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Plant-driven variation in decomposition rates improves projections of global litter stock distribution

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Abstract

Plant litter stocks are critical, regionally for their role in fueling fire regimes and controlling soil fertility, and globally through their feedback to atmospheric CO₂ and climate. Here we employ two global databases linking plant functional types to decomposition rates of wood and leaf litter (Cornwell et al., 2008; Weedon et al., 2009) to improve future projections of climate and carbon cycle using an intermediate complexity Earth system model. Implementing separate wood and leaf litter decomposabilities and their temperature sensitivities for a range of plant functional types yielded a more realistic distribution of litter stocks in all present biomes with except of boreal forests and projects a strong increase in global litter stocks and a concomitant small decrease in atmospheric CO₂ by the end of this century. Despite a relatively strong increase in litter stocks, the modified parameterization results in less elevated wildfire emissions because of litter redistribution towards more humid regions.

1 Introduction

Extensive ground-based measurements of plant biochemistry, physiology, and ecology have led to a much better quantification of ecosystem processes during the last decades (Hassan et al., 2005). Recent assimilation of many thousands of measurements of species traits in global databases (Wright et al., 2004; Kattge, 2011) opens a new perspective to specify plant parameters used in ecosystem models which predominantly operate at the level of large-scale plant units such as plant functional types (PFTs) (Cramer et al., 2001). Instead of constraining model parameters using values from a few publications, a novel approach aggregates plant traits from the species level to the PFT level using trait databases (Kattge et al., 2009).

Models of the terrestrial carbon cycle are composed of a part related to the functioning of living plants and a part describing the decomposition of plant litter and soil organic matter. While the former processes are quantified relatively well (Denman

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et al., 2007), the decomposition processes are much less constrained by observations, essentially because of long time scales involved and limited applicability of remote sensing data. In particular, litter decomposition is poorly quantified in ecosystem models used at a global scale (Cornwell et al., 2009) although it is an important integrative part of the carbon cycle. Besides, litter serves as a fire fuel and is therefore a central part of the fire disturbance process which drives ecosystem changes. Moreover, decomposition, especially of leaf litter, is a key component of nutrient (nitrogen, N, and phosphorus, P) cycling in ecosystems. The nutrient feedback of litter and soil decomposition to plant productivity has long been neglected in most Earth system models used for future carbon cycle projections (Denman et al., 2007), although there are recent advances both for N (Churkina et al., 2009; Gerber et al., 2010; Sokolov et al., 2008; Thornton et al., 2007; Zaehle et al., 2010) and P cycling (Wang et al., 2009). The litter decomposition is driven not only by nutrient content of the litter, by also other chemical components such as lignin (Parton et al., 1993), and accounting for litter quality is an essential further step in the global vegetation models.

Here, we demonstrate the critical consequences of accounting for PFT-specific variation in litter decomposition parameters, compiled in global trait databases, upon litter stocks and fire disturbance using the Lund-Potsdam-Jena (LPJ) global dynamic vegetation model (DGVM) (Gerten et al., 2004; Sitch et al., 2003), complemented by a diagnostic representation of N and P stocks.

2 Methods

2.1 PFT-dependent leaf litter decomposition

PFT-dependent decomposition rates of leaf litter, k , were derived based on strong correlations between litter lignin (lig, in %), nitrogen contents (N, in %) and decay rates (Parton et al., 2007). Litter decomposition experiments from the ART-DECO dataset (Cornwell et al., 2008), for which both lignin contents and nitrogen contents were available, were analysed to derive k used in this study. After correction for

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environmental conditions (temperature), both lignin and nitrogen were highly significantly ($P < 0.001$) related to k (Fig. 1). F -values were 55.685 and 116.159 for nitrogen and lignin, respectively. The effects of the litter traits on litter k were thus strong and standard errors of the regression coefficients were small (0.045 for log-lignin and 0.056 for logN, respectively). Together, the two litter traits and environmental conditions explained most of the variance (75 %) of the litter k values, with a rest of variance most likely to be explained by non-accounted factors such as leaf chemical composition such as tannins and soil macro-detritivores (Hattenschwiler and Jorgensen, 2010).

The decomposition rate at a reference temperature of 10 °C (Table 1) was parameterized as:

$$\frac{{}^{10}\log k_{10}^{\text{PFT}}}{{}^{10}\log k_{10}^{\text{ref}}} = \frac{a \cdot \text{lig}^{\text{PFT}} + b \cdot \text{N}^{\text{PFT}}}{a \cdot \text{lig}^{\text{ref}} + b \cdot \text{N}^{\text{ref}}}. \quad (1)$$

Parameters $a = -0.350$ and $b = 0.417$ were obtained from statistical analysis of the ART-DECO (Cornwell et al., 2008) trait database containing decomposition and litter chemistry data for 818 species from 66 experiments on six continents. Index ref refers to the reference litter site. The assignment of species to PFTs was based on botanical information on leaf habit, life-form and the biome of origin according to the definitions in LPJ. Arithmetic means of litter chemistry per PFT and overall averages across the ART-DECO database were applied.

We acknowledge the importance of other litter chemical parameters besides C:N stoichiometry and accounted for lignin content in Eq. (1). Although our leaf litter database also included tannin contents, we did not include tannins in Eq. (1) for three reasons: 1) tannins were less well covered in our database, 2) the relation between tannins and k (in particular, important in some tropical studies) was generally weaker than the relation between lignin and k , and 3) lignin and N together have been most frequently used to predict global patterns in k (e.g., Parton et al., 2007) and therefore using these parameters allows comparing our estimates with the those derived in previous studies.

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2.2 PFT-dependent woody litter decomposition rates

PFT-dependent woody litter decomposition rates are based on the analysis of another trait database, Functional Ecology of Trees (FET), developed by the Organismic Biogeochemistry Group at the Max-Planck-Institute for Biogeochemistry in Jena. FET contains 1511 data entries for k -values for 340 tree species from 66 plant families studied in 166 different locations across the world extracted from a total of 99 publications. Studies reporting wood decomposition rates and meeting the following criteria were considered:

- Decomposition rates, k , were based on observations on loss of mass, carbon, or density, but not volume;
- Only k -values from a single-exponential decay model were used (i.e. no linear or lag-time models etc.);
- The time axis was derived either from long-term observations or from chronosequences. Mass balance estimates based on woody detritus mass divided by input were excluded;
- Only whole organs including bark were studied (i.e. no wood chips etc.). This requirement was relaxed for tropical studies to include the comprehensive dataset from Usher and Ocloo (Usher and Ocloo, 1979) where wooden planks had been used;
- Only wood pieces exceeding a diameter of 1 cm were considered.

Decomposition is an ecosystem-level process and depends on the activity of the decomposer community, which is controlled by abiotic factors (temperature, moisture, oxygen availability) and biotic factors (substrate quality and litter accessibility). To be able to account for these factors, information on important covariates were collected along with decomposition rates. Mean annual temperature, mat, and annual precipitation sum, ap , were included as climate data. Where available the values given in the

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publications were used. Otherwise data from Climatic Research Unit for years 1960–1999 (New et al., 1999) were used. The diameter of logs, d , was included as covariate controlling both, accessibility and quality, the latter given that the fraction of chemically protected heartwood increases with size. The position of a tree, pos , influences the moisture content of the wood. Downed logs with soil contact exhibit greater moisture contents than standing snags. The assignment of PFTs was based on botanical information on leaf habit, life-form and the biome of origin according to the LPJ definitions (Sitch et al., 2003). The seven woody PFTs in LPJ were aggregated to evergreen broadleaved trees, deciduous broadleaved trees and needleleaved trees. This was done to obtain more reliable estimates for the temperature sensitivity by increasing the temperature range.

The abovementioned information was used to derive the following general formulation of the statistical model:

$$k_i = k'_{j(i)} \exp \left(\sum_l \beta_{j(i)l} c_{il} \right) q_{j(i)}^{\frac{T_i}{T_{ref}}} + \varepsilon_{ij} \quad (2)$$

where k = observed k -value, and k' = reference k -value when

- all covariates c attain a value of zero (see below), and
- the mean annual temperature T (°C) is at a reference temperature T_{ref} (set to 10°C).

In Eq. (2), $q = Q_{10}$ is the relative increase in k upon a temperature increase of 10°C, ε is the residual error component, i is a subscript for individual observation ($i = 1, \dots, n$), j is a subscript for the aggregated PFTs ($j = 1, 2, \text{ or } 3$), and l is subscript for different covariates (ap, d, pos). The β 's are parameters of the statistical model and the notation $j(i)$ indicates that observation i belongs to PFT j . The three covariates c used here are the annual precipitation sum ap (in mm), the initial diameter d (in cm) and a binary position indicator, pos , that takes of 1 when elevated and 0 for soil contact. The

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continuous covariates ap and d were z -transformed [(value-mean)/SD]. Temperature was not transformed in order to be compatible with the standard Q_{10} -formulation. The data matrix was full with the exception of the initial diameter d (with 119 missing values out of 1511) and the missing data were imputed within the estimation algorithm.

5 After log-transformation on both sides, Eq. (2) yields

$$\underbrace{\ln k_i}_{k^*} = \underbrace{\ln k'_{j(i)}}_{k'^*} + \sum_l \beta_{j(i)l} c_{il} + \underbrace{\ln q_{j(i)}}_{q^*} \cdot \frac{T_i - 10}{T_{\text{ref}}} + \varepsilon'_{ij} \quad (3)$$

where, i.e. the errors are normally distributed around the predicted log-transformed k -value with the estimated variance σ_j^2 .

10 Equation (3) was analyzed with WinBUGS (Lunn et al., 2000) using only non-informative (“flat”) priors to avoid the introduction of prior information into the estimation. The resultant estimates of parameters k^* and q^* were back-transformed to their original units (see Table 1), which resulted in log-normal error distributions at the original scale. Comparison of observed versus predicted decomposition rates of coarse woody debris is shown at Fig. 2 and modelled sensitivity of coarse woody debris decomposition rates to mean annual temperature is presented on Fig. 3.

2.3 Setup of model experiments

Similar to many DGVMs, the original formulation of the LPJ decomposition module did not consider separating litter into leaf and woody components. The decomposition rate, k , a reciprocal to the mean residence time of litter, was the same for all sources of litter (leaf, sapwood, and heartwood) and equalled 0.3 yr^{-1} for the reference temperature of 10°C and maximum soil moisture for all PFTs. Recent global compilations of ground-based observations of decomposition rates allowed for a new parameterization of litter decomposition for the nine PFTs used in LPJ. Firstly, the leaf and woody litter components were treated as separate pools and specified for each PFT. This is important because woody (especially coarse detritus) decomposition is slower by an

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order of magnitude than leaf decomposition. This simulation uses k values averaged from the trait databases. Secondly, k was specified for each PFT based on data for their species representatives in litter databases for leaf litter (Table 1, see Sects. 2.1 and 2.2 above). Thirdly, dependence of woody litter decomposition on temperature was re-parameterized to account for PFT-dependent temperature sensitivity rates (Q_{10}) using the FET dataset instead of the original uniform LPJ parameterization (Lloyd and Taylor, 1994). These three steps are noted as W (for woody and leaf litter separated), K (for k by PFT based on trait databases), and Q (for Q_{10} parameterization). Here we present results from four 2,000-yr pre-industrial equilibrium LPJ simulations noted as CTL (original LPJ parameterization), W, WK, and WKQ. The latter three simulations add one after the other the three implementation steps of the new PFT-dependent litter decomposition parameterization introduced above.

The new PFT-parameterizations were incorporated in LPJ (Gerten et al., 2004; Sitch et al., 2003), designed to represent land surface processes at a high spatial resolution (Kleinen et al., 2010). The LPJ model simulates natural vegetation dynamics without accounting for the anthropogenic land cover changes. Four equilibrium simulations were performed to quantify effects of the new parameterizations step-by-step. In addition, two transient runs were done by coupling LPJ to the intermediate complexity climate model CLIMBER-2 (Petoukhov et al., 2000) containing a oceanic biogeochemistry model (Brovkin et al., 2002). In the transient simulations, CLIMBER2-LPJ was driven by the SRES A2 scenario of fossil fuel and landuse emissions as in the C4MIP simulations (Friedlingstein et al., 2006) starting from pre-industrial equilibrium at the year 1750.

3 Results

The original LPJ parameterization (CTL) results in the largest litter stocks in the boreal and tundra regions of the Northern Hemisphere (Fig. 4, top). The litter stocks in the polar tundra region are overestimated, in particular in North-Eastern Siberia, where

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observations (Bazilevich, 1993) report litter stocks of 0.3–1 kg C m⁻² while the model simulates 4 to 8 kg C m⁻². At the same time, comparison with data for woody litter stocks (Fig. 5) reveals that woody litter is underestimated in all other regions and increasingly so towards tropical regions, in particular because of unrealistically high *k* values. This cumulates in a global litter amount of 184 Gt C which is beyond or at the upper range of estimates of litter stocks based on observations (68–97 Gt C) or models (47–196 Gt C) (Matthews, 1997), respectively. Accounting for the omission of anthropogenic deforestation in the model simulations, the total global CTL litter stock estimate is plausible, but ground observations demonstrate clearly that the original CTL parameterization shifts the litter stocks erroneously from forested temperate regions towards the tundra region.

In the WKQ simulation, the global total amount of litter (191 Gt C) is very similar to the results of the CTL simulation. However, the spatial patterns of litter distribution are distinct from the CTL simulation as the largest litter stocks are located in the boreal forest zone while the polar region has much less litter (Fig. 4, bottom). The litter stock in the tropical regions increases. When comparing to empirical woody litter stock data, the WKQ results are closer to the observations (Fig. 5). The model slightly underestimates the litter stocks in all regions except in the boreal needleleaved forests where the woody litter stocks are at the high end. At the northern boundary of boreal forests, the model overestimates the living biomass stocks by a factor of two, in particular because of the absence of a permafrost parameterization which otherwise would limit tree growth substantially, and this is reflected in the high litter stocks. Despite this bias, the new parameterization of the litter decomposition leads to a much improved worldwide distribution of litter stocks. The statistical analysis of woody litter data reveals a significant underestimation of litter stocks in all regions in the CTL simulations while the data and model results of the WKQ simulations are in much closer agreement (Table 2). The ANOVA *F* value is less for WKQ simulation than for CTL simulation for all PFTs, including boreal needleleaved trees. However, because of a bias in living biomass stocks, a mean litter stock in boreal needleleaved forests is overestimated

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by ca. 80 % (Table 2). This calls for improvement of modelling of biomass distribution in high northern latitudes, as discussed above. The global flux of leaf litter in the WKQ simulation ($19.9 \text{ Gt C yr}^{-1}$) is almost two times higher than the woody litter flux ($11.0 \text{ Gt C yr}^{-1}$). Despite smaller input flux, the woody litter dominates in total litter stocks (ca. 75 %) because its decomposition rate is by an order of magnitude slower than the decomposition rate of the leaf litter (Table 1).

Results from the W simulation suggest that the main improvement in the global distribution of litter is due to separation of litter into leaf and woody components (Fig. 6). The bias in the polar tundra region is partly removed. The W simulation uses k values averaged from the trait databases (0.94 and 0.057 yr^{-1} for the leaf and woody litter at 10°C , respectively). Accounting for the PFT-dependent decomposition constants in the WK simulation completely removes the litter stock bias in north-eastern Siberia, and the PFT-dependent Q_{10} values in the WKQ simulation decreases litter stocks in tropical regions towards more realistic values, where the relatively higher sensitivity to temperature ($Q_{10} = 2.75$, Table 1) partly reflects the greater contribution of xylophagous insects, especially termites, to wood turnover in warmer biomes (Cornwell et al., 2009) (see Sect. 2.2 and Fig. 3 for more details on Q_{10} constraining procedure). The W, WK, and WKQ simulations excluded the modulation by soil moisture on litter decomposition (Foley, 1995; Sitch et al., 2003). Higher moisture can promote decomposition of soil organic matter and leaf litter, but for woody litter the contact with soil moisture is much less and excess moisture may even reduce decomposition, especially in the tropics (Torres and Gonzalez, 2005).

Using the ART-DECO (Cornwell et al., 2008) and FET databases (Weedon et al., 2009), we assigned N and P contents to the leaf and woody litter of each PFT (Table 3). In the CTL simulation, the global litter stock holds 2.9 and 0.16 Pg of N and P, respectively. Despite higher litter stocks, the WKQ simulation keeps much less nutrients in litter pools (1.5 PgN and 0.09 PgP), because the bulk of the stock consists of nutrient-poor woody litter. Smaller nutrient litter content could reduce nutrient supply during the growing season and may lead to a progressive nutrient limitation under

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elevated CO₂ concentrations (Luo et al., 2004), stressing an importance of further analysis using a model that includes interactive N and P cycles.

To test the consequences of this improved litter parameterization for atmospheric CO₂ concentration and climate in the future, we used an Earth system model of intermediate complexity, CLIMBER2-LPJ (Kleinen et al., 2010), in simulations with a representative climate scenario, SRES A2 (see Sect. 2). In response to fossil fuel emissions and climate change, the atmospheric CO₂ concentration increases during the entire 21st century by 380 ppm and 377 ppm in the CTL-T and WKQ-T simulations (T for transient), respectively (Table 4). Lower CO₂ concentration in the WKQ-T experiment is explained by a 31 GtC higher total litter stock accumulation counteracted by a decrease of 24 GtC in biomass stocks. While the global increase of litter stocks at the end of the 21st century is rather similar for both experiments, the geographical patterns of these changes are different. The CTL-T simulation results in a rather homogeneous increase in litter stocks in the tropics and subtropics and elevated litter aggregation in the polar region. The WKQ parameterization predominantly leads to greater carbon storage at the southern boundary of boreal forests. Both CTL-T and WKQ-T simulations show a strong increase by 50 % in wildfire emissions during the 21st century (Table 4). The burned area increases mostly in subtropical dryland areas following elevated litter stocks due to a CO₂ fertilization effect and woody encroachment. Despite a relatively stronger increase in litter stocks, the WKQ-T simulation has slightly lower wildfire carbon emissions (Table 4), because of litter redistribution towards more humid regions.

4 Discussion and conclusions

Earth system models are extremely simple in representing plant functional diversity in general, but particularly when it concerns plant effects on its environment. In most, if not all, models variation in responses of plant traits and their afterlife effects on litter quality are neglected. Our study thus represents one of the first attempts to incorporate

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variation in these trait responses. We acknowledge that many improvements can still be made, but it is also important to acknowledge the principal step forward taken by our approach and the biological simplicity of current generation of Earth system models.

The litter decomposition rates vary within PFTs. As far as that variation is due to prevailing environmental conditions, our model accounts for it, thus capturing a major fraction of the variability in decomposition within PFTs. We cannot account for differences in litter quality within PFTs in a given environment because ESMs do not calculate the necessary traits that are known to determine k values. Only recently ESM started to simulate leaf nitrogen contents, an important driver of k , but no ESM accounts for lignins, phenolics, tannins or any other key chemical determinant of litter quality, let alone that ESMs allow these characteristics to vary within PFTs. However, given that we estimated k values based on global relations between k and litter N and lignin (explaining a large percentage of the variation in k ; see Fig. 1), our approach can easily be extended to include the variation in k within PFTs as soon as estimates on global variation in litter traits become available.

The databases that we used to derive the k values reported in Table 1 are currently the largest global databases in its kind, derived from studies that measured leaf litter k alongside litter chemical characteristics. We linked the k values to litter chemistry to predict the variation in k within and between PFTs. This led to highly robust estimates of k (see Figs. 1 and 2 for illustration of variation in k_{leaf} and k_{wood} , respectively). Subsequently, we predicted k from the average litter lignin and litter N contents of that PFT.

While we included the effects of temperature, precipitation and litter quality, there is a number of other factors affecting decomposition such as soil decomposers. Soil decomposers have been included implicitly, however, because decomposition experiments were run at local conditions with local soil fauna, albeit that macro-detrivores had been excluded due to the use of litter bags (but including meso- and micro-detrivores). In those cases where soil macro-detrivores do account for substantial additional variation in decomposition rates, notably in the tropics (see tropical forest

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studies by Hattenschwiler and Jorgensen, 2010), they must be part of the 25 % residual variance in the k -values. Our two litter chemical and environmental parameters explained the other 75 % of variation in decomposition rates. We therefore assume that soil decomposers are less important than these parameters which is confirmed by global studies (Aerts, 1997; Berg et al., 1993; Meentemeyer, 1978; Cornelissen et al., 2007 for a cold-biome example). Even if we had included additional k variance due to soil decomposers in our decomposition studies, we still would not have been able to account for them in our numerical experiments given that ESMs do not model soil decomposers. The effects of temperature and precipitation incorporated in our model have been derived from global relations between environmental conditions and decomposability and are generally accepted.

Plant litter dynamics are essential for the land-atmosphere carbon flux because this organic carbon stock is easily available for microbial decomposition and for abrupt release to the atmosphere through wildfires. Despite a large amount of local data on litter stocks across the globe, a synthesis of the global litter distribution is not readily available. Uncertainty in global litter storage remains high (Denman et al., 2007; Matthews, 1997), in particular, because woody litter storages are difficult to quantify on a global scale. It is therefore inevitable that, for some time, carbon cycle models will be utilized as the best available source of information on the spatial distribution of litter stocks used for carbon cycle projections. Using most recently compiled datasets on the litter decomposition (Cornwell et al., 2008; Weedon et al., 2009), we remarkably improved the modelled distribution of litter stocks (Fig. 4), although model results are still far from perfect when compared to local data.

Re-parameterisation of models based on trait datasets is not entirely free from biases. Woody litter estimates, for example, are often done for mature forests and this can partly explain the disagreement between the data and global models such as LPJ which simulate averaged forest stands without accounting for the tree age structure. Removing this kind of structural biases is an essential part of model improvement. Altogether, incorporating trait-based relationships into Earth system models constitutes

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a major step forward for better forecasting of land ecosystem processes including carbon and nutrient cycling, and fire regimes.

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Table 1. Litter decomposition parameters, k , at 10 °C and litter temperature sensitivities (Q_{10}) used in the WKQ simulation¹.

| LPJ plant functional type | Leaf litter k , yr ⁻¹ | Woody litter k , yr ⁻¹ | Woody litter Q_{10} ² |
|--|---------------------------------------|--|---------------------------------------|
| Tropical broadleaved evergreen trees (TrBE) | 0.93 | 0.039 | 2.75 |
| Tropical broadleaved raingreen trees (TrBR) | 1.17 | 0.039 | 2.75 |
| Temperate needleleaved evergreen trees (TeNE) | 0.70 | 0.041 | 1.97 |
| Temperate broadleaved evergreen trees (TeBE) | 0.86 | 0.104 | 1.37 |
| Temperate broadleaved summergreen trees (TeBS) | 0.95 | 0.104 | 1.37 |
| Boreal needleleaved trees (BoN) | 0.76 | 0.041 | 1.97 |
| Boreal broadleaved summergreen trees (BoBS) | 0.94 | 0.104 | 1.37 |
| C ₃ grass (H C3) | 1.20 | – | – |
| C ₄ grass (H C4) | 0.97 | – | – |

¹ In the CTL simulation, decomposition rates for the leaf and woody litter at 10 °C were set uniformly to 0.3 yr⁻¹. The sensitivity to temperature and soil moisture was defined following parameterizations by Lloyd and Taylor (1994) and Foley (1995), respectively.

² Q_{10} represents the relative increase in decomposition upon a 10 °C temperature rise.

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Table 2. Summary of the Analysis of Variance (ANOVA) on the differences between woody litter stocks as represented in the FET dataset (noted as Data) and according to model simulations CTL and WKQ (presented in the box-and-whisker plots in Fig. 2). For the model outputs, only grid cells where the simulated fractional projection cover of the PFT in question was higher than 50% were taken into account.

| LPJ PFT | <i>n</i> (number of sites or grid cells) | | | Mean litter stocks, kg C m ⁻² | | | Standard deviation of litter stocks, kg C m ⁻² | | | <i>F</i> value, ANOVA ¹ | |
|------------|---|------|------|---|------|------|--|------|------|---------------------------------------|-------|
| | Data | CTL | WKQ | Data | CTL | WKQ | Data | CTL | WKQ | CTL | WKQ |
| TrBE | 40 | 5443 | 5394 | 0.84 | 0.32 | 0.84 | 0.67 | 0.14 | 0.38 | 482.8 | 0.0 |
| TrBR | 9 | 2430 | 2444 | 1.22 | 0.15 | 0.29 | 0.94 | 0.08 | 0.21 | 1080.0 | 178.2 |
| TeNE | 100 | 1214 | 1238 | 6.47 | 0.61 | 2.40 | 6.86 | 0.31 | 1.30 | 873.9 | 298.9 |
| TeBE | 13 | 822 | 679 | 6.26 | 0.39 | 0.94 | 6.74 | 0.20 | 0.43 | 637.1 | 370.2 |
| TeBS | 53 | 448 | 434 | 1.75 | 0.60 | 1.25 | 2.39 | 0.24 | 0.44 | 97.0 | 11.5 |
| BoN | 68 | 9049 | 9051 | 2.35 | 1.58 | 4.32 | 2.71 | 0.64 | 1.87 | 86.0 | 76.4 |
| BoBS | 8 | 3662 | 3626 | 0.84 | 0.92 | 0.80 | 1.07 | 0.27 | 0.27 | 0.8 | 0.13 |

¹ The ANOVA used quantifies the difference between two independent datasets: observed data from the FET dataset and results of either CTL or WKQ simulations. The difference between observed data and models was always statistically significant at the $p < 0.05$ level (except of the TrBE PFT for the WKQ simulation) due to the very high number of observations. Although the differences may be statistically different, they might not represent biologically relevant differences. Therefore, the *F*-values, representing the variance explained by differences among dataset over the residual variance, was used to compare model outputs. The *F* values for the WKQ experiment were always lower than for the CTL experiment implying that the WKQ results were closer to the observed data than the CTL results.

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Table 3. N and P content of litter used to diagnose leaf litter nutrient stocks¹ following ART-DECO dataset (Cornwell et al., 2008). Carbon content of dry matter was taken as 50 %.

| LPJ Plant Functional Type | C : N (g : g) | C : P (g : g) |
|--|---------------|---------------|
| topical broadleaved evergreen tree | 56.6 | 1546 |
| tropical broadleaved raingreen tree | 33.2 | 871 |
| temperate needleleaved evergreen tree | 82.3 | 965 |
| temperate broadleaved evergreen tree | 68.2 | 2119 |
| temperate broadleaved summergreen tree | 53.4 | 548 |
| boreal needleleaved tree | 56.5 | 898 |
| boreal broadleaved summergreen tree | 60.3 | 1031 |
| C ₃ perennial grass | 43.3 | 763 |
| C ₄ perennial grass | 63.9 | 1511 |

¹ For woody litter, C : N and C : P ratios we taken as 156 and 2340 for broadleaved, and as 454 and 6474 for needleleaved trees, respectively, based on results by Weedon et al. (2009).

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Table 4. Results of transient CLIMBER-LPJ simulations.

| Years/variable | 1891–1900 ¹ | | 1991–2000 | | 2091–2100 | |
|--|------------------------|-------|-----------|-------|-----------|-------|
| | CTL-T | WKQ-T | CTL-T | WKQ-T | CTL-T | WKQ-T |
| Atmospheric CO ₂ concentration, ppm | 287 | 287 | 345 | 344 | 725 | 722 |
| Litter stocks, Gt C | 184 | 191 | 191 | 196 | 242 | 277 |
| Biomass, Gt C | 597 | 597 | 709 | 716 | 1112 | 1095 |
| Soil carbon, Gt C | 1349 | 1368 | 1356 | 1374 | 1452 | 1469 |
| Wildfire emissions, Gt C yr ⁻¹ | 3.1 | 2.9 | 3.6 | 3.3 | 5.3 | 5.0 |

¹ Decadal averaged values.

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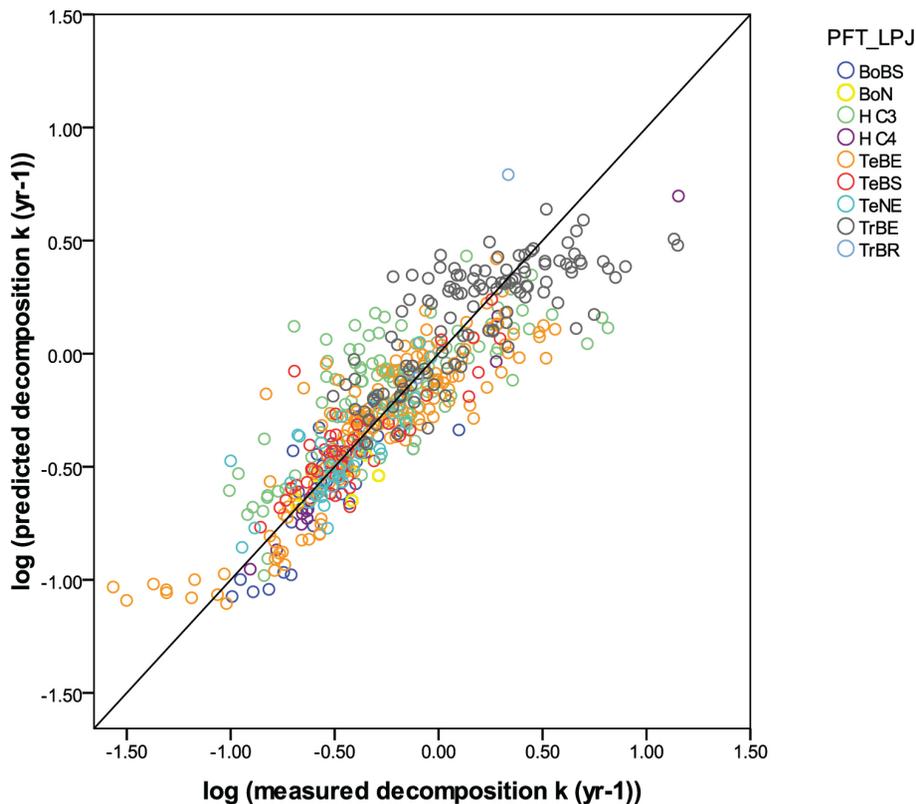


Fig. 1. Correspondence between measured k (x-axis) versus predicted k (y-axis) using Eq. (1) on a log-log scale. Acronyms for LPJ woody PFTs are the same as in Table 1.

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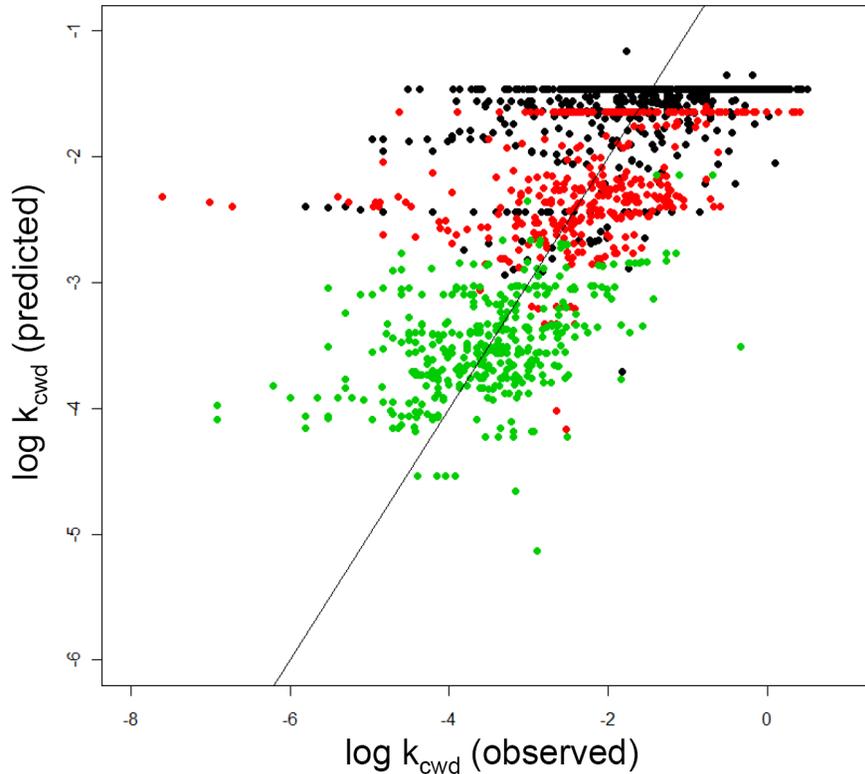


Fig. 2. Observed (x-axis) versus predicted (y-axis) decomposition rates of coarse woody debris at the log-scale. Green = evergreen needleleaved (boreal and temperate), red circles = deciduous broadleaved (boreal to tropical), black = evergreen broadleaved (mostly tropical). The model controls for effects of log size, precipitation, and soil contact. The large residual variation (and the low overall R^2 of 0.43) compared to litter decomposition is due to strong species-specific variation in decay preventing chemical constituents and decomposer communities.

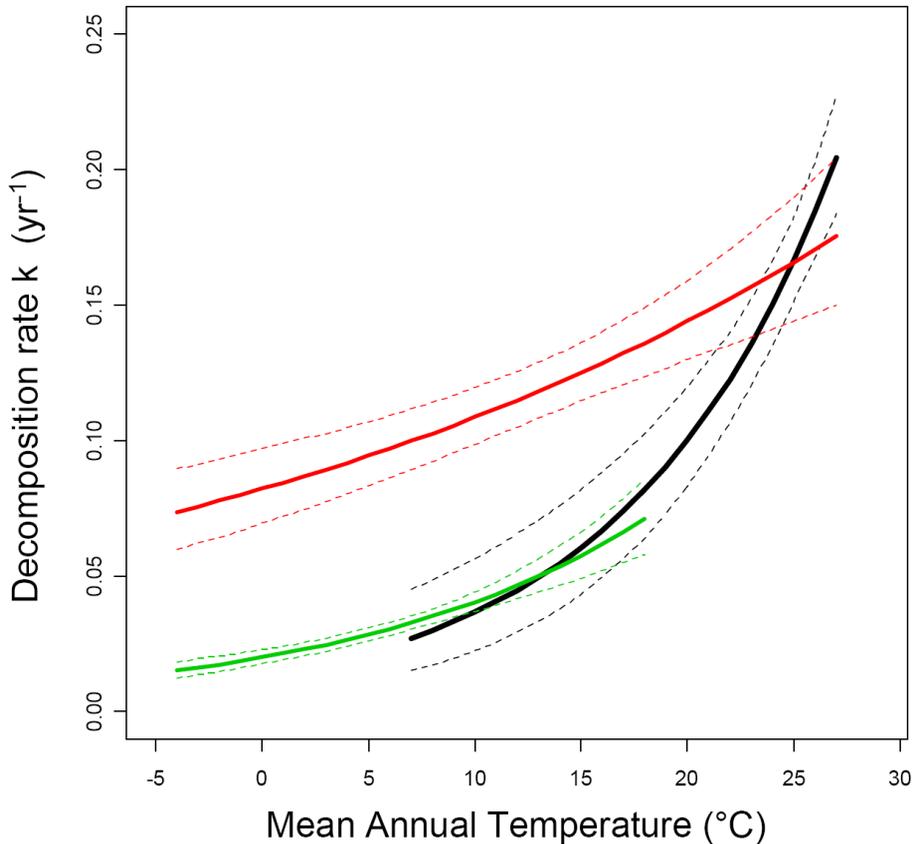


Fig. 3. Modelled sensitivity of coarse woody debris decomposition rates (yr^{-1}) to mean annual temperature (bold lines). The steepness of the curvature indicates differences in Q_{10} . The 95 % confidence intervals (dash lines) are with respect to the mean predictions and does not contain the residual variation. Green = evergreen needleleaved, red = deciduous broadleaved, black = evergreen broadleaved.

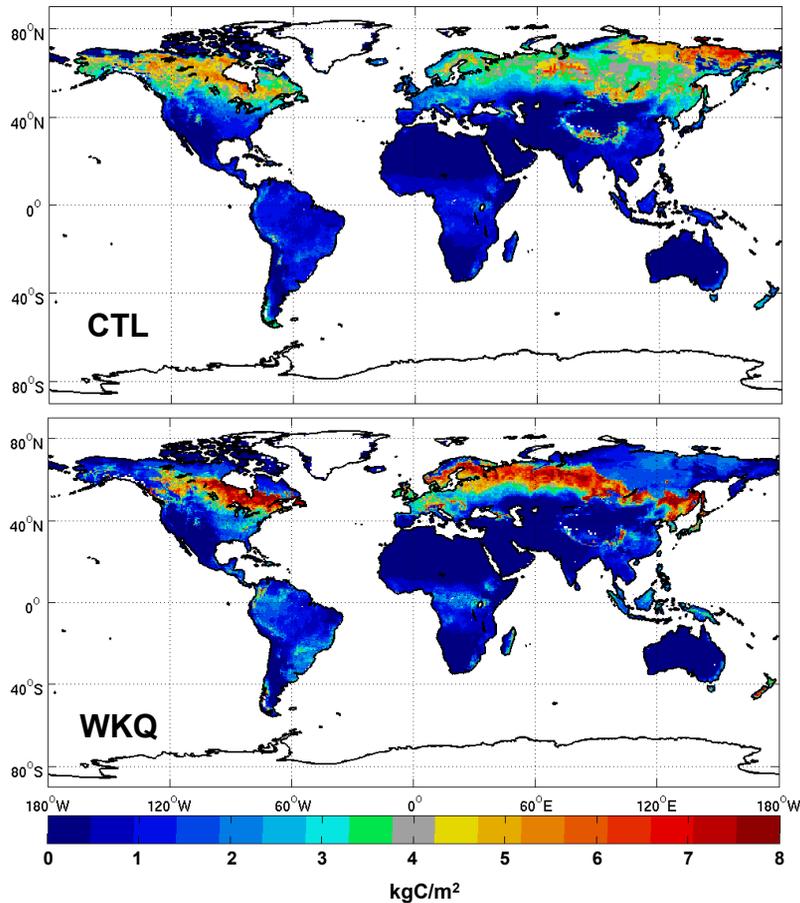


Fig. 4. Distribution of total litter stocks (kgC m^{-2}) in the CTL (top) and WKQ (bottom) simulations. Effects of anthropogenic changes in land cover on vegetation distribution and carbon stocks were not accounted for.

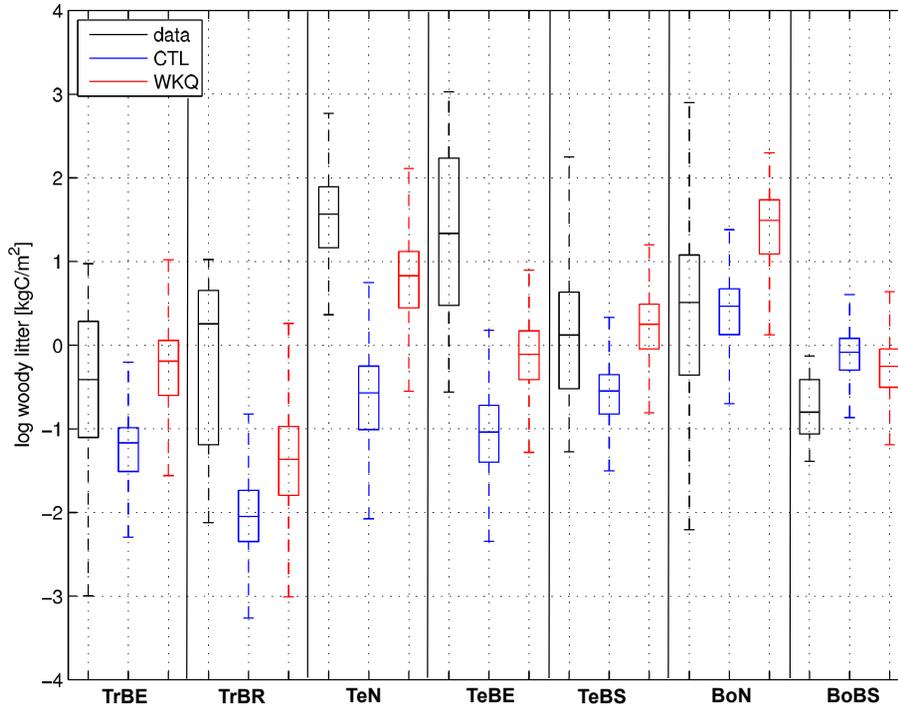


Fig. 5. Woody litter stocks (kg C m^{-2} , natural logarithm scale) simulated in the CTL and WKQ simulations compared to the Functional Ecology of Trees (FET) trait database aggregated to 7 woody Plant functional types (PFTs), see Table 1 for the PFT acronyms and Table 2 for statistical analysis. For representing the model outputs, only grid cells where the simulated fractional projection cover of the PFT in question was higher than 50 % were taken into account to allow adequate comparison with the observations. In the CTL experiment, woody and leaf litter stocks were calculated separately for comparison.

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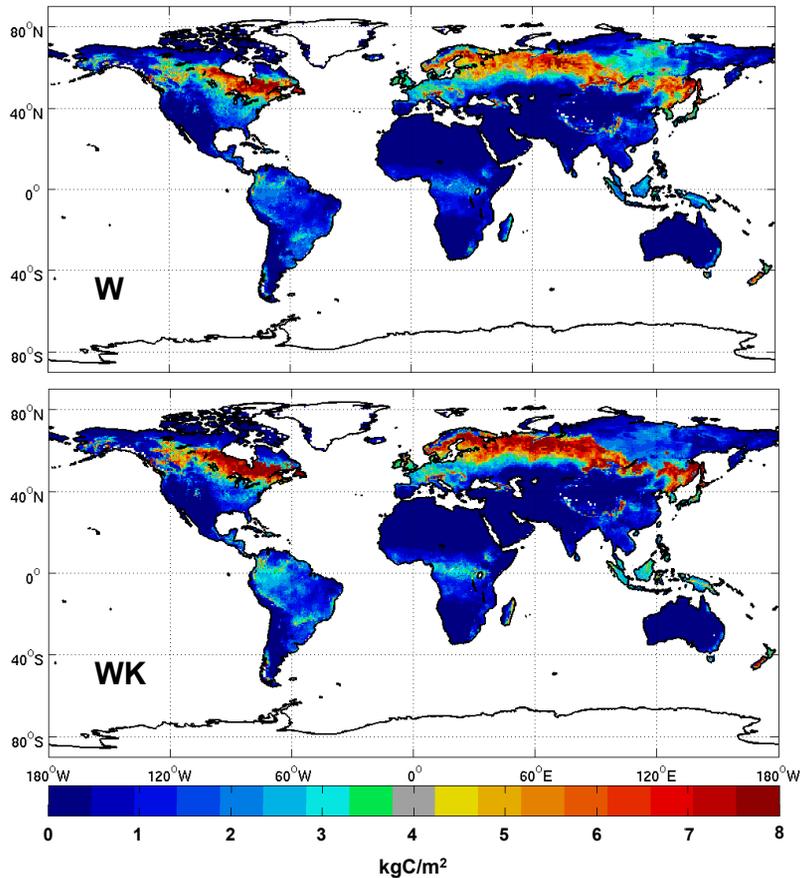


Fig. 6. Distribution of total litter stocks (kg C m^{-2}) in the W (top) and WK (bottom) simulations. Effects of anthropogenic changes in land cover on vegetation distribution and carbon stocks were not accounted for.