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SPECIAL FEATURE – STANDARD PAPER

WHETHER IN LIFE OR IN DEATH: FRESH PERSPECTIVES ON HOW PLANTS AFFECT BIOGEOCHEMICAL CYCLING

A deteriorating state of affairs: How endogenous and exogenous factors determine plant decay rates

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Summary

1. Woody plants store large quantities of carbon (C) and nutrients. As plants senesce and decay, these stores transfer to the soil or other organisms or are released to the atmosphere.

2. Exogenous factors such as topographic position and microclimatic and edaphic conditions tied to locations affect decay rates; however, we know less about how exogenous relative to endogenous factors such as morphological, anatomical and chemical construction tied to plant species affect these rates, especially across different tissue types.

3. We monitored stem, fine branch and leaf decay over 1 year in 'rot plots' distributed across four watersheds in ridge top and valley bottom habitats in a temperate deciduous oak-hickory forest at Tyson Research Center, MO, USA, in the Ozark Highlands for 21 species of woody plants that vary in their constructions.

4. We found poor coordination across tissues in construction and decay, which likely reflects how functional constraints on living tissues influence recalcitrance to decay. Additionally, for all three tissues, species membership and construction were better predictors of decay than was location. Of the construction traits, chemical composition including total fibre, lignin, cellulose, hemicellulose and concentrations of multiple microelements were the best predictors of decay, although the strength of these relationships differed among tissues.

5. *Synthesis.* We have long known that rates of biogeochemical cycling are influenced by exogenous factors, such as climatic and edaphic factors. Here, we show across plant tissues that endogenous factors, including species identity and tissue construction, can have stronger controls on rates of decay within our study system than do exogenous factors. However, it is likely that the relative strengths of these different controls change through time and among tissues. We predict that anatomical and morphological controls may be more important at early stages and exogenous factors may be more important at later stages of decay.

Key-words: anatomy, carbon and nutrient cycling, chemistry, decomposition, fine branch, leaf litter, morphology, plant traits, plant–climate interactions, stems

Introduction

Woody plants are a large biotic store of carbon (C) and nutrients (Chambers *et al.* 2000; Denman 2007; Luyssaert *et al.* 2008; Chave *et al.* 2009). These resources can remain locked in plant tissues for days to millennia depending on the longevity and decay rates of the different tissues (Currey 1965; Chave *et al.* 2009; Cornwell *et al.* 2009; van Mantgem *et al.* 2009; Pietsch *et al.* 2014). In the temperate zone, deciduous species lose leaves seasonally, while evergreen species may retain leaves for years to decades (Kikuzawa 1991; Botta *et al.* 2000). Larger branches and stems can last for the lifetime of the plant, while fine branches are likely shed faster than large branches but slower than leaves (Boddy & Swift 1984;

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Harmon, Brown & Gower 1993; Bernier *et al.* 2007). Once tissues senesce and begin to decay, their released C and nutrients may be incorporated back into soil or other organisms (e.g. fungal saprobes, wood-chewing insects, other plants) within the ecosystem (Stevenson & Cole 1999; Luyssaert *et al.* 2008; Cornwell *et al.* 2009). Carbon can also be respired to the atmosphere (Melillo *et al.* 1990) where it feeds back through the climate system, especially if rates of senescence and/or turnover are altered (Manion 1987; Harmon, Brown & Gower 1993; Cornwell *et al.* 2009; van Mantgem *et al.* 2009).

Decay rates of plants are dependent on several factors including exogenous ones such as topographic position and climatic and edaphic conditions and endogenous ones such as construction of tissues (Harmon *et al.* 1986; Chambers *et al.* 2000; Cornwell *et al.* 2009; Cusack *et al.* 2010; Bradford *et al.* 2014). Decay occurs more rapidly in warm and wet locations and seasons, when saprobic organisms are most active (Ayerst 1969; McClaugherty & Linkins 1990). For instance, fungal saprobes, which are important decay agents throughout the globe, are dependent on adequate moisture to effectively break down plants (Petersen *et al.* 1999; Forest Products Laboratory 2000). Recently, it has been shown that local factors can take precedence over large climatic gradients as predictors of decay (Bradford *et al.* 2014). Topographic position has strong influence on microclimatic and edaphic differences (Hanna, Harlan & Lewis 1982; Whitney 1991; Hook & Burke 2000; Johnson *et al.* 2000) and can influence the presence and distribution of living trees and coarse woody debris (Rubino & McCarthy 2003; Webster & Jenkins 2005). Nutrients such as nitrogen (N), phosphorus (P) and C tend to accumulate downslope (Hook & Burke 2000) with water runoff and slippage. As water, soils and deadwood move downslope, they carry decay agents with them. These organisms are dependent on availability of various macro- and micronutrients, such as N, P, manganese (Mn) and calcium (Ca) for decay. Some of these elements may limit fungal growth and function if they are not present in sufficient quantities (Sterner & Elser 2002; Luo *et al.* 2008). Because of the downslope movement of nutrients and water and potential concentration of decay agents, it is likely that decay will occur more rapidly in valley bottoms than ridge tops.

Additionally, it is now well-established that endogenous species-specific differences in plant morphological, anatomical and chemical construction can affect rates of decay in diverse climates (Hobbie 1996; Cusack *et al.* 2010; Jackson, Peltzer & Wardle 2013; Pietsch *et al.* 2014). Construction, however, differs within and among tissue types. Wood is a complex, three-dimensional tissue that displays vast interspecific variation in construction (Carlquist 2001; Evert & Esau 2006; Chave *et al.* 2009; Zanne *et al.* 2010). Anatomically, the water-transporting vessel and tracheid lumens vary considerably in size (80X-fold in diameter and 18 000X-fold in length) (Feldman 1985; Carlquist 2001; Evert & Esau 2006). These lumens may serve as pathways for saprobic microbes and wood-chewing insects, with larger lumens facilitating access to wood (Cornwell *et al.* 2009). Chemically, wood is C-rich, with structural C found largely as hemicellulose, cellulose and lignin, listed in increasing recalcitrance (Harmon *et al.* 1986; Sjostrom 2013). Wood also contains various macro- and micronutrients (N, P, Mn and Ca) important for decay organisms. Anatomical and chemical characteristics of wood give rise to its bulk density, with decay often slower in dense tissue (Chambers *et al.* 2000; Mori *et al.* 2014; Pietsch *et al.* 2014), but see Van Geffen *et al.* (2010). Leaves are constructed differently to wood due to their different functions (Zimmermann, Brown & Tyree 1975; Lambers, Chapin & Pons 1998). Their relatively flattened shape allows for greater initial surface contact with the soil than wood. Species vary in their leaf (or leaflet) sizes (Falster & Westoby 2003) and amount of leaf area they carry for a given cross-sectional area of sapwood (leaf area:sapwood area; LASA) (Pickup, Westoby & Basden 2005; Gotsch *et al.* 2010). Additionally, species differ in how they deploy leaf area for a given unit of mass (specific leaf area; SLA), with species with high SLA also typically having high N and P contents (Wright *et al.* 2004) and decay rates (Cornwell *et al.* 2008). Generally, leaves contain higher minerals, proteins and assimilable C compounds and lower recalcitrant lignin than woody tissues (Schlesinger & Bernhardt 2013).

Previous meta-analyses have brought together data for decay rates and traits from studies around the world for a given tissue (Cornwell *et al.* 2008, 2009; Weedon *et al.* 2009) or across tissues (Pietsch *et al.* 2014). However, when traits and decay for different tissues are measured on the same species but in different sites, this can potentially add noise to analyses. A few studies have examined coordination in decay rates across tissues in relation to traits (Freschet, Aerts & Cornelissen 2012a; Jackson, Peltzer & Wardle 2013), but the rates were measured in a common garden or laboratory microcosm experiment and not in contrasting locations. While these studies provide insight into how construction affects decay, they do not account for the relative roles of exogenous factors such as topographic position and microclimatic and edaphic conditions vs. endogenous factors such as tissue construction in driving decay. Here, we provide, to our knowledge, the first field experiment explicitly partitioning the relative roles of exogenous and endogenous factors in determining decay across different tissue types for numerous woody species. Furthermore, we examine a wider breadth of traits that potentially influences decay than has previously been studied. In addition to measuring typical functional (e.g. wood density, SLA, leaf size, LASA) and chemical (C fractions, N, P) traits, we also included anatomical conduit lumen sizes (diameters and lengths) that may regulate access of wood to decay organisms and micronutrients known to be critical for microbial decay. We use information on exogenous and endogenous factors and decay rates to gain a better understanding of the coordination in decay within and across different tissue types (i.e. stems, fine branches and leaves).

To this end, we examined rates of decay over 1 year for 21 woody species among different tissue types, including stems, fine branches and leaves from the same species in ridge top and valley bottom locations in a temperate oak-hickory deciduous forest in MO, USA. We asked the following questions:

(i) Is there coordination across tissues in rates of decay and construction traits? (ii) Is decay predicted best from A) location where rotting occurs, B) species identity or C) tissue construction (morphologically, anatomically and chemically)? (iii) Additionally, we ask whether the best predictors differ among tissue types. Because leaves and wood provide different functions to the plant and are constructed differently, we hypothesized they would be poorly coordinated in construction traits and decay rates (Pietsch *et al.* 2014). We hypothesized valley bottom locations should have faster decay than ridge top locations, as they tend to be wetter with greater nutrients available for decay agents. Additionally, we hypothesized that species- and tissue-specific anatomical and chemical traits should be strong predictors of variation in decay across samples. More specifically, we expected to observe fast decay in less dense wood with large conduits, leaves with high SLA, and in all tissues containing small amounts of C (especially lignin) relative to amounts of limiting minerals.

Materials and methods

STUDY SITE

This study was carried out at Washington University in St. Louis' Tyson Research Center (1966.5 acres; 38.5178, −90.5575) in Eureka, MO, USA. The forest is dominated by *Quercus* and *Carya* with alfisol soils and steep topographic relief (172–233 m: 61 m; Anderson-Teixeira *et al.* 2015). It has a temperate climate (mean annual temperature from nearby St. Louis, MO, USA: 1895–2014: 13.5 °C, 2009–2013: 14.6 °C and mean annual precipitation: 1874–2014: 1.0 m, 2009–2013: 1.1 m; http://www.crh.noaa.gov/lsx/?n=cli_archive).

EXPERIMENTAL SET-UP

Eight 'rot plots' were established in June 2009 across Tyson by selecting a paired ridge top (ridge) and valley bottom (valley) in each of four watersheds. Ridges and valleys should represent the most extreme differences in microclimatic and edaphic conditions in our system. To compare microclimates, we measured differences at 10-min intervals for 1 year (June 2011–June 2012) at each plot using Onset weather stations (Onset Computer Corporation, Bourne, MA, USA). We monitored air temperature and relative humidity (RH; %) at 60 cm above the soil surface using radiation-shielded temperature/RH Onset smart sensors and soil moisture content (ECH_2O Dielectric Aquameter Onset sensors) and temperature (12-bit temperature smart Onset sensors) at 10 cm below the soil surface. To compare edaphic factors, we also collected and homogenized eight soil cores (0–10 cm deep) per plot. We completed in-field N extraction by mixing soil from each plot in 2 M potassium chloride. The N samples were agitated for 1 h and passed through filter paper and 50% sulphuric acid was added as preservative. A sample from each plot was also incubated in foil pouches for 7 days. These samples were processed for N mineralization using the same steps as for N extraction. Additionally, ~35 g of soil from each plot was weighed, placed in a drying oven at 105 °C for ≥24 h and reweighed. Remaining soil samples were air-dried. Samples were sent to the Soils Lab, Smithsonian Tropical Research Institute, Panama, for analysis (http://stri.si.edu/sites/soil/analytical_charges.html). There were no significant differences in microclimatic or edaphic conditions among watersheds. Ridge plots were warmer and drier than valley plots (air relative humidity: ridge = 71.5, valley = 79.8; air temperature: ridge = 15.1 °C, valley = 14.0 °C), and ridge plots had lower pH and base-saturated cations and higher Mn than valley plots (pH: ridge = 5.3, valley = 6.6; base-saturated cations: ridge = 95.9%, valley = 99.6%; Mn: ridge = 142.4 mg kg^{-1}, valley = 22.8 mg kg^{-1}). Ridge and valley plots did not differ in other soil variables.

In each rot plot, recently harvested tissues (stems, fine branches and leaves) from 21 species of woody plants were allowed to decay for 1 year. For stem decay, two cohorts of samples were examined starting in June 2009 (cohort 1) and June 2011 (cohort 2). The first cohort included stems from 16 species (*Acer rubrum*, *Aesculus glabra*, *Amelanchier arborea*, *Asimina triloba*, *Carya tomentosa*, *Celtis occidentalis*, *Cornus florida*, *Diospyros virginiana*, *Gleditsia triacanthos*, *Juniperus virginiana*, *Pinus strobus*, *Platanus occidentalis*, *Prunus serotina*, *Quercus velutina*, *Ulmus rubra* and *Vitis vulpina*). The second cohort expanded on the first by adding stems from an additional five species (*Fraxinus americana*, *Juglans nigra*, *Lonicera maackii*, *Pinus echinata* and *Quercus alba*). To evaluate differences in decay between cohorts, the second cohort also included stems from *C. occidentalis*, *J. virginiana* and *Q. velutina*. At least three healthy individuals per species of adequate size as specified by the experiments were harvested. Individuals were felled and cut into stem log sections (5–9 cm diameter × 22 cm long) leaving bark intact. We selected this diameter range to compare decay across a range of species with different growth forms and wood constructions. The shrubs and vines seldom achieve branch diameters >7 cm at our site. This size is small compared to the diameter of a full grown individual for some of these species, meaning logs in our study likely had elevated rates of decay compared to larger logs. Some of the material included juvenile wood; however, we did see heartwood development in individuals of species known to have visible changes in the heartwood to sapwood transition (e.g. *J. nigra* and *J. virginiana*). Additionally, 4- to 7-cm-long discs were cut at the top and bottom of each individual. All logs and discs were weighed for initial stem fresh mass. Discs were dried at 103 °C to constant mass. Based on the dry/fresh mass for discs, we estimated initial dry mass of experimental log replicates.

After cleaning and homogenizing surface litter by cutting back small shrubs and large herbs and using a rake to clear away accumulated litter, we randomly allocated one replicate per species per plot. All logs were labelled and secured to the ground. After 1 year (June 2010 for cohort 1 and June 2012 for cohort 2), logs were collected. Any obvious fungal fruiting bodies, insects, plant roots and soil were removed. Any parts of the log bark and wood that passed through a 0.5-cm^2 mesh screen were considered converted to soil and discarded. Logs were dried at 103 °C to constant mass to determine final stem dry mass.

In a third cohort for fine branches and leaves, live branches and senescing leaves were collected from at least three individuals from the same 21 species in autumn 2011. We collected branches approximately 1 cm in diameter and senesced leaves either from or directly underneath the canopy, the latter onto a sheet. We air-dried samples indoors until deployment in autumn 2012. Fine branches with bark intact were cut to 10 cm lengths and weighed for initial fresh branch mass. Leaves were divided into approximately ~1 g samples. In October 2012, fine branches and leaves were wrapped in 1-mm polyethylene window mesh to maximize recovery after 1 year of decay. Samples were randomly staked next to the stem rot plots. Subsamples of leaves and fine branches were also weighed for initial fresh mass. Subsamples of leaves were dried at 60 °C and fine branches at 103 °C to constant mass and reweighed to determine dry/fresh mass for subsamples for conversion of initial fresh to initial dry mass for fine branches and leaves. Fine branches and leaves were harvested after 1 year (October

2013). Obvious fungal fruiting bodies, insects, soil and plant roots were removed. Harvested leaves were dried at 60 °C and fine branches at 103 °C to constant mass and reweighed to determine final dry mass.

It should be noted that differences in microclimatic conditions among years and presence of window mesh could have caused differences in decay among cohorts. Cohort 1 (stems) was conducted during wetter and cooler conditions than cohort 2 (stems); cohort 3 (leaf and fine branch) was conducted during conditions intermediary between the other cohorts (average annual temperature and annual precipitation – cohort 1: 13.6 °C and 1.3 m, cohort 2: 16.5 °C and 1.1 m and cohort 3: 14 °C and 1.1 m; http://www.crh.noaa.gov/lsx/?n=cli_archive). Additionally, window mesh likely retains moisture while excluding some leaf- and wood-chewing insects, potentially affecting decay rates in opposite directions. In a separate experiment, stems enclosed in window mesh showed slower decay than unenclosed stems, suggesting protection from insects is important (A. E. Zanne, unpubl. data). Microclimatic differences did not cause differences in decay between the two stem cohorts (cohorts 1 and 2) ($R^2 = 0.07$, $F_{1,46} = 3.3$, $P = 7.53\text{E-}2$), but we are unable to account separately for treatment vs. tissue effects between stems (cohorts 1 and 2) vs. leaves and fine branches (cohort 3).

TRAITS

For each of the 21 species, we measured a series of morphological, anatomical and chemical leaf and wood traits from recently harvested samples.

Morphology

An outer canopy branch at ~1 cm diameter was collected from five individuals for each species. From each branch, we took a 2.5-cm end section and removed bark. Branch cross-sectional area was estimated from the end diameter (cm^2). Wood density from this section was determined following (Osazuwa-Peters & Zanne 2011) as dry mass per fresh volume ($g\ cm^{-3}$). All branch leaves were removed and leaf blades were separated from petioles. Five fully expanded leaves per branch (or leaflets for compound species) with no obvious signs of damage were imaged on a flatbed scanner. Leaf area (cm^2) was determined using ImageJ (http://imagej.nih.gov/ij/), and leaves were dried at 60 °C to constant mass. SLA was estimated as fresh leaf area per dry leaf mass ($cm^2\ g^{-1}$). The remaining leaves per branch were dried at 60 °C to constant mass, and total leaf mass and area per branch were determined. LASA was estimated as total leaf area divided by branch cross-sectional area ($cm^2\ cm^{-2}$).

Anatomy

For angiosperms, we examined vessel vascular anatomy in 2–3 branches collected from outer crowns of each species. To estimate vessel length (m), we injected stems acropetally with fluorescently dyed silicone, sectioned stems at 1, 3, 5, 9, 17, 33 and 40 cm, scored vessels for the presence of silicone dye under UV microscopy and estimated vessel lengths under a Weibull distribution using a hierarchical Bayesian model that accounted for sampling error within and among species (B. Oberle, unpubl. data). We estimated vessel diameter (μm) from the same cross-sectional images. For conifers, we measured tracheid length (m) from 3 branches per species. Branch samples were macerated in Franklin's solution (1 part glacial acetic acid:1 part hydrogen peroxide) in a test tube at 60 °C for 2 days. Macerated wood stained with safranin was imaged at 10× (Olympus microscope BX40 with a Canon A640 digital camera, Tokyo, Japan), and tracheid lengths were measured in ImageJ. Species-specific average tracheid diameters (μm) were taken from the literature (Lewis 1935; Maherali *et al.* 2006).

Chemistry

Wood samples were removed from harvested discs with a drill. Wood and leaves remaining from morphology samples were ground in a coffee grinder followed by a Spex 8000D Dual Mixer/Mill (Spex SamplePrep, Metuchen, NJ, USA). Samples were sent to Cumberland Valley Analytical Services (Cumberland, MD, USA) for wet chemistry analyses, including crude protein (CP, used as an estimate of N) (% dry matter (DM)), P (%DM), lignin (%DM), neutral detergent fibre (NDF or total fibre, used as an estimate of total C) (%DM), acid detergent fibre (ADF) (%DM), Ca (%DM) and Mn (PPM). Cellulose was calculated as the difference of ADF and lignin, and hemicellulose was calculated as the difference of NDF and ADF (%DM). Ratios of fibre : CP and lignin : CP were calculated (%DM/%DM).

ANALYSES

We estimated exponential decay constants from mass loss data as $k = -\ln(\text{final dry mass per initial dry mass})$ ($g\ g^{-1}$). A leaf sample from two species (*V. vulpina* and *L. maackii*) had 100% mass loss; we replaced these values with 0.99999999 in all further analyses, giving a k of 18.421. Replicates of morphological and anatomical traits were averaged at the species level. To meet distribution assumptions, we log10-transformed LASA, CP, Mn, lignin, lignin : CP, hemicellulose, fibre : CP and $k + 1$ for all tissue decay values. To examine degree of coordination in decay among tissue types, k values were averaged across all plots for each tissue per species otherwise variation in k values was examined at the individual level. General linear models were used for all analyses. No differences in decay were found between watersheds ($P > 0.05$), so this variable was removed from analyses. No differences were found in decay for the three overlapping species between cohorts 1 and 2 ($P > 0.05$); species-specific k values were averaged between the cohorts and analysed together. All analyses were run in the R software environment (version 3.1.2; http://cran.r-project.org/). Data are available at Dryad (Zanne *et al.* 2015).

Results

SAMPLE-LEVEL VARIATION IN DECAY

Considerable variation in decay (k) occurred both within and across tissues (stem k – mean: 0.266; range: 0.001–0.672; fine branch k – mean: 0.182; range: −0.006 to 1.260; leaf k – mean: 0.901; range: −0.028-undefined).

IS THERE COORDINATION ACROSS TISSUES IN RATES OF DECAY AND CONSTRUCTION TRAITS?

Decay rates were poorly coordinated among tissues at the species level. Stem decay was positively related to fine branch decay (Fig. 1), although this relationship was driven by *Aesculus glabra*, which had the largest k values for both tissues. When this species was removed from analyses, decay rates between these tissues were no longer significantly related ($R^2 = 0.057$, $P = 0.270$, $N = 20$). Decay rates for leaves were unrelated to decay rates for stems and fine branches.

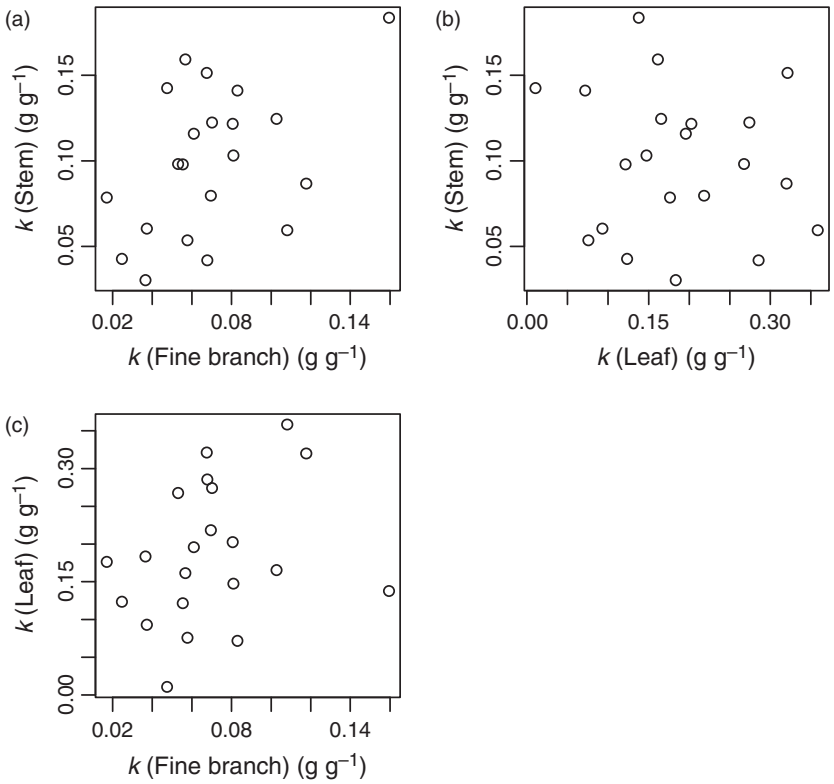

Fig. 1. Relationships among average k values for 21 species among the different tissue types. (a) Stem vs. fine branch ($R^2 = 0.214$, $F_{1,19} = 5.2$ $P = 0.035$), (b) stem vs. leaf ($R^2 = 0.021$, $F_{1,19} = 0.4$, $P = 0.535$) and (c) leaf vs. fine branch ($R^2 = 0.081$, $F_{1,19} = 1.7$, $P = 0.210$). k values were log10(k + 1)-transformed.

Weak relationships between decay rates across tissues can be partially explained by differences in tissue construction (Table S1 in Supporting Information, Fig. 2). No significant relationships were found between morphological leaf (leaf size, SLA and LASA) and wood (wood density) constructions. A few chemical traits were significantly (positively) related between leaves and wood, including CP, Mn, C, fibre:CP and lignin:CP (Table S1, Fig. 2).

WHAT ARE THE BEST PREDICTORS OF SAMPLE-LEVEL VARIATION IN DECAY AND DO THESE PREDICTORS DIFFER AMONG TISSUES?

Location (ridge vs. valley) was a significant but relatively weak predictor of variation in k especially as compared to species identity (Table 1, Figs 3 and 4), with location explaining 3.6%, 4.6% and 5.9% and species explaining 82.9%, 46.5% and 40.7% of variation in k in stem, fine branch and leaf samples, respectively. When analysed together, location and species membership explained separate and significant amounts of variation in k for all three tissue types (stem: 86.5%, fine branch: 51.0%, leaf: 54.2%; Table 2).

To better understand species-specific differences in decay, we examined the influence of morphological, anatomical and chemical traits on variation in decay. Generally, tissue chemistry was a better predictor of decay in all three tissues than was anatomy or morphology (Table 2, Fig. 5). In bivariate relationships, wood density was the only significant anatomical or morphological predictor of stem k (explaining 17% of variation), while SLA and LASA were significant predictors of leaf k (explaining 5.9% and 3.1% of variation, respectively). Nitrogen and P were the strongest chemical predictors of stem k (positively related, explaining 12% and 18% of variation, respectively), with fibre, lignin, fibre:CP, lignin:CP and Ca also significantly related to stem k. Lignin:CP was the best predictor of k in fine branches (negatively related, explaining 14% of variation), with CP, P, lignin, cellulose, fibre:CP and Ca also significantly related. Calcium was the best predictor of leaf k (positively related, explaining 20% of variation), with CP, fibre, lignin, cellulose, hemicellulose, fibre:CP and lignin:CP also significantly related. In multivariate analyses, traits together explained 62% in stem, 31% in fine branch and 29% in leaves of variation in k.

Discussion

To our knowledge, this is the first time within a study site that the relative effects of endogenous (i.e. species membership and construction traits) and exogenous (i.e. location) factors have been examined on decay rates of different plant tissues.

COORDINATION ACROSS TISSUES IN DECAY RATES

Only a handful of studies have examined whether coordination occurs across tissues in their rates of decay. Freschet, Aerts & Cornelissen (2012a), Freschet *et al.* (2013) found support for positive relationships in decay across tissues in a common garden experiment in Sweden and in a global meta-analysis. Jackson, Peltzer & Wardle (2013) found some degree of coordination among leaves, twigs and wood traits from a New Zealand study but poor coordination in decay

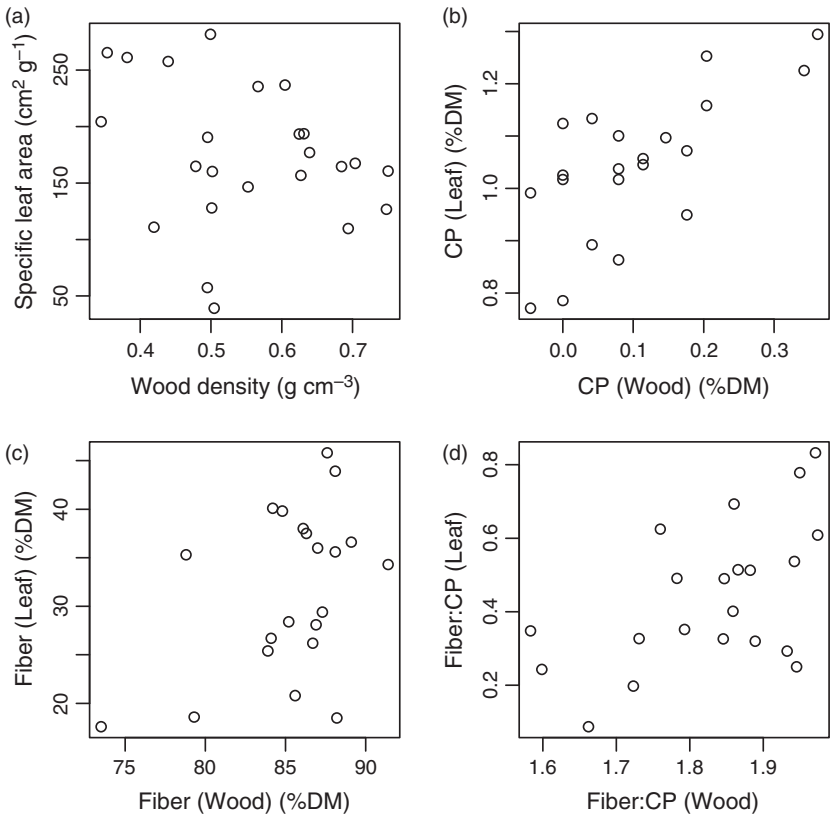

Fig. 2. Relationships between morphological traits. (a) Wood density vs. SLA and chemical traits, (b) Crude protein (CP), (c) fibre and (d) fibre: CP for wood and leaves. CP and fibre:CP were log10-transformed.

Table 1. General linear models (R^2, F, P and direction of relationship, with valley bottom = V and ridge top = R). Location and species membership are predictors, and decay rates (k values) for stem, fine branch, and leaf samples are response variables. Significant relationships are in bold

		Stem	Fine branch	Leaf
Location	R^2	**0.036**	**0.046**	**0.059**
	$F_{1,166}$	**6.3**	**7.9**	**10.4**
	P	**1.32E-02**	**1.84E-02**	**5.51E-03**
	Direction	**V>R**	**V>R**	**V>R**
Species	R^2	**0.829**	**0.465**	**0.407**
	$F_{20,147}$	**35.6**	**6.4**	**5.0**
	P	**<2.20E-16**	**4.06E-12**	**2.43E-09**
Location + Species	R^2	**0.865**	**0.510**	**0.542**
	$F_{21,146}$	**44.7**	**7.2**	**8.2**
	P	**<2.20E-16**	**3.79E-14**	**5.19E-16**
Location	$F_{1,146}$	**39.5**	**13.6**	**43.0**
	P	**3.59E-09**	**3.24E-04**	**9.02E-10**
	Direction	**V>R**	**V>R**	**V>R**
Species	$F_{20,146}$	**45.0**	**6.9**	**6.5**
	P	**<2.20E-16**	**3.60E-13**	**2.73E-12**

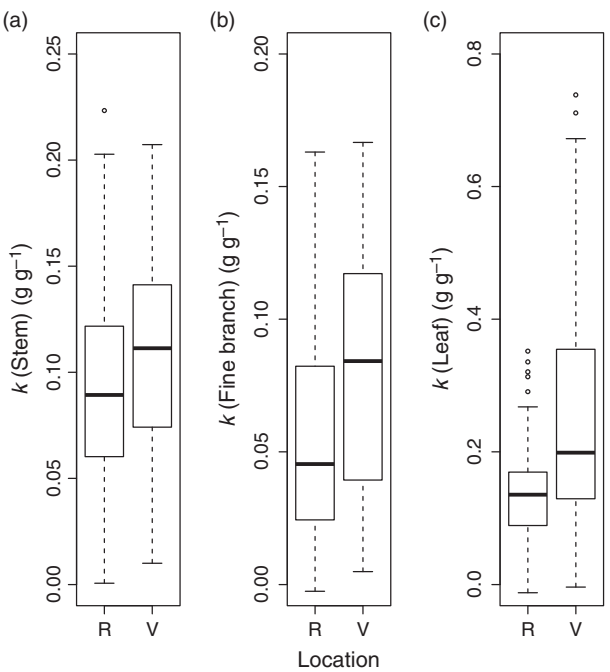

Fig. 3. Boxplots of decay rates (k values) for (a) stems, (b) fine branches and (c) leaves by location with valley bottom plots = V and ridge top plots = R. k values were log10(k + 1)-transformed. Note: An *A. glabra* fine branch sample from a ridge plot was an outlier (log 10(k + 1) = 0.354) and a *V. vulpina* and *L. maackii* leaf each from valley plots were completely decayed and are also outliers (log 10(k + 1) = 1.288). These values are not displayed to reduce the y-axis length for ease of visualization.

across tissues in microcosm experiments. Similar results were found by Pietsch *et al.* (2014) in a global meta-analysis with leaf and wood decay being significantly positively related only when considered across angiosperms and gymnosperms, but not within these groups.

In our work, we found some evidence for weak positive relationships in decay across tissues, but much of this

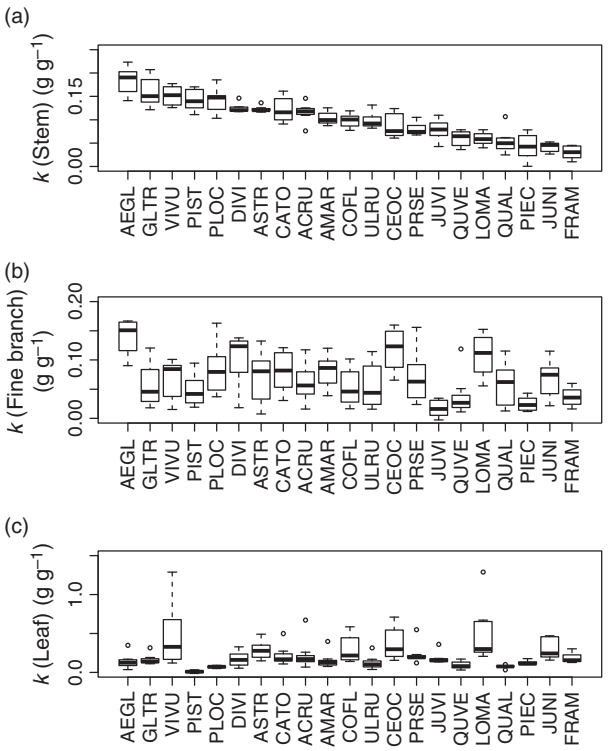

Fig. 4. Boxplots of decay rates (k values) for (a) stems, (b) fine branches and (c) leaves for 21 species with order of species displayed from highest to lowest stem k along the x-axes. The following species were included with abbreviations in parentheses: *Acer rubrum* (ACRU), *Aesculus glabra* (AEGL), *Amelanchier arborea* (AMAR), *Asimina triloba* (ASTR), *Carya tomentosa* (CATO), *Celtis occidentalis* (CEOC), *Cornus florida* (COFL), *Diospyros virginiana* (DIVI), *Fraxinus Americana* (FRAM), *Gleditsia triacanthos* (GLTR), *Juglans nigra* (JUNI), *Juniperus virginiana* (JUVI), *Lonicera maackii* (LOMA), *Pinus echinata* (PIEC), *Pinus strobus* (PIST), *Platanus occidentalis* (PLOC), *Prunus serotina* (PRSE), *Quercus alba* (QUAL), *Quercus velutina* (QUVE), *Ulmus rubra* (ULRU), *Vitis vulpina* (VIVU). k values were log10(k + 1)-transformed. Note: An *A. glabra* fine branch sample from a ridge plot was an outlier (log 10 (k + 1) = 0.354) and is not displayed to reduce the y-axis length for ease of visualization.

evidence was driven by inclusion or exclusion of a single species, *Aesculus glabra*, which had particularly high stem and fine branch rates of decay, while its leaves had average rates of decay. As leaves are typically broad thin surfaces constructed to facilitate gas exchange and light harvesting for photosynthesis, while wood is constructed to transport sap between roots and leaves, store C and nutrients, and mechanically support leaf tissues against gravity to access light (Zimmermann, Brown & Tyree 1975; Lambers, Chapin & Pons 1998; Tyree & Zimmermann 2002), it is clear that leaves and wood have very different functions. It seems there need not be *a priori* expectations that tissue construction (Baraloto *et al.* 2010) and decay rates should be similar within a plant. That said, if coordination in tissue senescence occurs with leaves and wood senescing on similar timeframes [e.g. low-nutrient environments may lead to selection for long nutrient retention in tissues, such as a sclerophyllous leaf habit (Wright & Cannon 2001)], one might expect coordination in tissue construction and decay. However, in a temperate site such as ours dominated by deciduous angiosperms, deciduous leaves are built to last at most one growing season, while wood is built to last numerous years. It follows for these deciduous species that coordination in tissue construction should be poor leading to a lack of coordination in decay rates. We included three evergreen conifers in our study. *Juniperus virginiana* occurs in specialized habitats on site, *Pinus echinata* is common in the region but locally absent, and *Pinus strobus* is introduced. Their longer leaf longevity, however, did not increase coordination in our study, albeit the sample size was small. Their fine branches decayed fairly slowly compared to other species in the experiment, but their other tissues had more variable rates. *Pinus strobus* had the slowest and *J. virginiana* had middle range leaf decay rates, while *P. echinata* had one of the slowest and *P. strobus* one of the fastest stem decay rates.

PREDICTORS OF DECAY

Wood and litter decay have received careful attention for decades (Witkamp 1966; Griffin 1977; Boddy 1983; Harmon *et al.* 1986; Pastor & Post 1986; Blanchette 1991; Pyle & Brown 1998; Chambers *et al.* 2000; Woodall 2010; Cornelissen *et al.* 2012; Bradford *et al.* 2014). This work has brought insight into where and why rates of decay are slower or faster. These studies have shown that decay happens more rapidly in warmer and wetter locations and times of the year (Witkamp & van der Drift 1961; Boddy 1983; Harmon *et al.* 1986; Hennon & DeMars 1997; Chambers *et al.* 2000). For instance, litter turnover rates decrease with latitude (Hennon & DeMars 1997; Cornwell *et al.* 2008). Recent work has emphasized the importance of local factors over large climatic gradients as important predictors of decay (Bradford *et al.* 2014). We pushed the extremes within our system by setting up rot plots on ridge tops and valley bottoms and found they differed in microclimatic and edaphic factors, although nutrients differed less than expected. We confirmed that ridge top habitats had slower rates of decay than valley bottoms; however, location only explained a modest 4–6% of variation in decay across samples for the three tissues. While our study captures variation in decay at the microclimatic and edaphic extremes within our system in part due to its steep topography (172–233 m: 61 m) (Anderson-Teixeira *et al.* 2015), greater differences in topographic relief and climatic and edaphic conditions can be found within and across other sites; location may be recovered in these systems as a stronger control of decay after 1 year than we find here.

From the literature, the relative importance of species-specific differences in decay is less clear. For instance, some studies have used mixtures of leaves in which leaves from different species are decayed together (Gartner & Cardon 2004). Others have marked deadwood on the landscape and followed its decay through time, which has allowed incorporation of species-specific effects when deadwood species identity can be determined (Chambers *et al.* 2000; Woodall 2010). However, when species cannot be identified, it becomes impossible to ascertain how much species member-

Table 2. General linear models, including bivariate and multivariate analyses (R^2, F, P, β and sign of relationship) with traits (wood density, conduit diameter, conduit length, crude protein (CP), P, fibre, lignin, cellulose, hemicellulose, fibre:CP, lignin:CP, Ca, Mn) as predictors of decay rates (k values) of stem, fine branch and leaf samples. Significant relationships are in bold. For multivariate analyses, significance traits are denoted as follows: '***' ≤ 0.001, '*' ≤ 0.05

		Stem	Fine branch		Leaves
Wood density	R^2	**0.170**	0.001	SLA	**0.059**
	$F_{1,166}$	**34.0**	0.2		**10.4**
	P	**2.84E-08**	6.61E-01		**1.54E-03**
	Sign	–			+
Conduit diameter	R^2	0.001	0.000	Leaf size	0.000
	$F_{1,166}$	0.1	0.1		0.0
	P	7.08E-01	7.95E-01		9.88E-01
Conduit length	R^2	0.003	0.002	LASA	**0.031**
	$F_{1,166}$	0.5	0.2		**5.4**
	P	5.00E-01	6.24E-01		**2.15E-02**
	Sign				+
CP	R^2	**0.123**	**0.061**		**0.044**
	$F_{1,166}$	**23.4**	**10.9**		**7.6**
	P	**3.05E-06**	**1.20E-03**		**6.62E-03**
	Sign	+	+		+
P	R^2	**0.178**	**0.048**		0.011
	$F_{1,166}$	**35.8**	**8.4**		1.9
	P	**1.28E-08**	**4.20E-03**		1.70E-01
	Sign	+	+		
Fibre	R^2	**0.059**	0.003		**0.127**
	$F_{1,166}$	**10.5**	0.6		**24.2**
	P	**1.46E-03**	4.50E-01		**2.07E-06**
	Sign	–			–
Lignin	R^2	**0.039**	**0.125**		**0.132**
	$F_{1,166}$	**6.8**	**23.8**		**25.22**
	P	**1.01E-02**	**2.48E-0**		**1.31E-06**
	Sign	–	–		–
Cellulose	R^2	0.006	**0.092**		**0.060**
	$F_{1,166}$	1.0	**16.9**		**10.6**
	P	3.13E-01	**6.20E-05**		**1.40E-03**
	Sign		+		–
Hemicellulose	R^2	0.009	0.007		**0.030**
	$F_{1,166}$	1.6	1.1		**5.2**
	P	2.14E-01	3.00E-01		**2.41-02**
					–
Fibre:CP	R^2	**0.146**	**0.062**		**0.150**
	$F_{1,166}$	**28.4**	**10.9**		**29.3**
	P	**3.23E-07**	**1.16E-03**		**2.10E-07**
	Sign	–	–		–
Lignin:CP	R^2	**0.106**	**0.142**		**0.161**
	$F_{1,166}$	**19.6**	**27.5**		**31.8**
	P	**1.73E-05**	**4.73E-07**		**7.29E-08**
	Sign	–	–		–
Ca	R^2	**0.070**	**0.045**		**0.202**
	$F_{1,166}$	**12.4**	**7.77**		**42.0**
	P	**5.45E-04**	**5.94E-03**		**9.90E-10**
	Sign	+	+		+
Mn	R^2	0.000	0.010		0.008
	$F_{1,166}$	0.0	1.7		1.3
	P	9.61E-01	1.91E-01		2.50E-01
Total traits	R^2	**0.620**	**0.306**		**0.289**
	$F_{10,157}$	**25.7**	**6.9**		**6.4**
	P	**<2.20E-16**	**6.50E-09**		**3.35E-08**
Wood density	β	**−0.286*** **	−0.063	SLA	**0.001***
Conduit length	β	**−0.590*** **	**−1.211*** **	Leaf size	0.000
Conduit diameter	β	**0.001***	0.000	LASA	**−0.373***
CP	β	−0.028	0.003		−0.090
P	β	**1.322*** **	0.414		−0.291
Lignin	β	**−0.225*** **	**−0.220*** **		**−0.238***
Cellulose	β	**−0.003*** **	−0.001		**−0.008***
Hemicellulose	β	**−0.163*** **	0.044		0.020
Ca	β	−0.009	0.046		**0.060*** **
Mn	β	0.007	**−0.015***		−0.021

(continued)

Table 2. (Continued)

ship, especially as driven by tissue construction, matters in determining why some samples or some locations have fast or slow rates of decay.

Recent work has narrowed in on species-specific effects. These studies have shown that plant traits can be good predictors of decay (Hobbie 1996; Cornwell *et al.* 2008, 2009; Weedon *et al.* 2009; Cusack *et al.* 2010; Freschet, Aerts & Cornelissen 2012a; Jackson, Peltzer & Wardle 2013; Pietsch *et al.* 2014). Wood density, conduit diameter and nutrient and C concentrations have been significantly related to wood decay (Weedon *et al.* 2009; Cusack *et al.* 2010; Freschet, Aerts & Cornelissen 2012a; Mori *et al.* 2014), while SLA and nutrient concentrations have been significantly related to leaf decay (Cornelissen *et al.* 1999; Santiago 2007; Cornwell *et al.* 2008; Pietsch *et al.* 2014) but see (Salinas *et al.* 2011). Within our system, we found that we could explain considerable variation in decay (41–83%) within a given tissue when we used species membership to compare decay rates. Additionally, when we explored differences in species-specific construction, we could explain a large amount of decay variation based on differences in morphological, anatomical and chemical traits (29–62%) for the different tissues.

In general, individual morphological and anatomical traits were poor predictors of decay, except for wood density being a relatively strong predictor of stem decay and SLA and LASA being significant but modest predictors of leaf decay. Interestingly, when conduit length was detected as significant (in multivariate analyses), longer conduits were negatively related to decay, suggesting that our initial hypothesis (Cornwell *et al.* 2009) in which longer conduits facilitate microbial and insect exploration of wood should result in high decay was not supported at least over a decay window of 1 year. Chemical traits were overwhelmingly the best predictors of decay with high nutrients leading to fast decay and high C leading to slow decay. On an individual basis, none of the chemical traits were very strong predictors of decay; the best predictor was Ca in leaves, which explained 20% of the variation in leaf decay. When significant, though, these chemical traits individually explained as much, or more, variation in decay as sample location (ridge vs. valley).

In examining chemical traits that were significant predictors, it is well known that most C in wood, especially in lignin form (Ruiz-Dueñas & Martínez 2009), is recalcitrant to decomposition by most organisms. It is also well-established that the macronutrients N and P are critical for wood- and litter-feeding micro- and macro-organisms (Sterner & Elser 2002; Luo *et al.* 2008) and they should be good determinants of decay (Santiago 2007; Cornwell *et al.* 2008; Weedon *et al.*

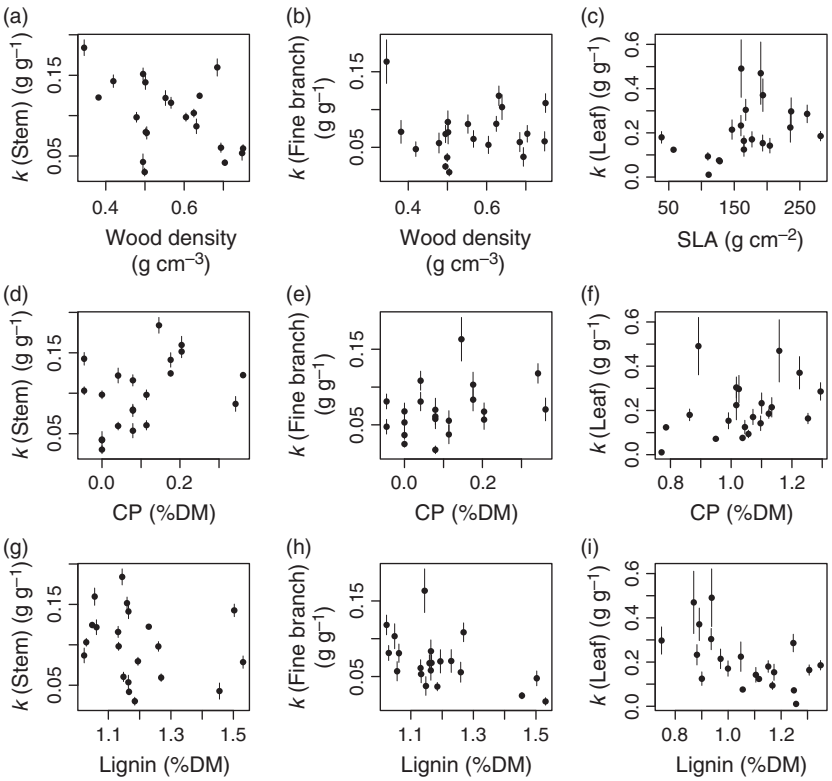

Fig. 5. Relationships between k values and traits for wood and leaf morphology with dots representing means and lines representing standard errors of the mean for (a, b) wood density and (c) SLA, and chemistry (d–f) crude protein (CP) and (g–i) lignin content for stems (a, d, g), fine branches (b, e, h) and leaves (c, f, i). For statistical analyses of relationships, see Table 2. k values were log10(k + 1)-transformed. Lignin and CP were log10-transformed.

2009). Additionally, we found Ca was positively related to decay across all tissues. It is vital for general fungal function and also components of wood decay enzymes (Jellison & Connolly 1997; Sutherland *et al.* 1997). Here, we explored the relationships between decay and a small suite of chemical traits. Further exploration of chemical traits in trait decay studies may provide greater insight into the biology of decay. For instance, pH can influence which fungi can colonize, grow on (Blaich & Esser 1975; Goodell *et al.* 1997; Boddy 2001) and decay (Freschet *et al.* 2012b) wood.

DIFFERENCES AMONG TISSUE TYPES IN PREDICTORS

When examining tissue-specific differences in predictors of decay, leaves tended to be slightly more sensitive to the location where they decayed and less sensitive to what species they came from and how that species was constructed than were stems. This result may be driven, in part, by a change in importance of plant construction through time. Early in decay, species differences may be particularly strong with the living 'green' traits strongly influencing ease of tissue colonization. As decay proceeds, however, samples begin to break down with physical integrity lost, C respired and nutrients transported into or away from tissues. For example, cord-forming fungi move nutrients into wood to facilitate decay in C-enriched tissues (Wells & Boddy 1995; Shortle & Jellison 2014). Because of these changes, samples may homogenize through time with differences among them decreasing (Witkamp 1966). As samples are broken down and a diversity of decay agents gain access, initial plant construction may become less important while relative roles of local microclimatic conditions may become greater. Since leaves generally decay more quickly than wood, this homogenization, if it is occurring, may be further along after 1 year for leaves than for wood, meaning that the timing of importance of species identity and construction differs among tissues.

Conclusions

In this study, we show poor coordination in construction traits between leaves and wood and in rates of decay among leaves, fine branches and stems over the course of a year. Considering the different roles that these plant tissues must carry out for a plant to successfully function, this result is probably not surprising. However, when considered individually, we found for the first time for each of the tissues that who species are and how they are constructed were much stronger predictors of decay than where they are decaying on the landscape. While the role of climatic conditions on rates of biogeochemical cycling has been carefully examined (Harmon *et al.* 1986; Chambers *et al.* 2000; Brovkin *et al.* 2012; Bradford *et al.* 2014), based on the results from our study, we suggest that it is at least as important to consider species composition when trying to understand how decay of plant tissues affects rates of C and nutrient flux within a site (Harmon *et al.* 1986; Cornwell *et al.* 2008; Jackson, Peltzer & Wardle 2013; Pietsch *et al.* 2014). The construction of these different species, especially chemically and perhaps also morphologically and anatomically, should be determined, because these traits will serve as the gatekeepers to different decay agents, allowing some and excluding others (Hibbett & Donoghue 2001; Cornwell *et al.* 2009; Eastwood *et al.* 2011). Within our site, flux

rates will be slower, at least over the time window considered here, first and foremost, based on endogenous factors such as C fractions and nutrient concentrations of plant tissues. Exogenous factors, such as topographic position and microclimatic and edaphic conditions, can speed up or slow down these rates but will likely have a less strong role than simply what species the sample comes from and how that sample is constructed.

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Data accessibility

Data deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.b3q08 (Zanne *et al.* 2015).

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Supporting Information

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

Table S1. General linear models (Pearson correlations: R^2, F, P and sign of relationship and paired t-tests: t, P and direction of relationship, with L = leaf and S = stem) between stems and leaves for morphological (wood density, leaf size, SLA and LASA) and chemical (CP, P, fibre, lignin, cellulose, hemicellulose, fibre: CP, lignin:CP, Ca, Mn) traits.