

Short- and Long-term Influence of Litter Quality and Quantity on Simulated Heterotrophic Soil Respiration in a Lowland Tropical Forest

Laëtitia Bréchet,^{1,2*} Valérie Le Dantec,³ Stéphane Ponton,^{4,5}
Jean-Yves Goret,² Emma Sayer,^{6,7,8} Damien Bonal,^{4,5} Vincent Freycon,⁹
Jacques Roy,^{10,11} and Daniel Epron^{4,5}

¹Department of Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YW, UK; ²INRA, UMR 0745, Ecologie des Forêts de Guyane, Campus Agronomique, BP 709, 97387 Kourou cedex, French Guiana; ³Toulouse III, Université Paul Sabatier, UMR 5126, Centre d'Etudes Spatiales de la Biosphère, 31401 Toulouse, France; ⁴INRA, UMR 1137, Ecologie et Ecophysiologie Forestières, Centre de Nancy, 54280 Champenoux, France; ⁵UMR 1137, Ecologie et Ecophysiologie Forestières, Faculté des Sciences, Université de Lorraine, 54500 Vandoeuvre-les-Nancy, France; ⁶Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK; ⁷Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancon, Panama, Republic of Panama; ⁸Department of Environment, Earth and Ecosystems, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK; ⁹CIRAD, UPR Forêts et sociétés, Campus International de Baillarguet, 34398 Montpellier Cedex 5, France; ¹⁰CNRS, UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive, 34293 Montpellier Cedex 5, France; ¹¹CNRS, UPS 3248, Ecotron Européen de Montpellier, 1 chemin du Rioux, Campus de Baillarguet, 34980 Montferrier-sur-Lez, France

ABSTRACT

Heterotrophic soil respiration (SR_H) alone can contribute up to 50% of total ecosystem respiration in tropical forests. Whereas the abiotic controls of SR_H have been extensively studied, the influence of plant traits is less well characterised. We used field experiments and a modelling approach to test the relative influence of plant traits on SR_H in lowland tropical forest in French Guiana. We measured leaf- and root litter traits for five common tree species

and conducted a root decomposition experiment to evaluate the influence of root chemistry on decay rates. We measured SR_H in trenched plots and used our field measurements to parameterize and test the Century model of soil C dynamics. Overall, the Century model performed well in simulating SR_H , and species-specific root decomposition in Century corresponded well to decomposition rates measured in situ. Root litter characterized by low lignin-to-nitrogen ratios decomposed more rapidly than low-quality root litter during the first 6 months. Model runs over different time scales revealed that litter quality substantially influenced SR_H on an annual time-scale by determining the rates of root- and leaf litter decomposition. However, litter mass had an overriding influence on SR_H over the longer term in 20-year model runs. *Synthesis* Using simple plant trait data to parameterise the Century model, we were able to accurately simulate changes in SR_H in a

Received 7 March 2016; accepted 30 October 2016;
published online 5 January 2017

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-016-0104-x) contains supplementary material, which is available to authorized users.

Author's contributions DE, VD and SP conceived of or designed study; DE, VD, SP and LB performed research; LB, VD, DE, SP and ES analyzed data; LB, VD, SP, DE, DB, VF, JR, ES and J-YG contributed new methods or models or data; LB, VD, ES, DE, SP, VF, JR and DB wrote the paper.

*Corresponding author; e-mail: l.brechet@lancaster.ac.uk

lowland tropical forest. Our results suggest that this approach could be used to predict changes in tropical soil C dynamics under global change scenarios by including data on changes in plant productivity and C inputs to the soil (for example litterfall and root turnover).

INTRODUCTION

Soil CO₂ efflux (soil respiration; 'SR') in moist tropical forests can contribute from 50% to over 80% to total ecosystem respiration (Meir 1996; Malhi and others 1999; Chambers and others 2004; Bonal and others 2008), with strong intra-annual variation and high spatial heterogeneity (Trumbore and others 1995; Sotta and others 2004; Powers and Schlesinger 2002; Epron and others 2006; Bréchet and others 2011). Previous studies in tropical forests have mainly investigated the role of soil water content and, to a lesser extent, soil temperature in determining the temporal variation of SR (Davidson and others 2000; Sotta and others 2004), whereas differences among sites have been attributed to topographic position and soil type (Epron and others 2006), to aboveground litter quality of tree species (Bréchet and others 2009; Keller and others 2013) or to fine root litter (Valverde-Barrantes 2007). However, SR rates can differ by an order of magnitude over distances of only a few metres within a site (Stoyan and others 2000; Ishizuka and others 2005; Kosugi and others 2007; Ohashi and Gyokusen 2007; Bréchet and others 2011). Some of this variation can be explained by the high diversity of tropical trees and their contribution to the autotrophic component of SR via root- and associated rhizosphere respiration but also by the spatial heterogeneity of plant inputs to the soil, which influences heterotrophic respiration (SR_H) during the decomposition of litter and litter-derived soil organic carbon (SOC).

Plant traits such as the lignin and nitrogen contents of leaf- and root litter could represent important controls on rates of SR_H because they affect decomposition rates (Melillo and others 1982; Aber and others 1990; Bloomfield and others 1993; Hobbie 1996; Berg and McClaugherty 2008) by altering microbial community composition (Brant and others 2006) and turnover (Russell and others 2007). In highly diverse tropical forests, the chemical composition of roots and leaves varies widely among tree species (Hattenschwiler and others 2008; Bréchet and others 2009). It is therefore conceivable that high spatial and temporal variation

Key words: Century model; decomposition; leaf litter; fine roots; heterotrophic soil respiration; sensitivity analysis; soil carbon dynamics; plant traits.

in the quality and quantity of plant litter will influence the rates of SR_H and the storage of SOC at different scales but there is currently insufficient data to assess this. Given that SR_H contributes an estimated 40–60% of total SR in tropical forests (Chambers and others 2004; Sayer and Tanner 2010), and tropical forest productivity and diversity could change substantially under future climate scenarios (Condit and others 2009), we need to improve our understanding of how plant traits influence the storage of organic C or the release of CO₂ during decomposition.

There have been considerable efforts to partition SR into autotrophic and heterotrophic components because they are likely to respond differently to environmental change (Boone and others 1998; Epron and others 2001). The heterotrophic component of soil respiration is particularly difficult to assess in situ (Subke and others 2006) because it is technically challenging to measure SR_H in isolation and because SR_H is influenced by the composition, activity and turnover of microbial decomposer communities, which in turn are strongly influenced by soil temperature and water content as well as by the quantity and quality of the available substrate (Chang and others 2007). Modelling approaches could help us overcome these difficulties, but most current models of SR_H do not account for the high species diversity and particular environmental conditions in tropical forests.

The Century model was initially developed to simulate SOC dynamics in grasslands (Parton and others 1987) and has since been adapted and tested for many other ecosystems, including agricultural systems (Smith and others 1997), boreal and temperate forests (Epron and others 2001; Kirschbaum and Paul 2002) and, to a lesser extent, tropical forests (Motavalli and others 1994; Wang and others 2002). In the Century model, SOC is partitioned into multiple pools that are defined kinetically as active, slow, and passive according to their potential decomposition rates. The decomposition of material in these C pools is associated with microbial activity; and SR_H is calculated for each of the flows. Simulations of C flows among these pools are controlled by decay rates, which in turn

Table 1. Chemical Composition, Given as % Dry Mass for Lignin (L), Nitrogen (N), Structural Carbon (Cs) of Fine Root and Leaf Litter of Five Tropical Tree Species Present in the Study Site (0.5-ha area) in the Paracou Experimental Forest, French Guiana

Species	<i>n</i> Leaf				Fine root (<2 mm)			
	L _{Leaf}	N _{Leaf}	L:N _{Leaf}	L:Cs _{Leaf}	L _{Root}	N _{Root}	L:N _{Root}	L:Cs _{Root}
<i>Carapa procera</i>	6 37.60 ± 4.30 (5)	1.10 ± 0.10 (5)	34.90	0.54	44.50 ± 1.50 (2)	1.20 ± 0.04 (5)	37.10	0.60
<i>Dicorynia guianensis</i>	2 44.40 ± 3.20 (6)	1.30 ± 0.12 (6)	34.70	0.59	44.00 ± 4.70 (2)	1.30 ± 0.07 (5)	33.80	0.57
<i>Eperua falcata</i>	5 34.10 ± 2.10 (6)	1.20 ± 0.10 (6)	27.90	0.52	41.80 ± 2.80 (2)	1.00 ± 0.03 (5)	42.70	0.63
<i>Platonia insignis</i>	1 18.20 ± 1.80 (6)	1.40 ± 0.14 (6)	12.80	0.30	20.10 ± 0.50 (2)	0.80	26.10	0.45
<i>Symphonia spI</i>	3 22.50 ± 7.60 (6)	1.10 ± 0.17 (6)	19.70	0.34	31.40	1.10 ± 0.04 (5)	28.50	0.54

n is the number of individuals per species among the 277 trees of the study site, L is the lignin content, N is the nitrogen content, L:N is the ratio of lignin to nitrogen, and L:Cs is the ratio of lignin to structural carbon for leaf- and root litter; means ± standard deviation are given for *n* = 5 (N) and *n* = 2 (L and Cs).

are controlled by soil water content, soil temperature, soil texture, litter chemistry and litter quantity. Although the description of the biological processes may be overly simplistic (Torn and others 2009), the Century model is robust, easy to implement and needs small number of parameters. Our study evaluated the use of the Century model of soil C dynamics to assess the relative influence of selected plant traits on the spatial and temporal variation in SR_H in a tropical forest.

We specifically aimed to test the following two hypotheses: (1) the Century model can be used to examine patterns of heterotrophic respiration (SR_H) and root decomposition in a highly diverse tropical forest; and (2) biotic factors related to litter quality and litter quantity are important drivers of heterogeneity in SR_H that change over time.

To achieve this, we parameterized and tested the model using detailed field measurements of soil respiration, plant litter chemistry and fine root decomposition in a highly diverse tropical forest in French Guiana. We then used the model to characterize the influence of different plant traits representing litter quality and quantity on simulated SR_H over the short-term (1-year model runs) and longer-term (20-year model runs).

MATERIALS AND METHODS

Study Site

The study site was located within the Paracou Experimental Forest in French Guiana, South America (5°16'54"N, 52°54'44"W; Gourlet-Fleury and others 2004). The moist tropical climate is characterized by a dry season from mid-August to mid-November, and a long wet season from November to August, which is interrupted by a short dry period in February/March (Appendix A1,

Figure A1 in Electronic Supplementary Material). The mean air temperature is 25.7°C and mean annual precipitation is 3041 mm (Gourlet-Fleury and others 2004; Bonal and others 2008), almost two-thirds of which falls between mid-March and mid-June. The soils in the area are mostly nutrient-poor Acrisols (IUSS Working Group WRB 2006).

Measurements were made within a 0.5 ha area within 50 m of the flux tower of the Guyaflux site (Bonal and others 2008). The forest in this area has a mean canopy height of *c.* 35 m and a mean tree density of 569 individuals ha⁻¹ (diameter at breast height > 10 cm). Tree species richness is *c.* 140 species ha⁻¹.

Field Data Collection

Carbon Inputs from Plant Litter, Microbial Biomass and Soil Characteristics

We estimated the carbon inputs from aboveground litter using monthly litterfall data for 2006–2007 (Bonal and others 2008). We calculated the ratios of lignin to nitrogen (L:N) and lignin to structural C (L:Cs) for the leaf litter of five common tree species, *Carapa procera* DC., *Dicorynia guianensis* Amsh., *Eperua falcata* Aubl., *Platonia insignis* Mart., *Symphonia spI* (~6% of all trees in the plot), using data from previous chemical analyses at the study site (Hattenschwiler and others 2008; Bréchet and others 2009). Structural C (Cs) was calculated by summing cellulose, hemicellulose and lignin content (Table 1).

Root biomass was measured in five soil samples randomly located within the study site (0.3-m × 0.3-m × 0.3-m) collected between April and May 2006. Roots were categorised as fine roots (<2 mm diameter) and medium roots (>2 mm diameter). Coarse roots (>10 mm diameter) were not included due to the difficulties in obtaining

representative samples from soil cores. Soil microbial C biomass at 0–15 and 15–30 cm depth was determined on five fresh soil samples per depth by fumigation–extraction (Vance and others 1987) in June 2007.

Previous work at the study site showed that variation in soil C content was minimal (Freycon, unpublished data) and differences in soil texture were related to slope and relative elevation (Allié and others 2015), neither of which varied among our measurement plots. Soil characteristics were therefore determined on samples taken from a soil pit at the study site. Soil cores were collected at 0–5, 15 and 45 cm depths. The soil samples were then air dried and sieved (2-mm mesh). Clay and C content were analysed for each sample. Clay content (0–2 μm particle size) was determined gravimetrically by the pipette method after soil organic matter oxidation with H_2O_2 (French standard NF X31-107, AFNOR 1994). Bulk density was calculated from mass and volume measurements of soil cores. Total soil C content was determined with a total C analyser (NF ISO 10694). As no carbonates were present in the soils, total C reflected organic C.

Root Decomposition

To obtain a range of patterns of root decomposition with which to validate the Century model, we conducted a decomposition experiment with litterbags containing fine roots of four of our five common tree species (*Carapa*, *Dicorynia*, *Eperua*, and *Symphonia*). Roots were collected at 0–10 cm soil depth in nearby monospecific plantations. We prepared 18 litterbags (10-cm \times 10-cm; 3-mm mesh) per species; each bag contained *c.* 1.5 g of recently cut, clean fine roots. Five additional root samples per species were oven-dried at 60°C to determine dry weight and then combusted at 500°C to determine the initial ash-free mass of roots. For each species, we analysed five replicate samples for root nitrogen (N) and C content using an elemental analyser (CHN NA2000, ThermoFisher, Courtaboeuf, France), and we analysed two replicate samples for soluble C, lignin, cellulose and hemicellulose C content using the van Soest method (Van Soest 1963). All the litterbags were buried horizontally in the soil at 5 cm depth in the forest in June/July 2006. Nine bags per species were retrieved after 6 and 12 months, respectively, and processed immediately upon return to the laboratory. The roots were carefully removed before being gently rinsed using a 1-mm mesh screen, oven-dried at 60°C, and weighed. An aliquot of each sample was combusted at 500°C to estimate

the ash-free mass and percentage mass remaining was calculated for each species separately after correction for mineral ash content (that is, contamination from the mineral soil). C content of each root sample was determined using an elemental analyser (CHN NA2000, ThermoFisher, Courtaboeuf, France).

Soil Respiration

To measure SR_H and exclude root-rhizosphere respiration, we installed four 1.5-m \times 1.5-m plots in April 2006, which were isolated from the surrounding soil by a 70-cm deep trench. To limit recolonization by roots, the trenches were lined with plastic before being back-filled and all trenches were recut in June 2007. As the trenching method can influence soil CO_2 efflux through the initial input of dead root mass and by altering soil water content (Epron and others 1999; Sayer and Tanner 2010), we differentiate heterotrophic respiration measured in trenched plots (SR_TP) from heterotrophic soil respiration (SR_H). As tree species diversity at the study site was high (*c.* 91 species), a specific test of the influence of individual species was beyond the scope of this study and the plots were installed at random locations. The four pairs of trenched and control plots were located 20–40 m apart and the plots within each pair were separated by 4–10 m. All five common tree species occurred over the plots.

Soil CO_2 efflux was measured (from 13/05/2006 to 24/08/2007) over permanent collars (52.5 cm internal diameter, 13 cm height) within the four trenched plots and four control plots using a closed chamber system described by Bonal and others (2008). Briefly, the system comprised four hemispherical automated flux chambers (one per plot; 20.5 cm height), connected to a closed-path infrared gas analyser (Li840; LI-COR Inc.) and a data logger (CR10X; Campbell Scientific Inc.). Measurements of the CO_2 concentration in the headspace of the four chambers were made sequentially every 30 min for 225 s per chamber. Average CO_2 concentrations were logged every 10 s and SR_TP was calculated by linear regression analysis of these values against time, excluding the first 40 s of each measurement to account for the equilibration period after chamber closure. Occasional measurements showing negative values or no increase in CO_2 over time were excluded from further analyses. Chambers were left open in between measurements.

Meteorological Data for Model Parameterization

We used daily means of air temperature, soil temperature, and soil water content for the study per-

iod (2006–2007) to parameterise our model. Half-hourly averages calculated from measurements recorded at the flux tower were used for air temperature at 12-m above the soil surface and soil temperature at 3 and 18-cm depth, as described by Bonal and others (2008). Soil water content was measured at 0–15 cm depth within each trenched and control plot using a frequency domain sensor (CS616, Campbell Scientific, UK) installed in September 2005, which logged measurements every 30 min. Soil water content at 20-cm depth was measured with a portable sensor (TRIME-T3, IMKO, Germany) at the flux tower twice a month and we calculated daily means by interpolation using the relationship between the values measured at 0–15 cm depth and those measured at 20 cm depth ($R^2 = 0.83$, $n = 15$).

Modelling Soil Carbon Dynamics

Model Description

To simulate SOC decomposition, we used the Century model (Parton and others 1987) adapted for application to forest ecosystems (Epron and others 2001). Briefly, the model includes above- and below-ground litter pools (excluding coarse woody debris) and three soil organic C pools (active, passive, and slow; Table 2); their potential decomposition rates i are calculated as:

$$\frac{dC_i}{dt}(j) = K_i(j) \times T_i(j) \times A_w(j) \times A_t(j) \times C_i(j) \quad (1)$$

where C_i is the total carbon in all litter and SOC pools; (j) is the corresponding soil layer; K_i is the

maximum decomposition rate and T_i the soil texture reducing factor affecting the decomposition of pool i (Table 2); A_w is the soil water content reducing factor, which accounts for the reduction in decomposition at low soil water content, and A_t is the corresponding soil temperature reducing factor. A full description of the model and C pools is given in Parton and others (1987).

In the model, the litter decomposition rates are determined by the structural fraction. The organic C of fresh plant litter is partitioned into metabolic (F_m) and structural fractions ($F_s = 1 - F_m$) based on the lignin to nitrogen (L:N) ratio. We determined F_m for litter from the soluble C content of leaf litter from 45 tree species growing at our study site (Hattenschwiler and others 2008) and of fine roots from the five common tree species; this gave F_m values of 31.2 and 33.3% for leaf- and root litter, respectively. We then used the slope of the relationship between the measured values of litter L:N ratios and the soluble C fraction to modify the original equation for F_m (Parton and others 1987) accordingly:

$$F_m = 0.85 - 0.016 \times \frac{L}{N} \quad (2)$$

We modified the soil water content reducing factor (A_w) to better account for tropical conditions, where heavy rainfall can result in sudden, transitory waterlogging. Soil water content was expressed relative to field capacity (SWCr), such that SWCr is >1 when the soil is waterlogged. We calculated the impact of soil water content on decomposition rates from the relationship between

Table 2. Parameters and Coefficients Used in the Century Model to Describe the Distribution of Organic Carbon (C) in Different Pools and Soil Horizons, Showing the Organic C in Each Pool Before Initialization of the Century Model and the Projections from 20-year Model ‘Spin-up-runs’ Using the 2006 Climate Data from the Paracou Experimental Forest, French Guiana

Parameter	Coefficient	Initial values			20-year model run		
		Organic	0–15 cm	0–30 cm	Organic	0–15 cm	0–30 cm
$F_{S_{Leaf}}$	$1 - F_m$	59.8	–	–	92.3	–	–
$F_{m_{Leaf}}$	0.32	28.6	–	–	2.4	–	–
$F_{S_{Root}}$	19×10^{-3}		1.9	1.9		3.8	4.8
$F_{m_{Root}}$	0.032×10^{-3}		3×10^{-3}	3×10^{-3}		0.1	0.1
Active C	$0.53 \times 10^{-2}/1.1 \times 10^{-2}/1.12 \times 10^{-2}$	11.6	1.1	1.1	5.3	0.8	0.8
Slow C [‡]	37.72×10^{-2}		37.3	37.3		26.4	20.0
Passive C [‡]	60.36×10^{-2}		59.7	59.7		68.9	74.3

Parameter values are given as a proportion of the total C within each horizon for comparison; $F_{S_{Leaf}}$, $F_{m_{Leaf}}$, $F_{S_{Root}}$ and $F_{m_{Root}}$ are the structural and metabolic fractions of leaf or root litter, respectively, and Active C is equivalent to the microbial biomass C pool, with different coefficients for each soil horizon.

[†] and [‡] indicate initial values for coefficients taken from Motavalli and others (1994) and Wang and others (2002), respectively; initial values for all other coefficients are based on in situ measurements at the Paracou study site.

SR_H and $SWCr$ measured during a two-week period when $SWCr$ was continuously > 1 . The relationship was described by a second-order polynomial equation (equation 3), which we added to the original function for $SWCr > 1$ in the model (Appendix B2, Figure B2 in Electronic Supplementary Material). Consequently, the soil water reducing factor (A_w) was calculated as:

$$A_w = \begin{cases} \frac{1}{(1+30 \times e^{(-8.3 \times SWCr)})}, & \text{if } SWCr < 1 \\ -5.8289 \times SWCr^2 + 10.191 \times SWCr - 3.3575, & \text{if } SWCr > 1 \end{cases} \quad (3)$$

Model Parameterization

For our study, the Century model included a three-layer soil profile: surface organic layer, superficial soil (0–15 cm), and deep soil (15–30 cm) layers; for these two mineral soil layers, we used mean values of soil C and clay content from the soil pit to initialize the model.

All model runs used a 1-day time step and corresponding daily means of air temperature and soil temperature. The fresh C input from aboveground litter was calculated assuming a C content of 49.5% dry mass (Hattenschwiler and others 2008) and litterfall remained constant between each monthly collection (Figure 1). The daily C input from root litter was estimated as the product of root biomass and turnover rates given by Gill and Jackson (2000), assuming a root C content of 48% dry mass (Table 3). For model validation, we used the daily means of SR_{TP} measurements for each trenched plot from May 2006 to August 2007.

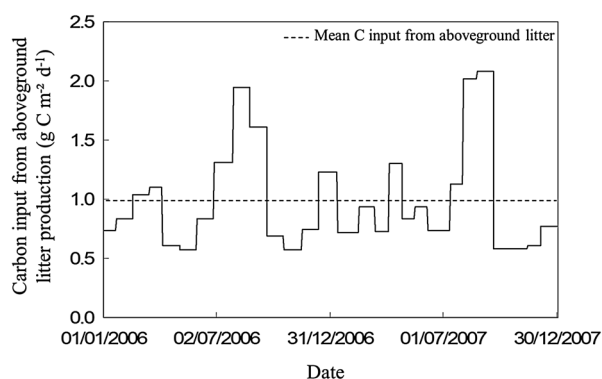


Figure 1. Seasonal variation in C input from aboveground fine litter production during 2006 and 2007 at the study plot in the Paracou experimental forest, French Guiana, calculated from four litter traps and used in the standard parameterisation of the Century model.

Model Initialization and Validation

The model initialization process was performed under the equilibrium-state assumption (that is, the measured C stock represents the equilibrium stock). The size of each initial C pool in the model was generated with the ‘spin-up-run’ method, which simulates the C content of each pool using constant mean annual parameters until an equilibrium state is reached (Smith and others 2005). For our study, we used a spin-up run of 20 years using the 2006 climate data and a standard parameterization based on the mean values of leaf- and root litter mass and chemical composition. The initialization was based on (1) the vertical distribution of soil C content from the soil pit at the study site and the relative proportions of each C pool reported by Motavalli and others (1994) and Wang and others (2002); (2) the residence times of soil C pools according to Waelbroeck (1995); and (3) the vertical distribution of the microbial biomass at the study site (Table 2).

The first model validation compared simulated SR_H to SR_{TP} measured in situ using the standard parameterization and the corresponding measurements of soil water content in the trenched plots. We performed the validation with and without the modified equation for A_w to ascertain whether accounting for transient waterlogging improved the performance of the Century model in wet tropical conditions. We also tested whether the model could reproduce the effects of trenching during plot establishment by comparing simulations using standard root litter inputs (that is, simulated SR_H) to simulations with an initial single large pulse of dead roots (that is, simulated SR_{TP}).

The second model validation compared the simulated values of root C during decomposition with the values measured in situ in the litterbag study, using the fine root chemistry of each of the four species to parameterize the model.

Statistical comparisons between measured and simulated values were performed using the linear regression procedure in SAS 9.1 (Statistical Analysis Systems, SAS Institute Inc., Cary, NC, USA).

Modelling the Influence of Plant Traits on SR_H

We conducted three sensitivity analyses to explore how changes in litter traits would affect simulated SR_H dynamics. The first test successively examined individual parameters of litter quantity and quality (Table 3) to identify potential variables that may account for spatial heterogeneity in annual SR_H . We assessed the effect size of changes to input parameters on the output variable SR_H by dividing

Table 3. Parameters and Their Ranges (where available) for the Quantity and Quality of Root and Leaf Litter and Soil Characteristics

Symbol	Description	Units	Value	References
L_{Leaf}	Leaf litter lignin content of 45 tree species	%	35.00 (18.20; 56.00)	Hattenschwiler and others (2008)
N_{Leaf}	Leaf litter nitrogen content of 45 tree species	%	1.09 (0.68; 2.00)	Hattenschwiler and others (2008)
Cs_{Leaf}	Leaf litter structural carbon content of 45 tree species	%	69.00 (50.00; 120.00)	Hattenschwiler and others (2008)
$L:Cs_{Leaf}$	Leaf litter L:Cs ratio		0.51	Hattenschwiler and others (2008)
M_{Leaf}	Aboveground litter production from 4 litter traps	$g C m^{-2} d^{-1}$	0.99 (0.09; 22.68)	Bonal et al. (2008)
L_{Root}	Fine root lignin content of 16 tree species	%	35.00 (20.10; 46.20)	This study
N_{Root}	Fine root nitrogen content of 16 tree species	%	0.91 (0.56; 1.43)	This study
Cs_{Root}	Fine root structural carbon content of 16 tree species	%	69.00 (44.00; 81.00)	This study
$L:Cs_{Root}$	Fine root L:Cs ratio		0.51	This study
M_{Root}	Fine root (<2 mm) production from 5 soil samples	$g C m^{-2} d^{-1}$	0.90 (0.56; 1.33)	This study
M_{Root}	Fine root (<2 mm) production from 5 soil samples	$g C m^{-2} d^{-1}$	0.30 (0.19; 0.41)	This study
M_{CRoot}	Medium root (>2 mm) production from 5 soil samples	$g C m^{-2} d^{-1}$	0.14 (0.13; 0.15)	This study
M_{CRoot}	Medium root (>2 mm) production from 5 soil samples	$g C m^{-2} d^{-1}$	0.03 (0.01; 0.06)	This study
T_{Root}	Fine root (<2 mm) turnover	%	80.00	Gill and Jackson (2000)
T_{CRoot}	Medium root (>2 mm) turnover	%	10.00	Gill and Jackson (2000)
Clay content, 0–15 cm		%	33.20	This study
Clay content, 15–30 cm		%	41.40	This study
Sand content, 0–15 cm		%	57.30	This study
Sand content, 15–30 cm		%	50.90	This study
Silt-clay mixture content, 0–15 cm		%	42.80	This study
Silt-clay mixture content, 15–30 cm		%	49.20	This study
Bulk density		$10^3 kg m^{-3}$	1.00	Epron and others (2006)

Means over the four litter traps and each litter trap separately to define the range, are given here for aboveground litter production (M_{Leaf}) but daily values were used for the standard parameterisation and sensitivity analyses (see Figure 1). All data are from studies carried out at our study site, except for root turnover (Gill and Jackson 2000).

the total range of measured values for each parameter into five equal ranges and using these to incrementally increase the parameter values. The second test estimated the variation in model outputs due to species-specific parameterizations. Finally, the third test aimed at investigating the potential use of the Century model in simulating spatial heterogeneity of SR_H . The test consisted of using 4000 model runs created from random selections of the measured parameters within their ranges of variation (that is, soil water content, leaf- and root litter mass, and leaf- and root litter chemistry) as an estimation of the maximum expected range of spatial heterogeneity in a highly diverse tropical forest.

The sensitivity index (I), used for the first and second tests, was calculated as a measure of the model output change in response to a change in a single value or group of parameter values. The partial derivative approach, $\partial y = \partial x$ was used to mathematically describe the dependence of the model output y on a parameter x (Lenhart and others 2002). In our model, the initial output y_0 was SR_H modelled using the standard parameterisation x_0 (mean parameter values). We then used the range of variation for each measured parameter to determine the maximum change in the values of x ($\pm\Delta x$). Thus, the maximum and minimum values for output y are determined by the range of values for parameter x , where $x_{\min} = x_0 - \Delta x$ and $x_{\max} = x_0 + \Delta x$. Thus, the finite approximation of the partial derivative is:

$$I = \frac{(y_{\max} - y_{\min})}{2\Delta x} \quad (4)$$

where $2\Delta x = x_{\max} - x_{\min}$

As the sensitivity index I is dimensionless, it is standardised to give:

$$I = \frac{(y_{\max} - y_{\min})}{2\Delta x} \times \frac{x_0}{y_0} \quad (5)$$

Absolute values of I were used to compare the degree of influence of different parameters on SR_H . Thus, the sensitivity index I for single parameters ranges from 0 to 1, where $I = 0$ if the parameter has no influence on the model output, $I = 1$ if a change in the value of parameter x results in an equivalent proportional change in SR_H , and $I > 1$ if a change in x results in a relatively greater change in SR_H .

We also conducted sensitivity analyses to assess the effect of species-specific litter traits on SR_H in second test, where x_{sp} for each species was the sum of the values of all measured traits of chemical composition and x_{mean} the mean x for all species.

Accordingly, the model output using species-specific parameterisation was y_{sp} and I_{sp} was calculated as:

$$I_{sp} = \frac{y_{sp}}{x_{sp}} \times \frac{x_{\text{mean}}}{y_0} \quad (6)$$

I_{sp} therefore indicates the degree of influence of a given species on SR_H , with values greater than 0, as above.

To differentiate between short-term and longer-term effects of plant inputs on soil C dynamics, we calculated I and I_{sp} using model runs of 1 and 20 years, respectively.

RESULTS

Field Measurements

Plant Litter, Microbial Biomass and Soil Properties

Average litter production in the Paracou experimental forest in 2006 and 2007 was 3.7 and 3.6 Mg C ha⁻¹ y⁻¹ (1.01 and 0.98 g C m⁻² d⁻¹), respectively. Carbon inputs from litterfall varied notably throughout the year with a distinct peak at the beginning of the dry season (~2.00 g C m⁻² d⁻¹ in August 2006 and September 2007) and the lower values the following 3 months (~0.50 g C m⁻² d⁻¹; Figure 1).

Root biomass at 0–15 cm depth (858 and 424 g m⁻² for fine and medium roots, respectively) accounted for approximately 74% of the root biomass at 0–30 cm depth (1742 g m⁻²). Soil C content at our study site decreased exponentially with depth, from 13.84 kg C m⁻² at 0–15 cm to 3.05 kg C m⁻² at 15–30 cm. Soil microbial biomass C was 2.4% of the total soil organic C at 0–15 cm and 0.4% at 15–30 cm depth. Soil clay content increased moderately from 33.2 to 41.4% with depth, whereas the sand content decreased (Table 3).

Litter Chemistry and Root Decomposition

The five studied tree species varied widely in their leaf- and root- litter chemistry, particularly in lignin content (Table 1). Leaf litter lignin content ranged from 18.2% dry mass in *Platonia* to 44.4% in *Dicorynia* with an average of 31.4% across all species. The L:N ratio of the leaf litter varied by a factor of 2.7 among the five species, whereby *Carapa* and *Dicorynia* had the highest L:N ratios and *Platonia* had the lowest. Similarly, the lignin content of fine root litter ranged from 20.1% dry mass in *Platonia* to 44.5% in *Carapa* and fine root L:N ratios varied by a factor of 1.6. The highest L:N ratio was measured in fine roots of *Eperua* followed by

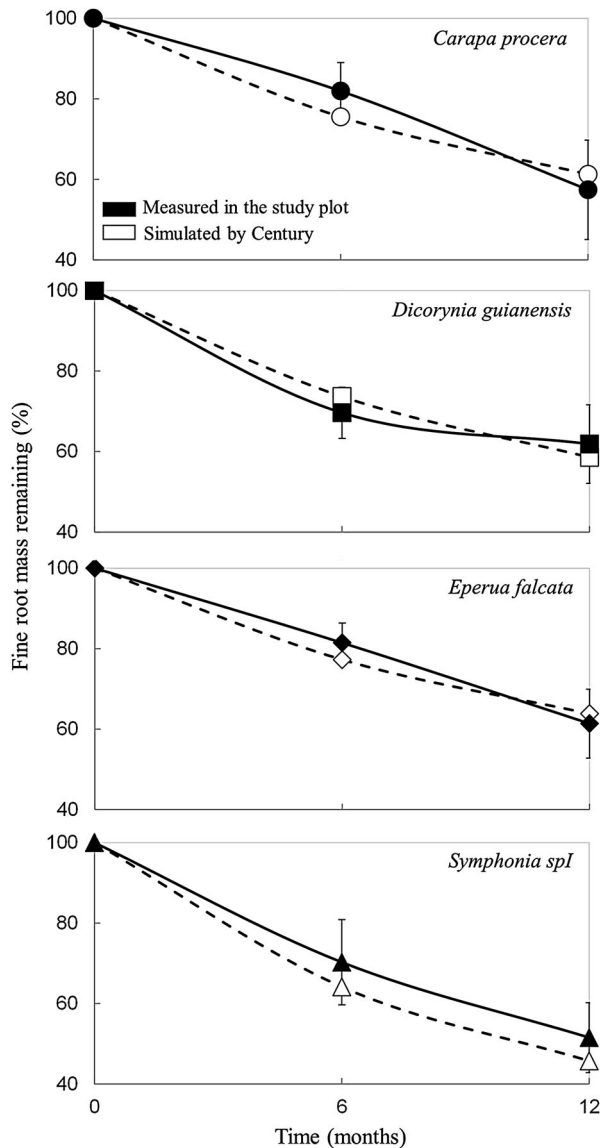


Figure 2. Comparison of measured (*solid symbols*) and simulated (*open symbols*) dry mass remaining during the decomposition of fine roots of four tropical tree species (*C. procera*, *D. guianensis*, *E. falcata*, *S. spl*) in the Paracou experimental forest, French Guiana; the simulations in the Century model used species-specific parameters of root chemical composition; bars indicate \pm standard deviation for $n = 9$ per species.

Carapa, *Dicorynia*, *Symphonia*, and *Platonia* (Table 1). The proportion of lignin in total structural C was generally lower for leaf litter (30–59%) compared to fine roots (44–63%; Table 1).

Mass loss during the first 6 months of root decomposition for the four measured species mirrored root L:N ratios, whereby *Eperua* had the lowest mass loss followed by *Dicorynia* and *Carapa*,

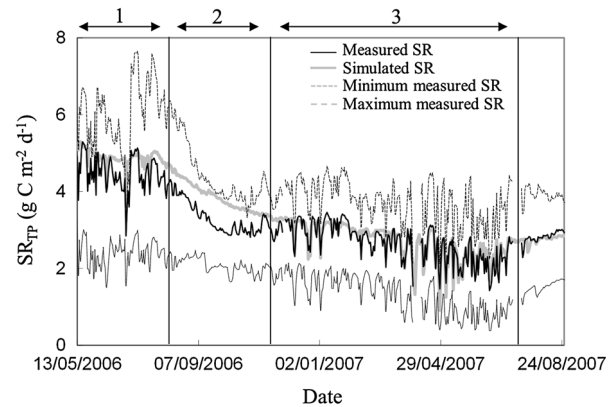


Figure 3. Mean seasonal variation of heterotrophic soil CO₂ efflux (SR_{TP}) measured in trenched plots (*black line*) in the Paracou experimental forest, French Guiana, and simulated SR_{TP} (that is, with an initial single large pulse of dead roots; *grey line*) from the Century model; *dashed* and *dotted lines* represent the maximum and minimum measured values, respectively. Three distinct periods defined by visual examination of the temporal course of SR_{TP} were: 1) the 3-month period after plot establishment; 2) the subsequent 3-month dry-season; and 3) the 7-month main study period.

and *Symphonia* had the highest mass loss. After 12 months, mass loss was notably greater in *Symphonia* compared to the other three species. Across all species, the proportion of fine root mass remaining was $76 \pm 7\%$ after 6 months and $58 \pm 5\%$ after 12 months (Figure 2).

Soil Respiration

Total SR in the control plots during the entire study period was higher and less variable [mean: $3.46 \text{ g C m}^{-2} \text{ d}^{-1}$, coefficient of variation (CV): 19%] than heterotrophic soil respiration measured in the trenched plots [that is, including the respiration related to the decomposition of roots killed during trenching (SR_{TP}); mean: $3.18 \text{ g C m}^{-2} \text{ d}^{-1}$, CV: 26%].

Three different periods of SR_{TP} were identified by visual examination (Figure 3): the ‘establishment period’ corresponded to 3 months immediately following plot establishment where SR_{TP} ($4.50 \pm 0.44 \text{ g C m}^{-2} \text{ d}^{-1}$) was higher than total SR ($3.71 \pm 0.66 \text{ g C m}^{-2} \text{ d}^{-1}$). The second period encompassed about 3 months during the dry season in which SR_{TP} was $3.35 \pm 0.43 \text{ g C m}^{-2} \text{ d}^{-1}$ and approximately 95% of total SR. Finally, the third ‘main period’ corresponded to *c.* 7-months during which mean SR_{TP} was $2.66 \pm 0.49 \text{ g C m}^{-2} \text{ d}^{-1}$, which was equivalent to 81% of total SR.

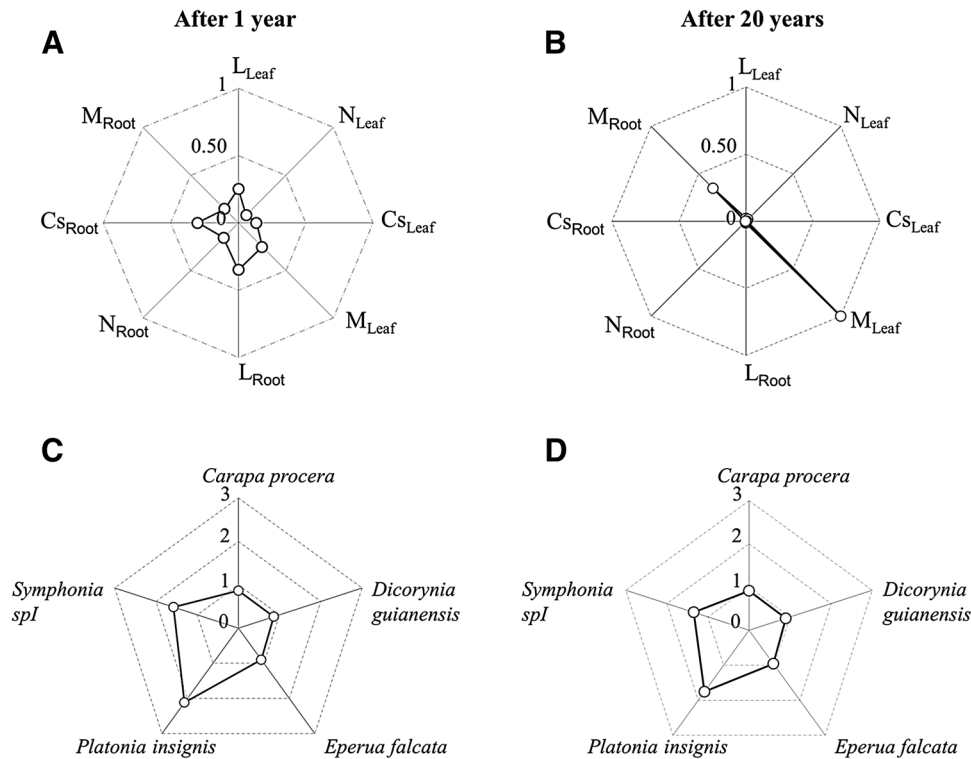


Figure 4. Sensitivity indexes (I) for the influence of (A, B) individual plant trait parameters and (C, D) species-specific groups of parameters (given in Table 1) on SR_H simulated by the Century model in 1-year and 20-year model runs, where L_{Leaf} , L_{Root} are the lignin contents, N_{Leaf} , N_{Root} are the nitrogen contents, CS_{Leaf} , CS_{Root} are the total structural carbon contents and M_{Leaf} , M_{Root} are the

mass of leaf- and fine root litter, respectively. Note that different types of sensitivity analyses were used for individual traits (A, B), for I , and species-specific groups of traits (C, D), for I_{sp} , and the scales are therefore not comparable (see section “Modelling the influence of plant traits on SR_H ”).

Model Performance and Validation Tests

Initial validation tests of the Century model using data from the field experiments and the relevant literature (summarised in Tables 2, 3), showed that the modified equation for the soil water content reducing factor (A_w ; equation 3) significantly improved the correlation between simulated and measured values ($R^2 = 0.86$ compared to $R^2 = 0.63$, $n = 222$; Appendix B2, Figure B2b in Electronic Supplementary Material). Hence, we used the modified equation for all subsequent model runs and tests.

Our simulations accounting for the large root litter input during trenching showed that the accuracy of the model in simulating SR_{TP} varied among the three distinct periods described from the field measurements above (Figure 3). During the initial 3-month after trenching, simulated SR_{TP} (mean: $4.87 \pm 0.22 \text{ g C m}^{-2} \text{ d}^{-1}$) was generally higher and less variable compared to measured SR_{TP} ($4.50 \pm 0.44 \text{ g C m}^{-2} \text{ d}^{-1}$). During the sub-

sequent dry season, simulated SR_{TP} (mean: $3.92 \pm 0.40 \text{ g C m}^{-2} \text{ d}^{-1}$) was slightly but consistently higher than measured values ($3.35 \pm 0.43 \text{ g C m}^{-2} \text{ d}^{-1}$). However, during the main 7-month period, there was a strong correlation between simulated and measured SR_{TP} ($R^2 = 0.86$; Appendix B2 in Electronic Supplementary Material), which also had very similar mean values (simulated SR_{TP} $2.73 \pm 0.47 \text{ g C m}^{-2} \text{ d}^{-1}$; measured SR_{TP} $2.66 \pm 0.49 \text{ g C m}^{-2} \text{ d}^{-1}$; Figure 3). When we used standard inputs of root litter to simulate SR_H during the main 7-month period, we observed a slightly weaker correlation between simulated SR_H and measured SR_{TP} ($R^2 = 0.76$; Appendix B2, Figure B2c in Electronic Supplementary Material).

The model performed well in simulating mass loss during the decomposition of fine roots (Figure 2). Using species-specific parameterizations (Table 1) for the four tree species, simulated decomposition after 6 and 12 months of decomposition (73 ± 6 and $57 \pm 8\%$ mass remaining, respectively) were consistent with measured values

(76 ± 7 and $58 \pm 5\%$, respectively; $R^2 = 0.83$, $n = 8$).

Relative Influence of Litter Traits on Decomposition Processes and SR_H

The sensitivity indices (I), calculated to test the influence on SR_H of changes in the parameter values of individual litter traits, varied between 0.003 and 1.00 (Figure 4) with a greater range of variation for the 20-year model run than the 1-year run. Of all tested parameters, leaf- and root litter mass and lignin contents (M_{Leaf} , L_{Root} , M_{Root} and Cs_{Root}) had the highest sensitivity indices, but their relative influence on SR_H changed between 1-year and 20-year model runs (Figure 4A, B). In the 1-year model run, L_{Root} had the greatest influence on annual SR_H ($I = 0.350$; Figure 4A), followed by Cs_{Root} and L_{Leaf} ($I = 0.301$ and 0.254 , respectively). In the 20-year run, a new equilibrium was reached and M_{Leaf} had the greatest influence on annual SR_H ($I = 1.00$; Figure 4B), followed by M_{Root} ($I = 0.346$), whereas L_{Root} and L_{Leaf} had almost no effect ($I = 0.013$ and 0.022 , respectively).

Simulations to assess the effects of species-specific litter traits on annual SR_H (Table 1; Figure 4C, D) showed that parameters from species characterised by low L:N and L:C:s ratios (*Platonia* and *Symphonia*) produced higher annual SR_H than species with higher L:N and L:C:s ratios (*Eperua*, *Carapa* and *Dicoryntia*; Table 1) in both the 1-year and 20-year model run (Figure 4C, D).

The final sensitivity analysis used 4000 model scenarios obtained by complete randomization of the parameters to test whether the Century model could be used to simulate spatial heterogeneity of SR_H . Although the mean simulated daily values of SR_H were in good agreement with measured SR_H , the standard deviation was consistently lower in the model simulations compared to the field measurements, indicating that other parameters contribute to the spatial heterogeneity of SR_H over small scales (Figure 5).

DISCUSSION

Root Decomposition

The importance of leaf litter traits, especially lignin content and L:N ratios, in controlling decomposition processes is well established (Meentemeyer 1978; Mellilo and others 1982; Cornwell and others 2008) but most studies of litter decomposition have focussed on leaf litter because root decomposition studies are notoriously difficult to conduct (Vogt

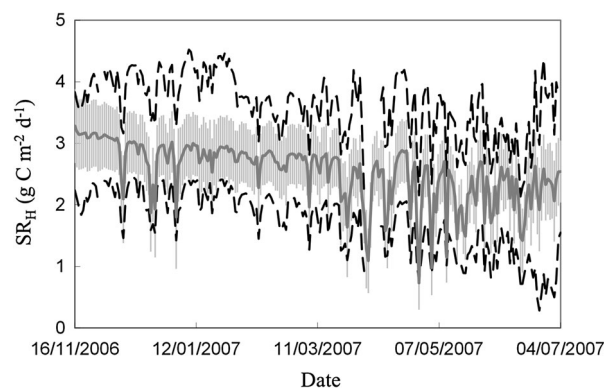


Figure 5. Comparison between measured and simulated values of SR_H for randomly selected sets of parameter values (soil water content, leaf- and fine root litter mass, and leaf- and root litter chemistry) with equilibrium conditions obtained after 20-year simulation in the Century model. The *dashed black lines* represent the maximum and minimum values of measured SR_H ; the *dark grey line* and *grey vertical bars* represent the mean and standard deviations, respectively, from 4000 model runs.

and others 1996). We show that, among the four tree species of the decomposition experiment, the relatively large range in fine root lignin concentrations (31.4–44.5%) explained much of the variation in root decomposition rates: mass loss at 6 months was related to L:N ratios and mass loss at 12 months was greatest in the species with the lowest root lignin content (Figure 2; Table 1). The 12-month mass loss of fine roots for the four species was similar to the range reported for a study in subtropical China (Lin and others 2010) but was much lower than the mass loss measured in Puerto Rico (Bloomfield and others 1993), which most likely reflects the higher lignin content of the roots in our study.

The high diversity of tropical trees and current lack of data on plant tissue chemistry for the majority of tropical species make it extremely difficult to quantify the effect of above- and below-ground litter traits on tropical soil C dynamics. Nevertheless, fine root mortality and decomposition represents a large flux of C and nutrients into the soil (*c.* 50% of the C in the top 10 cm of mineral soil; Silver and others 2000), and we were able to accurately simulate root decomposition rates in Century using species-specific data on lignin, nitrogen and structural carbon content (Figure 2) without accounting for other factors that are thought to control root decomposition processes (for example pH, soil nutrient availability and the dynamics of microbial decomposers) (Swift 1979).

Measured and Simulated soil CO₂ Efflux

We estimated that respiration in the trenched plots (SR_{TP}) was 80% of total soil respiration measured in control plots (SR) during the wet season in 2006 and 2007, which is remarkably similar to a previous estimate for lowland tropical forest (Sayer and Tanner 2010). Our estimate is based on the main 7-month period of the study because decomposition of cut roots can influence soil CO₂ efflux for several weeks up to months after trenching (Uchida and others 1998; Sayer and Tanner 2010). Accordingly, we measured higher respiration in trenched plots compared to the controls for the first 3 months of the study. Soil water content was higher in the trenched plots compared to the control plots, particularly during the dry season (that is, 13 and 26% in control and trenched plots, respectively; data not shown). Consequently, SR_{TP} was equivalent to about 95% of total SR for during the 3-month dry season. A study in lowland tropical forest in Panama reported a similar pattern of disturbance after trenching and high respiration rates in trenched plots during the dry season, which was attributed to greater soil water content in trenched plots (Sayer and Tanner 2010).

Our model provided a good simulation of SR_{TP} during the main 7-month period when we accounted for the decomposition of roots killed by trenching (Figure 3) and the simulation was improved with the modified equation for A_w to account for waterlogging, which can drastically decrease soil organic matter decomposition rates (Trumbore 1997). The heavy rains that occur frequently in the wet tropics can strongly reduce, and even temporarily halt, soil respiration within a short period of time by saturating soil pores and limiting gas diffusion (Linn and Doran 1984; Sotta and others 2004). The original Century model did not account for changes in soil CO₂ efflux during a rapid increase in soil water content and consequently overestimated SR_H for water-saturated soils.

It is noteworthy that the simulations of SR_{TP} were inaccurate during the initial establishment period. Although we accounted for the dead root biomass in the trenched plots, simulated SR_{TP} was still higher and also less variable than measured SR_{TP} for the 3 months following trenching (Figure 3, period 1). This discrepancy is most likely because Century's decomposition dynamics are described by a single-phase first order kinetic function (Smith and others 1997) and are based on assumptions of steady-state conditions in which root turnover occurs constantly and gradually,

whereas trenching constitutes a major disturbance. Large, sudden inputs of fresh organic matter can also alter microbial activity and dynamics, which are not accounted for in the model. Furthermore, the early stages of decomposition in tropical forests can be particularly rapid, as frequent and heavy rains cause substantial leaching of soluble compounds (Swift 1979; Couteaux and others 1995) and hence simulations could underestimate the initial stages of decomposition and then overestimate the amount of C remaining in the soil during the following months. In our study, simulated SR_H was representative of in situ measurements 6 months after plot establishment, which coincides with the start of main study period identified by the comparison of trenched and control plots in the field; this demonstrates that Century performs well under steady-state conditions but is not currently able to model strong disturbances.

Shift in Predominant Drivers of SR_H Over Time

Our sensitivity analyses demonstrate the influence of litter quality on rates of SR_H in the short term (1-year model runs). The simulations parameterized using litter traits of individual tree species showed that modelled rates of SR_H were higher for species with lower leaf- and root litter L:N ratios, which reflects the rapid decomposition and turnover of C in high-quality plant material (Berg 1986; Prescott and others 2000). However, the mass of plant litter was the most important predictor of SR_H in the 20-year model run, whereas litter chemistry had almost no influence. This can at least partly be attributed to the change in the relative contribution of different soil C pools to SR_H over time in the Century model. The turnover of the active C pool is determined by the metabolic fraction of organic matter during decomposition whereas the structural fraction of plant material is assumed to go directly to the slow C pool (Parton and others 1987). The size of the slow C pool increases with the duration of the model run and as a result, SR_H derived from the slow C pool also increases (Appendix C3 in Electronic Supplementary Material). Litter manipulation experiments in different forest ecosystems have emphasized the predominant role of litter mass on soil C cycling (Sayer 2006; Liu and others 2009; Sayer and others 2011). Our findings emphasised the role of litter chemistry in the short-term decomposition dynamics but also highlighted the importance of litter quantity in regulating longer-term soil C dynamics. Nonetheless, litter

quality is likely to play an indirect role in SR_H over decadal times scales by influencing the transfer of C to the slow pool (Berg and McClaugherty 2008; Grandy and Neff 2008).

Spatial Heterogeneity in SR_H

We tested whether we could use the Century model to simulate spatial heterogeneity in SR_H by running 4000 different model scenarios in which random combinations of measured plant traits represented small-scale differences in the quality of litter inputs in highly diverse tropical forests. Even though our in situ measurements probably underestimated the full range of variation in the studied parameters, the simulated standard deviation was still lower than measured values (Figure 5), which shows that the model was only able to capture part of the spatial heterogeneity in SR_H observed at our study site. Arguably, Century was not developed to model spatial heterogeneity and capturing the full extent of small-scale spatial heterogeneity is thus unfeasible, especially in highly diverse tropical forests. However, although we included species-specific data for litter chemistry, we used mean rates of litterfall and soil characteristics across the site, which does not account for the large differences in productivity and root turnover rates among tree species or spatial heterogeneity in soil properties. Consequently, it could be possible to improve simulations of spatial heterogeneity by incorporating information on species-specific litter production and fine-scale measurements of soil properties. Given the strong evidence for species-specific effects on SR and soil C storage (Bréchet and others 2009; Potvin and others 2011), this possibility merits further investigation because the ability to model variation in SR as a function of specific plant traits would allow us to simulate soil C dynamics in response to changes in forest productivity and diversity, for example, under global change scenarios.

CONCLUSIONS

We assessed the influence of plant traits on SR_H in a lowland tropical forest and provide insights into the role of litter quality in the variability of SR_H . By using field measurements to test and parameterize the Century model, we demonstrated that data on specific plant traits can be used to improve simulations of SR_H . Although litter quality was important for SR_H linked to short-term decomposition dynamics, litter quantity was more important for determining SR_H under steady-state conditions. In

future, additional data such as species-specific patterns of litterfall could allow us to model soil C dynamics and soil C storage in response to changes in forest productivity and diversity, for example, in response to future global change, and may also improve simulations of spatial heterogeneity in SR_H .

ACKNOWLEDGEMENTS

We wish to thank Cyril Douthe and Louis Maire for their help during data acquisition in the field and laboratory. We are grateful to Nick Ostle and Ed Tanner for their helpful comments on improving the earlier drafts of the manuscript. We also acknowledge two anonymous reviewers who provided thoughtful comments that improved this manuscript. LB was funded by a PhD Grant from the French ‘‘Ministère de l’Education Nationale et de la Recherche’’. The UMR EEF is supported by the French National Research Agency through the Laboratory of Excellence ARBRE (ANR-12-LAB-XARBRE-01). EJS was supported by funding from the European Research Council under the European Union’s Seventh Framework Programme (FP/2007-2013), ERC Grant Agreement No. 307888.

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