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Is there a tree economics spectrum of decomposability?

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ABSTRACT

The plant economics spectrum (PES) integrates trade-offs and coordination in resource traits among species within and between organs, and affects ecosystem processes such as litter decomposition. This PES is currently based on trait variation among a wide range of plant types and growth forms. Here we ask whether the PES also features within the same growth form, i.e. within and between organs among temperate tree species. If so, is there a tree economics spectrum (TES) of decomposability driving the decomposition rates across the coarse branches, twigs and leaves of different species? And how robust would this TES of decomposability be to different environmental conditions?

To investigate these questions, we conducted a "common garden decomposition experiment" with ten temperate tree species in two contrasting forest environments in the Netherlands for 47 months. We evaluated the effects of functional traits of leaves, twigs, branch wood and branch bark on the decomposition rates of those organs. We measured the same resource traits for all those organs of the ten tree species and assessed whether there was a multivariate axis of functional traits explaining decomposition rates in both environments.

We report three key findings. First, tree organ specific economics spectra were significantly correlated with each other for the studied tree species. Second, tree organs differ significantly in decomposition rates, i.e. leaves were consistently more decomposable than twigs and twigs more than coarse branches. Third, we found some evidence of a TES with important afterlife effects driving coordinated decomposability of twigs and leaves but not of coarse branches across the tree species, and the effects of this TES on decomposition rates strongly depended on local forest environment.

The consistent contrasting decomposability between tree organs across species confirms an important role of plant litter inputs of different organs in forest biogeochemistry and carbon storage. There is also substantial coordination of interspecific trait variation between the finer tree organs. Knowledge about relationships of the TES and decomposability taking interactions with environmental variation into account can help for predicting whole-tree carbon and nutrient turnover as dependent on forest and soil type, even within the same climate zone.

1. Introduction

Plant litter decomposition is a major driver of carbon and nutrient cycling in terrestrial ecosystems (Parton et al., 2007), and affects local soil formation and global atmospheric composition (Canadell et al., 2007). Decomposition of plant material is strongly determined by climate (Berg et al., 1993; Parton et al., 2007), substrate quality (Aerts, 1997; Cornwell et al., 2008), and activity of soil organisms (Lavelle

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et al., 2006; Swift et al., 1979). These controls operate hierarchically to influence the decomposition. At regional to global scales, climate and litter quality were found as co-dominant factors (Cornwell et al., 2008; Wall et al., 2008; Bradford et al., 2016). Bradford et al. (2017) found decomposers strongly regulate decomposition at regional scales. Within biomes, climate often fails to predict decomposition rates (Bradford et al., 2014), while local environmental parameters, such as soil fertility, decomposer activity, and litter quality are strong predictors of the decomposition rates. On the plot scale, litter quality is known to explain much of the variation in decomposition rates, especially when measured as plant functional traits associated with plant acquisitive or conservative resource strategies (Chambers et al., 2000; Cornelissen et al., 2004; Cornwell et al., 2008; Weedon et al., 2009; Pietsch et al., 2014). Plant litter derives from different plant parts such as leaves, flowers, seeds, wood and bark. A wealth of information exists on leaf litter decomposition and the factors that drive their decay rates (e.g. Cornelissen et al., 1999; Cornwell et al., 2008; Makkonen et al., 2012). However, much less is known about the decomposition of twigs and coarse branches, although these woody plant components represent a substantial proportion of total litter fall and organically bound elements in forest soils (Harmon et al., 1986; Dearden et al., 2006; Chave et al., 2009; Cornwell et al., 2009). Moreover, the question arises if species with rapidly decaying leaf litter also have rapidly decaying twigs and branches; in other words whether organ specific decomposability within species covaries. Understanding the variation of decomposition within and between plant organs across species is of vital importance for predicting biogeochemical cycles under global change (Chapin et al., 2009; Brovkin et al., 2012; Pietsch et al., 2014).

Plant organs have marked differences in function, morphology, physiology and microenvironment, which imply a large variation in ecology and associated functional traits. If traits are coordinated among plant organs and affect decomposability, there might be a cross-species economics spectrum driving parallel decomposition relationships across plant organs. In one of the few studies on coordinated traits for litter decomposition, Freschet et al. (2012a) found a plant economics spectrum (PES) of litter decomposability which integrates trade-offs and coordination in resource traits among species within and between organs. They demonstrated that the PES had important afterlife effects on carbon turnover by driving coordinated decomposition rates of different organs (leaves, stem, roots) across a wide range of subarctic plants. However, this PES was investigated across a wide range of growth forms, from small herbaceous plants to large trees. Whether resource economic traits are also coordinated and affect decomposability across organs within a single growth form, as hypothesised by Reich (2014), has not been proven yet. Recent studies have not shown any convincing evidence in support of a PES within growth forms (Jackson et al., 2013; Pietsch et al., 2014; Zanne et al., 2015). For example, Zanne et al. (2015) found endogenous factors, including species identity and tissue construction, had stronger control on decay rates than exogenous factors across plant tissues. Perhaps one source of deviation from a general PES of decomposability is that it may manifest itself differently in different sites varying in other biotic (e.g. decomposer communities) and abiotic (e.g. soil, micro- and macroclimatic) drivers. Local forest environment may vary in both abiotic and biological parameters that determine decomposition. Trees can respond to abiotic conditions physiologically and biochemically and, as a consequence, produce litter of different qualities (Flanagan and Van Cleve, 1983; Hobbie, 1992). Soil moisture, and composition of both microbial and faunal decomposer communities, can directly influence the decomposition process (Bradford et al., 2002). The interactions with environment can confound the decomposition drivers.

The aim of this study was therefore to assess the effects of multiple abiotic and biotic factors, tree species, organ type and incubation environment, on decomposition rates across the three tree organs, i.e. leaves, twigs, and coarse branches, varying in resource trait values. We asked whether the PES also exists within the dominant growth form in forest ecosystems, as a tree economics spectrum (TES) in temperate forests. We hypothesise that if economics spectra are coordinated in dead tree crown organs, then the TES combining these organs might drive coordinated interspecific variation in the decomposabilities of different organs but this coordination might interact with environment. We expect, (1) leaves, twigs and branches of species with trait values reflecting an acquisitive resource strategy would decompose faster than those of species with a conservative resource strategy (*sensu* Freschet et al., 2012a; Reich, 2014; Diaz et al., 2016). Therefore, the predictive power of TES for decomposition will be consistent with each organ's specific economics spectrum. (2) At a local scale, decomposition is controlled by plant functional trait variation determining litter quality, heterogeneity in soil, microclimate and the decomposer community and their interactions (Hättenschwiler et al., 2005; Cornelissen et al., 2012; Freschet et al., 2012b; Bradford et al., 2014), however the effect strengths of functional traits and TES′ predictive power of decomposability will be robust to such interactions.

To test the hypothesis and predictions, we carried out a “common garden decomposition experiment” sensu Cornelissen (1996) studying the traits of different plant organs, i.e. leaves, twigs, branches (wood and bark), and the decomposition rates of those organs for 47 months, among ten co-occurring tree species in two contrasting temperate forest types and their environments on infertile sandy soil and fertile clayey soil.

2. Materials and methods

2.1. Study area and tree species

To test the impact of soil environment on decomposition of different plant organs, two environmentally contrasting sites were selected to represent two predominant temperate forest types and soils in NW Europe: (1) the Hollandse Hout forest plantation in Flevoland (hereafter site F) (Lat. 52.46 N, Long. 5.42 E) and (2) the forest estate Schovenhorst in the Veluwe region (hereafter site S) (Lat. 52.25 N, Long. 5.63 E). Both sites are located in the central part of the Netherlands. Site F was reclaimed from the former Zuiderzee in the 1960s; it has a relatively young marine clay soil, and is calcareous, moist and fertile, with a pH close to neutrality. This site mainly consists of monospecific plantations used for commercial forestry. In contrast, site S is much older and has a sandy and podzolic soil that is well-drained. The soil is acidic and has low fertility. Further site details are given in Cornelissen et al. (2012).

The incubation plot at site F was a relatively light-open *Populus x canadensis* Moench stand with a dense herb layer dominated by the nitrophylic herbs *Urtica dioica* L. and *Galium aparine* L. The incubation plot at site S was *a Larix kaempferi* (Lambert) Carriere stand that was also relatively light-open. It had a low and dense ground layer of predominantly the acidophilic grass *Deschampsia flexuosa* (L.) Trin. intermingled with mosses and patches of the dwarf shrub *Vaccinium myrtillus* L. More information about the incubation sites can be found above and in Cornelissen et al. (2012).

2.2. Sampling

Six tree species were sampled per site, with two species overlapping, giving in the two sites combined a total of ten species, i.e. six broad-leaved and four coniferous species (see tree species list, extraction site and abbreviations in Table 1). All selected species are important and representative for NW European forests or forestry plantations. *Quercus robur* L. and *Picea abies* (L.) Karst. were sampled from both sites in order to compare the effects of growing conditions on intraspecific variability in plant organ functional traits and decomposability. Because the collection site had a significant effect on traits (Fig. S1, Supplementary material) and litter mass loss for *Q. robur* and *P. abies* (Table S1, Supplementary material), we treated the same species collected from two

Table 1
Tree species and their two environmentally contrasting collection sites in the experiment (Cornelissen et al., 2012). F, site Flevoland-Hollandse Hout; S, site Schovenhorst -Veluwe. Species in bold typeface were extracted from both sites. All species were incubated in both sites.

Collection Site	Tree species	Abbreviation	Family	
F	*Betula pendula*	FBET	Betulaceae	Angiosperms
F	*Fagus sylvatica*	FFSY	Fagaceae	Angiosperms
F	*Fraxinus excelsior*	FFEX	Oleaceae	Angiosperms
F	***Picea abies***	FPAB	Pinaceae	Gymnosperms
F	*Populus x canadensis*	FPOP	Salicaceae	Angiosperms
F	***Quercus robur***	FQRO	Fagaceae	Angiosperms
S	*Abies grandis*	SAGR	Pinaceae	Gymnosperms
S	*Larix kaempferi*	SLKA	Pinaceae	Gymnosperms
S	***Picea abies***	SPAB	Pinaceae	Gymnosperms
S	*Populus tremula*	SPTR	Salicaceae	Angiosperms
S	*Pseudotsuga menziesii*	SPME	Pinaceae	Gymnosperms
S	***Quercus robur***	SQRO	Fagaceae	Angiosperms

sites as separate "species" when analyzing the relationship of functional traits and decomposability.

Between mid-January and mid-February 2012, we extracted in total 120 trees from the two forest sites. Ten healthy trees of each species with a trunk diameter of approximately 25 cm at mid-height were cut and samples from plant organs were collected. From each tree crown we cut six 20-cm long branch sections of 5 ± 0.5 cm diameter (5 for incubation decomposition experiment, 1 for initial trait measurements), and at least 40 terminal twigs (cut from the end part of small branches) of 15 cm in length. In autumn 2012, we collected undecomposed leaf litter of each tree species from the two tree extraction sites at time of leaf fall. At the same time naturally senesced but undecomposed twigs (cut to 15 cm length) of two tree species from each site were sampled from the ground in order to compare the effects of life stage (freshly cut versus naturally senesced) on intraspecific variation of functional traits and decomposability. All the plant materials were air dried (20 °C) and stored in open paper bags in the laboratory. We chose to use different life stages (freshly cut versus naturally senesced) for different plant organs because of field relevance; leaves of most species turn over and are shed on an annual basis (and evergreens after 1–3 years), so leaf litter is the most relevant stage to enter the decomposition cycle. Many fresh branches and twigs are left after forestry operations and after wind throw, so the proportion of non-senesced branches and twigs entering the decomposition subsystem is rather high in our forests. Twigs are intermediate in this respect, with both living twigs (forestry, storms, see above) and dead twigs (natural senescence with intermediate shedding time compared to leaves and branches) entering the litter layer in significant proportions.

2.3. Plant organ functional trait measurements

All collected plant organs were measured for initial functional trait values including dry matter content (DMC), carbon (C), nitrogen (N), phosphorus (P) and lignin content, and pH_{H2O}. Leaf litter, twigs and branches were measured for DMC following Cornelissen et al. (2003). The samples were immersed in tap water till a constant weight to ensure homogeneous filling of air spaces, then wiped gently with a dry tissue and measured for their water saturated weight. Subsequently dry weight was measured after drying in an oven until constant weight at 70 °C. DMC was expressed as the ratio between dry weight and water saturated weight (to the nearest 0.001 g for leaves and twigs, 0.01 g for branches). For all other analyses, air-dried subsamples were ground using a MM200 ball mixer (Retsch, Haan, Germany), and subsequently oven-dried for 24 h at 70 °C. For branches, bark and wood were ground separately because they have different trait values which might drive decomposition differently.

C and N content was measured by dry combustion on a Flash EA 1112 elemental analyser (Thermo Scientific, Rodana, Italy). For P content, a 50 mg subsample was digested in 1 ml of a 1: 4 mixture of 37% (v / v) HCl and 65% (v / v) HNO_3, in a closed Teflon cylinder for 6 h at 140 °C. Samples were then diluted with 4 ml demineralized water and total P content was quantified by spectrophotometry, using the ammonium molybdate method (Murphy and Riley, 1962).

Lignin content was determined following Poorter and Villar (1997). Briefly, the ground material were put through 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 content, were measured. The lignin content was then calculated based on the difference in C content of lignin and cellulose, after correction for remaining proteins.

The pH_{H2O} was measured following Cornelissen et al. (2006), by shaking 0.15 ml ground sample with 1.2 ml demineralized water in an Eppendorf tube for 1 h at 250 rpm. After shaking, the tubes were centrifuged for 5 min at 13,000 rpm and the supernatant measured using a narrow (5 mm diameter) SenTix Mic electrode connected to an Inolab Level 2 pH meter (both: WTW, Weilheim, Germany).

2.4. Reciprocal decomposition study

In December 2012, leaf, twig and branch samples were introduced in the two incubation sites. Before incubation, samples of air dried leaves (around 1.0 g) were weighed and sealed into separate nylon litter bags (10 cm × 8 cm, 1 mm mesh size). For needle-leaf litter 0.5 mm mesh size was used for the bottom part of the litter bag to retain the needles. Twigs (around 4 pieces of 15 cm long) were weighed and sealed in 20 cm × 3 cm litterbags (1 mm mesh size). Samples of air-dried single branches (20 cm long × 5 ± 0.5 cm diameter) were weighed, then sealed into litter bags (28 cm × 10 cm, 10 mm mesh size). To compare the effect of 1 mm and 10 mm mesh size, freshly cut twig subsamples of 6 tree species were weighed and sealed in 20 cm × 3 cm litterbags (10 mm mesh size). The result showed that after 5 months of decay, the mass loss of freshly cut twig did not differ significantly between the mesh sizes (Table S2, Supplementary material). In total 1660 litter bags were made. In total 360 litter bags for leaf litter (6 tree species × 2 collection sites × 5 replicates × 2 incubation environments × 3 harvest times), 480 litter bags for freshly cut twigs (6 tree species × 2 collection sites × 5 replicates × 2 incubation environments × 4 harvest times), 160 litter bags for naturally senesced twigs (2 tree species × 2 collection sites × 5 replicates × 2 incubation environments × 4 harvest times), and 600 litter bags for branches (6 tree species × 2 collection sites × 5 replicates × 2 incubation environments × 5 harvest times) were included in this study. An additional subset 60 litter bags for freshly cut twig in 10 mm mesh size (3 tree species × 2 collection sites × 5 replicates × 2 incubation environments × 1 harvest times) was included for comparison with 1 mm mesh size.

At the two incubation sites, material from each tree individual had its own plot representing a statistical block. The five blocks per site measured 12 by 12 m each with minimum distances of 20 m between blocks. Logs and branches already present in the blocks were removed before litter bag placement. Each of the blocks in site S had a 1.2 m high fence to keep out the wild boar that are abundant in this area. Within each block, the litter bags were positioned on the soil surface making good contact with the soil by means of a large-mesh net stretched rather tightly across (Cornelissen et al., 2012).

Litter bags were harvested at different time intervals after incubation to account for differences in decomposition rate of the various plant organs. The intervals between harvests differed between organ

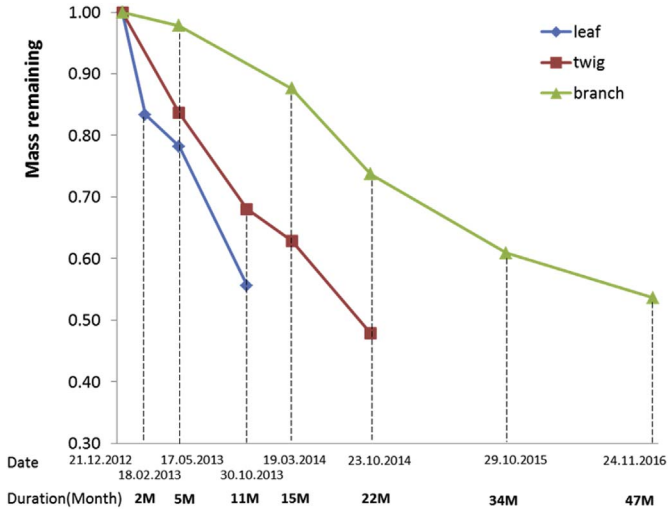

Fig. 1. Average fraction of initial litter mass remaining at all harvest dates and durations since decomposition started for each litter type. This graph, in which species averages integrate species and incubation sites, is meant to justify the harvesting regime.

type, and decreased from branches via twigs to leaf litter (Fig. 1). Leaf litter bags were retrieved three times, after 2, 5 and 11 months and twigs four times, after 5, 11, 15 and 22 months, while branches were sampled five times, after 5, 15, 22, 34 and 47 months, respectively.

2.5. Data analysis

Branch functional traits were measured separately for bark and wood, and those two components were treated as two separate organs when analysing the initial traits. In order to quantify the main axes of overall functional trait variation in the plant organs a Principal Component Analysis (PCA) was performed. In the PCA we included leaf litter, freshly cut twigs and branches, but not the senesced twigs because (1) we wanted to avoid that the same organ was included twice in the analysis, and (2) senesced twig material was not collected for all tree species which would have resulted in an unbalanced analysis.

To test for differences in decomposition rates between plant organs we calculated decay rates (k) through the first order decay function: $M_t = M_0 e^{-kt}$, where M_t denotes plant organ dry mass at the time t, and M_0 gives the initial plant organ dry mass of the sample. k was first calculated for each replicate, and then average over the five replicates.

Pearson's correlation analysis was used for correlations between the first PCA axis scores of tree organs and between each organ with TES combining all organs; and for the relationships between functional traits and decomposition rates. Linear regression was used to test the relationship between decomposition rate and the first PCA axis scores across tree species, for each organ and for TES combining all organs. Normality and homogeneity of residual variances were visually estimated by residual plots and normal probability plots using the plot function in *R* (R Core Team, 2014).

To test the effects of different factors (tree species, organ type, incubation site) for plant organ decomposition rate simultaneously, we performed a three-way repeated measure ANOVA, with organ as within-subject factor (3 levels; leaf, twig and branch), and tree species (12 levels, the actual species) and incubation site (2 levels; high fertility site F and low fertility site S) as between-subject factors. Normality of the data was visually checked by Q-Q plots, and k values were $\log_{10}(k+1)$ transformed to correct for residuals deviations from normality. Mauchley's test was used to test for sphericity.

To test the effects of tree species and incubation sites on decomposition rate for each plant organ a two-way factorial ANOVA was used with tree species and site as factors, as well as for the comparison of the two decay stages of twigs, i.e. freshly cut *vs* senesced.

All statistical analyses were performed in *R* language version 3.0.3 (R Core Team, 2014).

3. Results

3.1. Correlation of organ specific and tree economics spectra

To assess whether functional traits were coordinated within organs, a separate PCA was carried out per organ. The first PCA axis (PC1) accounted for 61.1% of the trait variation for leaf litter (Fig. S2a, Supplementary material), 48.9% of that for twigs (Fig. S2b) and 32.5% for branches (Fig. S2c). The PC1 axes of three organs were significantly related to each other (Fig. 2). To assess whether traits were also coordinated across organs, a single PCA was carried out for all organ traits (Fig. S2d), with the first two axes accounting for 59.0% of the total trait variation. The PC1 axis, accounting for 39.8% of the variance, was mostly determined by structure-related traits (DMC, and C and lignin content), nutrient content (mostly P) and pH. The PC1 axis of tree (all organs) was significantly related to PC1 axis of each organ (Table S3, Supplementary material). PCA ordination characterised and separated the tree species in two groups, i.e. angiosperms and gymnosperms (Fig. S2).

3.2. Correlation of tree organs decomposibilities

At their respective last harvesting date (i.e. after 11 months for leaves, 22 months for twigs and 47 months for branches), leaf litter displayed an average mass loss of 44.4% (ranging from 15.6% to 93.2% across species), freshly cut twigs 52.2% (ranging from 23.4% to 93.7%), senesced twigs 38.0% (ranging from 8.3% to 71.3%) and branches 46.4% (ranging from 11.0% to 96.9%) (Fig. 1, Table S4, Supplementary material for mass loss of each organ and each tree species). The harvesting regime in which the time intervals were longer for branches than for twigs and longer for twigs than leaves, ensured that the material decayed through more or less similar decomposition stages while also having overlap in absolute decomposition time.

The three factors, tree species, organs and incubation sites, all had significant effects on the decomposition rates. These factors also interacted (Table S5a, Supplementary material). The incubation site affected the decomposability of all plant litter (Table S5b) with generally

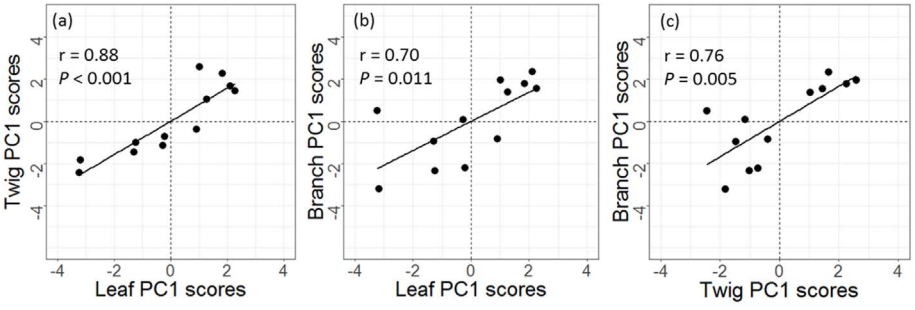

Fig. 2. Correlations between organ specific economics spectra for leaves, twigs and branches (combined branch DMC, branch bark and branch wood), as indicated by PCA first axis score. (a) leaf litter and twigs, (b) leaf litter and branches, (c) twigs and branches. The dots are the tree species.

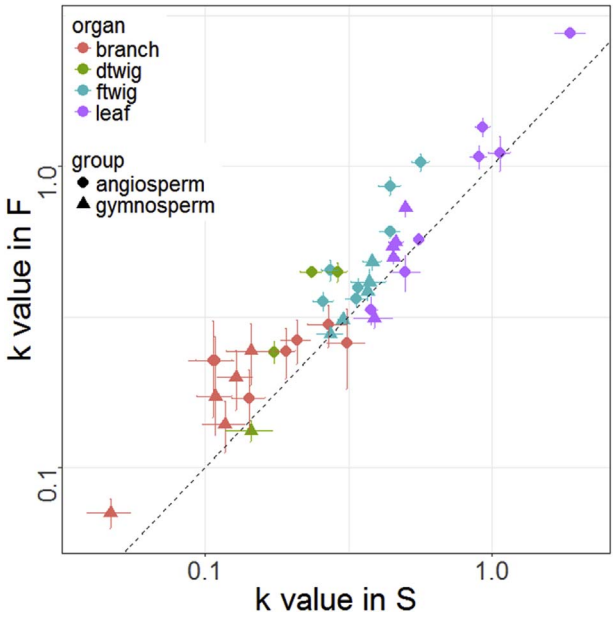

Fig. 3. Comparison of decomposability (k values) between two environmentally contrasting site. This is for different organs, leaf, twig and branch, for 10 sampled tree species; dead twig for 4 subsampled tree species. Tree species were separate to two groups, angiosperm and gymnosperm. The dashed line is the 1:1 line. Ftwig = freshly cut twig, and dtwig = dead (naturally senesced) twig. Bars indicate ± SE. Note axes are log10 scaled.

higher decomposition rates in the more fertile site F compared to less fertile site S. This is illustrated with the position of the *k*-values above the 1:1 line in Fig. 3.

Leaves decomposed generally faster than both twigs and branches, whereas twigs decomposed generally faster than branches (Fig. 3 and 4). Interspecific variations in leaves, twigs and branches were mostly not or weakly coordinated and showed several differences for plant organs and sites (Fig. 4). The covariation relationship was only significant for leaf vs. twig in site F. There was a lack of any co-variation between organs in the S site, i.e. the evidence for a coordination pattern depended on decomposition site.

3.3. Species, organ and local environment influenced on decomposability

When plant organs were analyzed separately, tree species had significant influence on decomposability for all organs (Table S5b). Within the same organ, in general angiosperms decomposed faster than gymnosperms (Fig. 3, Fig. S3, Supplementary material), and both decomposed faster in site F than in site S although not always significantly so (Fig. S3). For the sub-experiment comparing freshly cut twigs and senesced twigs, freshly cut twigs decomposed faster than senesced twigs, and consistent with the general pattern that decomposition rates were higher in site F than in site S (Fig. S4, Supplementary material).

The strong predictor traits driving decomposability were organ specific, but with overlap (Table S6, Supplementary material). All traits related to organ structure (DMC, and C and lignin content) and pH were good predictors of interspecific variation in decomposition of leaf litter in both sites. C and P content were good predictors of twig decomposition in both sites, while N content was a good predictor of twig decomposition but only in site F. The lignin content of branch wood was a good predictor of branch decomposition in both sites, branch wood C: N and lignin: N ratios were good predictors of branch decomposition in site F. More significant relationships between traits and decomposability were found with higher decomposition rates, i.e. for leaves than for branches.

3.4. Organ specific and tree economics spectra predicted decomposability

The PC1 axis score for leaves was a good predictor of litter decomposition rate in both sites (Fig. 5a), the PC1 axis score for twigs was a good predictor for decomposition rate in site F (Fig. 5b), while the predictive power of the PC1 axis score for branches was not significant for either site (Fig. 5c). Correlation analyses revealed significant relationships between the PC1 axis scores among all pairs of plant organs except for the pairs including bark (Fig. 2, Table S3). However, there was not a single organ trait axis that had an overall relationship with decomposability of all organs (Table S7, Supplementary material). PC1 axis combined all the organ traits representing the TES (Fig. S2), and was a highly significant predictor of the decomposability in both sites for leaf litter (Fig. 5d), while for twigs this relationship was only significant in site F (Fig. 5e) and for branches the relationship was not significant in either of the sites (Fig. 5f).

4. Discussion

Leaf, twig and branch economics spectra were related with each other to form a tree economics spectrum (TES) in terms of interspecific trait variation. Tree crown economics predicted decomposability for leaf litter and twigs reasonably well, while no clear prediction was found for the branches. Overall, the predictive power of the TES for decomposability was organ dependent and interacted with decomposition environment. Tree species, their organs, the growing environment of the trees and the decay environment, as well as interactions between these drivers, all influenced litter decomposition rates. Below, we discuss in more detail the effects and interactions of those multiple factors that control tree decomposition.

4.1. Correlation between functional traits of organs

We found that organ specific economics spectra were significantly correlated with each other. Our results are consistent with previous research finding coordinated trait variation between plant organs (Freschet et al., 2010; Kerkhoff et al., 2006; Reich, 2014). In contrast, Baraloto et al. (2010) found no correlation between coarse wood and leaf traits across tree species of tropical rain forests. Whether wood and leaf traits are coordinated or not differs strongly amongst studies (Wardle et al., 1998; Wright et al., 2007; Baraloto et al., 2010; Freschet et al., 2010; Pietsch et al., 2014), perhaps partly due to differences in tree life strategies and environmental factors in different biomes and partly to whether fine or coarse wood is involved. When branch bark was analyzed separately in our study, its economics spectrum was not

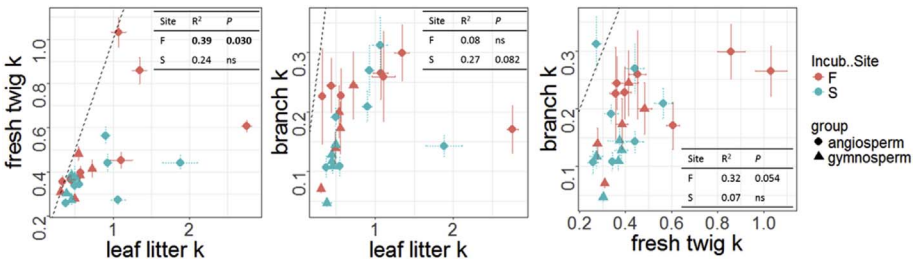

Fig. 4. Comparison of decomposability k values between tree organs. Inset: linear regressions (R^2 and *P* values) between k values of leaves, twigs and branches; k values were $\log_{10}(k+1)$ transformed.

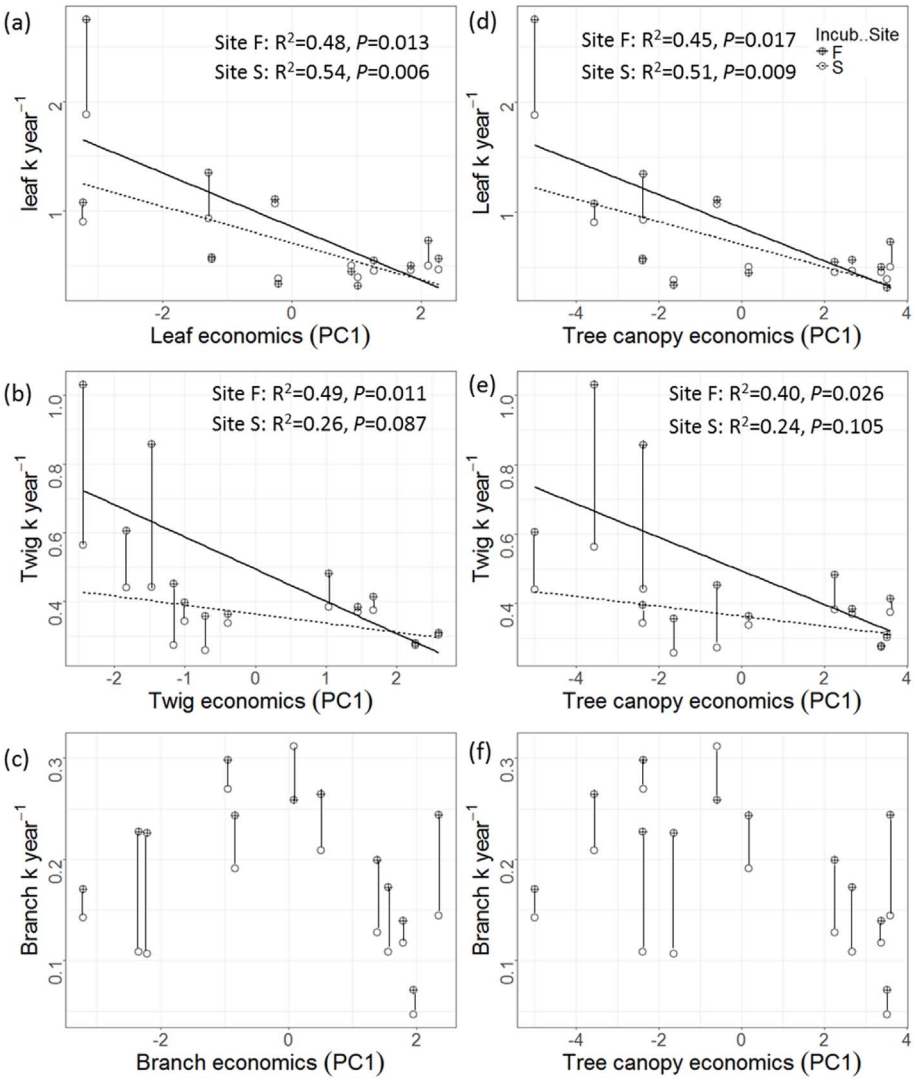

Fig. 5. Relationships between the PCA first axis (PC1) and decomposability. (a)–(c), relationships between organ specific PC1 and decomposability of (a) leaves, (b) twigs, and (c) branches. (d)–(f), relationships between tree economics spectra (combining all organs, PC1) and decomposability of (d) leaves, (e) twigs, and (f) branches. Vertical pairs of points are for the same tree species. The results are not different at all for any of the relationships if only including material of *Picea abies* and *Quercus robur* collected from the S site (Fig. S5, Supplementary material).

correlated with that of wood or other organs (Table S3). For bark traits, Rosell et al. (2015) found covariation of certain bark traits with some wood traits, and to a lesser degree with some leaf traits in tropical rainforests. We investigated different bark traits to explain dissimilar functions of the organs in this study, focusing on the afterlife traits that might predict decomposition. During decomposition, bark trait variation may relate to specific additional effects, e.g. to the colonisation by the decomposer fauna community (Zuo et al., 2016).

4.2. Effects of tree economics spectrum on decomposability

Whether or not the traits and decomposabilities of different tree organs are associated across species of different ecological strategies is important, as it indicates whether, at the whole-plant level, species either accelerate or slow down forest carbon and nutrient turnover (Freschet et al., 2013). The overall differences in decomposability between tree organs, decay of leaves > twigs > coarse branches, mainly because of variance in litter quality, confirmed previous findings (Zhang et al., 2008). We found that multiple chemical and structural factors affected litter decomposability of different organs within a single growth form, i.e. temperate tree species. Structure related traits (DMC and C and lignin concentrations) decreased leaf litter decomposability, and pH increased decomposability, confirming previous findings (Cornelissen et al., 2006; Fortunel et al., 2009; Freschet et al., 2012a). The effects of the other traits were organ or site specific. Decomposability of twigs was negatively related to C and positively to P content in both sites, but positively to N content, although only significantly so at the nutrient-rich site F. Branch decomposability was only related to P content and pH in the fertile site F. In this study the freshly cut branches were used principally. While this is an important primary form of branch matter input onto the forest floor in temperate forest, where e.g. heavy wind or logging activity can bring down large amounts of living branches, these branches might differ from naturally senesced branches in traits and their relationship with decomposability. There was evidence from twigs (Fig. S4) that life stage (freshly cut living versus naturally senesced) affected decomposition rates, freshly cut twigs decomposed faster than naturally senesced but undecomposed twigs of the same species. Thus, it appears that traits partly differ in their predictive power of decomposability for different organs, living versus senesced and between incubation sites. Such differences and interactions warrant in-depth investigation as they may have help to delimit the constraints on upscaling from site-level decomposition studies.

Coordination between decomposabilities of tree organs was expected to be driven by their economics spectra. But the coordination was found to depend on the pair of tree organs and the decay environment. Other studies (Jackson et al., 2013; Zanne et al., 2015) found that decomposability of wood is decoupled from that of leaves and twigs because wood decomposition is largely influenced by structural properties, whereas decomposition of leaves and twigs is related

to tissue chemistry. Pietsch et al. (2014) demonstrated that coarse wood and leaf traits are not correlated globally, except for the contrast between generally slow-decomposing leaves and wood in gymnosperms compared to angiosperms. In contrast, a certain degree of covariation in the decomposability of different tree crown organs was evident in our study, although only significantly so for leaves vs. twigs in site F. This means that tree species with faster decaying leaf litter had faster decaying twigs. Interactions were more important between species and organ, and weaker including site (Table S5).

The contrasting decomposabilities between tree organs suggest including all tree organs in decomposition studies will improve our understanding of overall forest ecosystem process, e.g. organic matter accumulation, nutrient dynamics and other aspects of biogeochemical cycling. In that sense, it would have been very valuable to include the decomposition rates of large logs as well, as they represent a major carbon pool, but four years would not have been enough to cover more than the initial log decomposition phase in the LOGLIFE experiment (Cornelissen et al., 2012). Another high priority for future contributions in this field would be to include roots of different tree species as a likely important component of the tree economics spectrum (Freschet et al., 2013).

Traits underpinning the leaf and twig economics spectra were good predictors for their decomposition rates, but there was not a single organ trait axis that had an overall relationship with the decomposability of all organs (Table S7). Instead of using one organ (mostly leaf traits) to explain litter afterlife effects, a more comprehensive method is to use a whole-tree economics spectrum (TES) approach which combines the decay of different organs. Freschet et al. (2010, 2012a) stated that at the whole-plant level, physiological and allometric connections between organs lead to coordinated trait variation across organs, which in turn drives organ decomposabilities across a large number of plant types. In support of our hypothesis, we found that the TES was consistent with the organ specific economics spectra. However, while we confirmed that the TES exists in temperate forests, reflecting integrated trait variation, the predictive power of TES for decomposition rate was weak to absent, organ specific and differed between two contrasting forests. In general, interspecific trait variation could predict decomposability of organs with relatively high decomposition rates (leaves and twigs) and failed to predict branch decomposability. Furthermore, while there was some effect of this TES on decomposability in fertile, base-rich F site, which had the higher decomposition rates overall, there was no clear evidence of coordinated decomposability in the infertile, acidic S site.

4.3. Forest environment influence the effect of litter traits on decomposition

The result that economics spectra of leaves, twigs, branch were coordinated with each other is consistent with previous research (e.g. Jackson et al., 2013), and we carried out the experiment *in situ* in forest stands and took decay environments into account. Our findings indicated that the pattern of decomposability across species was influenced by incubation site, i.e. environmental factors.

Within a biome, the local environmental parameters and litter quality determine decomposition rates (e.g. Freschet et al., 2012b). These local environmental parameters consist of abiotic factors and the adapted decomposer community. In a more nutrient-rich environment, litter decay is generally faster. In this study, this was generally the case but there were several exceptions for individual species and organs. This indicates that the litter quality of our samples may have interacted with the quality of the matrix litter and its decomposer community (Freschet et al., 2012b). The mesh size would make effects dependent on species and site, as it includes the interactions with fungal and faunal decomposers (Bradford et al., 2002). While we found evidence for leaves and twigs that the TES controlled the decomposability across tree species, the predictive power of TES differed between the two contrasting forest environments. Thus our third prediction that the TES of decomposability should be robust to environmental variation was not supported. The forest environment where trees had grown may also have influenced the litter quality, and thereby decomposition, as indicated by the finding that *Q. robur* and *P. abies* sampled from both sites had variability in functional traits (Fig. S1) and litter mass loss (Table S1). The two incubation sites were located in the same climate zone but differed in terms of soil chemistry, texture, moisture and vegetation type. The local environment (especially soil type) strongly influences the composition of the decomposer community (Berg et al., 2008). Zuo et al. (2014) also found that the macro-detritivore community composition was influenced by the environment in which decomposition took place. The macro-detritivore abundance at site F was higher than at site S, as was expected due to the moister and more fertile, base-rich soil in site F. In general, clay soils, with a higher pH and soil moisture during the drier months of the year are more favorable to macro-detritivores; they tend to have a higher diversity and abundance. Well drained sandy soils, as in site S, are often dry in summer, posing drought stress to soil fauna (Paoletti and Hassall, 1999; Berg et al., 2008). Moreover, the soil at site S is acidic, adding an additional potential stress factor to the decomposer community.

4.4. Outlook and conclusion

Consistent with the previously reported plant economics spectrum of decomposability over a wide range of plant types, we confirmed the existence of an economics spectrum within a single life form, i.e. trees. However, the relationship between plant economics spectra and decomposability differed with the organ type and local environment. Taking into account all of the different organs is a useful approach to describe the impact of whole plant strategies on ecological processes such as decomposition. An important addition in view of whole-tree carbon turnover, not covered here, is to account for the different total biomass pools of different organs entering the decomposition subsystem (Freschet et al., 2013). In general, a better understanding of the relationship between functional traits and ecological processes across contrasting tree organs and contrasting environments, will greatly improve the understanding of forest ecosystem functions and services under global change.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2018.01.019.

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