

LETTER

Global meta-analysis of wood decomposition rates: a role for trait variation among tree species?

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Abstract

The carbon flux from woody debris, a crucial uncertainty within global carbon-climate models, is simultaneously affected by climate, site environment and species-based variation in wood quality. In the first global analysis attempting to explicitly tease out the wood quality contribution to decomposition, we found support for our hypothesis that, under a common climate, interspecific differences in wood traits affect woody debris decomposition patterns. A meta-analysis of 36 studies from all forested continents revealed that nitrogen, phosphorus, and C : N ratio correlate with decomposition rates of angiosperms. In addition, gymnosperm wood consistently decomposes slower than angiosperm wood within common sites, a pattern that correlates with clear divergence in wood traits between the two groups. New empirical studies are needed to test whether this difference is due to a direct effect of wood trait variation on decomposer activity or an indirect effect of wood traits on decomposition microsite environment. The wood trait–decomposition results point to an important role for changes in the wood traits of dominant tree species as a driver of carbon cycling, with likely feedback to atmospheric CO₂ particularly where angiosperm species replace gymnosperms regionally. Truly worldwide upscaling of our results will require further site-based multi-species wood trait and decomposition data, particularly from low-latitude ecosystems.

Keywords

Angiosperm, decay, gymnosperm, lignin, wood density, woody debris.

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INTRODUCTION

Forecasting the direction and pace of global change requires knowledge about the processes controlling carbon flux between the biosphere and atmosphere (Cao & Woodward 1998). Simultaneous and substantial increases in global temperatures and atmospheric CO₂ levels in this century (IPCC 2007) are expected to affect the levels of storage and flux rates of carbon in the biosphere, potentially producing complex feedbacks between climate, vegetation and the

natural carbon sink in terrestrial ecosystems (Knorr *et al.* 2005).

Forests represent a large pool of carbon in global budgets. They contain *c.* 50% of carbon in the terrestrial biosphere (Malhi 2002) despite covering only 30% of the Earth's land surface (FAO 2006). A significant proportion of forest carbon is in the form of coarse woody debris, which can constitute as much as 20% of the total in old-growth forests (Harmon *et al.* 1990; Delaney *et al.* 1998). Despite the importance of coarse woody debris to local and

global carbon budgets, the factors determining flux rates and pool sizes are relatively poorly understood (Harmon *et al.* 1986). As a result, the inclusion of wood decomposition in vegetation and climate models is usually in a highly generalized form (e.g. Cramer *et al.* 2001).

Empirical studies have revealed that local environmental conditions, in particular temperature and humidity, exert strong controls on the rate of coarse woody debris decomposition (Moore *et al.* 1999; Kueppers & Harte 2005). Recent studies have suggested that species-based variation in wood traits may also contribute to the observed variations in wood decomposition rate (Yin 1999; Chambers *et al.* 2000). Tree species vary in the physical, chemical and structural properties of their wood (Panshin & de Zeeuw 1980; Chave *et al.* 2006), and consequently in the decomposability of the substrate that they contribute to the detrital pool of an ecosystem (Cadisch & Giller 1997; Berg & Laskowski 2006). The effects of these differences on the rates of mineralization, comminution, leaching and respiration of decomposing material (Lavelle *et al.* 1993; Cadisch & Giller 1997) may have profound effects on the carbon storage capacity of forests, and thereby on climate (Sitch *et al.* 2003).

Wood traits represent important dimensions of plant functional variation with important implications for the abundance and distribution of woody species in different habitats. Woody tissue – xylem – has two primary roles in living plants: mechanical support of photosynthetic tissue, which allows for onward height growth, and the transport of water from the soil to the leaves. Among species, xylem shows a tremendous amount of variation with respect to the types of cells present (i.e. absence of vessels in gymnosperms), relative abundance of cell types, the sizes and biochemical stoichiometry of those cells, and the distribution of complex lignin molecules within the wood. Such variation in wood characteristics is well illustrated by the striking differences between wood of angiosperms and that of gymnosperms (Panshin & de Zeeuw 1980), which represent the two major extant clades of woody species. Research in functional ecology has focused on the constraints acting upon wood traits, and preliminary studies suggest likely relationships between wood traits and ecological strategy (Loehle 1988; Falster & Westoby 2005; Chave *et al.* 2006; Preston *et al.* 2006). For example, wood density in a diverse Australian tropical forest is related to growth rate and successional stage (Falster & Westoby 2005); and xylem architecture and wood density correlate with tolerance of highly negative water potential and maximum height in Californian chaparral species (Preston *et al.* 2006). Interspecific variation in wood traits may translate into predictable variation in decomposition rates. There is therefore the potential for trait-ecosystem process coupling analogous to that found between leaf economics

and nutrient cycling (Hobbie 1992; Cornelissen *et al.* 1999; Cornwell *et al.* 2008).

In this study, we gathered data from 36 wood decomposition studies conducted on all five forested continents. Here we test the hypothesis that interspecific differences in wood traits are associated with differences in decomposition rate within a common climatic environment. We expect that, among species, wood with higher macronutrient concentration and less lignin will decompose faster, as observed for decomposing leaf tissues (Melillo *et al.* 1982), and wood that is less dense and/or has larger vessels will decompose faster by improving the microenvironment experienced by decomposing organisms (Yoneda 1975; Dix & Webster 1995). In particular, we expect that variation is driven by the considerable differences in wood architecture and chemistry between angiosperms and gymnosperms (Panshin & de Zeeuw 1980). Our approach differs from previous studies in that we repeatedly compare wood decomposition rates within single sites, thus isolating, to the extent possible, the effects of traits independently of climate. This is the first quantitative attempt to explicitly test for correspondence of variation in wood decomposition rates with that in wood traits on a global scale.

METHODS

Literature survey and data selection criteria

We identified data for the meta-analysis from literature searches in *Web of Science*, *CAB Abstracts*, forestry databases and book series. Abstracts of articles and chapters obtained by these searches were screened for explicit measurements of decomposition rates of wood (defined as any woody plant tissue of any size including ‘twigs’ or ‘fine woody debris’) in terrestrial field conditions. Reference lists from every study were systematically examined for additional suitable articles that were then incorporated into the bibliographic databases as above.

We limited the meta-analyses to the 36 studies (details in Table 1) that examined at least two species simultaneously in the same climate zone or site, and published either decomposition rate constants (k values; Olson 1963) or mass loss or density loss data from which k values could be calculated.

Higher k values indicate a greater proportional mass loss per unit time. There were two main methodologies in the literature: (1) studies that determined these decomposition rate constants from direct experimental measurement of woody tissues incubated in field conditions for known time periods (henceforth ‘Direct’ studies), and (2) studies that estimated k values by comparing mass per volume (density) of woody debris fragments of known or

Table 1 Summary of papers collected and used in the meta-analysis

Reference	Location	Methodology	Sites	No. species	Timescale (years)	Mean annual temperature (°C)	Annual precipitation (mm)	Diameter (cm)
Brais <i>et al.</i> (2006)	Canada	Chronosequence	1	4	75	1.2	1380	
Brown <i>et al.</i> (1998)	CO, USA	Chronosequence	1	2	140	0.1	462	> 30
Erickson <i>et al.</i> (1985)	WA, USA	Chronosequence	4	4	9.75	3.7–10.0	912–2380	1–12
Foster & Lang (1982)	NH, USA	Chronosequence	1	2	64	6.5	1057	> 10
Graham & Cromack (1982)	WA, USA	Chronosequence	1	2	100	4.9	2786	> 15
Harmon <i>et al.</i> (2000)	Russia	Chronosequence	1	3	70	4.3	1182	
Harmon <i>et al.</i> (2005)	Western USA	Chronosequence	7	17		0.0–9.5	1184–3016	25–52
Janisch <i>et al.</i> (2005)	WA, USA	Chronosequence	1	2	70	9.3	2303	
Johnson & Greene (1991)	Canada	Chronosequence	2	2	220	–1.4	1522	
Krankina & Harmon (1995)	Northwest Russia	Chronosequence	1	3	70	4.3	605	> 10
Kueppers <i>et al.</i> (2004)	CO, USA	Chronosequence	3	2	600	–0.5	560	> 10
Mackensen & Bauhus (2003)	South-eastern Australia	Chronosequence	3	3	11	11.7–15.7	961–1137	10–30
Macmillan (1988)	IN, USA	Chronosequence	1	4	25	11.8	1117	> 5
Sollins <i>et al.</i> (1987)	Northwestern USA	Chronosequence	1	3	90	7.7	1715	> 15
Tarasov & Birdsey (2001)*	Russia	Chronosequence	1	4	105			5–60
Yatskov <i>et al.</i> (2003)	Russia	Chronosequence	4	10	75	–1.4–4.3	605–805	> 10
Alban & Pastor (1993)	MN, USA	Direct	2	4	17	4.1	667	5–22
Brown <i>et al.</i> (1996)	Western Australia	Direct	3	6	5	18.3	774	10–15
Contrufo & Ineson (2000)†	UK	Direct	1	1	3	8.7	1703	2
Devries & Kuyper (1988)	The Netherlands	Direct	6	3	7	8.9	759	5–10
Eaton & Lawrence (2006)	Southern Mexico	Direct	1	4	1.5	24.7	1141	5–13
Edmonds <i>et al.</i> (1986)	WA, USA	Direct	1	2	5	8.1	1968	1–12
Edmonds (1987)	WA, USA	Direct	1	4	5	3.2	1935	1–10
Frangi <i>et al.</i> (1997)‡	Argentina	Direct	3	3	4	3.2–4.7	470–538	1–16
Gosz <i>et al.</i> (1973)	NH, USA	Direct	2	5	1	5.2	1105	0.5
Harmon <i>et al.</i> (1995)	Yucatan, Mexico	Direct	1	12	4	25.9	1316	1–30
Laiho & Prescott (1999)	Alberta, Canada	Direct	3	3	14	1.7	620	15
Mattson (1987)	NC, USA	Direct	1	17	6	12.1	1854	6–22
Mukhin & Voronin (2007)*	Western Siberia	Direct	6	5				1–3
O'Connell (1997)	Western Australia	Direct	1	4	2	15.9	1098	1–5
Romero <i>et al.</i> (2005)	FL, USA	Direct	5	3	2	23.5–23.9	1326–1405	8–10
Rosswall <i>et al.</i> (1975)	Finland	Direct	2	2	3	–2.6–0.1	434–601	
Scowcroft (1997)	HI, USA	Direct	1	2	1	21.7	2766	< 0.5
Songwe <i>et al.</i> (1995)	Cameroon	Direct	1	2	1	26.4	3101	2
Swift <i>et al.</i> (1976)	UK	Direct	1	4	3	8.7	1703	> 2
Taylor <i>et al.</i> (1991)	Canada	Direct	3	3	3	1.7	620	1–3

See Methods for description of methodology codes. Ranges for climatic and geographic data are only available when multiple site locations were published. When diameter is given as a range, only diameter classes repeated across all species within a study were used in the analysis. Bibliographic references for all papers used in the analysis are in Appendix S1.

*There was insufficient information reported on site locations to generate climate data.

†Wood samples from plants grown in elevated and ambient CO₂ were incubated in the field. We treat the two treatments as separate species as chemical traits were reported for both.

‡ ϵ values were reported as a function of diameter, we used the value of the function at diameter = 8 cm for the analysis.

estimable age across a chronosequence (Harmon *et al.* 1986) (henceforth: 'Chronosequence' studies). A separate literature on ecosystem-scale rates of decomposition based on pool size calculations that did not include species-specific estimates was not included in the final analysis. All

studies we used determined decomposition for woody debris laying on the surface of the soil. A few papers also provided data for standing, suspended or buried material, but these were not numerous enough to warrant inclusion in the analysis.

Data assembly

The meta-analytical procedures incorporated data in two linked databases. First, the 'site' database contains an entry for each study site (given that some studies ranged over different sites) detailing site characteristics including latitude, longitude, altitude, methodology (Direct or Chronosequence), time scale of study and number of species. When location coordinates were not supplied, we approximated them using maps and geographical references in the text. To use a consistent source for long-term climatic averages, we determined mean annual temperature, and mean annual precipitation values for each site by extraction from a global climate dataset (New *et al.* 2002).

The second database contains records for each site \times species combination. Each record includes species name, taxonomic information, wood fragment diameter and k value, and if available, any wood trait data explicitly reported by the particular study. If multiple k values were reported for different size classes, we entered a unique record for each size class. Only those size classes that were common to all species in a study were included, as surface area/volume ratio generally decreases with size, thereby potentially reducing access by decomposing organisms and affecting decomposition rates. Diameter of decomposing fragments is thus uniform across species within each study. If single-exponential decay models were fitted by the original authors, k values were taken directly from the papers. In the case of multiple-exponential or linear decay models, we converted these to equivalent single-exponential decay models using

reported data. In cases where only graphical data were presented, we used graphical data extraction software to obtain a mass loss time series to which we fitted single-exponential decay models. In all cases, k values were expressed in year^{-1} units. We acknowledge that single-exponential decay models do not in all specific cases give the best description of the decay pattern, especially on long time scales (e.g. Berg & Matzner 1997). However, it has been by far the most reported model for several decades. Also, for our analyses, the absolute k values are themselves less important than the relative difference in k between different plant groups within the same study (i.e. derived with the same method over the same time scale).

We assembled 36 published studies (56% direct measurement, 44% chronosequence studies; Table 1, Appendix S1 in Supporting information), which comprised data from 83 sites (sites per study range: 1–7, median = 1 site) across all continents that host woody species (Fig. 1). Roughly half of the studies were conducted in forests managed for timber production (47%) with the remainder conducted in forests subject to natural disturbance regimes (41%) or a mixture of the two (12%). Time scales (length of incubation for Direct studies and estimated age of oldest site in Chronosequence studies) ranged from 1 to 600 years (median = 10 years). This range reflects the difference in woody litter turnover times between tropical and boreal/alpine environments. In total, k values for 99 different species were reported (species per study range: 2–17, median = 3 species). Other climatic and methodological details of each study are in Table 1.

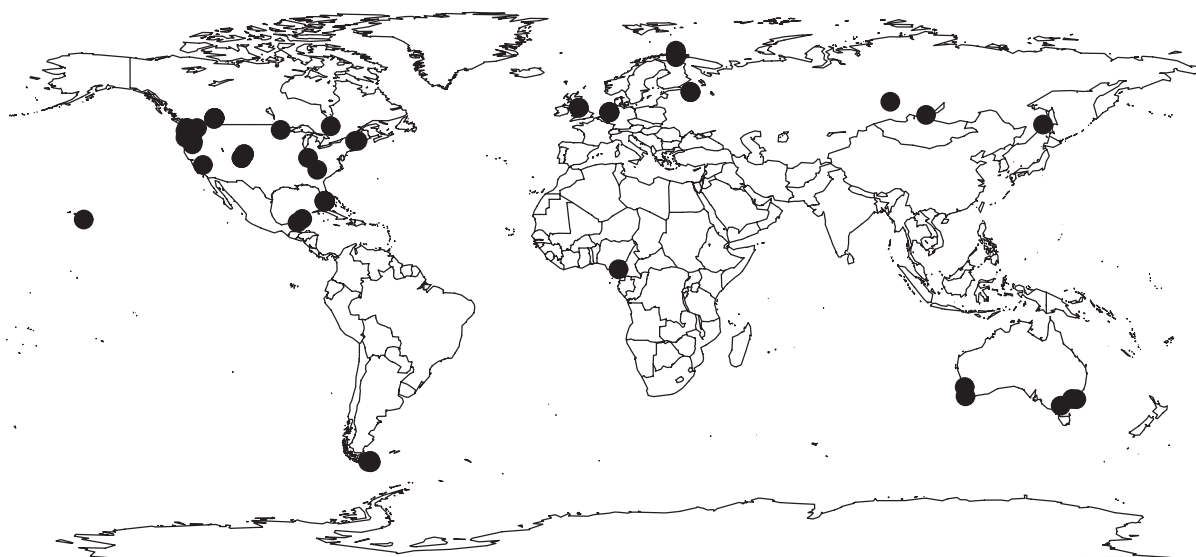


Figure 1 Geographical distribution of site locations from studies used in the meta-analysis. North America accounted for 52% of the studies, with Russia, Western Europe and Australia also represented by multiple studies (Table 1). Thus, the majority were conducted in temperate, alpine or boreal forests in North America or Europe. Tropical rainforests are represented by only two studies, coastal mangroves by only one and (semi)-arid shrublands not at all.

Traits used as explanatory variables in the meta-analysis were selected based on (1) *a priori* hypotheses about their effect on decomposition and (2) data availability. We used wood density, lignin, carbon, phosphorus and nitrogen concentration data (standardized to per cent by mass) from the original studies, and wood density and mean conduit area values from a wood anatomy database (A. E. Zanne & D. A. Coomes, unpublished data) containing a variety of forestry and personal datasets. Values from this database were applied to all matching species in the site \times species database, although we did not use gymnosperm conduit area in gymnosperm-only analyses (see below) due to the small variation of values relative to the inherent measurement error for this trait.

We obtained trait values for the following proportion of the 99 species: wood density, 82%; conduit area, 33%; nitrogen concentration, 34%; phosphorus concentration, 28%; lignin concentration (and lignin : N ratio), 18%; and carbon concentration (and C : N ratio), 11%.

Data analysis

Preliminary data inspection indicated strongly rightward skew for the distributions of both k values and wood traits. To satisfy the assumption of normality for parametric statistical tests, we therefore log-transformed explanatory and response variables before analysis.

To estimate the effects of continuous traits T on k values we used a linear mixed effects model in the NLME package of R (<http://www.r-project.org>) with either site or study as the random factor j according to the following statistical model:

$$\log k_i \sim N(\beta_{j[i]} + \alpha_{j[i]} \log T_i, \sigma_k^2),$$

for $i = 1, \dots, n$ observations

The rationale for treating j as a random factor is that we cannot account for between-study heterogeneity in such factors as climate, soils, methodology, localization, decomposer community and size of wood fragments. The β_s (intercepts) and α_s (slopes) vary between J groups (sites or studies) and are themselves modelled as coming from a joint normal distribution described by the mean slope and intercept μ_α and μ_β , their respective variances σ_α^2 and σ_β^2 , and their between-group correlation parameter ρ .

$$\begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim N \left[\begin{pmatrix} \mu_\alpha \\ \mu_\beta \end{pmatrix}, \begin{pmatrix} \sigma_\alpha^2 & \rho\sigma_\alpha\sigma_\beta \\ \rho\sigma_\alpha\sigma_\beta & \sigma_\beta^2 \end{pmatrix} \right],$$

for $j = 1, \dots, J$ groups

In Table 2, we report the estimates for μ_α and their 95% confidence intervals to characterize the relationship between k values and traits. This approach for continuous variables is

Table 2 Results of linear mixed effects models estimating effects of wood traits on k values (both log-transformed) for angiosperm species only (a,b) and gymnosperm species only (c,d)

	Observations	Groups	Lower	Estimate	Upper
(a) Angiosperms only, grouped by site					
Wood density	79	19	-0.96	-0.40	0.17
Conduit area	15	4	-0.45	-0.18	0.09
% Nitrogen	66	23	0.06	0.35	0.64
% Phosphorous	44	14	0.14	0.50	0.87
% Lignin	28	8	-1.41	0.26	1.92
C : N ratio	16	6	-1.12	-0.65	-0.18
Lignin : N ratio	20	7	-1.10	-0.51	0.08
(b) Angiosperms only, grouped by study					
Wood density	90	12	-1.09	-0.51	0.06
Conduit area	15	4	-0.45	-0.18	0.09
% Nitrogen	66	9	0.02	0.38	0.74
% Phosphorous	44	5	0.00	0.50	1.00
% Lignin	28	5	-1.82	0.13	2.08
C : N ratio	16	3	-1.17	-0.56	0.06
Lignin : N ratio	20	4	-1.26	-0.51	0.23
(c) Gymnosperms only, grouped by site					
Wood density	88	36	0.00	0.93	1.87
% Nitrogen	27	10	-0.43	0.77	1.97
% Phosphorous	13	5	-0.23	0.29	0.81
% Lignin	26	10	-1.54	1.44	4.42
C : N ratio	18	6	-2.81	-1.28	0.26
Lignin : N ratio	18	6	-3.80	-1.88	0.04
(d) Gymnosperms only, grouped by study					
Wood density	108	22	-0.18	0.80	1.78
% Nitrogen	30	8	-1.41	-0.10	1.22
% Phosphorous	16	6	-0.10	0.34	0.78
% Lignin	26	4	-2.48	1.20	4.89
C : N ratio	21	4	NA	-0.52	NA
Lignin : N ratio	18	3	-3.43	-1.18	1.07

Each analysis was repeated using either site (a,c) or study (b,d) as the random grouping variable in the model. For each model number of observations, groups (sites or studies) and lower and upper confidence limits (95% confidence, n = number of groups) are reported along with the slope estimate. Significantly non-zero slope estimates are highlighted ($P < 0.05$). For discussion of trait covariance see Appendix S3 in Supporting information.

analogous to the test for discrete variables using the random model in the MetaWin program (see below and Rosenberg *et al.* 2000). We therefore provide estimates of the global mean trait – k relationship, the distributions of which will reflect the influence of climate, other site factors and methodological differences between studies. Analyses were performed on combined data (Appendix S2), and on subsets containing only gymnosperm or angiosperm species. In all cases, we limited the analysis to groups that contained at least two levels of the explanatory variable.

To aid in the interpretation of the preceding analyses, we generated covariance half-matrices for each data subset (combined, angiosperm, gymnosperm) for the seven

continuous explanatory variables. An additional set of analyses that used genus-level means for wood anatomy traits (thus increasing the number of usable entries where species-level traits were not available) produced qualitatively similar results and is not reported here.

To test for the effect of phylogeny (gymnosperm vs. angiosperm species) on k values, we calculated effect sizes using the log-response ratio metric [i.e. $L = \ln(\text{mean } k_{\text{angiosperms}}) - \ln(\text{mean } k_{\text{gymnosperms}})$] for each site that included at least two k values from both groups and generated a 95% confidence interval for the mean effect size using the random effects model in MetaWin (Rosenberg *et al.* 2000). The requirement of this type of analysis for calculation of standard deviations (and therefore multiple observations per taxonomic group) limited the effective dataset, and we performed the analysis on two subsets. The first included only studies for which each observation within a study corresponded to a different species (four studies); this represents the most independent set of observations but the small number of studies limits inferences. The second dataset added three studies with only one species in angiosperms and/or gymnosperms but with multiple observations across sites (seven studies in total). As a second test of the hypothesis, which allowed us to incorporate yet more studies into the analysis (i.e. those with only one observation for one of the groups), we calculated mean decomposition rates for angiosperms and gymnosperms in each study and performed a paired t -test. This procedure allows the use of more of the data set but obscures any variation within groups within each study and does not weight studies by sample size and variance in the same way as the classical meta-analysis.

RESULTS

Trait–decomposition relationships without consideration of phylogeny

The linear mixed effects models yielded significant trait – k value relationships for all seven explanatory variables when all species were considered together, and site was used as the random grouping variable (Appendix S2). Closer examination of the patterns and comparison with the angiosperm- and gymnosperm-only analyses (see below) reveal that the significant relationships are driven by strong divergence in trait values and k values between angiosperms and gymnosperms. This confounding leads to artificially significant results, presented and discussed in Appendix S2.

Comparison of angiosperms and gymnosperm wood decomposition

Pair-wise comparisons of trait values by taxon reveal consistent differences in wood traits between angiosperms

and gymnosperms (Fig. 2). Angiosperm wood tends to be denser, and have larger conduits (vessels compared to tracheids), lower lignin concentration, and higher N and P concentration. These differences lead to higher lignin : N ratios in gymnosperms (Welch's t -test, $P < 0.05$). There were no significant differences due to taxon for C and C : N ratio (Welch's t -test, $P > 0.05$).

One of our *a priori* expectations was that a large proportion of interspecific differences in decomposition rates could be associated with the dramatic anatomical and biochemical differences between angiosperm vs. gymnosperm xylem. The random effects meta-analysis model estimated a mean effect size (ln RR) of 0.88 from the conservative four-study subset and 0.84 from the seven-study subset with more relaxed selection criteria (Fig. 3). These translate respectively to angiosperm k values 141% and 131% higher than gymnosperms in the same decomposition environment. Only the seven-study result is significant at $P < 0.05$, which is unsurprising given the low sample size for the other. A t -test of differences between mean angiosperm and gymnosperm decomposition rates from 16 studies reached a similar conclusion – with angiosperms having k values 77% higher (95% CI: 25–158 higher, $P = 0.0034$) (Fig. 4). These consistent patterns, for both the few multiple-species studies and the many studies with few species, together suggest that the significant trait – k value relationships in Appendix S2 are driven by systematic differences in the trait values of gymnosperms and angiosperms.

We used the coefficients from the mixed model analysis (described above) to calculate an estimate (with confidence intervals) for the magnitude of the wood quality effect using data subsets containing angiosperm or gymnosperm species only. Here we present the effects of a twofold increase in each wood trait value (converted from Table 2 for retransformed trait and k values).

When angiosperms are considered separately, there are positive relationships between k and N (change with twofold increase in trait = 27%, 95% CI: 4–56), and P (41% increase, CI: 10–83), and a negative relationship between k and C : N ratio (36% decrease, CI: 12–54). The estimates of slope from this dataset are smaller than from the pooled data, and the nitrogen relationship remains significant when the data are grouped by site or study (Table 2a,b). In the gymnosperm subset (Table 2c,d), there are no significant trait – k value relationships, regardless of grouping.

As all the traits used as explanatory variables are potentially related, knowledge of their covariance structure is crucial for interpretation of the preceding analyses. Full covariance matrices for all data subsets are reported and discussed in Appendix S3 but the key features are that: (1) denser wood tends to have lower lignin concentration

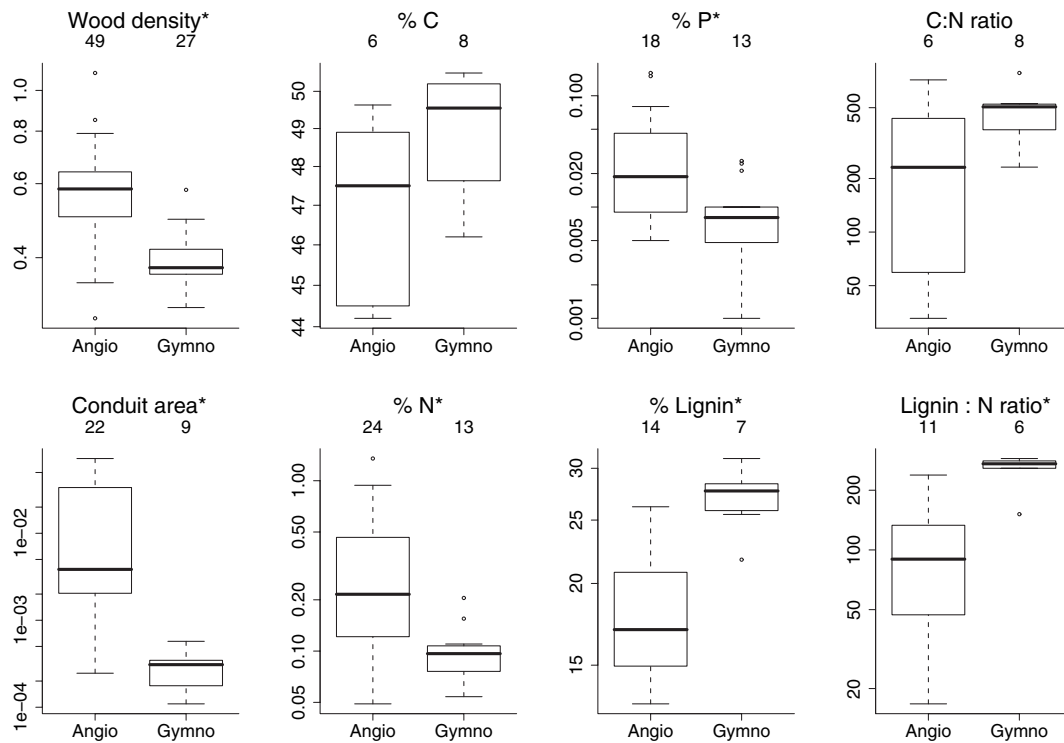


Figure 2 Comparisons of wood trait values between angiosperm and gymnosperm species. Units are g cm^{-3} for density, mm^{-2} for conduit area, and per cent by mass for chemical traits. Note \log_{10} scale. Numbers above each plot indicate number of species in sample. Asterisks against trait name indicate significant differences between angiosperm and gymnosperm species (Welch's *t*-test, $P < 0.05$).

and C : N ratios in angiosperms, but have higher lignin concentration and therefore higher C : N and lignin : N ratios in gymnosperms; and (2) P and lignin are positively correlated in gymnosperms and negatively correlated in angiosperms.

DISCUSSION

The linear mixed-effects model found strong effects of several chemical wood traits on decomposition of angiosperm wood. We found that decomposition is faster at higher N and P concentration, and slower at higher C : N ratio. These results broadly agree with the established idea that decomposition rate of plant material is constrained by the availability of macronutrients (Swift *et al.* 1979; Cadisch & Giller 1997; Berg & Laskowski 2006), and support the conclusions of several individual studies of wood decomposition that each identify one or both of N and P as important controllers of decay rates (e.g. Edmonds 1987; Alban & Pastor 1993). Mechanistic explanation of this pattern is provided by the simple economic model of Sinsabaugh *et al.* (1993) – as wood mass loss is related to lignocellulase enzyme production and activity, low substrate N and P can divert microbial energy investment away from

lignocellulase synthesis and towards N and P acquisition, slowing decomposition rates.

The gymnosperm-only analyses did not find any significant relationship between wood traits and decomposition rates within groups, despite generally having a larger sample size (Table 2). This is probably a result of a narrower range of values for some traits, particularly N, lignin and conduit area (Fig. 2). When angiosperm and gymnosperm wood fragments decay in a common environment, the latter consistently decomposes more slowly (Figs 3 and 4). This difference cannot be explained by wood density, which was generally lower in gymnosperms than in angiosperms, contradicting our hypothesis of a negative relation between wood density and decomposition rate. However, the generally low decomposition rates of gymnosperm wood do correspond with their higher lignin concentration and lower N and P concentration compared to angiosperm wood (Fig. 2).

It is also possible that angiosperm/gymnosperm differences in wood decomposability could be driven by other characteristics of their wood. Angiosperm and gymnosperm woods contain lignin formed from different alcohols (sinapyl and coniferyl respectively), which may have important effects on their degradation by microbes

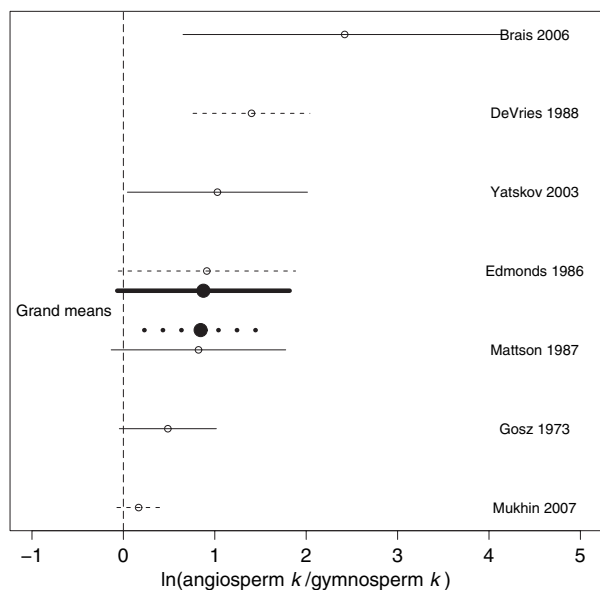


Figure 3 Confidence limits for estimates of mean effect size of angiosperm vs. gymnosperm on k values (log ratio of angiosperm to gymnosperm k values within each group). Points indicate mean effect size per study; lines are 95% confidence intervals. Solid lines indicate studies with different species for each group, dashed lines indicate studies with the same species but repeated at different sites, with bolder lines showing grand means (\pm 95% confidence interval) for the conservative subset (solid line) and the combined dataset (dashed line) (see Methods).

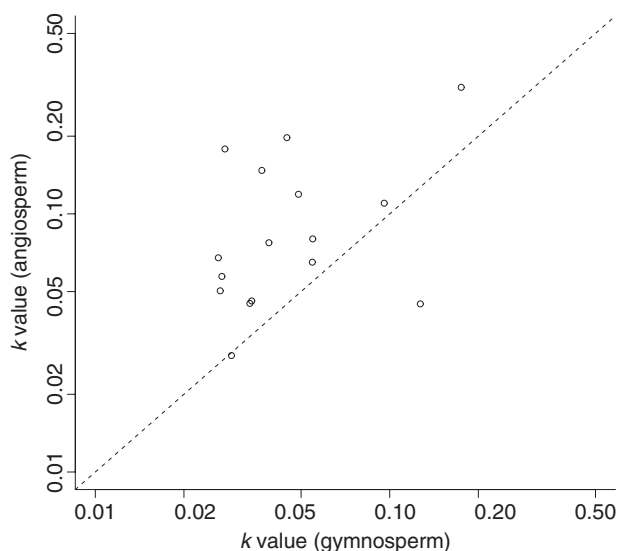


Figure 4 Log-log scatterplot of mean k values (year^{-1}) for angiosperms vs. gymnosperms calculated for each study that contained at least one observation of each. Dashed line is slope = 1, i.e. predicted values for no difference between groups. Mean difference is angiosperms 77% higher k (t -test, $P < 0.05$).

(Dix & Webster 1995; Kogel-Knabner 2002). They also differ consistently in the quality of hemicelluloses; the microscopic distribution of lignin and other structural compounds in tracheids; and the presence of non-structural phenolics and other aromatics such as those contained in resin (Dix & Webster 1995; Kogel-Knabner 2002). These chemicals, highly diverse and often present in low concentrations, may be more important controls of decomposition rates than macronutrient or lignin concentrations (Scheffer & Cowling 1966; Panshin & de Zeeuw 1980). It has been reported that brown-rot fungi (with minimal lignin degradation capacity) are more commonly associated with conifer forests than lignin-degrading white-rot fungi, which preferentially attack angiosperm wood (Boddy & Watkinson 1995), a pattern that may be related to the aforementioned differences in hemicelluloses. Such differences may also lead to differential conversions of wood chemistry over time; interactions that merit in-depth investigation.

Both wood density and xylem architecture may have important consequences for the micro-environmental conditions that decomposing fungi and bacteria experience in decaying material. Less dense wood potentially desiccates more rapidly (Yoneda 1975, but see Berry & Roderick 2005), and in situations where substrate moisture could limit fungal activity, this may affect decomposition rates. However, this is unlikely to control the slow decomposition of gymnosperm wood in our analysis, as most data came from boreal forests where soil moisture is not a predominant limiting factor for fungal activity. Alternatively, the large vessel elements of angiosperm wood may provide favourable microsites for fungal activity in terms of moisture and oxygen conditions, as well as increased physical access for fungal hyphae to a larger proportion of wood fragment volume (Dix & Webster 1995).

Implications for synthesis

Other investigators have looked for global patterns in wood decomposition by relating k values to climatic variables such as temperature and evapotranspiration (Yin 1999; Chambers *et al.* 2000; cf. Meentmeyer 1978). Our goal is complementary to that effort; we compared different species decomposing within the same sites to specifically test for correspondence of variation in wood traits with that in decomposition rates. Decomposition is a process controlled by a hierarchy of constraining factors (Lavelle *et al.* 1993) and complete understanding will require the integration of both climatic and substrate variables. We still do not know whether and how different biomes, with different woody plants and different nutrient budgets, may differ in the hierarchy of chemical drivers of decomposition.

In addition, the local decomposer community may exert strong effects on decomposition rates, particularly in regions where invertebrates such as termites are important processors of woody material (Torres & Gonzalez 2005). At an even finer scale, within-site horizontal heterogeneity in soil environment, some of which may have been caused by different species with different traits growing and shedding debris in the past, may have explained some of the variation in k in our dataset. Also, vertical variation in the microsite and microclimatic characteristics that occur as woody debris moves from the canopy to the ground, and potentially to burial or aquatic environments, has a demonstrated effect on decomposition rates (Van der Wal *et al.* 2007), as does wood fragment size, although not in a clearly predictable way (Abbott & Crossley 1982). Moreover, older trees of the same species may have greater proportions of heartwood with higher concentrations of recalcitrant compounds and important differences in wood quality may occur both radially and longitudinally within a tree (Panshin & de Zeeuw 1980; Finer & Kaunisto 2000). It is likely that each of these factors is controlled by species identity to a greater or lesser degree – leading to species-level effects on decomposition alongside the trait effects examined in this study. The challenge of understanding the relative importance and interaction of these controlling factors, and to upscale these regionally, remains open.

In spite of these complications, our results have important implications for the study of the effects of climate change on ecosystem function. One of the predictions of global climate–vegetation models is an increase in deciduousness (as associated with angiosperm dominance) of forests, particularly at the southern edge of the current boreal zone (IPCC 2007). Such changes may occur within the next 100 years under current climate projections (Cramer *et al.* 2001). Higher decomposition rates of angiosperm compared with gymnosperm wood therefore have the potential to influence carbon storage within large areas of forest. We should note that both the main climate effect – increased mean temperature – and vegetation feedback – increased dominance of angiosperms – will speed the decomposition of woody material. Even without temperature effects, our most conservative estimate of the difference in k values of angiosperm wood compared to gymnosperm wood (77% higher) will translate to a 44% reduction in the size of the woody debris pool, which equates to between 4.4 and 9.7 tonnes C ha⁻¹ based on estimates of Russian boreal forest woody debris pool sizes (Krankina & Harmon 1995, see Appendix S4 for more detail and relation to forest productivity). This estimate of emissions is an order of magnitude higher than the calculated effect of a beetle outbreak on carbon storage in Canadian boreal forests (0.36 tonnes C ha⁻¹), an event that transiently converted

large areas of forest from carbon sink to source (Kurz *et al.* 2008). This pattern may be further augmented by the generally faster decomposition of angiosperm tree leaves compared with gymnosperm leaves, as was recently demonstrated in a global meta-analysis following a similar common-site approach (Cornwell *et al.* 2008). Extending this approach to whole trees, explicitly comparing within-species patterns in wood, leaf and root traits across tree species and types, is important for better understanding vegetation feedback to carbon storage (De Deyn *et al.* 2008). Increased woodiness of tundra and alpine regions is also likely through shrubland expansion (Tape *et al.* 2006). Knowledge of the relationships between wood traits and decomposition rates will allow more accurate prediction of the effect of these expansions on carbon cycling. Decomposing wood can also act as sources or sinks for a variety of soil nutrients (e.g. Arthur & Fahey 1990; Laiho & Prescott 1999) – changes to decomposition dynamics will therefore also influence ecosystem nutrient cycling.

In many systems, woody material is released to the ecosystem episodically through burning as well as gradually via biological decomposition. Wood traits and plant architecture can determine flammability of woody species (Lavorel & Garnier 2002; Schwilk 2003). Plant flammability can directly affect decomposition processes through the formation of pyrogenic carbon, the ecological properties of which are determined by fire temperature and wood type (Gundale & DeLuca 2006). Pyrogenic carbon can both contribute to a highly recalcitrant soil C pool, as well as alter soil biochemistry through adsorption of a variety of compounds, e.g. plant allelopathic substances (Preston & Schmidt 2006). The relationship between wood traits and carbon and nutrient cycling thus involves both decomposability and flammability, the relative importance of each will depend on local climatic conditions and overall plant community structure and trait composition, both now, and in a warmer future.

Our analysis has identified the likely importance of wood traits in determining decomposition rates of woody tissues in a range of ecosystems. Wood traits are in turn determined by a range of ecological trade-offs, such as the various relationships between succession strategy, growth rate, wood density and water relations (Falster & Westoby 2005; Preston *et al.* 2006). We suggest a comparison between wood trait coordination and decomposition rates as a fruitful avenue of future investigation. The relationship between leaf traits, decomposition and ecosystem nutrient cycling is comparatively well established (Hobbie 1992; Aerts 1997; Cornelissen *et al.* 1999) and comprises possible feedback from decomposition to plant traits (Berendse 1994); very similar dynamics could occur within the slower-turnover wood pool.

Current state of data and future work

Meta-analysis seeks to find general patterns from a collection of individual studies, but the generality of the conclusions are necessarily limited by the coverage of the data used. Although we believe our coverage of the literature is good and our results robust, we propose a number of caveats. First, the biogeographical coverage of the dataset is rather limited (Fig. 1), with the majority of studies conducted in North American and Western European boreal and temperate forests. Increasing the geographical coverage, especially to include more data from shrublands and subtropical and equatorial forests, would provide more general conclusions, as well as the opportunity to investigate the relative importance of different traits in different biomes. The wide variation in wood traits within tropical forests (Chave *et al.* 2006) suggests that the effects described here could be even more important in equatorial forests. Second, we used single values for each species for wood density and mean conduit area – this ignores the potentially important intraspecific variation in these traits (Panshin & de Zeeuw 1980; Kaakinen *et al.* 2004; Kostianen *et al.* 2006). For chemical traits, we used values that were site-matched and therefore more realistic. Third, values of some traits were missing for a majority of species. This decreases the effective size of the dataset and further limits the generality of results.

Our understanding of species effects on wood decomposition will benefit from more standardized field experiments explicitly measuring decomposition rates of wood types with a range of traits along climatic gradients. In addition, the continued growth of databases of a range of structural and chemical traits (e.g. Chave *et al.* 2006; A. E. Zanne & D. A. Coomes, unpublished data; Plant Functional Types (TRY) initiative of IGBP/DIVERSITAS) will allow us to identify the most important drivers of wood decomposition, and the environmental and phylogenetic constraints on their coordination. An important goal for future trait screening efforts should be to extend their coverage to traits not traditionally measured but with potentially important effects on ecosystem function, e.g. micronutrient contents.

Decomposition of woody plant tissue is an important component of the terrestrial carbon cycle, and a better understanding of its controlling factors is essential for predicting ecosystem responses to global change. Using a global dataset, we have provided evidence that, within a given climatic context, wood decomposition rates can be correlated with a range of wood traits: macronutrients, lignin concentration and xylem architecture. These trait effects are most apparent when comparing angiosperm and gymnosperm wood, which we have shown to differ systematically in a range of traits, as well as in their

decomposition rates. Further knowledge of wood trait–decomposition relationships, as well as the connections with processes at different scales, will enable us to better predict the future interplay between global change and terrestrial carbon cycles.

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SUPPORTING INFORMATION

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

Appendix S1 Bibliographic information for the studies used in the meta-analysis.

Appendix S2 Results of linear mixed-effect model using pooled dataset.

Appendix S3 Covariance matrices for wood traits.

Appendix S4 Estimation of effect of changes to decomposability of wood on carbon storage.

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