
6

CHAPTER 6

The plant economics spectrum of litter decomposition

Grégoire T. Freschet, Rien Aerts, Johannes H. C. Cornelissen

Submitted manuscript

Setup of the common-garden decomposition experiment

SUMMARY

(1) Recent evidence indicates tight control of plant resource economics over interspecific trait variation among species, both within and across organs. Here we demonstrate that this 'Plant economics spectrum' has important afterlife effects on carbon turnover by driving coordinated decomposition rates of different organs across species.
(2) To that end, we conducted a common-garden decomposition experiment bringing together leaves, fine stems, coarse stems, fine roots and reproductive parts from a wide range of subarctic plant types, clades and environments and measured all plant parts for the same (green and litter) plant economics traits.
(3) All organ decomposabilities were consistently controlled by the same structure-related traits (lignin, C and dry matter content) while nutrient-related traits (N, P, pH, phenols) had more variable influence, likely due to their contrasting functions across organs. Consistent shifts in elevation of parallel trait-decomposition relationships between organs indicate that other traits relating to organ dimensions, configuration or chemical contents co-determine litter decomposition rates.
(4) While the coordinated litter decomposabilities across species organs imply a coordinated impact of plant aboveground and belowground litters on plant-soil feedbacks, the contrasting decomposabilities between plant parts suggest a major role for the relative inputs of organ litter as driver of soil properties and ecosystem biogeochemistry.

Keywords: plant economics spectrum; plant functional traits; litter decomposition; leaf; stem; root; coarse woody debris; lignin

INTRODUCTION

Plant litter decomposition, a major driver of carbon and nutrient cycling in terrestrial and freshwater ecosystems, controls the provision of fundamental ecosystem services such as soil formation, nutrient availability and atmospheric composition, with feedback to vegetation composition. One major aim of ecology is to model how functional features of vegetations differing in species composition feed back to soil carbon turnover, and thereby atmospheric chemistry and climate, in different biomes (Sitch *et al.* 2003; Cornwell *et al.* 2009). Here we make a leap forward towards this aim by presenting the first empirical multi-species study to take an explicit whole-plant functional approach to assessing litter decomposition rates, more specifically by linking the 'plant economics spectrum' (PES, Freschet *et al.* 2010a) to litter decomposability.

While leaf litter decomposition rates are strongly determined by climate (Berg *et al.* 1993; Parton *et al.* 2007) and community composition of soil organisms (Lavelle *et al.* 2006), local-scale interspecific variation in litter quality ('species identity') is their predominant driver (Cornwell *et al.* 2008). Structural and chemical leaf traits have 'afterlife' effects on litter decomposability (Cornelissen *et al.* 2004). Indeed, interspecific variation in traits of fresh leaves and that of leaf litter tend to be strongly correlated (e.g. Freschet *et al.* 2010b). Thus, lignin content (Meentemeyer 1978), physical toughness (Pérez-Harguindeguy *et al.* 2000), polyphenol content (Coq *et al.* 2010), or specific leaf area (SLA) and dry matter content (DMC) (Garnier *et al.* 2004;

Kazakou *et al.* 2006) can substantially affect leaf decomposition rates. Also, the high nutrient requirement of decomposer organisms creates nutrient-limited conditions for decomposition processes (Enríquez *et al.* 1993). Thus, nitrogen (N), phosphorus (P) and calcium (Ca) contents (Enríquez *et al.* 1993; Aerts 1997) and pH (as a proxy for basic cation content and antimicrobial organic acids; Cornelissen *et al.* 2006) are usually significant predictors of leaf litter decomposition rates.

Most litter turnover studies linking vegetation composition to decomposition have focused on the relation between leaf traits and leaf litter decomposability. Some evidence exists that interspecific variation in litter quality is also the predominant driver of root litter decomposition (Silver & Miya 2001) and the huge range in wood functional trait values (Chave *et al.* 2009) and within-site wood decomposition rates (Harmon *et al.* 1995; van Geffen *et al.* 2010) suggests that similar pattern may exist for plant stems too. Indeed, several chemical traits related to leaf decomposition, such as N, Ca and lignin concentrations, also impact root decomposition (Silver & Miya 2001; Vivanco & Austin 2006), whereas N, P and tissue density affect stem decomposition (Chambers *et al.* 2000; Weedon *et al.* 2009). However, with only few studies available on interspecific variation in stem and root decomposability, we still do not know whether the traits underpinning decomposition rates, or their relative contributions, have the same effect across plant parts. While it seems likely that the same traits will have broadly similar effects on litter decomposition of distinct plant organs, differences in the magnitude of their impact are likely. For instance, while litter N or P contents are major determinants of colonization-degradation by soil organisms (Cornwell *et al.*, 2008), whether these nutrient pools are active (e.g. in enzymes for leaf photosynthesis, root adsorptive capacity) or passive (e.g. stem or root storage, recalcitrant defence compounds) will partly determine their chemical form after senescence and thereby modulate their availability to decomposers. Traits related to physical support functions, expressed in plant allometric relationships including organ sizes, may play important roles too; for instance tree trunk diameter predicted variation in decomposition rates among 15 Bolivian tree species (van Geffen *et al.* 2010). Any such differences in organ function, as expressed in structural and physiological differences, might cause shifts in trait-decomposability relationships between organs.

Empirical evidence is growing that plant species possess integrated strategies across their organs with regards to C and nutrient economy (Freschet *et al.* 2010a), which are moreover robust to geographical scaling (Kerkhoff *et al.* 2006; Liu *et al.* 2010). In other words, (i) each vegetative plant organ (leaves, twigs, main stems, coarse roots, fine roots) seems to obey a fundamental trade-off between traits inferring rapid resource acquisition and traits leading to resource conservation, owing to direct and indirect mutual dependencies between these traits (Reich *et al.* 2003; Chave *et al.* 2009; Elser *et al.* 2010); and (ii) those traits seem to be generally coordinated across vegetative organs, likely due to plant physiological, ontogenetic and allometric constraints (Niklas & Enquist 2002; Wright *et al.* 2006; but see Baraloto *et al.* 2010 for decoupling of coarse wood and leaf traits among tropical trees). As over half the global variance in these traits is at local to plant community scale (Wright *et al.* 2004; Freschet *et al.* 2010c), many contrasting plant economic strategies are already found within a local flora (e.g. Freschet *et al.* 2010a).

Assuming that consistent traits and economic strategies drive decomposition across plant organs, decomposability is probably coordinated across organs too. This would

indicate tight control of plant economics on the carbon and nutrient turnover in ecosystems.

At present, however, there is very little empirical evidence for this. Wang *et al.* (2010) observed significant correlation between leaf and root decomposition of four tree species only, while Hobbie *et al.* (2010) did not find any consistent relationship for eleven tree species. Here we present the first empirical evidence of a clear association between the PES and litter decomposability, in a comprehensive multi-species, multi-organ decomposition study covering a wide range of subarctic plant functional types and aquatic, riparian and terrestrial habitats. More precisely, we test the hypotheses that (i) the decomposability of distinct plant organs (leaves, fine stems, coarse stems, fine roots and reproductive parts) is controlled by the same structure-related (lignin, DMC, C) and chemical (N, P, phenolic contents, pH) traits, although the relative influence of these traits might shift across organs. Considering the strong trait coordination found across leaves, stems and roots in a subarctic flora (Freschet *et al.* 2010a), we further hypothesize that (ii) interspecific variation in litter decomposability is coordinated across plant vegetative organs. Finally, assuming the validity of the two previous hypotheses, we test that (iii) the locally operating PES is a good predictor of the decomposability of vegetative plant organs.

MATERIALS AND METHODS

Study area, species types and sampling

The plant species were sampled 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. During the 1999-2008 decade this area had a mean annual rainfall of 352mm and mean January and July temperatures of -9.7 and 12.3°C, respectively (meteorological data, Abisko Research Station). The forested area, which was the focus of this study, features strongly organic Podsol soils and covers most of the landscape below 700m a.s.l. except for occasional treeless mires, fens and bogs. The three most distinct ecosystem types within the selected forested sites were: dry birch forest with ericaceous understory, riparian birch forest with herbaceous and shrubby understory and forested freshwater systems (ponds and streams). Seven sampling sites (c. 20m transects) each including all three ecosystem types were used to identify the dominant vascular species (roughly 80-90% of total plant annual biomass production) of each plant community (see Cornelissen *et al.* 2003). These included 15 species from the dry forest, 18 from the riparian forest and 7 from aquatic systems, altogether covering seven growth forms and six higher clades (see Appendix S1 in Supporting Information for species list and characteristics).

All 40 species were sampled for leaves, 38 for fine stems (<3mm Ø), 11 for fine roots (<2mm Ø), 19 for reproductive organs (ovary plus receptacle), all 6 tree species for coarse stems (~50mm Ø) and 2 species for coarse roots (~50mm Ø). All these materials were sampled both fresh and as litter (except reproductive organs: only as litter). 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. The details of coarse stem and coarse root sampling, for which several stages of decay were collected, are in Appendix S2. To ensure fair comparison of fine root types in terms of function, only the finest root branch order visible to the naked eye was

considered for each species. Twigs of woody species (<3mm Ø) were considered analogous to stems of forbs and graminoids in terms of function.

For each organ, one part of the collected sample was placed in paper bags and air-dried for chemical analyses and incubations while the other was immediately placed in a closed plastic bag for DMC analysis. For root sampling, plant individuals were excavated and brought to the lab. Soil and alien material were washed off the root system before both mature, undamaged roots and darkening, turgescence-losing roots (i.e. root litter) were collected. Large mycorrhizal rhizomorphs were brushed off. For dead woody fine stems, only those that looked similar to living ones except for the absence of leaves were selected. 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 living leaves and fine stems were collected while fully mature, in late July or early August 2007 (see Freschet *et al.* 2010a). All litters of leaves, fine stems and reproductive organs were sampled when fully senesced between mid-August and mid-October 2007 (see Freschet *et al.* 2010b). Fine roots were collected partly in August 2007 and partly in August 2008 owing to the labour-intensive process involved.

Plant trait measurements

All collected materials were measured for C, N, P and lignin content, as well as pH. For these analyses air-dried sub-samples were ground and subsequently oven-dried for 24h at 60°C. Carbon and nitrogen concentrations were measured by dry combustion on a NA 1500 elemental analyser (Carlo Erba, Rodana, Italy). Phosphorus was measured by acid digestion as referred to in Freschet *et al.* (2010a). Lignin concentration was determined by extraction of non-ligneous compounds as described in Freschet *et al.* (2010a). For pH, 0.15ml of each ground sample was shaken with 1.2ml demineralised water in an Eppendorf tube for 1h at 250rpm. After centrifugation at 13,000rpm for 5min, pH of the supernatant solution was measured (Cornelissen *et al.* 2006).

All materials except reproductive organs were measured for DMC (dry weight (mg) to water saturated weight (g) ratio) following Cornelissen *et al.* (2003). The protocol was modified for woody fine stems and coarse stems-roots, which were submersed in water for 3 and 9 days respectively in order to ensure homogeneous filling of air spaces.

Leaves, fine stems and coarse stems-roots were measured for tannins and non-tannin phenols using the Folin-Ciocalteau method, as described by Waterman & Mole (1994), modified according to Makkar (2003).

Decomposition study

All litter materials were incubated in an outdoor litter-bed (see details below) at Abisko Research Station, following Cornelissen *et al.* (2004). Our experiment was not designed to capture natural *in situ* decomposition rate (G. T. Freschet, R. Aerts & J. H. C. Cornelissen, unpublished manuscript, for *in-situ* incubations of several litter types across contrasting ecosystems – not included in this thesis), but rather to provide standardized ('common-garden') environmental conditions for large interspecific, inter-organ comparisons. Decomposition was measured over two full years of incubation, but for leaf litter additionally after one year.

Coarse stem and coarse root litter decomposition followed a new protocol allowing for reconstruction of long-term decomposition rates using a number of short-term

incubations of woody debris from various stages of decay (details in Appendix S2 and G. T. Freschet, J. T. Weedon, R. Aerts, J. R. van Hal & J. H. C. Cornelissen, unpublished manuscript, i.e. Chapter 5 of this thesis). Briefly, for each wood species and type (stem or root) wood samples of a broad range of stages of decay were collected, split in four replicate sub-samples, sealed in mesh (see below) and then incubated for 2 years in the litter-bed. After retrieval, the changes in relative density (proxy for litter mass per volume) for fragments of each wood type were entered into an iterative optimization procedure which modelled the best-fit parameters of each of three possible decay functions (most commonly used to describe wood decay: linear, exponential, sigmoid). For each wood type, the model providing the best fit was subsequently used for $T_{1/2}$ calculation (see below).

For all other materials, four subsamples (eight for leaves) of each air-dry litter sample were weighed and sealed into litterbags. An additional subsample was oven-dried (60°C, 72h) in order to correct air-dry mass of litterbag samples for residual humidity. The amount of material and the dimensions of the bags were adjusted to each material type in order to standardize litter densities and textures inside the bags. A 1mm mesh was used for most material given the absence of large soil invertebrates in this sub-arctic area and 0.3mm for very thin materials (providing access to microbes and micro-invertebrates). In a control test no significant difference in 2-year mass loss % was found between litters sealed into 0.3 versus 1mm mesh for *Betula pubescens* and *Vaccinium uliginosum* (paired t-tests).

The litter-bed for incubation consisted of rectangular wooden frames sunk into the ground, including a free-draining foundation layer of grit stones (particle sizes 10-20mm) on top of the original soil profile. They were covered by a 20mm layer of mixed fresh and old litter collected in September 2007 from nearby dry and wet birch forests and ponds, together representing the ecosystems sampled for litter. This way, all litter types were presumably inoculated with the microbial communities of all ecosystem types. On 23 April 2008, all litter-bags were laid out flat, without overlap, and covered by a 10mm layer of the same mixed litter. Four separate blocks hosted the four groups of replicates per litter type. The litter-bags were subject to the local climatic influences and did not receive any treatment. They were harvested after two years of incubation (23 April 2010, and 23 April 2009 for first leaf harvest), while still frozen and stored at -16°C. After defrosting, the adhering soil, soil fauna and other alien material were removed from the decomposed litter by gentle brushing and rinsing with tap water. Litter samples were then dried (60°C, 96h) and re-weighed. For all litter materials except coarse stems and roots (see above), single negative exponential models were used to derive decomposition constants (k) from % mass loss against time. Finally, half-lives of decomposing material ($T_{1/2}$; time (y) needed to reach 50% mass loss) were derived from their respective decomposition models to obtain comparable measures of decomposability across all litter types (including stem and root woody debris which required the use of linear or sigmoid models).

Data analysis

To comply with normality assumptions of all subsequent parametric tests, $T_{1/2}$ of all organs and most organ functional traits (except DMC, C, pH and C/N) were $\log_{10}$-transformed. The predictive value of plant functional traits for $T_{1/2}$ of each organ was assessed using ordinary least squares (OLS) regressions. Coarse stems and coarse roots were considered similar in structure and function and pooled for this analysis. Once we

had identified the best predictor of $T_{1/2}$ across organs (i.e. lignin content), we looked within each organ for complementarity and interaction between this and the other traits as possible predictors of $T_{1/2}$ using multiple linear regressions.

We compared the slopes and intercepts of trait-decomposability relationships for different vegetative organs by standardized major axis (SMA) regressions and routine procedures from the SMATR freeware (Warton *et al.* 2006) (Fig. 1). Bivariate relationships between organs' $T_{1/2}$ were described with SMA regressions (Fig. 2). We compared decomposition rates of leaves to those of fine stems and of fine stems to those of fine roots using paired t-tests. OLS regressions were used to test the predictive power of leaf, fine stem and fine root organ economics spectra on their respective organ $T_{1/2}$ (Fig. S2); and of the PES on each organ $T_{1/2}$ (Fig. 3). Data on the carbon and nutrient economics spectrum for each organ and the PES were taken from Freschet *et al.* (2010a), who performed principal component analyses (PCA) on trait data for living leaves, fine stems and fine roots of the same 35 species. Separate PCAs were thus performed for each organ and for all three organs together (see Table S1 for main axes respective factor loading of each PCA, as well as proportion (%) variance explained by each economics spectrum axis). Following the high proportion of variance explained by each first PCA axis and the relatively homogeneous impacts of variables on each first PCA axis, first axis species scores of leaf, fine stem, fine root and whole-plant PCAs were used to quantify leaf, fine stem, fine root and whole-plant economics spectra, respectively.

RESULTS

Over the two years of incubation, leaf materials displayed an average 69% mass loss (from 32 to 99%), fine stems 39% (from 8 to 96%), fine roots 28% (from 8 to 65%) and reproductive organs 58% (from 17 to 95%).

Relationships between plant organ litter traits and litter decomposability

All structure-related traits (DMC, C, lignin content) were good predictors of the interspecific variation in decomposability of any given organ (except DMC vs. fine root decomposability; Table 1). In contrast, the goodness-of-fit of relationships between several chemical traits (pH, N, non-tannin phenols) or structural to chemical trait ratios (lignin/N, C/N) and decomposability varied widely among organs. Only leaves displayed significant relationships between N and $T_{1/2}$ and pH scaled with leaf, fine stem and coarse stem-root $T_{1/2}$ but not with fine root or reproductive organ $T_{1/2}$. Tannin and P contents showed no clear trends with $T_{1/2}$ within any organ.

Lignin consistently explained >53% of the variance in organ $T_{1/2}$ and was generally the best single trait predictor of decomposability, followed by DMC (>56%; except for fine roots) and C content (>30%; Table 1). Combining lignin and DMC in multiple regressions against $T_{1/2}$ added substantial explanatory power to lignin predictions alone for leaves (+13% explained variance; $P<0.05$) and fine stems (+8%; $P<0.001$) but not for fine roots and coarse stems or roots. Litter chemical traits did not significantly increase predictive power of lignin with respect to $T_{1/2}$ variance, except N content for leaves (+15% explained variance; $P<0.05$), fine stems (+5%; $P<0.05$) and reproductive parts (+21%; $P<0.01$). Combining lignin, DMC and N significantly explained over 76% of the variance in leaf $T_{1/2}$ ($P<0.001$) and 90% of stem $T_{1/2}$ variance ($P<0.001$). With

respect to organ decomposabilities, the information provided by structural and nutritional traits was thus partially redundant or complementary depending on the organ.

Table 1. Relationships between traits of litter (or living organs; the value between brackets) and 'decomposition half-life' ($T_{1/2}$) across species for each organ.

	Leaves (n = 40)			Fine stems (n = 38)			Fine roots (n = 11)			Coarse stems & roots (n = 8)			Reproductive parts (n = 19)	
	R		P-value	R		P-value	R		P-value	R		P-value	R	P-value
Lignin (%)	**0.73**	**(0.66)**	< 0.001	**0.90**	**(0.87)**	< 0.001	**0.91**	**(0.82)**	< 0.001	**0.85**	**(0.86)**	0.007	**0.73**	< 0.001
DMC (mg g^{-1})	**0.75**	**(0.86)**	< 0.001	**0.88**	**(0.94)**	< 0.001	0.40	(0.34)	ns (0.22)	**0.89**	(-0.28)	0.003	na	na
Carbon (%)	**0.55**	**(0.63)**	< 0.001	**0.88**	**(0.90)**	< 0.001	**0.63**	**(0.73)**	0.036	**0.80**	(0.37)	0.017	**0.85**	< 0.001
Nitrogen (%)	**-0.42**	**(-0.45)**	0.007	0.04	**(-0.39)**	ns (0.83)	-0.15	(0.44)	ns (0.66)	-0.36	(-0.67)	ns (0.39)	0.08	ns (0.75)
Phosphorus (%)	-0.03	(-0.16)	ns (0.84)	-0.01	**(-0.41)**	ns (0.97)	-0.34	(0.15)	ns (0.31)	-0.40	(-0.79)	ns (0.33)	-0.32	ns (0.18)
pH	**-0.43**	**(-0.45)**	0.006	**-0.61**	**(-0.51)**	< 0.001	-0.33	(0.05)	ns (0.32)	**-0.96**	(-0.39)	< 0.001	0.00	ns (0.99)
Lignin + N	**0.80**		*** / *	**0.92**		*** / *	**0.92**		ns / ns	**0.86**		ns / ns	**0.86**	*** / **
Lignin + DMC	**0.81**		*** / ***	**0.94**		*** / ***	**0.94**		* / ns	**0.93**		ns / ns	na	na
Lignin + N + DMC	**0.87**		* / ns / ns	**0.95**		* / ns / ns	**0.96**		ns / ns / ns	**0.99**		ns / ns / ns	na	na
C/N	**0.47**	**(0.55)**	0.002	0.12	**(0.51)**	ns (0.46)	0.27	(-0.14)	ns (0.43)	0.48	**(0.78)**	ns (0.23)	0.27	ns (0.26)
Lignin/N	**0.75**	**(0.71)**	< 0.001	**0.74**	**(0.82)**	< 0.001	**0.72**	**(0.73)**	0.013	0.62	**(0.88)**	ns (0.10)	**0.52**	0.022
Tannins (mg g^{-1})	na	(0.26)	ns (0.11)	na	(0.07)	ns (0.67)	na	na	na	na	(-0.47)	ns (0.51)	na	na
Non-tannin phenols (mg g^{-1})	na	(0.27)	ns (0.09)	na	**(0.52)**	< 0.001	na	na	na	na	(-0.79)	ns (0.07)	na	na

OLS regression coefficients (R) are displayed for litter material (and for living material within brackets); bold characters are used for significant relationships. Single regression significances (P-value) relate to litter material, with ns (non-significant P-value). For multiple regressions, significance is displayed for each paramater except interactions (* P <0.05; ** <0.01; *** <0.001). na is non-available data. n is the number of species.

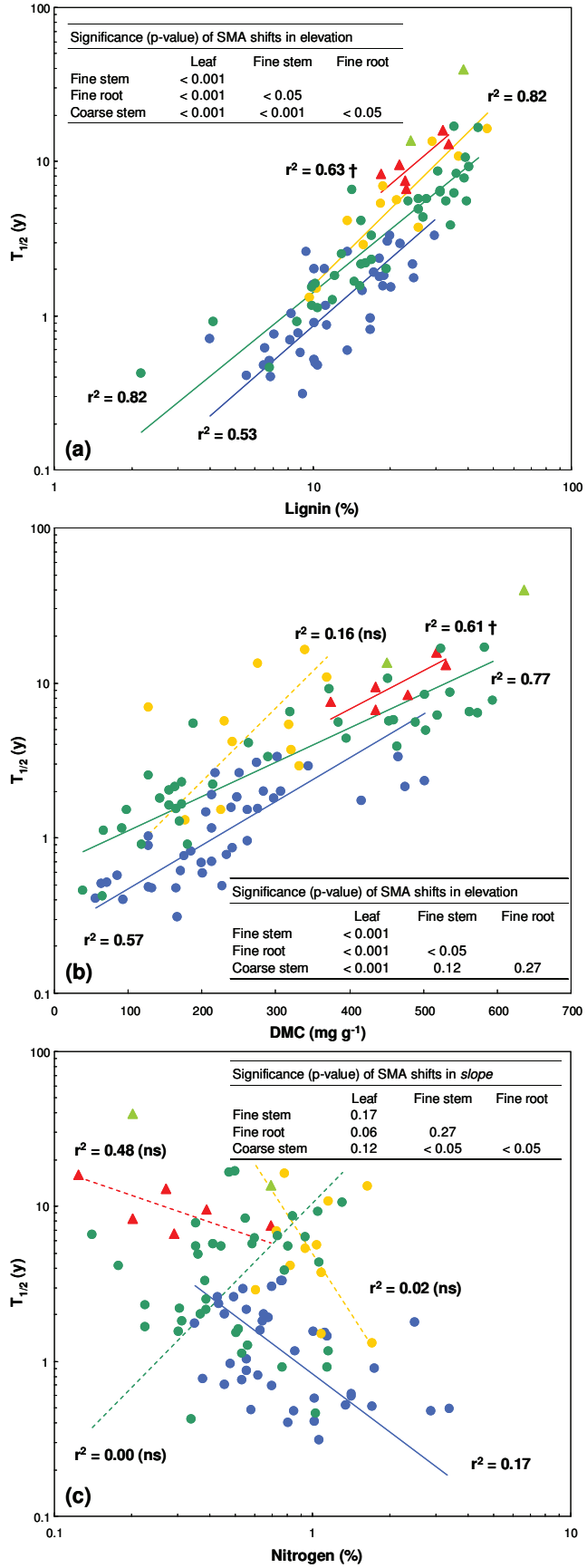


Fig. 1. Standardized major axis (SMA) regressions (r^2) between each organ litter decomposition half-life ($T_{1/2}$) and **(a)** lignin content, **(b)** dry matter content (DMC), **(c)** nitrogen content. Symbols: ● leaves, ● fine stems, ● fine roots, ▲ coarse stems, ▲ coarse roots; † marginally significant; (ns) non-significant. Inset: significance of shifts in slope **(c)** or elevation — **(a)** **(b)** following non-significant differences in slope — between each separate plant organ SMA regression.

Trait-decomposability regressions typically revealed similar slopes between organs, with consistent shifts in elevations (intercepts). For instance, at a given lignin content, decomposition rates ranked as leaves > fine stems > fine roots > coarse stems and roots (Fig. 1a). However, the change (slope) in decomposition rate per unit change in lignin content was similar across organs. Very similar patterns of common slope and significant elevation shifts were found for DMC (Fig. 1b), P, C, pH, tannins, non-tannin phenols and lignin/N (data not shown). In contrast, N (Fig. 1c) and C/N displayed some dissimilarities between slopes. For instance, the N-$T_{1/2}$ relationship of coarse stems had flatter slope than those of any other vegetative organ (Fig. 1c).

Strong co-variation of decomposability of different vegetative plant organs

Interspecific variations in leaf, fine stem and fine root $T_{1/2}$ were strongly coordinated (Fig. 2). Coarse stem and reproductive organ $T_{1/2}$ were not significantly coordinated with that of any other organs (data not shown).

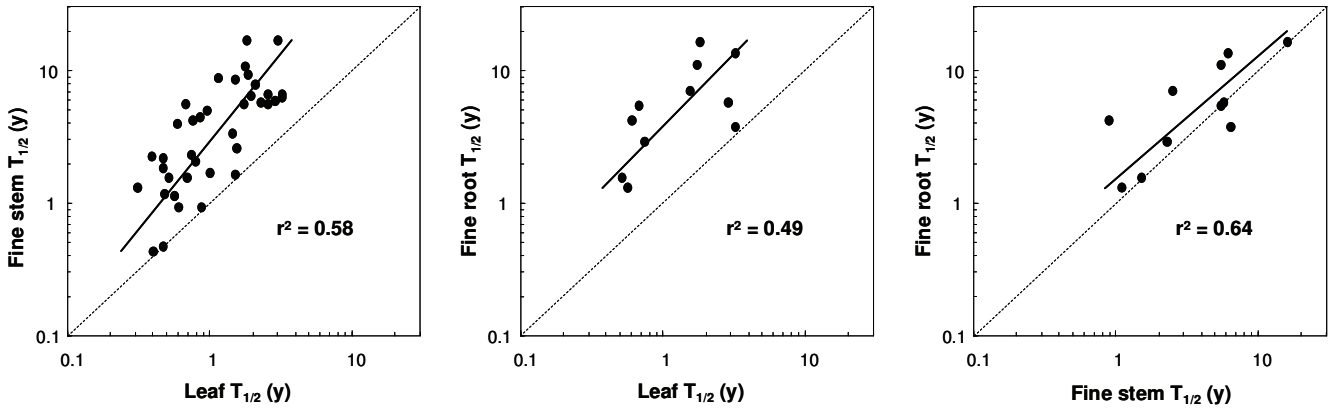


Fig. 2. SMA regressions (r^2) between litter decomposition half-lives ($T_{1/2}$) of leaves, fine stems and fine roots.

The position of species relative to the 1:1 axes of each regression (Fig. 2) illustrates that leaves decomposed generally faster than fine stems ($P<0.001$), which themselves decomposed marginally slower than fine roots ($P=0.08$). Visual inspection of those relationships indicated that the coordinated pattern of $T_{1/2}$ across organs was partly due to relationships within but also between phylogenetic, plant type or environmental groups (Figure S1). Nevertheless, we observed no clear phylogenetic, plant type or environmental group clustering away from the general regression lines, for any organ. In other words, despite a few outliers no plant type or clade seemed to consistently offset either the slope or intercept of organ decomposability relationships. Similarly, plants from aquatic, riparian and terrestrial environments fitted consistently in the pattern of interspecific decomposability co-variation between vegetative organs.

Consistent with the above results, leaf and fine stem economics spectra were good predictors of interspecific variation in their respective organ decomposability (R^2 of 0.57 and 0.76, respectively, $P<0.001$ in both cases; Figure S2). In contrast, the fine root economics spectrum did not significantly predict fine root decomposability ($R^2=0.02$; $P=0.70$; Figure S2). Nevertheless, the PES was a highly significant predictor of the decomposabilities of each of the vegetative organs (Fig. 3). Thus, following a gradient

from the most nutrient acquisitive to the most nutrient conservative species, the decomposition half-lives of leaves (R^2=0.53), fine stems (R^2=0.64), fine roots (R^2=0.49) and coarse stems (R^2=0.86) decreased exponentially (P<0.05 in all cases; Fig. 3).

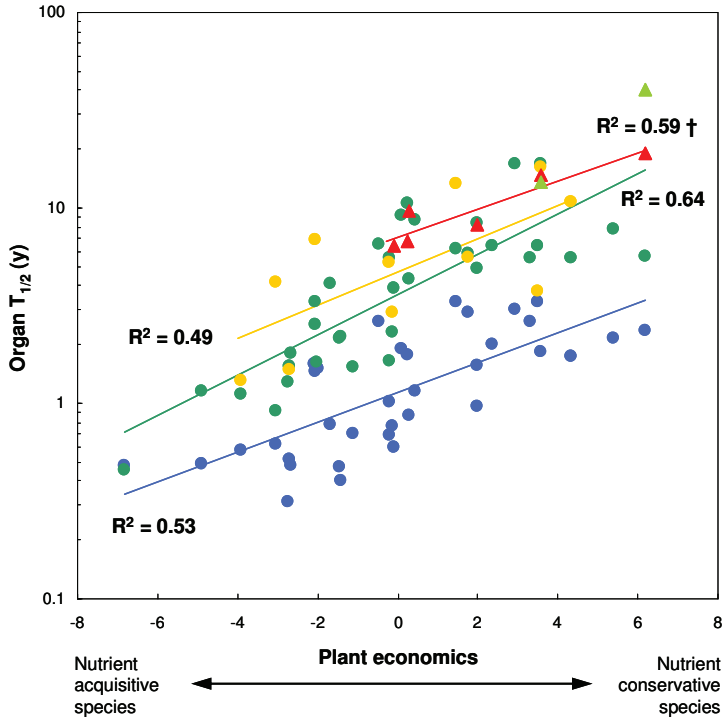


Fig. 3. Relationships between the PCA first axis score representing the plant economics spectrum and decomposition half-lives of different organs. Symbols: ● leaves, ● fine stems, ● fine roots, ▲ coarse stems, ▲ coarse roots.

DISCUSSION

This is the first study comparing litter decomposabilities of the main plant organs among multiple species ranging widely in taxonomy and ecology. We have found remarkable interspecific coordination between organs resulting in a 'plant economics spectrum of litter decomposability', concomitant with consistent shifts in intercept of trait-decomposability relations between organs. Below we synthesize these findings and their ecological implications.

The same structure-related traits determine interspecific variation in decomposability for different plant organs

Our results show that the relative investment of plants in dense, long-lived, mechanically reinforced structures (reflected by traits such as DMC, C and lignin content) is what predominantly drives the (interspecific variation in) decomposability of every plant organ. In contrast, nutrient and phenolic contents were typically weaker predictors, with diverging predictive powers across organs. Nevertheless, structural (lignin, DMC) and chemical (N) traits together were better predictors than structural traits alone for several high-turnover organs (leaves, fine stems and reproductive parts). Our first hypothesis is thus not unequivocally supported by our findings.

In line with our findings, the few studies that investigated the role of structural traits on non-leaf litter decomposition also attributed a major role for lignin (e.g. Taylor *et al.* 1991; Vivanco & Austin 2006; Weedon *et al.* 2009). However, whilst Taylor *et al.* (1991) suggested a disruption in lignin-decomposition relationship for materials of high (>28%) lignin content, we found a linear relationship encompassing plant material with over 40% lignin (Fig. 1). The strong impact of structural features on litter decomposabilities is supported by the complementarity of lignin and DMC in predicting litter decomposition rates, especially for leaf and fine stem litter (Table 1). As DMC represents the proportion of light to dense tissues, it differentiates for instance between the soft, nutrient-rich mesophyll of leaves and the tough supportive and conductive tissues of leaf veins (Garnier & Laurent 1994; Kazakou *et al.* 2006). For stems, which generally consist mostly of supportive and conductive tissues, this distinction appeared almost as relevant as for leaves. This confirms the value of DMC as a predictive plant trait for litter decomposability (Garnier *et al.* 2004). The poor relation with fine root decomposability is inconclusive in our study, given the low number of species represented. The predictive power of C content for decomposability is particularly good for highly lignified tissues such as fine and coarse stems where it correlates strongly with lignin and DMC. However, C is also abundant in non-structural compounds and can therefore only be a crude indicator of litter structural composition.

Whilst Wardle *et al.* (1998) observed a consistent effect of organ N on leaf, stem and root decomposition of 20 herbaceous species, we found inconsistent effects of N content on decomposition, depending on the organ considered. While leaf nitrogen content influenced leaf decomposition, this relation was not apparent in any other organs. To explain these contrasting findings, we hypothesize that initial N content substantially affects litter decomposition only if it is higher than that of the surrounding litter substrate. In low N litters, decomposers rely largely on exogenous N sources (Parton *et al.* 2007). When N availability is higher in the surrounding substrate than in the litter under study, such as non-leaf litter incubated in the abundant (young and old, thus less N-immobilizing) leaf-dominated litter mixture matrix in our litter-bed, decomposers of the non-leaf litter may have relatively steady access to exogenous N sources. Additionally, the relationship between N and decomposition could reach a threshold at high litter N content where microbial growth is no longer N-limited (Taylor *et al.* 1991). The N-decomposition relationship may thus hold only for intermediate values of litter N, explaining the weak impact of N on leaf decomposability and its non-significant impact on all other plant organs.

The differential influences of litter pH and the amount of low-molecular weight phenolic compounds on the decomposability of different plant organs suggest that these traits may have different meanings across organs with respect to the decomposition process. Indeed, while pH is a good proxy of basic cation content and/or antimicrobial organic acids in leaf, fine stem and wood litters, pH variation in fine roots does not seem to be associated with the same properties. Similarly, while a large proportion of low-molecular weight phenolic compounds may have anti-microbial properties in fine stems, they seem to predominantly serve different functions in leaves (see also Aerts *et al.*, 2006).

The consistency of trait-decomposability relationships across organs is confirmed by the similarities in regression slopes between organs (except for N and C/N), which supports our first hypothesis. At the same time, major differences between organs in

terms of trait-decomposability regression elevation (intercept) reflect substantial intrinsic differences between organs. For instance, at a given lignin content (e.g. 20%), leaves decomposed 1.6 times faster than fine stems, 2.1 times faster than fine roots and 3.1 times faster than coarse stems. These elevation shifts suggest the predominant impact of additive effects (several co-varying traits, e.g. lignin, DMC, N) rather than interactions between traits, which would imply slope heterogeneity. However, these shifts may also stem, at least partly, from the changing ecological or physiological function of some traits across organs. For instance, potential differences in the configuration of lignin deposition between organs would lead to more or less recalcitrant structures for decomposers. Contrasting proportions of different forms of organic N may also affect the decomposability of different organs. Organs key to uptake and assimilation, such as leaves and fine roots, hold more easily degradable forms of organic N (particularly photosynthetic enzymes or transmembrane proteins) than organs with predominant support and transport functions, in which most N might be in recalcitrant fibrous structures (e.g. microtubules, phloem proteins). Large differences between organ structure and function are also likely to explain shifts in organ decomposability. For instance, the typically flat structure of leaves should provide a relatively larger surface for microbial attacks and selective feeding by soil fauna compared to cylindrical organs such as stems. Relative access to decomposers, as reflected by the area/volume ratio of plant parts, may also explain why stem diameter (inversely proportional to the area/volume ratio) is an important factor for stem decomposition (Harmon *et al.* 1995; van Geffen *et al.* 2010), potentially explaining part of the shift in decomposability between fine and coarse stems and roots. Besides, the surface properties of each organ differ strongly. The barrier created by the bark of coarse stem and root litter likely provides better protection against decomposers than the lower side of leaves, with relatively thin cuticles and high densities of stomata providing microbial access, or absorptive fine root tissues. This is illustrated by the often 'empty bark' (of highly lignified or suberized phloem) of highly decomposed roots or stems compared to the vein skeletons of decomposed leaves.

Coordinated variation of plant organ decomposabilities: the 'afterlife' of the plant economics spectrum

In support of our second hypothesis, we demonstrate for the first time that, across a large number of plant functional types, contrasting clades and both aquatic and terrestrial species, plant decomposability is coordinated across its vegetative organs. This striking coordination could be a direct consequence of, simultaneously, the consistent role of functional traits on decomposition across organs identified here *and* the consistent co-variation of those traits between vegetative organs (Kerkhoff *et al.* 2006; Freschet *et al.* 2010a). The absence of a relationship between leaf and fine root decomposabilities of 11 woody deciduous and evergreen species (Hobbie *et al.* 2010) suggests that the positive coordination reported in our study might be partly driven by plant functional type or clade differences. Visual inspection of our data appears to partly support this (Figure S1), although no formal test could be performed with the low number of species per plant functional type or clade.

In line with the idea that the leaf economics spectrum drives leaf decomposability (Grime *et al.* 1997; Santiago 2007), we found here that not only leaf but also fine stem economics drive their respective organ decomposabilities. Thus, *within* aboveground organs, the numerous trade-offs between economic traits (Reich *et al.* 1997; Roumet *et*

al. 2006) also constrain parallel co-variation in decomposability. This was not found for fine roots. However, in support for our third hypothesis, we show here that the plant economics spectrum, reflecting an integrated plant strategy (Freschet *et al.* 2010a), controls the decomposability of every of its vegetative organs. This is consistent with the links between herbaceous species' growth rates and leaf, stem and root decomposabilities found previously (Wardle *et al.* 1998). Thus, at the whole-plant level, physiological and allometric interactions between organs (e.g. Wright *et al.* 2006; Maire *et al.* 2009) lead to coordinated trait variation across organs (Kerkhoff *et al.* 2006; Freschet *et al.* 2010a) which in turn drive coordinated organ decomposabilities.

At the ecosystem level, such coupling between plant strategy and organ decomposability yields considerable implications for plant control over soil processes. Litter decomposition drives biogeochemistry including nutrient turnover and immobilization, soil formation and atmospheric composition. Soil properties, in turn, have been shown to have strong feedback effects on plant performance and thus plant selection (Aerts 1999; Wardle *et al.* 2004). The coordinated litter decomposabilities across species organs imply a coordinated impact of plant aboveground and belowground litters on the direction and magnitude of this potential feedback loop. Whether the impact of this whole-plant decomposability coordination is substantial with regards to soil properties is nevertheless uncertain. Considering the substantial differences found here between organ decomposabilities, both the absolute and the relative fluxes of litter inputs from each organ could indeed be an even stronger control on soil properties and ecosystem biogeochemistry. In freshwater systems however, where detritus displacements generally occur, it is less likely that such plant-sediment feedback be of much influence. The relationships underpinning the afterlife effects of the plant economics spectrum on whole-plant litter decomposability will provide comprehensive input of vegetation composition feedback to soil carbon turnover, which is urgently needed in next-generation global models linking carbon dynamics to climate.

ACKNOWLEDGEMENTS

We are grateful to the Abisko Scientific Research Station (ANS) for providing facilities and ideal working conditions, Jurgen van Hal for his dedicated help with the final litter harvest, Richard van Logtestijn for assisting with the litterbag making, James Weedon for his help with wood decay models and Emilie Kichenin, Maxime Belondrade and Damien Lamouroux for their invaluable input during the experiment setup. G.T.F. was supported by EU Marie Curie host fellowship grant MEST-CT-2005-MULTIARC 021143; R.A. 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).

REFERENCES

Aerts R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship *Oikos* **79**: 439-449.

Aerts R. 1999. Interspecific competition in natural plant communities: Mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* **50**: 29-37.

Aerts R, van Logtestijn RSP, Karlsson PS. 2006. Nitrogen supply differentially affects litter decomposition rates and nitrogen dynamics of sub-arctic bog species. *Oecologia* **146**: 652-658.

Baraloto C, Timothy Paine CE, Poorter L, Beauchene J, Bonal D, Domenach AM, Hérault B, Patiño S, Roggy JC, Chave J. 2010. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters* **13**: 1338-1347.

Berg B, Berg MP, Bottner P, Box E, Breymeyer A, de Anta R, Couteaux M, Escudero A, Gallardo A, Kratz W, *et al.* 1993. Litter mass loss rates in pine forests of europe and eastern united states: Some relationships with climate and litter quality. *Biogeochemistry* **20**: 127-159.

Chambers JQ, Higuchi N, Schimel JP, Ferreira LV, Melack JM. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central amazon. *Oecologia* **122**: 380-388.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* **12**: 351-366.

Coq S, Souquet J-M, Meudec E, Cheynier V, Hättenschwiler S. 2010. Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of french guiana. *Ecology* **91**: 2080-2091.

Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, Steege Ht, Morgan HD, Heijden MGAvd, *et al.* 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**: 335-380.

Cornelissen JHC, Quested HM, Gwynn-Jones D, Van Logtestijn RSP, De Beus MAH, Kondratchuk A, Callaghan TV, 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 JHC, Quested HM, van Logtestijn RSP, Pérez-Harguindeguy N, Gwynn-Jones D, Díaz S, Callaghan TV, Press MC, 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 WK, Cornelissen JHC, Allison SD, Bauhus J, Eggleton P, Preston CM, Scarff F, Weedon JT, Wirth C, Zanne AE. 2009. Plant traits and wood fates across the globe: Rotted, burned, or consumed? *Global Change Biology* **15**: 2431-2449.

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N, *et al.* 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**: 1065-1071.

Elser JJ, Fagan WF, Kerkhoff AJ, Swenson NG, Enquist BJ. 2010. Biological stoichiometry of plant production: Metabolism, scaling and ecological response to global change. *New Phytologist* **186**: 593-608.

Enríquez S, Duarte C, Sand-Jensen K. 1993. Patterns in decomposition rates among photosynthetic organisms: The importance of detritus c:N:P content. *Oecologia* **94**: 457-471.

Freschet GT, Cornelissen JHC, van Logtestijn RSP, Aerts R. 2010a. Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology* **98**: 362-373.

Freschet GT, Cornelissen JHC, van Logtestijn RSP, Aerts R. 2010b. Substantial nutrient resorption from leaves, stems and roots in a sub-arctic flora: What is the link with other resource economics traits? *New Phytologist* **186**: 879-889.

Freschet GT, Dias ATC, Ackerly DD, Aerts R, van Bodegom PM, Cornwell WK, Dong M, Kurokawa H, Liu G, Onipchenko VG, *et al.* 2010c. Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. *Global Ecology & Biogeography* **in press**.

Garnier E, Cortez J, Billes G, Navas M-L, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, *et al.* 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630-2637.

Garnier E, Laurent G. 1994. Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. *New Phytologist* **128**: 725-736.

Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, *et al.* 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**: 259-281.

Harmon ME, Whigham DF, Sexton J, Olmsted I. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the northeastern yucatan peninsula, mexico. *Biotropica* **27**: 305-316.

Hobbie SE, Oleksyn J, Eissenstat DM, Reich PB. 2010. Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. *Oecologia* **162**: 505-513.

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.

Kerkhoff AJ, Fagan WF, Elser JJ, Enquist BJ. 2006. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *The American Naturalist* **168**: E103-E122.

Lavelle P, Decaëns T, Aubert M, Barot S, Blouin M, Bureau F, Margerie P, Mora P, Rossi JP. 2006. Soil invertebrates and ecosystem services. *European Journal of Soil Biology* **42**: S3-S15.

Liu G, Freschet GT, Pan X, Cornelissen JHC, Li Y, Dong M. 2010. Coordinated variation in leaf and root traits across multiple spatial scales in chinese semi-arid and arid ecosystems. *New Phytologist* **188**: 543–553.

Maire V, Gross N, da Silveira Pontes L, Picon-Cochard C, Soussana J-F. 2009. Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology* **23**: 668-679.

Makkar HPS. 2003. *Quantification of tannins in tree and shrub foliage: A laboratory manual*: Kluwer Academic Publishers.

Meentemeyer V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* **59**: 465-472.

Niklas KJ, Enquist BJ. 2002. On the vegetative biomass partitioning of seed plant leaves, stems, and roots. *The American Naturalist* **159**: 482-497.

Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC, *et al.* 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* **315**: 361-364.

Pérez-Harguindeguy N, Díaz S, Cornelissen JHC, Vendramini F, Cabido M, Castellanos A. 2000. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central argentina. *Plant and Soil* **218**: 21-30.

Reich PB, Walters MB, Ellsworth DS. 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 PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB. 2003. The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences* **164**: S143-S164.

Roumet C, Urcelay C, Díaz S. 2006. Suites of root traits differ between annual and perennial species growing in the field. *New Phytologist* **170**: 357-368.

Santiago LS. 2007. Extending the leaf economics spectrum to decomposition: Evidence from a tropical forest. *Ecology* **88**: 1126-1131.

Silver W, Miya R. 2001. Global patterns in root decomposition: Comparisons of climate and litter quality effects. *Oecologia* **129**: 407-419.

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, *et al.* 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the lpj dynamic global vegetation model. *Global Change Biology* **9**: 161-185.

Taylor BR, Prescott CE, Parsons WJF, Parkinson D. 1991. Substrate control of litter decomposition in 4 rocky-mountain coniferous forests. *Canadian Journal of Botany* **69**: 2242-2250.

van Geffen KG, Poorter L, Sass-Klaassen U, Van Logtestijn R, Cornelissen JHC. 2010. The trait contribution to wood decomposition rates of 15 neotropical tree species. *Ecology* **91**: 3686–3697.

Vivanco L, Austin A. 2006. Intrinsic effects of species on leaf litter and root decomposition: A comparison of temperate grasses from north and south america. *Oecologia* **150**: 97-107.

Wang H, Liu S, Mo J. 2010. Correlation between leaf litter and fine root decomposition among subtropical tree species. *Plant and Soil* **in press**.

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH, Wall DH. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629-1633.

Wardle DA, Barker GM, Bonner KI, Nicholson KS. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology* **86**: 405-420.

Warton DI, Wright IJ, Falster DS, Westoby M. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* **81**: 259-291.

Waterman PG, Mole S. 1994. *Analysis of phenolic plant metabolites*. Oxford: Blackwell Scientific.

Weedon JT, Cornwell WK, Cornelissen JHC, Zanne AE, Wirth C, Coomes DA. 2009. Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? *Ecology Letters* **12**: 45-56.

Wright IJ, Falster DS, 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.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M*, et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821-827.

Supporting information

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

Species	Abbreviation	Phylogeny	Plant type	Environment
Alnus incana	A.i	Core eudicot	Woody deciduous	Riparian
Angelica archangelica	A.a	Core eudicot	Forb	Riparian
Betula nana	B.n	Core eudicot	Woody deciduous	Terrestric
Betula pubescens	B.p	Core eudicot	Woody deciduous	Terrestric
Calamagrostis lapponica	C.l	Monocot	Graminoid	Terrestric
Caltha palustris	Ca.p	Early eudicot	Aquatic forb*	Aquatic*
Carex rostrata	C.r	Monocot	Graminoid	Riparian
Comarum palustre	Co.p	Core eudicot	Forb	Riparian
Cornus suecica	C.s	Core eudicot	Forb	Terrestric
Deschampsia cespitosa	D.c	Monocot	Graminoid	Riparian
Deschampsia flexuosa	D.f	Monocot	Graminoid	Terrestric
Empetrum nigrum	E.n	Core eudicot	Woody evergreen	Terrestric
Epilobium angustifolium	E.a	Core eudicot	Forb	Riparian
Equisetum fluviatile	E.f	Pteridophyte	Fern ally	Aquatic
Equisetum palustre	E.p	Pteridophyte	Fern ally	Riparian
Equisetum sylvaticum	E.s	Pteridophyte	Fern ally	Terrestric
Filipendula ulmaria	F.u	Core eudicot	Forb	Riparian
Geranium sylvaticum	G.s	Core eudicot	Forb	Riparian
Hippurus vulgaris	H.v	Core eudicot	Aquatic forb	Aquatic
Juniperus communis	J.c	Gymnosperm	Woody evergreen	Terrestric
Lycopodium annotinum	L.a	Lycophyte	Fern ally	Terrestric
Menyanthes trifoliata	M.t	Core eudicot	Aquatic forb	Aquatic
Pinus sylvestris	P.s	Gymnosperm	Woody evergreen	Terrestric
Populus tremula	P.t	Core eudicot	Woody deciduous	Terrestric
Potamogeton alpinus	P.a	Monocot	Aquatic forb	Aquatic
Prunus padus	P.p	Core eudicot	Woody deciduous	Riparian
Ribes spicatum	Ri.s	Core eudicot	Woody deciduous	Riparian
Rubus saxatilis	Ru.s	Core eudicot	Forb	Riparian
Salix caprea	S.c	Core eudicot	Woody deciduous	Riparian
Salix lapponum	S.l	Core eudicot	Woody deciduous	Riparian
Salix phylicifolia	S.p	Core eudicot	Woody deciduous	Riparian
Saussurea alpina	Sa.a	Core eudicot	Forb	Riparian
Sorbus aucuparia	So.a	Core eudicot	Woody deciduous	Riparian
Sparganium angustifolium	Sp.a	Monocot	Aquatic forb	Aquatic
Trientalis europaea	Tri.e	Core eudicot	Forb	Terrestric
Trollius europaeus	Tro.e	Early eudicot	Forb	Riparian
Utricularia vulgaris	U.v.	Core eudicot	Aquatic forb	Aquatic
Vaccinium myrtillus	V.m	Core eudicot	Woody deciduous	Terrestric
Vaccinium uliginosum	V.u	Core eudicot	Woody deciduous	Terrestric
Vaccinium vitis-idea	V.v	Core eudicot	Woody evergreen	Terrestric

Nomenclature follows Mossberg et al. (1992). * Although being rather riparian than aquatic, *Caltha palustris* was found mostly in and collected from ponds

Mossberg, B., Stenberg, L. & Ericsson, S. (1992). Den Nordiska Floran. Wahlström & Widstrand, Stockholm, Sweden.

Appendix S2. *Assessing long-term coarse stem and root decomposition rates from short-term experimental setup* – Protocol for coarse stem & root sampling and the fitting of decomposition models via iterative optimization procedure

Sampling

All six tree species (*Betula pubescens*, *Pinus sylvestris*, *Alnus incana*, *Populus tremula*, *Sorbus aucuparia* and *Salix caprea*) were sampled for woody stems and two of them, *Betula p.* and *Pinus s.*, were also sampled for woody roots. The sampling was done from mid-August to mid-October 2007 and complemented in April 2008. Owing to the young age and low stature of the forest, the average diameter of woody debris fragments (WD) was relatively low. To ensure a homogeneous sampling, only the most represented size class of WD was considered, that is, logs of 5 ± 1.2 cm diameter. Only WD with a minimum length of 50 cm were sampled in order to get four replicate subsamples of 10 cm for the decomposition experiment and a central subsample of 10 cm for chemical and structural measurements. To ensure the representativeness of the central subsample with respect to the neighbouring subsamples used for the decomposition experiment, WD with heterogeneous external or internal appearance were discarded. In particular, WD with large branching knots or irregular shapes were avoided.

For each woody debris type (each species, stem and root), between two and three samples of newly dead material were identified and sampled in the field, on standing trees, according to both internal and external appearance of the wood. Following density measurements (see below), only the densest wood sample of each woody debris type was kept as representative of newly dead wood and other newly dead wood samples were discarded. For each woody debris type, WD were also sampled from various stages of decay. We aimed thereby to cover the widest possible range of wood decay stages. WD of which state of fragmentation did not allow the direct estimation of initial wood density were avoided. After sawing them into five 10-cm long cylindrical subsamples, WD were cleaned of alien material, then air-dried and stored in paper bags pending further treatments and analyses.

Decomposition study

We used the central subsample of each WD to estimate density, residual moisture and chemical and structural traits of the whole WD. Residual moisture of each sample was estimated as the ratio of the difference between air-dry and oven-dry weight to air-dry weight. Oven-dry weight was measured after 96h at 60°C. We estimated wood density (mg cm^{-3}) as the ratio of wood oven-dry weight (mg) to volume (cm^3). The volume was estimated on the air-dry central subsample both by volume displacement in a graduated glass column and by measurement of length and diameter (taken as the average of three cross-section segments, applying the cylinder formula to each) and, considering the low deviation between the two measures, taken as the mean of both estimations.

For each WD (from newly dead to the most decayed ones), the four remaining air-dry subsamples were weighed separately and sealed into nylon litter bags of 1 mm mesh-size, which allowed exchange of microorganisms and small soil invertebrates. Measured air-dry weights were corrected for residual moisture. The litter-bags were incubated in outdoor litterbeds of Abisko Research Station, on 23 April 2008, following the same protocol as for other litter materials, as described in the main manuscript.

The litter-bags were harvested after two full years of incubation, on 23 April 2010, while still frozen and stored at -16°C pending further processing. After defrosting, adhering soil, soil fauna and other alien material were removed from the decaying WD subsamples by gentle brushing and rinsing with tap water. WD subsamples were then dried (60°C, 96 h) and re-weighed. The % mass loss of each replicate subsample was calculated from the fraction of its dry weight after decomposition to its original dry weight. For each replicate subsample, wood density after decomposition was estimated by recalculating the wood density of the related WD central subsample after accounting for the replicate subsample % mass loss. These calculations assumed a constant volume before and after incubation in order to avoid biases related to material fragmentation leading to density underestimation (Christensen 1984). Original volume, and therefore density, can not always be derived as accurately from very strongly decayed WD as it can from fresh WD.

Data analysis

For each woody debris type (e.g. *Betula p.* stem) all density measurements (*n* 'WD decay class' × pre- and post-incubation × 4 replicate subsamples) were standardized, i.e. divided by the density of the densest newly dead WD, to give relative wood density (RD) values, which ranged from 1 to 0. For each pair of pre- and post-incubation RD, the set of 4 replicate subsamples was averaged to produce one single average "two-year-decay-vector" (*sensu* Harmon *et al.* 2000). We obtained thus for each woody debris type a set of *n* vectors (with *n* from 5 to 16 depending on the woody debris type).

For each dataset (set of *n* vectors) three decay models were fitted using an iterative optimization procedure to describe the dynamics of RD. The models were (i) linear decay: $RD = 1 - mt$, (ii) negative exponential decay: $RD = e^{-kt}$ and (iii) sigmoid decay: $RD = 1 - (1 - e^{-at})^b$, where t is time in years and m, k, a and b are constants describing the species-specific decay. Each of these models assume RD = 1 at $t = 0$, with m, k and $a > 0$, $b \geq 1$ and $t \geq 0$.

Thus, the densest newly dead WD vector, with a pre-incubation RD of 1, was set at $t = 0$, which logically set the post-incubation end of the two-year-decay-vector at $t = 2$ (i.e. the incubation period, in years). The optimization then involved finding the position along the t axis of the remaining '$n - 1$' vectors that minimized the residual variance (σ^2) for a given decay model. Optimization was carried out using the optim() function in R (R Development Core Team, 2009) combined with lm() function for the linear decay model and nls() function for the negative exponential and sigmoid decay models.

Prior testing using simulated datasets indicated that success or failure of the nls() fitting was sensitive to the choice of starter values for the optimization, both for values of t and the parameters a and b in the sigmoid regression procedures. To decrease the risk of failure we provided the sigmoid model with realistic initial t values for each vector based on a linear decay model (based on the average slope of all vectors) and used the same mean slope as the starting value for a. For consistency we set the same initial t values for the linear and exponential model optimization procedures and used the same mean slope as the starting value for m and k. For each woody debris type, once optimization procedures had been performed for each distinct model (linear, exponential, sigmoid), the decay model that provided the lowest σ^2 was selected and used to calculate the woody debris type decomposition half-life ($T_{1/2}$). Because these $T_{1/2}$ were derived from simultaneous incubations with those of litter samples from other

plant organs, in the same litterbeds, $T_{1/2}$ of all litters could be compared directly to represent decomposability.

References

Christensen O. (1984). The states of decay of woody litter determined by the relative density. *Oikos*, 42, 211-219.

Harmon M.E., Krankina O.N. & Sexton J. (2000). Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Canadian Journal of Forest Research*, 30, 76-84.

R Development Core Team (2009). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Table S1. Contributions (%) of organ traits to the construction of 1st and 2nd axis of **(a)** each organ PCA and **(b)** whole-plant PCA

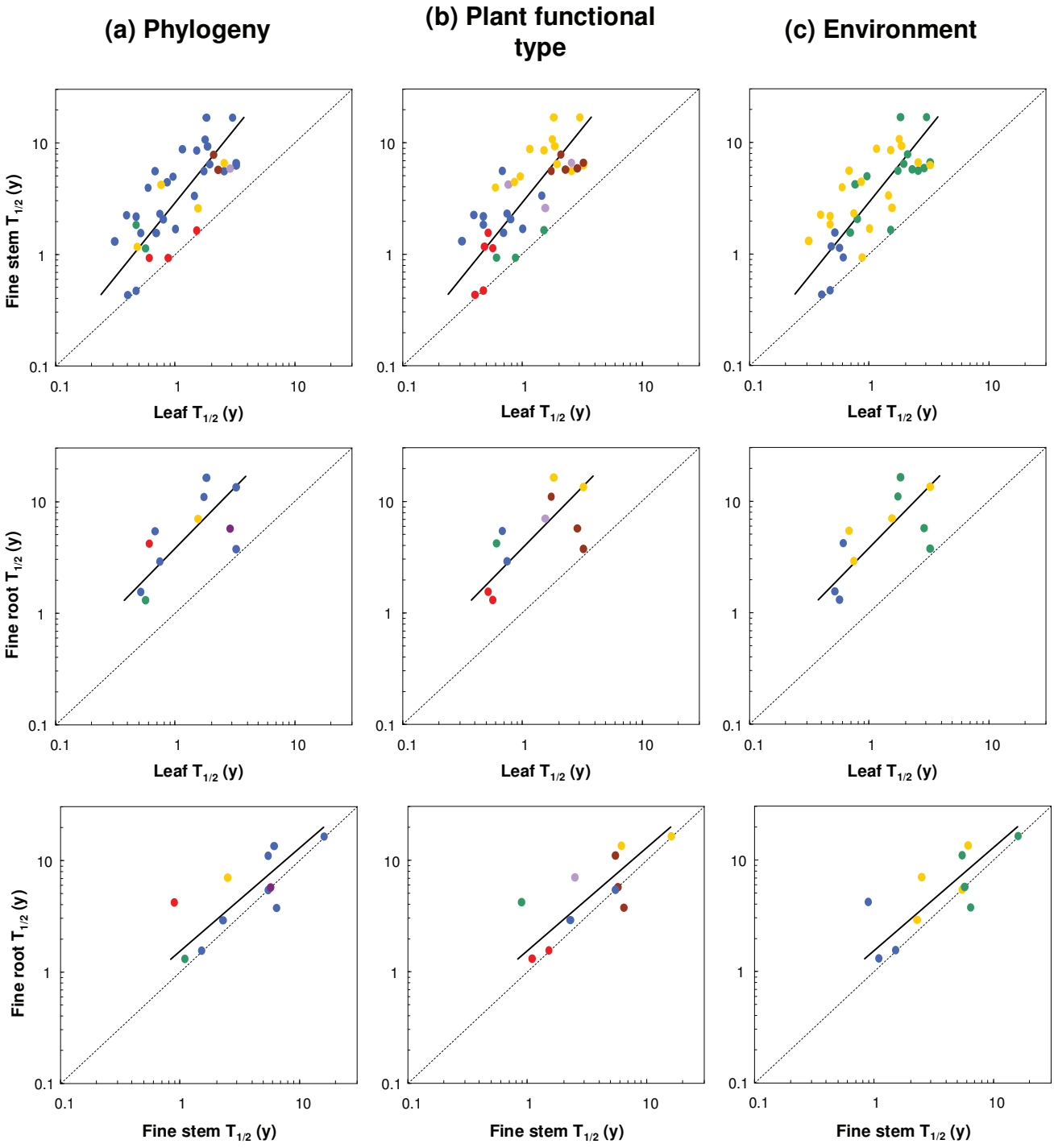
(a)	Leaf PCA		Stem PCA		Root PCA	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
SLA (mm^2 mg^{-1})	12.3	10.4	–	–	–	–
DMC (mg g^{-1})	21.2	0.4	24.7	5.8	16.4	5.3
N (%)	17.7	0.6	10.9	44.3	25.5	6.8
C / N	20.4	0.3	17.3	25.8	28.5	1.8
P (%)	1.8	87.7	7.9	3.1	3.0	62.8
Lignin (%)	13.0	0.0	23.2	4.2	10.4	11.2
pH	13.6	0.7	16.0	16.8	16.3	12.0
% variance explained	54.2	14.4	57.0	22.3	47.3	19.9

Axis 1 represents the leaf, stem and root economics spectra, respectively.

(b)		Whole-plant PCA	
		Axis 1	Axis 2
Leaf	SLA (mm^2 mg^{-1})	5.9	6.1
	DMC (mg g^{-1})	9.4	0.9
	N (%)	5.3	3.6
	C / N	6.7	1.3
	P (%)	0.6	0.0
	Lignin (%)	6.0	7.9
	pH	6.3	1.4
Stem	DMC (mg g^{-1})	8.9	6.0
	N (%)	3.4	10.8
	C / N	6.2	5.3
	P (%)	2.3	0.8
	Lignin (%)	8.0	5.3
	pH	6.8	10.3
Root	DMC (mg g^{-1})	4.7	0.0
	N (%)	3.5	13.7
	C / N	4.8	6.1
	P (%)	0.0	0.6
	Lignin (%)	7.7	8.3
	pH	3.8	11.5
% variance explained		43.3	11.6

Axis 1 represents the plant economics spectrum (PES).

Figure S1. Biplots of leaf, fine stem and fine root decomposability relationships (with SMA regression lines), as seen from environmental, plant functional type and phylogenetic perspectives. Symbols: **(a)** ● Basal eudicot, ● Core eudicot, ● Gymnosperm, ● Lycophyte, ● Monocot, ● Pteridophyte; **(b)** ● Aquatic forb, ● Fern ally, ● Forb, ● Graminoid, ● Woody deciduous, ● Woody evergreen; **(c)** ● Aquatic, ● Riparian, ● Terrestrial.



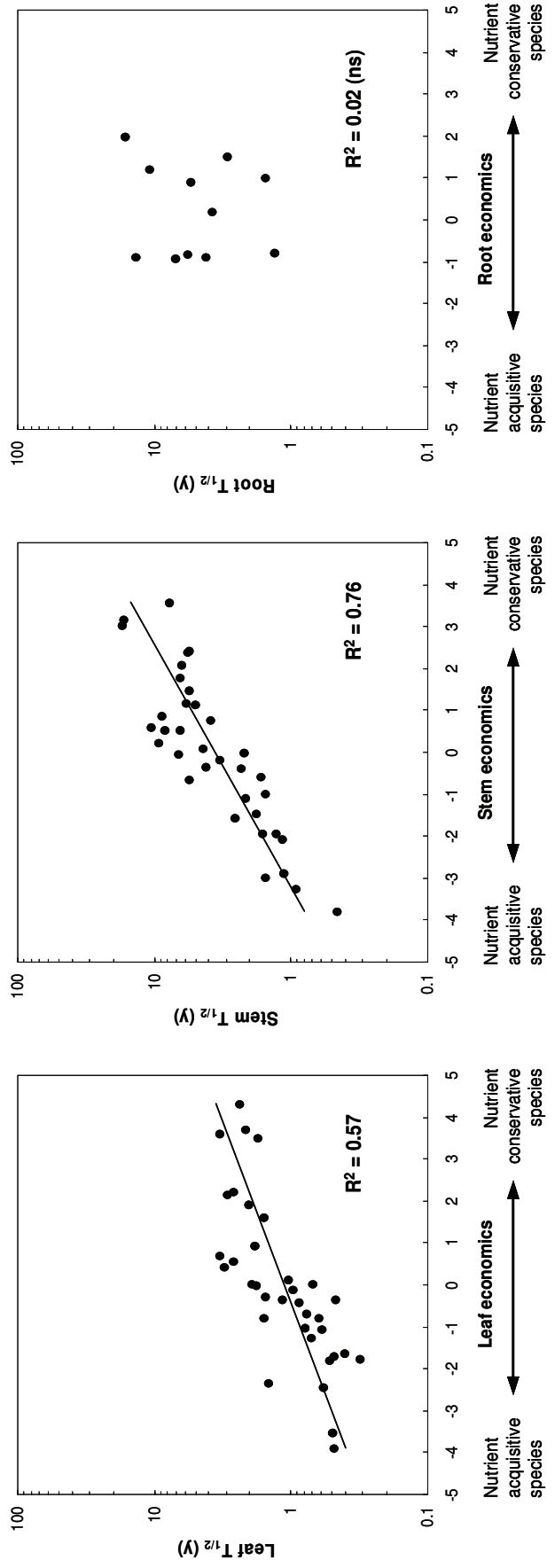


Figure S2. Relationships between leaf, fine stem and fine root economics and their respective decomposition half-lives ($T_{1/2}$). R^2: OLS regression coefficient; ns: non-significant P-value