LETTER

Plant species traits are the predominant control on litter decomposition rates within biomes worldwide

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Abstract

Worldwide decomposition rates depend both on climate and the legacy of plant functional traits as litter quality. To quantify the degree to which functional differentiation among species affects their litter decomposition rates, we brought together leaf trait and litter mass loss data for 818 species from 66 decomposition experiments on six continents. We show that: (i) the magnitude of species-driven differences is much larger than previously thought and greater than climate-driven variation; (ii) the decomposability of a species' litter is consistently correlated with that species' ecological strategy within different ecosystems globally, representing a new connection between whole plant carbon strategy and biogeochemical cycling. This connection between plant strategies and decomposability is crucial for both understanding vegetation–soil feedbacks, and for improving forecasts of the global carbon cycle.

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Litter decomposition in terrestrial ecosystems has a profound effect on global carbon cycles (Prentice *et al.* 2001; Canadell *et al.* 2007) through litter carbon respiration as well as litter accumulated as potential fuel for wildfires (Sitch *et al.* 2003; Friedlingstein *et al.* 2006). Forecasts of strong climate warming and other global environmental changes for the remainder of this century (IPCC 2007) have put feedbacks to climate through changes in litter turnover and thereby carbon stocks high on the international research agenda. The multiple drivers of decomposition include the effects of environment, at both regional and micro-site scales, the substrate quality of litter, and composition of the decomposer community (Cornelissen 1996; Aerts 1997; Parton *et al.* 2007). Climate sets broadly similar conditions for long-term litter decomposition within biomes (Berg *et al.* 1993; Moore *et al.* 1999; Raich *et al.* 2006; Parton *et al.* 2007). In contrast, interspecific differences in green leaf traits and the subsequent quality of litter produced following leaf senescence are associated with the diversity of plant resource-acquisition strategies in a given biome (Aerts 1996; Reich *et al.* 1997; Aerts & Chapin 2000; Grime 2001; Diaz *et al.* 2004; Wright *et al.* 2004).

Green leaf traits are modulated only modestly by climate (Wright *et al.* 2005), and over 40% of global variation for particular leaf traits can be found within individual sites (Wright *et al.* 2004). The pronounced within-site variation among species can be due to finer-scale environmental heterogeneity in space (e.g. soil fertility and hydrology) and time (e.g. disturbance) and/or tradeoffs among other physiological traits that produce roughly similar fitness levels among coexisting species with alternate physiological strategies (Grime 2006; Marks & Lechowicz 2006; Ackerly & Cornwell 2007).

Many of the physiological and protective features of green leaves persist through senescence, in part because the resorption of nutrients by the plant is incomplete, leading to a strong correlation between green leaf tissue chemistry and the chemical composition of discarded leaf litter (Aerts 1996; Killingbeck 1996). The carbon and nutrient chemistry and stoichiometry of the litter, and its physical features, can then have a strong effect on the abundance and activity of decomposers leading to different rates of decomposition (Melillo *et al.* 1982; Taylor *et al.* 1989). We therefore hypothesized (i) that variation in leaf litter decomposition rates *within climate regions* worldwide would be a function of the traits of living plant species; and (ii) that this species-driven variation would equal direct climate-driven variation in leaf litter decomposition across biomes.

We tested these hypotheses by synthesising data from published and unpublished experiments (Assembly of Research on Traits and DECOmposition: ART-DECO project). Our focus was on data sets from experiments that incubated leaf litter of many species in a common environment, holding climate, soil environment, decomposer community, and incubation period constant within each study. In total, the database contains 1196 records of species-by-site combinations from 66 sites on six continents including 818 species from 165 plant families. The sampled diversity largely parallels the mix of diversity among higher plant taxa: the data set includes 580 eudicot species, 118 monocots, 22 species from the Magnoliid lineage, 39 Gymnosperms, 37 Pteridophytes (ferns and fern allies), and 20 Bryophytes. The broad coverage of our data set and meta-analytic methods allowed us to isolate species-specific decomposability within each study, and to search for decomposition relationships with continuous traits, plant functional types, and phylogenetic groups that are consistent across studies.

METHODS

Species-specific decomposition records and the traits of green leaves and undecomposed leaf litter were collected from published and unpublished sources based on experimental multi-species incubations (see Appendix S1). In most cases, the data were contributed directly by the lead author of the original experiment, allowing the original researcher to classify species functional traits and to include unpublished values for particular traits. In experimental studies (e.g. when decomposition included fertilization of the decomposition environment) only the control groups were used. Species decomposition records were collected as percent mass loss for each successive harvest, and decomposition constants (k) were calculated for each species-experiment combination (Chapin *et al.* 2002). The number of harvests (1–10), the length of the decomposition period before each harvest (< 30 days to > 1700 days), the fertility of the decomposition site, and the experimental methods (e.g. position of litterbags during decomposition) varied from study to study as appropriate for the questions asked in the particular study. In this meta-analysis, we sought to analyze repeated within-study patterns.

Species-based variation in decomposition rates were quantified both as the total range observed within each study and also the range of the middle 90% of species within each study (calculation following type 7 from Hyndman & Fan 1996). Climate-driven variation was calculated using the same statistical methods from published studies (fig. 1a in Parton *et al.* 2007 and Berg *et al.* 1993). Standard meta-analysis techniques (METAWIN v2.0; Rosenberg *et al.* 2000) were used to quantify the degree of congruence among results from studies undertaken under a variety of climatic and experimental conditions. Response ratios were used to compare effect sizes from the set of studies, with study included in the model as a random factor. Uncertainty surrounding estimates of effect size were described using

(nonparametric) bootstrap confidence intervals. For pairwise comparisons of group-mean effect size (e.g. deciduous vs. evergreen woody species), only studies with > 2 species were included in each group. We derived mean slope estimates and statistical significance of trait-decomposition relationships using mixed-effects ANCOVA, with study treated as a random factor and traits used sequentially as covariates (R v2.6: function 'lme'), and we calculated weighted estimates of regression coefficients for the trait-decomposition relationships (Sokal & Rohlf 1995).

RESULTS

How wide is the variation in leaf decomposition rates due to species traits, compared with climate-driven variation? To calculate the magnitude of the species-based effect within an ecosystem while holding climate constant, we considered only studies that sampled > 20 species from one climatic zone, leaving 14 studies. On average, these studies found a 18.4-fold range in decomposition rate. Considering only the

middle 90% of the species in each study (that is, between the 5th and 95th quantile), there was a 10.5-fold average difference in species decomposition rates (size of circles in Fig. 1). We compared these results with those of two large-scale experiments decomposing the same litter in very different climate conditions. In North America, Parton *et al.* (2007) found a 5.5-fold range in decomposition rate of a common substrate, with the fastest decomposition in a wet tropical forest and the slowest in the tundra. In another large study spanning sites in Europe and North America Berg *et al.* (1993) found a 5.9-fold range in the rate of decomposition for pine litter across sites.

For each study, we quantified the relationship between decomposition rate and leaf traits (both of green leaves and of litter). Both green leaf and litter traits were correlated with decomposition with roughly equal variance in decomposition explained by each green leaf or litter trait (Fig. 2). There was also significant collinearity among predictors: litter %N was positively correlated with litter %P ($r = 0.50$, $P < 0.001$), and negatively correlated with LMA ($r = -0.45$, $P < 0.001$), but
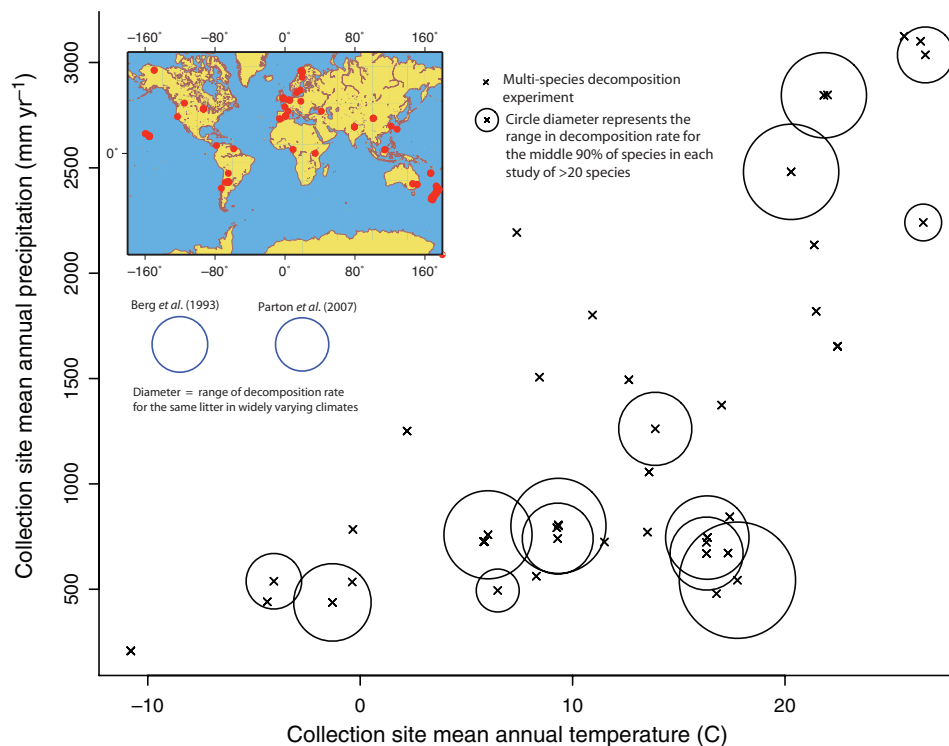

Figure 1 The magnitude of the species effect on decomposition within regional floras located in widely varying climate conditions across the world. Each cross in the figure and dot on the map represents a multi-species decomposition study at the modelled long-term climate (New *et al.* 1999). For 14 large sample size (> 20 species) studies, we calculated the change in decomposition rate for the middle 90% of species (from the 5th to the 95th quantile). We then represent the proportional difference within each study as the diameter of the circles (arbitrary scale). This species-based effect (holding climate constant within each study) can be compared with published measures of the range of decomposition rates observed due solely to climate-based variation (holding species constant). Two large across-climate studies of the same litter found 5.5- and 5.9-fold ranges in decomposition rates among different biomes. On average, species-based effects were substantially larger than climate-driven effects, showing an 18.4-fold mean difference when all data were considered, and 10.5-fold mean difference when only the central 90% of species were included in the analyses.
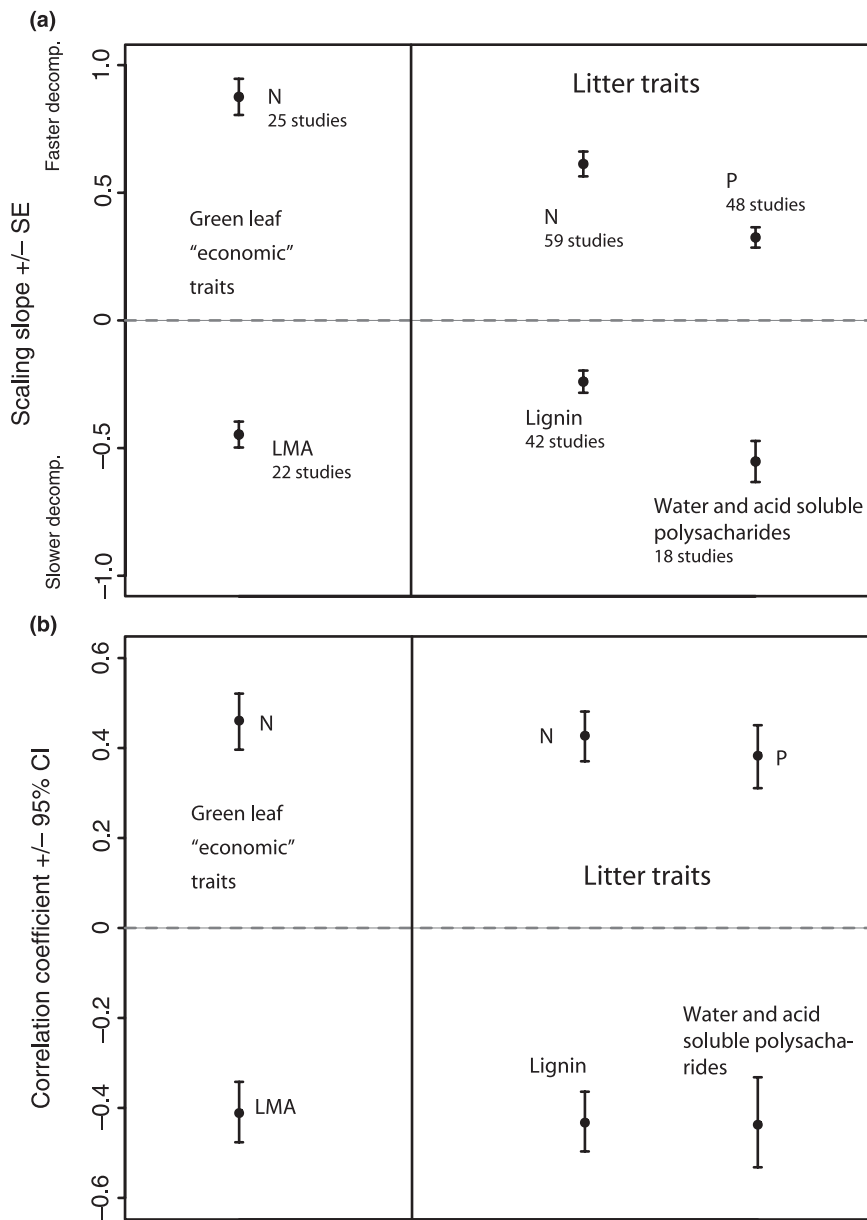
(a)

(b)

Figure 2 Meta-analysis of the relationships between green leaf or leaf litter traits and decomposition rate (k) within studies across the world. All comparisons are within studies with climate and experimental methods held constant. The number of studies that measured each trait varies and is reported in panel (a). Panel (a) shows the log–log scaling slope for each trait. Panel (b) shows the sample size weighted mean correlation coefficient. Water and acid soluble polysaccharide fraction consists largely but not exclusively of cellulose and hemicellulose. Associated ANCOVA found each of the six traits significant at $P < 0.01$.

uncorrelated with litter lignin ($r = 0.01$, NS). Thus, positive effects of P and/or negative effects of thicker leaves on decomposition may contribute to the positive relationship between decomposition and leaf and litter %N.

We found consistent large differences in decomposability among vascular functional groups (Fig. 3) and among the large clades within the higher plant phylogeny (Fig. 3a). The main differences are discussed below.

DISCUSSION

On average, studies that sampled many species across the world found an 18.4-fold range in decomposition rate. This

is a much larger range than previous estimates (Chapin *et al.* 2002). Further, large variation in litter decomposition rates was observed among species in all climate zones from the Arctic to the Tropics (see distribution of circles, Fig. 1), demonstrating that a wide range of decomposition rates among species is a common feature of natural ecosystems worldwide.

What underlies the large differences in species decomposition rates? Plant species range from those that obtain a strategically slow return on carbon invested, often coupled with efficient nutrient use and/or extended durability, as indicated by high leaf mass per area (LMA) or low mass-based leaf nitrogen concentration
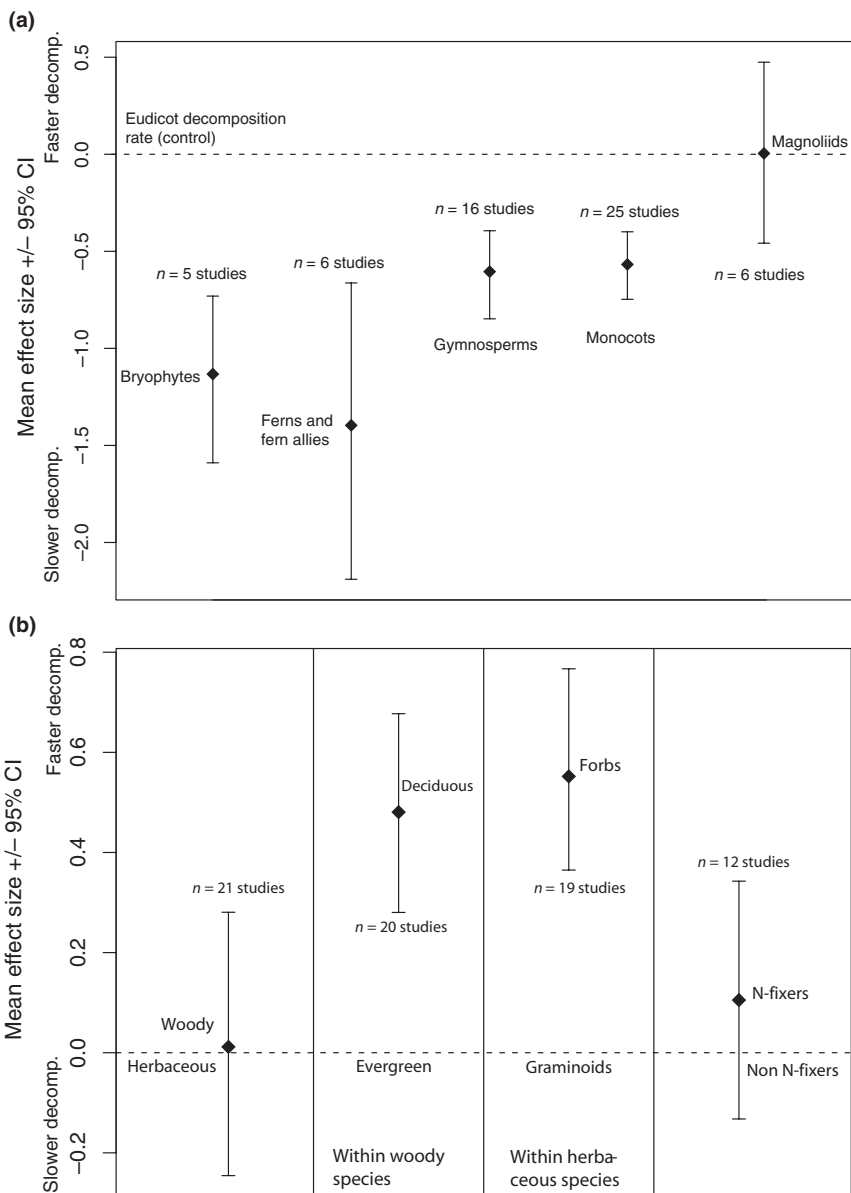
Figure 3 Effect size estimates from meta-analysis for pairwise phylogenetic and functional group comparisons, including studies that had a minimum of two species in each group. Effect sizes correspond to a percent change in decomposition rate (see text). All comparisons are within studies with climate and experimental methods held constant. In panel (a), the decomposition of bryophytes, ferns and fern allies, gymnosperms and Magnoliids are compared with the eudicots. In panel (b), we make pairwise comparisons between woody and herbaceous species, evergreen woody and deciduous woody species, herbaceous forbs and herbaceous graminoids, and species with and without the ability to fix atmospheric N. Error bars represent the 95% confidence intervals obtained through bootstrapping. Please note the shift in the y-axis scale between panel (a) and panel (b).

(N_{mass}), to those capable of gaining a fast return on leaf carbon associated with the opposite traits. This continuous array of species' strategies has been termed the 'leaf economics spectrum' (Reich *et al.* 1997; Wright *et al.* 2004), because it represents fundamental biochemical and structural tradeoffs globally (Reich *et al.* 1997). Here, we show, for the first time at a global scale, that these leaf 'economic' traits lead influential afterlives, affecting the rate of decomposition, which is a key component of the global carbon cycle.

Consistent with previous work on smaller scales (Melillo *et al.* 1982; Taylor *et al.* 1989), litter N and litter lignin both had effects on decomposition (Fig. 2). Litter N was strongly related to green leaf N, an economic trait related to

physiological capacity, and uncorrelated with litter lignin. This suggests that both immobile carbon chemistry – litter lignin – and traits associated with the green leaf economics spectrum are important in influencing decomposition.

We found consistent large differences in decomposability among vascular functional groups (Fig. 3). Woody deciduous species – generally faster-return plants with shorter individual leaf lives than woody evergreens (Reich *et al.* 1997) – produced litter that decomposed 60% faster than woody evergreen species. This was true whether the evergreen species included both gymnosperms and angiosperms or only the latter. Surprisingly, herbaceous species in general did not produce litter that decomposed faster than woody species. This was due to slow decomposition among

graminoids (grasses and grass-like monocots), which balanced fast decomposition among forbs (eudicot herbs). These differences in decomposition are consistent with differences in mean green leaf %N and structure among angiosperm graminoids, forbs, shrubs and trees, when comparing species with comparable tissue longevities (Reich *et al.* 2007). In contrast to the large differences between forbs and graminoids, species that have the capacity to fix atmospheric N produced litter that decomposed only slightly (and nonsignificantly) faster than non-N fixers.

Decomposability of litter also differs systematically among the large clades within the higher plant phylogeny (Fig. 3a). Eudicot litter decomposed faster than four out of five more basal clades both across all species and within specific growth forms. Global mean effect sizes demonstrate that eudicot litter decomposed on average four times faster than bryophyte litter, three times faster than litter of ferns and their allies, 1.8 times faster than gymnosperm litter and 1.6 times faster than monocot litter.

One of the key uncertainties in forecasts of the carbon cycle are potential shifts in the identity and traits of the dominant plant species, which have feedbacks to the climate cycle through numerous mechanisms including decomposition rate (Chapin *et al.* 2005; Cornelissen *et al.* 2007; Suding *et al.* 2008). Within biomes across the world there are numerous predictions for shifts in the traits of the dominant species due to anthropogenic change. To list just three: a decrease in the abundance of slow decomposing bryophytes in the tundra (Hobbie 1996), a shift from evergreen gymnosperm to deciduous angiosperm dominance at the southern edge of the boreal forest (Cramer *et al.* 2001), and a shift to greater graminoid biomass with greater N deposition (van Wijk *et al.* 2004; Soudzilovskaia *et al.* 2007). The magnitude of the differences reported here suggests that shifts in the relative abundance of these already co-existing groups in response to anthropogenic change could have large effects on regional carbon cycles (Garnier *et al.* 2004; Cortez *et al.* 2007).

In summary, the traits of green leaves of different species vary widely within particular biomes and sites. This variation is associated with different 'economic' strategies for carbon gain and growth and with different phylogenetic groups (Reich *et al.* 1997; Wright *et al.* 2004). This functional differentiation has large and consistent afterlife effects on the rate of decomposition of senesced leaves. Based on this worldwide data set, we calculate that species-based variation in leaf composition has a very strong effect on decomposition rate, larger than both previous estimates and the effect of global climatic variation. These results demonstrate that the leaf afterlife features of differentiation in plant functioning should be considered a predominant control on the rate of decomposition of organic matter in ecosystems. Correctly forecasting the abundance and distribution of plant species traits and their associated decomposability under future climates and atmospheric CO_2 concentrations is crucial for accurate forecasts of the future carbon cycle.

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SUPPORTING INFORMATION

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

Appendix S1 The ART-Deco database includes data from unpublished work and these published papers.

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