the purpose of chemical analyses while the other was immediately placed in a closed plastic bag to be analysed for DMC – and SLA for leaves – within 5 h (see Cornelissen *et al.* 2003, for more details). For root sampling, plant individuals were excavated and brought to the laboratory. Soil and alien material were washed off the root system before living and undamaged roots were collected. Large mycorrhizal rhizomorphs were brushed off the roots. For all organs, parts with obvious symptoms of damage, infection or herbivore activity were avoided. Petioles and rachides were included as part of the leaf. To avoid effects of seasonal variation, all leaves were collected while fully mature and before the onset of senescence (see Quedest *et al.* 2003), i.e. between 28 July and 3 August 2008. Accordingly, stems were all sampled between 4 and 10 August 2008. Roots were collected partly in August 2007 and partly in August 2008 owing to the labour-intensive process involved.

PLANT TRAIT MEASUREMENTS

All collected plant material was measured for C, N, P and lignin content. For that purpose, air-dried subsamples of each material were ground and subsequently oven-dried for 24 h at 60 °C. Carbon and N concentrations were measured by dry combustion on a NA 1500 elemental analyser (Carlo Erba, Rodana, Italy). For P, 50 mg of sample was digested in 1 mL of a 1 : 4 mixture of 37% (v/v) HCl and 65% (v/v) HNO₃ in a closed Teflon cylinder for 6 h at 140 °C. Samples were then diluted with 4 mL demineralized water and total P concentration was quantified by spectrophotometry, using the ammonium molybdate method (Murphy & Riley 1962). Lignin concentration was determined as described in Poorter & Villar (1997). Briefly, the ground material underwent several polar (water, methanol) and non-polar (chloroform) extraction steps, to extract soluble sugars, soluble phenols and lipids. Acid hydrolysis removed starch, fructan, pectin and part of the hemi-cellulose. Apart from some recalcitrant hemi-cellulose, proteins and possibly silicates, the residue should contain almost only lignin and cellulose. The mass of the residue, corrected for ash content (including silicates), and its C and N concentrations, were measured. The lignin concentration was thus calculated based on the difference in C content of lignin and cellulose, after correction for remaining proteins.

Each sample was also measured for pH by shaking 0.15 mL ground sample with 1.2 mL demineralized water in an Eppendorf tube for 1 h at 250 rpm. After centrifugation at 9000 × *g* for 5 min, pH of the supernatant solution was measured.

For DMC the samples (10–50 pooled leaves per species, 10–20 stems and 10–50 fine roots) were immersed in tap water overnight (leaves, fine roots and non-ligneous stems) or for 3 days

(woody stems), then wiped gently and measured for their water-saturated weight. Subsequently dry weight was measured after drying for 48 or 72 h (woody stems) at 60 °C. DMC was expressed as the ratio between dry weight (mg) and water-saturated weight (g).

For SLA measurements, 10 random fresh leaves per species were scanned individually using an Area Meter (Delta-T; Burwell, Cambridge, UK), then oven-dried (60 °C, 48 h) and weighed separately. SLA of each leaf was then expressed as the ratio between leaf area (m²) and leaf dry mass (kg). The mean of all 10 ratios was used as species SLA.

ENVIRONMENTAL VARIABLES

Three distinct environments, upland dry birch forest, riparian birch forest and forested freshwater system were measured for soil C and N and soil litter temperature and humidity during the growing season. Soil litter temperature and humidity were measured from mid-May to mid-September with one automatic data logger (Hobo Weather Station, Onset Computer Corporation, Cape Cod, MA, USA) per environment. Temperature (°C) of the litter was measured with four probes per station and four probes were used in terrestrial and riparian environments to measure litter water content (m³ water m⁻³ litter). Probes for water content (Hobo Soil Moisture Smart Sensor) were calibrated for each litter substrate at the start of the experiment. Aquatic environments were assumed to have litter water content of 1 m³ m⁻³. For soil nutrient measurement, 12 soil samples were taken randomly from the 0–10 cm soil layer of each ecosystem using a metal corer. Coarse litter was brushed off the soil gently prior to sampling. The 12 samples were pooled, dried at air temperature and homogenized. Living roots and gravel were extracted manually, weighed and discarded. Remaining samples were weighed and a subsample per environment was then ground and subsequently used for C and N analyses following the same methods as for plant material (see above). The weight percentages of gravel were then used to correct total average soil C and N content (%) of each environment.

DATA ANALYSIS

For each trait, cross-species Pearson's correlations were performed between the different plant parts. Some data (leaf C:N and P; stem DMC, N and P; root N, C:N and P) needed log transformation to correct for deviations from normality. Biplots of leaf–stem and leaf–root relationships were constructed for DMC, lignin, pH and N. Linear regressions were used to provide the slopes of the linear relationships. For N, leaf–stem and leaf–root relationships were slightly improved by using logarithmic transformations on stem N and root N; nevertheless, slopes of linear regression were still provided for additional information. Linear regressions were used to display regression lines of each separate environment. Due to the small number of observations for several clades and plant types, we could not test the influence of each clade and plant type on regression slopes in a robust way. We were, however, able to test for environment influence (≥ 5 observations per group) with standardized major axis (SMA) tests using SMATR freeware (Warton *et al.* 2006). Principal component analyses (PCA) were performed with the total plant trait set (19 traits), leaf traits only, stem traits only, root traits only and stem-plus-root traits pooled. Because of the generally high proportions of variance explained by the first PCA axis, these scores were used in all subsequent analyses as a proxy for the whole plant or plant organ economics. To test for significant differences between groups of species, ANOVAS were carried out – followed by *post hoc* multiple

pairwise comparisons (Tukey's test) – on the species scores on the first PCA axis for the complete plant trait set, with either plant environment, plant type or plant clade as qualitative variable. Linear regressions were used to test the predictive value of environmental variables (soil C, N and C:N, soil litter temperature and water content) on the whole-plant PCA first-axis species scores. Finally, Pearson's correlations were performed between the species scores on each pair of first axes derived from the PCAs for the different organs. This allowed us to test the degree of association of the spectrum for each different plant organ with the whole-plant spectrum and those of each of the other organs.

Results

When comparing plant functional traits of different vegetative organs – leaves, stems and roots – across multiple subarctic species representing a broad spectrum of vascular plant taxa, growth forms and habitats, significant positive correlations were found in most cases (Table 2). Lignin and C content, DMC and C:N all showed robust significant correlations between the different plant parts. Significant correlations were also found for N and pH between leaves and stems and leaves and roots, but stem and root N and pH did not show significant correlations. Phosphorus content did not display any particular pattern.

As seen in Fig. 1 for a subset of traits, all – significant – relationships were linear except for leaf–stem N and leaf–root N (slightly exponential). Slopes of linear regressions were, however, not always close to 1, revealing different structural and chemical allocations across organs. Thus, DMC displayed a narrower range of variation and was generally lower in roots than in leaves and stems. Lignin content of roots and stems was similar but higher than in leaves. Leaf pH reached lower values in leaves than in stems and roots. Nitrogen content was highest in leaves, intermediate in roots and lowest in stems. Visual inspection showed no phylogenetic or plant type (Figs S1 and S2, respectively) group clustering away from the general regression lines, whichever trait or organ relationship was considered. In other words, although a few outliers were observed, no plant type or clade seemed to consistently offset either slope or intercept of organ trait relationships. Standardized major axis tests on environments (Fig. 1) demonstrated

also that terrestrial, riparian and aquatic groups of species did not display any significant difference in slope or intercept for any trait. All clades, plant types and environments fitted thus consistently in the emerging patterns of trait covariation among organs.

The first PCA axis based on 19 traits from all vegetative plant parts accounted for 43% of overall variation, as against only 12% for axis 2 (Fig. 2). All plant traits, except P content of the different plant parts, contributed substantially to the first axis. With increasing scores on the first PCA axis, variables representative of the resource acquisitive strategy, i.e. SLA, N content and pH, decreased while variables representative of plant nutrient conservation strategy, i.e. DMC, lignin content and C:N, increased. Consistent with this plant strategy axis, all terrestrial species – except *Cornus suecica*, *Deschampsia flexuosa* and *Equisetum sylvaticum* – were clustered on the nutrient-conservative side of the spectrum; all aquatic species were grouped at the far end of the acquisitive side of the spectrum; and riparian species were spread in-between these two extremes (Fig. 2A). Pairwise comparison of the first-axis species scores for the plant environment variable confirmed this ($P < 0.001$ for terrestrial versus riparian and $P < 0.002$ for riparian versus aquatic). Environmental variables representative of soil organic matter quantity (C, $R^2 = 0.55$, $P < 0.0001$), quality (N, $R^2 = 0.53$, $P < 0.0001$; C:N, $R^2 = 0.37$, $P < 0.0001$) and mineralization rate (average humidity and temperature of the soil litter layer during growing season, $R^2 = 0.52$ and 0.34 , respectively, $P < 0.0001$ and $P = 0.0003$, respectively) were significant predictors of the plant PCA first-axis scores (see Fig. 3, for N and litter moisture regressions). The more fertile the environment was (high soil N, litter temperature and moisture; low C:N ratio), the more negative the PCA first-axis scores were, i.e. the more nutrient acquisitive the species strategies. The different plant-type groups were ranked from woody evergreens to aquatic forbs (Fig. 2B). Woody evergreens and woody deciduous were significantly different from all other groups except club mosses ($P = 0.31$ and $P = 0.99$, respectively). Aquatic forbs were significantly different from all other groups except fern allies ($P = 0.48$). Fern allies, forbs, graminoids and club mosses, occupying a

Table 2. Pearson correlations (r) of species traits across plant parts

	Leaves versus stems ($n = 39$)		Leaves versus roots ($n = 36$)		Stems versus roots ($n = 35$)	
	r	P -value	r	P -value	r	P -value
Carbon (%)	0.81	<0.0001	0.66	<0.0001	0.84	<0.0001
Lignin (%)	0.69	<0.0001	0.70	<0.0001	0.82	<0.0001
DMC (mg g ⁻¹)	0.85	<0.0001	0.48	0.003	0.68	<0.0001
C/N	0.59	<0.0001	0.45	0.005	0.41	0.014
pH	0.66	<0.0001	0.61	<0.0001	0.27	NS (0.12)
Nitrogen (%)	0.47	<0.002	0.35	0.035	0.28	NS (0.11)
Phosphorus (%)	0.21	NS (0.20)	-0.14	NS (0.43)	0.22	NS (0.21)

r is Pearson's correlation coefficient; P is significance of the correlation, with NS (non-significant P); n is the number of species.

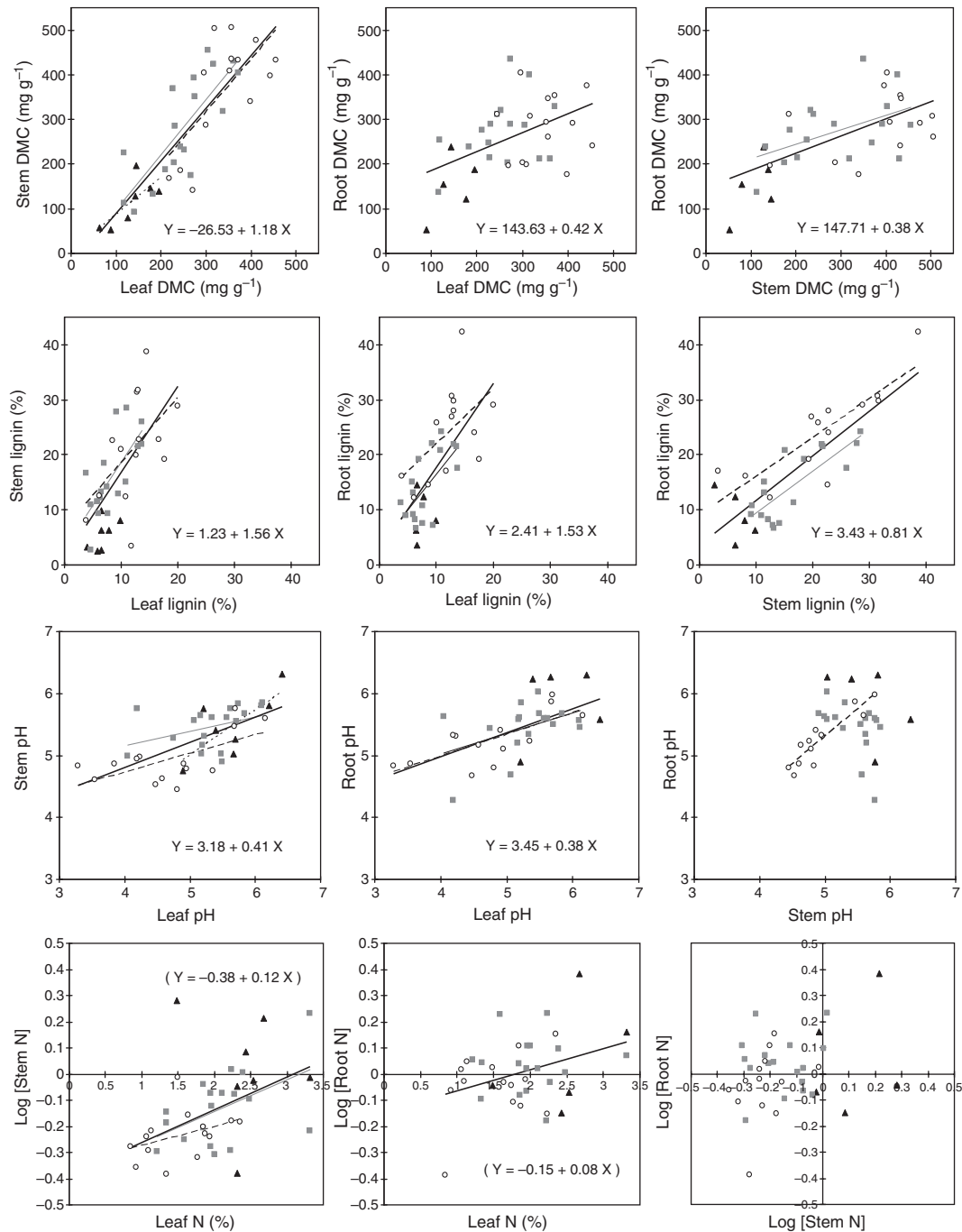


Fig. 1. Biplots of leaf, stem and root trait relationships. Type I regression lines are shown for the total species pool (—) along with the regression equations, and for each environment, terrestrial (---), riparian (— · —) and aquatic (· · ·), when significant. Species are distinguished according to their environment: ○ Terrestrial; ■ Riparian; ▲ Aquatic. Distributions of higher taxa and plant types are available in Figs S1 and S2, respectively.

central position on the spectrum, were not significantly different from each other. As for phylogenetic groups (Fig. 2C), only gymnosperms showed a significant difference from the other groups except for lycophytes ($P = 0.73$).

Similarly to the whole-plant PCA, organ PCAs all displayed highly informative first axes (47%, 57% and 54% of overall variation explained for root, stem and leaf PCA, respectively), whereas second axes were not consistent (Table S2). Despite different contributions of variables to the root, stem and leaf

first PCA axes, a common pattern of organ economy emerged along all three axes. All three organs showed a similar pattern with variables representative of the resource acquisitive strategy at one end of first PCA axis and variables representative of the resource conservative strategy at the other. Pearson's correlations between species first-axis scores of plant trait-based PCA (leaf, stem and root traits pooled) versus PCAs based on leaf, stem and root traits, separately, displayed high correlation coefficients (r) of 0.93, 0.92 and 0.79, respectively, with

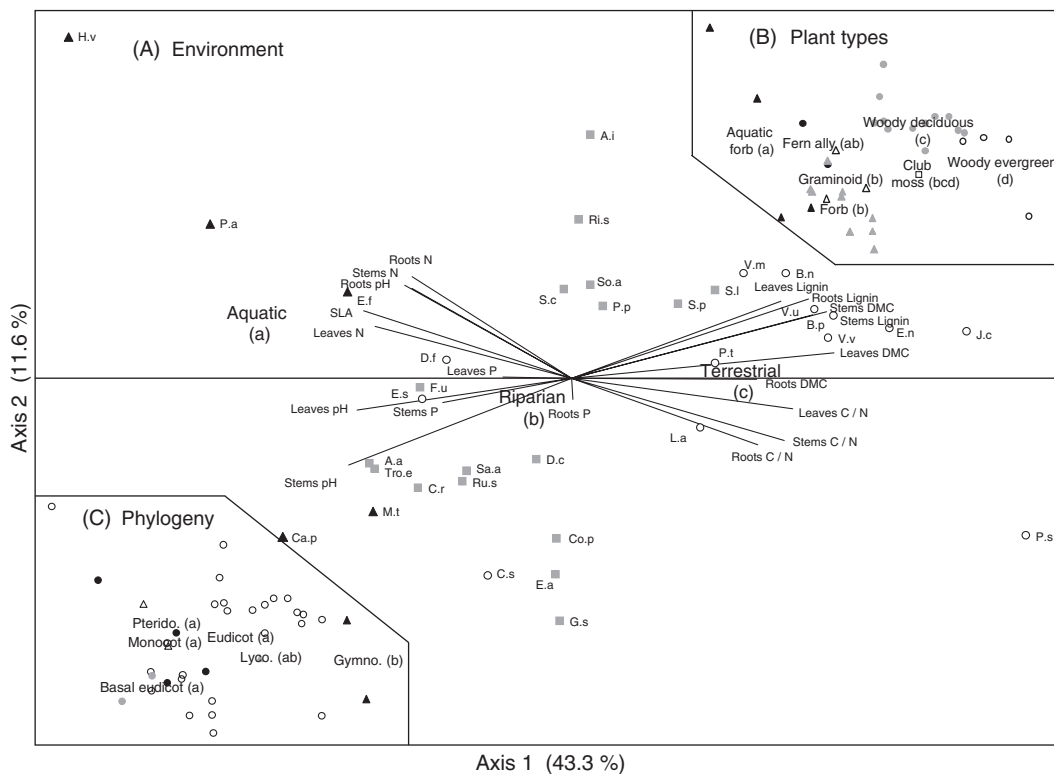


Fig. 2. The plant economics spectrum, from fast-growing (left) to nutrient-conservative (right) species. Variables (plant traits) used for the PCA are displayed with their vector. The plant economics spectrum is represented as a straight horizontal line (axis 1). Species name abbreviations are provided next to their position on the graph; see Table S1, for details of the abbreviations. (A), (B) and (C) are three representations of the same PCA with different grouping of species (i.e. supplementary qualitative variables). Centroids of each species group – plant environment in (A), plant type in (B) and plant phylogeny in (C) – are displayed with an index of their statistical difference (a, b, c, d, ...; result of pairwise comparisons of axis 1 species scores). Symbols: (A) ▲ Aquatic; ■ Riparian; ○ Terrestrial; (B) ▲ Aquatic forb; △ Graminoid; ▲ Forb; ● Fern ally; □ Club moss; ● Woody deciduous; ○ Woody evergreen; (C) ● Basal eudicot; ● Monocot; △ Pteridophyte; ○ Core eudicot; ▲ Lycophyte; ▲ Gymnosperm.

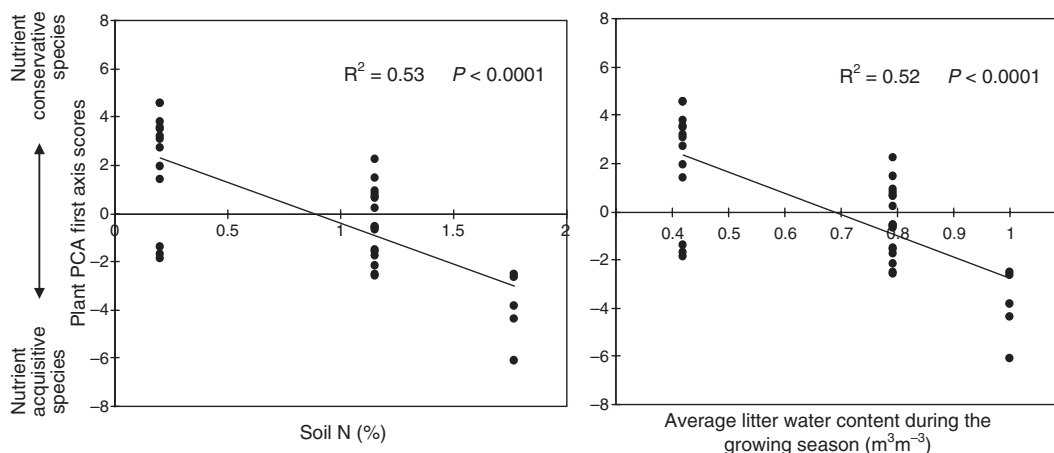


Fig. 3. Linear regressions between environmental variables and the species economic strategies.

$P < 0.0001$ (data not shown). Correspondingly, Pearson’s correlations performed between species first-axis scores of leaf trait-based PCA versus stem-plus-root trait PCA (Fig. 4d), leaves versus stems (Fig. 4a), leaves versus roots (Fig. 4b) and stems versus roots (Fig. 4c) displayed relatively strong correlations as well (r of 0.81, 0.78, 0.64 and 0.63, respectively, with $P < 0.0001$).

Discussion

THE LINK BETWEEN PLANT ORGAN ECONOMICS AND THE CHOSEN TRAITS

The traits involved in this study were chosen to represent the trade-off between fast acquisition and conservation of

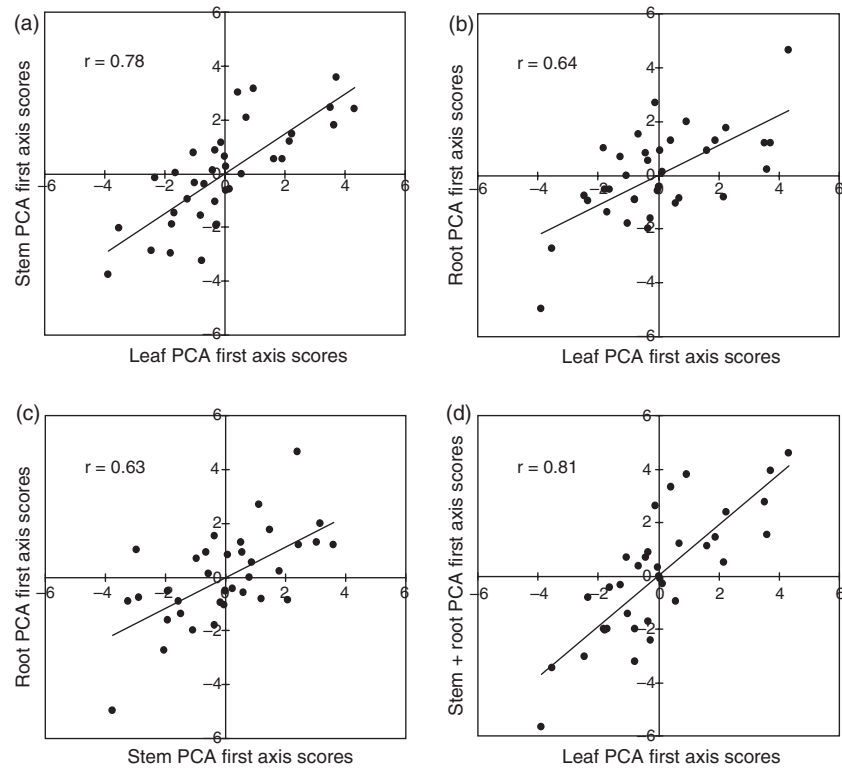


Fig. 4. Correlations between economics spectra, as indicated by PCA first axis score, of different plant parts.

resources. They are, however, not exhaustive. To get a more comprehensive picture, other important traits representative of growth rate or nutrient uptake could have been used such as respiration rate, tissue life span, specific root length, tissue density or type of mycorrhizal association. The chosen traits, focusing on structural and chemical investments, are nevertheless fairly representative of these plant traits and functions. For instance, N content relates to respiration (Reich *et al.* 2008) and to mycorrhizal type (Cornelissen *et al.* 2001), while DMC is representative of tissue density (Wahl & Ryser 2000), life span and growth rate (Cornelissen, Diez & Hunt 1996; Ryser 1996; Wright & Cannon 2001). Lignin is inversely correlated with digestibility (Cornelissen *et al.* 2004). Phosphorus and pH, representative of plant nutrient content, are part of leaf growth and defence strategy (Wright *et al.* 2004; Cornelissen *et al.* 2006). While clearly established for leaf economics, the link between these traits and the root and stem functions has, however, not yet been clearly demonstrated and remains partly speculative. As a result of this coordinated choice of traits, all traits involved in this study are highly inter-correlated, except P content (Fig. 2). This is surprising, as leaf and root P contents usually covary with other nutrients (Thompson *et al.* 1997; Gordon & Jackson 2000), notably N. Moreover, leaf P, which tends to covary with plant relative growth rate (e.g. Kazakou *et al.* 2006), is supposed to reflect plant life strategy (Thompson *et al.* 1997). In the present work, leaf, stem and root P contents hardly contribute to the plant resource economics axis. We hypothesize that in some other ecosystems of the world, with strong phosphorus limitation of biological processes, e.g. certain (sub)tropical, temperate and boreal forests, wetlands and drylands (see Wardle, Walker & Bardgett 2004;

Wassen *et al.* 2005; Lambers *et al.* 2008), P contents of the different organs will correspond more closely to this axis.

Independent of the plant part considered, nutrient content variables – here N and pH (i.e. cation content) – are inversely correlated with structural variables – DMC, lignin, C:N – confirming at the whole-plant level a pattern well-established at leaf level (e.g. Cornelissen *et al.* 2004; Garnier *et al.* 2004). Evidence is accumulating that such patterns of trait correlations represent evolutionary and/or biophysical constraints on leaf structure and function (Reich *et al.* 2003b). The present results provide strong evidence that interspecific variation in this suite of traits is consistent not only at the level of individual plant organs but also at the whole-plant level.

TIGHT ACROSS-SPECIES COORDINATION BETWEEN LEAF, STEM AND ROOT TRAITS, ACROSS ENVIRONMENTS, CLADES AND PLANT TYPES

Finding strategic dimensions of trait variation and correlation is a predominant goal of functional ecology. At present, the relationship between root and shoot traits is still poorly understood and, for many traits, inconsistent (see Table 1 but also Wright *et al.* 2006). The cross-species positive correlations found in this study between the three main plant parts, leaves, stems and roots, for any particular trait, are generally good. Interestingly, traits representative of structural investment, such as DMC, C and lignin contents, are more strongly correlated across organs than mineral nutrient traits such as pH, N or P. This contrasts with the world-wide correlations found by Kerkhoff *et al.* (2006) for N and P across all organs and indicates that regional differences exist with respect to those

relationships. The present results indicate that strong correlations exist also for structural traits, seemingly independent of phylogenetic or plant-type constraints. However, inconsistent results found in the literature for the same structural traits imply that these relationships are influenced by spatial scale or geographical area of study. Further empirical data and meta-analysis are still much needed to settle this issue. Kerkhoff *et al.* (2006) showed that both the contingencies of evolutionary history and some degree of environmental convergence have led to a common set of rules that constrain the partitioning of N and P among plant organs. Similarly, we found here that, while a trade-off in plant resource investment may exist across plant organs within individual vascular plants, it is constrained within a rather narrow range of variation, especially in terms of structural investments.

As demonstrated by the differences between slopes of leaf–stem and leaf–root correlations (not always equal to 1; Fig. 1), this goes in conjunction with a differential investment between organs. With regard to the intercepts (rather close to zero, except for pH), this pattern of investment is, however, fairly similar between leaves and stems across all species studied here, whichever environment, plant type or clade they belong to. Conversely, the much larger values of intercepts found for leaf–root correlations imply differential investments across species, in relation to their position on the nutrient acquisition–conservation trade-off. We hypothesize that internal physiological, ontogenetic and allometric constraints may be responsible for the reduced range of differential investment between leaves and stems (see also Niklas 1999; Wright *et al.* 2006) and for the consistent differential investments between leaves and roots.

Although the small aquatic data set limits its scope, it is nevertheless striking to see that aquatic plants seem to fall into the same pattern of trait coordination among organs as terrestrial ones. With regard to the contrasted habitats and abiotic conditions faced by aquatic and terrestrial species, one would expect major differences between their respective organs in terms of roles and adaptations (Niklas 1992) and therefore trade-offs. Physical properties of fluids enveloping organisms profoundly influence every biological function. For instance, terrestrial plant organs suffer desiccation, as opposed to aquatic ones. Aquatic stems and leaves face much stronger forces than terrestrial organs when exposed to the same fluid flow due to the respective viscosities of water and air. Aquatic and terrestrial stems, whose main function is plant support in both cases, obey furthermore different constraints, the former adapting to pulling forces by a tensile body while the latter adapt to downward gravity forces by a compressive body. Besides, the main function of aquatic roots may be less related to nutrient uptake than to anchorage and they may thus take a different form compared to terrestrial roots. Although all these (among many other) shifts in environmental constraints affect plant organ forms and functions, they do not seem to affect dramatically the trait coordination between the different organs. Part of the answer may lie in the similar paths taken by all plant organs to adapt to their environment. In this regard, all

organs of aquatic species need lower structural investments and, along with that, higher nutrient contents than their terrestrial counterparts.

EVIDENCE OF A 'PLANT ECONOMICS SPECTRUM'

We identified in the first PCA axis for all organs (Fig. 2), a coherent 'plant economics spectrum' that is the result of multiple covarying leaf, stem and root traits around which the species cluster. This axis of specialization is, however, built mostly out of plant vegetative organ structural and chemical investment variables and represents therefore only a partial picture of the plants' resource economics. With respect to stems and roots, more confident interpretation of the data would require further assessment of the linkages between the present traits and plant economics. This spectrum is nevertheless fully consistent with the current knowledge on the influence of environment on plant traits and life strategies (e.g. Diaz, Cabido & Casanoves 1998; Hendricks *et al.* 2000; Ackerly & Cornwell 2007). Plant-type clustering (Fig. 2B) along this spectrum is also concordant with the literature (e.g. Diaz & Cabido 1997; Grime *et al.* 1997; Diaz *et al.* 2004 for the nutrient acquisitive character of aquatic plants), confirming further the link with well-established plant strategy schemes. The novelty of our approach comes from the rigorous characterization of the *same* traits across *all* vegetative organs, thus allowing a consistent comparison of interspecific trait variation between plant organs. Some non-leaf traits, mostly allometric and regenerative traits, have previously been integrated into well-known strategy schemes (e.g. Grime *et al.* 1997; Westoby 1998; Craine *et al.* 2001; Ackerly 2004; Díaz *et al.* 2004), and leaf traits were found to be the strongest representatives of the resource acquisition–conservation axis. Conversely, leaf, stem and root traits merged here into one 'plant economics spectrum'.

Since literature on the relevance of plant traits across the terrestrial–aquatic boundary is still scarce, some caution is necessary concerning the position of aquatic plants on this spectrum. Some evidence exists nevertheless with regard to the positive role of lignin and C:N ratio on herbivory defence (Hanley *et al.* 2007) and the positive correlation of N and P with plant growth rate (Nielsen *et al.* 1996). Other traits such as density might, however, be needed to complete the picture, since the chosen traits do not reflect adaptations such as the presence of internal gas spaces, which have an important role in oxygen and carbon dioxide diffusion (Sorrell & Dromgoole 1989; Raven 1996) and thereby plant growth.

LOCAL ENVIRONMENTAL FEATURES PLAY A PIVOTAL ROLE IN EXPLAINING PLANT FUNCTIONAL TRAIT VARIATION

This study emphasizes the importance of local environmental variation as a driver of functional trait diversity. In line with Wright *et al.* (2004), we found great variation in species traits at the local scale. Besides, surrogates for environmental variables such as soil organic matter quantity (C), quality (N, C:N)

and mineralization rate (litter temperature and moisture) during the growing season are good predictors of species economics, as defined by their scores on the plant economics axis. Below-ground and above-ground systems are under strong mutual influence through complex feedbacks between plant community composition and soil fertility (Aerts 1999; Wardle *et al.* 2004). The link identified here between plant traits and ecosystem properties is a direct consequence of those strong interactions. It reinforces the idea that plant traits can be used to capture ecosystem properties (e.g. Chapin *et al.* 1996; Garnier *et al.* 2004). The spatial changes occurring within and across environments can thus potentially explain a large part of the local plant species and plant trait diversity. The fact that groups of dominant species sorted by environmental features, all found within 20-m transects, are very significantly different from each other and show little overlap (Fig. 2A) also supports that claim. Microenvironmental variation is in general mostly driven not only by heterogeneity in microtopography and consequent surface hydrology, but also by local heterogeneity in soil depth, biotic factors and successional time (e.g. Grime 2001). These results suggest that this microvariation might be the missing key to our understanding of the tremendous functional diversity generally found at the local scale (see also Cornwell & Ackerly 2009).

CONCLUSION: EVIDENCE OF A STRONG LINK BETWEEN THE 'LEAF ECONOMICS SPECTRUM' AND THE 'PLANT ECONOMICS SPECTRUM' AT HIGHER LATITUDES

Looking for consistency of species ranking between the spectra for the different plant organs, we have unravelled promising relationships, the most closely coordinated organs being leaves and stems, while roots exhibit a slightly less tight but still coordinated pattern. The similarity of the species ranking for all three plant parts in multivariate space (Fig. 4a–c) supports our hypothesis that leaves, stems and roots occur at the same position on the resource acquisition versus conservation trade-off. This similarity is based on the strong coherence between plant traits of the different organs, across clades, plant types or plant environments represented in this study. Moreover, the wide spread of eudicots and monocots along the plant economics spectrum demonstrates the spectrum's overall existence not only between but also within large clades. The non-coordinated part of the trait variation between leaves and roots (see Table 1; Fig. 4b) and stem and roots (Fig. 4c) might stem not only from the somewhat different meanings plant traits carry depending on the environmental context but also across plant types and clades (Ryser 2006; Lusk *et al.* 2008). The subarctic leaf economics spectrum is representative of the rest of the plant (stem and root PCA, Fig. 4d) and reflects remarkably well the plant economics spectrum (leaf, stem and root PCA, $r = 0.93$; data not shown). These findings support the view that evolution works on the entire plant rather than just isolated plant traits (e.g. Reich *et al.* 2003b; Kerkhoff *et al.* 2006), and they shed new light on the function of plants as connectors of above-ground and below-ground systems (see Wardle *et al.* 2004). However, since our work is based on data from high-lat-

itude ecosystems only, with several important traits to complete the picture lacking, it needs to be extended to other plant traits and further tested on other floras and biomes across the world. These results, if widely applicable, would imply promising perspectives for functional ecology, as they strongly suggest that plant resource economics can to some significant degree be studied through the prism of leaves. In the present context of rapid human-induced changes of ecosystems world-wide (Millennium Ecosystem Assessment 2005), being able to use leaf trait changes to predict whole-plant functional trait changes, including trait changes below-ground, would indeed be of great help for better forecasting ecosystem consequences of changes in vegetation composition.

Acknowledgements

We are grateful to the Abisko Scientific Research Station (ANS) and its staff for their kind assistance and hospitality. G.T.F. was supported by EU Marie Curie host fellowship grant MEST-CT-2005-MULTIARC 021143; R.A. and R.S.P.L. by EU ATANS grant Fp6 506004; and J.H.C.C. by grants 047.017.010 and 047.018.003 of The Netherlands Organisation for Scientific Research (NWO). We are thankful to anonymous referees who provided constructive comments on the manuscript.

References

- Ackerly, D. (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs*, **74**, 25–44.
- Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters*, **10**, 135–145.
- Aerts, R. (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*, **50**, 29–37.
- APG II (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society*, **141**, 399–436.
- Castro-Díez, P., Puyravaud, J.P., Cornelissen, J.H.C. & Villar-Salvador, P. (1998) Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. *Oecologia*, **116**, 57–66.
- Chapin, F.S., III, Bret-Harte, M.S., Hobbie, S.E. & Zhong, H. (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, **7**, 347–358.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Cornelissen, J.H.C., Diez, P.C. & Hunt, R. (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology*, **84**, 755–765.
- Cornelissen, J.H.C., Aerts, R., Cerabolini, B., Werger, M. & van der Heijden, M. (2001) Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*, **129**, 611–619.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.T., Morgan, H.D., Heijden, M.G.A.v.d., Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- Cornelissen, J.H.C., Queded, H.M., Gwynn-Jones, D., Van Logtestijn, R.S.P., De Beus, M.A.H., Kondratyuk, A., Callaghan, T.V. & Aerts, R. (2004) Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology*, **18**, 779–786.
- Cornelissen, J.H.C., Queded, H.M., van Logtestijn, R.S.P., Pérez-Harguindeguy, N., Gwynn-Jones, D., Diaz, S., Callaghan, T.V., Press, M.C. & Aerts, R. (2006) Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? *Oecologia*, **147**, 315–326.
- Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.

- 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 root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos*, **93**, 274–285.
- Craine, J.M., Lee, W.G., Bond, W.J., Williams, R.J. & Johnson, L.C. (2005) Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology*, **86**, 12–19.
- De Deyn, G.B., Cornelissen, J.H.C. & Bardgett, R.D. (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, **11**, 516–531.
- Diaz, S. & Cabido, M. (1997) Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science*, **8**, 463–474.
- Diaz, S., Cabido, M. & Casanoves, F. (1998) Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, **9**, 113–122.
- Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. et al. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.
- Garnier, E., Cortez, J., Billes, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Gordon, W.S. & Jackson, R.B. (2000) Nutrient concentrations in fine roots. *Ecology*, **81**, 275–280.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Wiley, New York.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H. et al. (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.
- Hanley, M.E., Lamont, B.B., Fairbanks, M.M. & Rafferty, C.M. (2007) Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 157–178.
- Hendricks, J.J., Aber, J.D., Nadelhoffer, K.J. & Hallett, R.D. (2000) Nitrogen controls on fine root substrate quality in temperate forest ecosystems. *Ecosystems*, **3**, 57–69.
- Kazakou, E., Vile, D., Shipley, B., Gallet, C. & Garnier, E. (2006) Covariations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology*, **20**, 21–30.
- Kerckhoff, A.J., 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. *The American Naturalist*, **168**, E103–E122.
- Lambers, H., Raven, J.A., Shaver, G.R. & Smith, S.E. (2008) Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution*, **23**, 95–103.
- Lusk, C.H., Reich, P.B., Montgomery, R.A., Ackerly, D.D. & Cavender-Bares, J. (2008) Why are evergreen leaves so contrary about shade? *Trends in Ecology & Evolution*, **23**, 299–303.
- Millennium Ecosystem Assessment (2005) *Living Beyond Our Means: Natural Assets and Human Well-being*. Millennium Ecosystem Assessment.
- Mossberg, B., Stenberg, L. & Ericsson, S. (1992) *Den Nordiska Floran*. Wahlström & Widstrand, Stockholm, Sweden.
- Murphy, J. & Riley, J.P. (1962) A modified single method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 31–36.
- Nielsen, S.L., Enriquez, S., Duarte, C.M. & Sand-Jensen, K. (1996) Scaling maximum growth rates across photosynthetic organisms. *Functional Ecology*, **10**, 167–175.
- Niklas, K.J. (1992) *Plant Biomechanics: An Engineering Approach to Plant Form and Function*. University of Chicago Press, Chicago, IL, USA.
- Niklas, K.J. (1999) A mechanical perspective on foliage leaf form and function. *New Phytologist*, **143**, 19–31.
- Poorter, H. & Villar, R. (1997) The fate of acquired carbon in plants: chemical composition and construction costs. *Plant Resource Allocation* (eds F.A. Bazzaz & J. Grace), pp. 39–72. Academic Press, San Diego, CA.
- Questaed, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F., Riemann, P., Gwynn-Jones, D., Kondratyuk, A. & Jonasson, S.E. (2003) Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology*, **84**, 3209–3221.
- Raven, J.A. (1996) Into the voids: the distribution, function, development and maintenance of gas spaces in plants. *Annals of Botany*, **78**, 137–142.
- 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 of the United States of America*, **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., Buschena, C., Tjoelker, M.G., Wrage, K., Knops, J., Tilman, D. & Machado, J.L. (2003a) 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.
- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. & Walters, M.B. (2003b) The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, **164**, S143–S164.
- Reich, P.B., Tjoelker, M.G., Pregitzer, K.S., Wright, I.J., Oleksyn, J. & Machado, J.-L. (2008) Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecology Letters*, **11**, 793–801.
- Roumet, C., Urceley, C. & Diaz, S. (2006) Suites of root traits differ between annual and perennial species growing in the field. *New Phytologist*, **170**, 357–368.
- 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. (2006) The mysterious root length. *Plant and Soil*, **286**, 1–6.
- Ryser, P. & Lambers, H. (1995) Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant and Soil*, **170**, 251–265.
- Sjögersten, S. & Wookey, P.A. (2002) Climatic and resource quality controls on soil respiration across a forest-tundra ecotone in Swedish Lapland. *Soil Biology and Biochemistry*, **34**, 1633–1646.
- Sorrell, B.K. & Dromgoole, F.I. (1989) Oxygen diffusion and dark respiration in aquatic macrophytes. *Plant, Cell and Environment*, **12**, 293–299.
- Suding, K.N., Lavorel, S., Chapin, F.S., III, Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. & Navas, M.-L. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.
- Thompson, K., Parkinson, J.A., Band, S.R. & Spencer, R.E. (1997) A Comparative study of leaf nutrient concentrations in a regional herbaceous flora. *New Phytologist*, **136**, 679–689.
- Tilman, D. (1982) *Resource competition and community structure*. Princeton University Press, Princeton, NJ, USA.
- 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.
- Wahl, S. & Ryser, P. (2000) Root tissue structure is linked to ecological strategies of grasses. *New Phytologist*, **148**, 459–471.
- Wardle, D.A., Walker, L.R. & Bardgett, R.D. (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **305**, 509–513.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science*, **304**, 1629–1633.
- Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006) Bivariate line-fitting methods for allometry. *Biological Reviews*, **81**, 259–291.
- Wassen, M.J., Venterink, H.O., Lapshina, E.D. & Tanneberger, F. (2005) Endangered plants persist under phosphorus limitation. *Nature*, **437**, 547–550.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution*, **21**, 261–268.
- Withington, J.M., Reich, P.B., Oleksyn, J. & Eissenstat, D.M. (2006) Comparisons of structure and life span in roots and leaves among temperate trees. *Ecological Monographs*, **76**, 381–397.
- Wright, I.J. & Cannon, K. (2001) Relationships between leaf lifespan and structural defences in a low-nutrient, sclerophyll flora. *Functional Ecology*, **15**, 351–359.
- Wright, I.J. & Westoby, M. (1999) Differences in seedling growth behaviour 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.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K. *et al.* (2005) Modulation of leaf economic traits and trait relationships by climate. *Global Ecology & Biogeography*, **14**, 411–421.
- Wright, I.J., Falster, D.S., Pickup, M. & Westoby, M. (2006) Cross-species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics. *Physiologia Plantarum*, **127**, 445–456.

Received 11 August 2009; accepted 9 November 2009
 Handling Editor: Richard Bardgett

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Biplots of leaf, stem and root trait relationships. Data are shown without transformation: regression lines are therefore only informative (not always complying with bivariate normality assumption). Species are distinguished according to their higher taxum:

○ Core eudicot; ● Basal eudicot; ● Monocot; Δ Pteridophyte; ▲ Lycophyte; ▲ Gymnosperm.

Figure S2. Biplots of leaf, stem and root trait relationships. Data are shown without transformation: regression lines are therefore only informative (not always complying with bivariate normality assumption). Species are distinguished according to their plant type: ○ Woody evergreen; ● Woody deciduous; ● Fern ally; Δ Graminoid; ▲ Forb; ▲ Aquatic forb; □ Club moss.

Table S1. Species list and characteristics. All leaf, stem and root trait data is available through the TRY database: <http://www.try-db.org>.

Table S2. Contributions (%) of organ traits to the construction of first and second axes of organ PCAs.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be reorganized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.