1   *Running headline:* Abiotic drivers of heterotrophic soil respiration

2   **Short- and long-term influence of litter quality and quantity on simulated heterotrophic**

3   **soil respiration in a lowland tropical forest**

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6   Laëtitia Bréchet[1*], Valérie Le Dantec[2], Stéphane Ponton[3,4], Jean-Yves Goret[1], Emma

7   Sayer[5,6,7], Damien Bonal[3,4], Vincent Freycon[8], Jacques Roy[9,10], Daniel Epron[3,4]

8

9   [1] INRA, UMR 0745, Ecologie des Forêts de Guyane, Campus Agronomique, BP 709, F-

10   97387 Kourou cedex, French Guiana

11   [2] Toulouse III, Université Paul Sabatier, UMR 5126, Centre d'Etudes Spatiales de la

12   Biosphère, F-31401 Toulouse, France

13   [3] INRA, UMR 1137, Ecologie et Ecophysiologie Forestières, Centre de Nancy, F-54280

14   Champenoux, France

15   [4] Université de Lorraine, UMR 1137, Ecologie et Ecophysiologie Forestières, Faculté des

16   Sciences, F-54500 Vandoeuvre-les-Nancy, France

17   [5] Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, United

18   Kingdom.

19   [6] Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancon, Panama,

20   Rep. Panama.

21   [7] Department of Environment, Earth and Ecosystems, The Open University, Walton Hall,

22   Milton Keynes, MK7 6AA, United Kingdom

23   [8] CIRAD, UPR BSEF, Campus International de Baillarguet, F-34398 Montpellier Cedex 5,

24   France

1   [9] CNRS, UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive, F-34293 Montpellier

2   Cedex 5, France

3   [10] CNRS, UPS 3248, Ecotron Européen de Montpellier, 1 chemin du Rioux, Campus de

4   Baillarguet, F-34980 Montferrier-sur-Lez, France

5

6   * Correspondence: L. Bréchet (l.brechet@lancaster.ac.uk)

7

Abstract

11

12   1)   Heterotrophic soil respiration (SR_H) alone can contribute up to 50% of total ecosystem

13   respiration in tropical forests. Whereas the abiotic controls of SR_H have been extensively

14   studied, the influence of plant traits is less well characterised.

15   2)   We used field experiments and a modelling approach to test the relative influence of

16   plant traits on SR_H in lowland tropical forest in French Guiana. We measured leaf- and root

17   litter traits for five common tree species and conducted a root decomposition experiment to

18   evaluate the influence of root chemistry on decay rates. We measured SR_H in trenched plots

19   and used our field measurements to parameterize and test the Century model of soil C

20   dynamics.

21   3)   Overall, the Century model performed well in simulating SR_H and species-specific

22   root decomposition in Century corresponded well to decomposition rates measured *in situ*.

3

Root litter characterized by low lignin-to-nitrogen ratios decomposed more rapidly than low-quality root litter during the first six months.

4)   Model runs over different time scales revealed that litter quality substantially influences SR_H in the short-term by determining the rates of litter decomposition. However, litter mass had an overriding influence on SR_H over the longer term.

5)   *Synthesis*: Models such as Century can accurately simulate changes in SR_H using a relatively small number of parameters and simple plant trait data, even in highly diverse tropical forests. By including data on tree phenology, it may be possible to use Century to model changes in soil C dynamics as a result of altered species composition.

1 Introduction

2 Soil CO_2 efflux (soil respiration; 'SR') in moist tropical forests can contribute from 50% to

3 over 80% to total ecosystem respiration (Meir 1996; Malhi and others 1999; Chambers and

4 others 2004; Bonal and others 2008), with strong intra-annual variation and high spatial

5 heterogeneity (Trumbore and others 1995; Sotta and others 2004; Powers and Schlesinger

6 2002; Epron and others 2006; Bréchet and others 2011). Previous studies in tropical forests

7 have mainly investigated the role of soil water content and, to a lesser extent, soil temperature

8 in determining the temporal variation of SR (Davidson and others 2000; Sotta and others

9 2004), whereas differences among sites have been attributed to topographic position and soil

10 type (Epron and others 2006), to aboveground litter quality of tree species (Bréchet and others

11 2009) or to fine root litter (Valverde-Barrantes 2007). However, SR rates can differ by an

12 order of magnitude over distances of only a few metres within a site (Stoyan and others 2000;

13 Ishizuka and others 2005; Kosugi and others 2007; Ohashi and others 2007; Bréchet and

14 others 2011). Some of this variation can be explained by the spatial arrangement of dominant

15 trees (Katayama and others 2009; Bréchet and others 2011; Ohashi and others 2015; Tan and

16 others 2013), which contribute to the autotrophic component of SR, including roots and

17 associated rhizosphere respiration, but can also influence heterotrophic respiration (SR_H) from

18 the decomposition of litter and soil organic matter (SOM).

19 Plant traits such as the lignin and nitrogen contents of leaf- and root litter could represent

20 important controls on rates of SR_H because they affect decomposition rates (Melillo and

21 others 1982; Aber and others 1990; Bloomfield and others 1993; Hobbie 1996; Berg and

22 McClaugherty 2008) by altering microbial community composition (Brant and others 2006)

23 and turnover (Russell and others 2007). In highly diverse tropical forests, the chemical

24 composition of roots and leaves varies widely among tree species (Hättenschwiler and others

1 2008; Bréchet and others 2009). It is therefore conceivable that high spatial and temporal

2 variation in the quality and quantity of plant litter will influence the rates of SR_H and the

3 storage of soil organic carbon (SOC) at different scales but there is currently insufficient data

4 to assess this. Given that SR_H contributes an estimated 40 - 60% of total SR in tropical forests

5 (Chambers and others 2004; Sayer and Tanner 2010), and tree species composition could

6 change substantially under future climate scenarios (Condit and others 2009), we need to

7 improve our understanding of how plant traits influence the storage of organic C or release of

8 CO_2 during decomposition.

9 There have been considerable efforts to partition SR into autotrophic and heterotrophic

10 components because they are likely to respond differently to environmental change (Boone

11 and others 1998; Epron and others 2001). The heterotrophic component of soil respiration is

12 particularly difficult to assess *in situ* (Subke and others 2006) because it is technically

13 challenging to measure SR_H in isolation and because SR_H is influenced by the composition,

14 activity and turnover of microbial decomposer communities, which in turn are strongly

15 influenced by soil temperature and water content as well as by the quantity and quality of the

16 available substrate (Chang and others 2007). Modelling approaches could help us overcome

17 these difficulties, but most current models of SR_H do not account for the high species

18 diversity and particular environmental conditions in tropical forests.

19 Our study evaluated the use the Century model of soil C dynamics to assess the relative

20 influence of selected plant traits on the spatial and temporal variation in SR_H in a tropical

21 forest. To achieve this, we made detailed field measurements of soil respiration plant litter

22 chemistry and fine root decomposition to parameterize and test the model before

23 characterizing the short-term and longer-term influence of litter quality and quantity on

24 simulated SR_H.

25

1 **Materials and Methods**

2 **Study Site**

3 The study site was located within the Paracou Experimental Forest in French Guiana, South

4 America (5º16'54''N, 52º54'44''W; Gourlet-Fleury and others 2004). The moist tropical

5 climate is characterized by a dry season from mid-August to mid-November, and a long wet

6 season from November to August, which is interrupted by a short dry period in February /

7 March (Appendix A1, Fig. A1). The mean air temperature is 25.7°C and mean annual

8 precipitation is 3041 mm (Gourlet-Fleury and others 2004; Bonal and others 2008), almost

9 two-thirds of which falls between mid-March and mid-June. The soils in the area are mostly

10 nutrient-poor Acrisols (IUSS Working Group WRB 2006).

11 Measurements were made within a *c.* 0.5 ha area within 50 m of the flux tower of the

12 Guyaflux site (Bonal and others 2008). The forest in this area has a mean canopy height of *c.*

13 35 m and a mean tree density of 569 individuals ha^{-1} (diameter at breast height > 10 cm). Tree

14 species richness is *c.* 140 species ha^{-1}.

15

16 **Field data collection**

17 *Carbon inputs from plant litter, microbial biomass and soil characteristics*

18 Carbon inputs from aboveground litter production were estimated from monthly litter

19 collections during 2006 - 2007, described in Bonal and others (2008). We calculated the ratios

20 of lignin to nitrogen (L:N) and lignin to structural C (L:Cs) for the leaf litter of five common

21 tree species, *Carapa procera* DC., *Dicorynia guianensis* Amsh., *Eperua falcata* Aubl.,

22 *Platonia insignis* Mart., *Symphonia spI* (~6% of all trees in the plot), using data from previous

23 chemical analyses at the study site (Hättenschwiler and others 2008; Bréchet and others

1 2009). Structural C (Cs) was calculated by summing cellulose, hemicellulose and lignin

2 content (Table 1).

3 Root biomass was measured in five soil samples randomly located within the study site (0.3-

4 m × 0.3-m × 0.3-m) collected between April and May 2006. Roots were categorised as fine

5 roots (< 2 mm diameter) and medium roots (> 2 mm diameter). Coarse roots (> 10 mm

6 diameter) were not included due to the difficulties in obtaining representative samples from

7 soil cores. Root nitrogen, lignin, cellulose and hemicellulose C contents were analysed for the

8 five common tree species listed above using an elemental analyser (CHN NA2000,

9 ThermoFisher, Courtaboeuf, France) and the van Soest method (Van Soest 1963),

10 respectively. Soil microbial C biomass at 0 - 15 cm and 15 - 30 cm depth was determined on

11 five fresh soil samples per depth by fumigation-extraction (Vance and others 1987) in June

12 2007.

13 Soil characteristics were determined on samples taken from a soil pit at the study site. Soil

14 cores were collected at 0 - 5 cm, 15 cm and 45 cm depths. The soil samples were then air

15 dried and sieved (2-mm mesh). Clay and C content were analysed for each sample. Clay

16 content (0 - 2 μm particle size) was determined gravimetrically by the pipette method after

17 soil organic matter oxidation with H_2O_2 (French standard NF X31-107, AFNOR 1994). Total

18 soil C content was determined with a total C analyser (NF ISO 10694). As no carbonates were

19 present in the soils, total C reflected organic C.

20

21 *Root decomposition*

22 We measured root decomposition rates using litterbags containing fine roots of four of our

23 five common tree species (*Carapa*, *Dicorynia*, *Eperua*, and *Symphonia*). Roots were collected

24 at 0 - 10 cm soil depth in nearby monospecific plantations. We prepared 18 litterbags (10-cm

25 × 10-cm; 3-mm mesh) per species; each bag contained *c.* 1.5 g of recently cut, clean fine

1 roots. Five additional root samples per species were oven-dried at 60°C to determine dry

2 weight and then combusted at 500°C to determine the initial ash-free mass of roots. All the

3 litterbags were buried horizontally in the soil at 5 cm depth in the forest in June / July 2006.

4 Nine bags per species were retrieved after six and twelve months, respectively, and processed

5 immediately upon return to the laboratory. The roots were carefully removed before being

6 gently rinsed using a 1-mm mesh screen, oven-dried at 60°C, and weighed. An aliquot of each

7 sample was combusted at 500°C in order to estimate the ash-free mass and percentage mass

8 remaining was calculated for each species separately after correction for mineral ash content

9 (*i.e.* contamination from the mineral soil). C content of each root sample was determined

10 using an elemental analyser (CHN NA2000, ThermoFisher, Courtaboeuf, France).

11

12 *Soil respiration*

13 To measure SR_H and exclude root-rhizosphere respiration, we installed four 1.5-m × 1.5-m

14 plots in April 2006, which were isolated from the surrounding soil by a 70-cm deep trench. To

15 limit re-colonization by roots, the trenches were lined with plastic before being back-filled

16 and all trenches were recut in June 2007. As the trenching method can influence soil CO_2

17 efflux through the initial input of dead root mass and by altering soil water content (Sayer and

18 Tanner 2010), we differentiate heterotrophic respiration measured in trenched plots (SR_{TP})

19 from heterotrophic soil respiration (SR_H).

20 Soil CO_2 efflux was measured (from 13/05/2006 to 24/08/2007) over permanent collars (52.5

21 cm internal diameter, 13 cm height) within the four trenched plots and four control plots using

22 a closed chamber system described by Bonal and others (2008). Briefly, the system comprised

23 four hemi-spherical automated flux chambers (one per plot; 20.5 cm height), connected to a

24 closed-path infrared gas analyser (Li840; LI-COR Inc.) and a data logger (CR10X; Campbell

25 Scientific Inc.). Measurements of the CO_2 concentration in the headspace of the four

1 chambers were made sequentially every 30 min for 225 s per chamber. Average CO_2

2 concentrations were logged every 10 s and SR_{TP} was calculated by linear regression analysis

3 of these values against time, excluding the first 40 s of each measurement to account for the

4 equilibration period after chamber closure. Occasional measurements showing negative

5 values or no increase in CO_2 over time were excluded from further analyses. Chambers were

6 left open in between measurements.

7

8 *Meteorological data for model parameterization*

9 Soil water content was measured at 0 - 15 cm depth within each trenched and control plot

10 using a frequency domain sensor (CS616, Campbell Scientific, UK) installed in September

11 2005, which logged measurements every 30 minutes. Measurements at 20 cm depth were

12 taken with a portable sensor (TRIME-T3, IMKO, Germany) at the flux tower twice a month

13 and we calculated daily means using linear regression between the values measured at 0 - 15

14 cm depth and those measured at 20 cm depth ($R^2 = 0.83$, $n = 15$). Air temperature at 12 m

15 above the soil surface and soil temperature at 3 and 18 cm depth were measured at the flux

16 tower as described by Bonal and others (2008), starting in December 2003.

17

18 **Modelling soil carbon dynamics**

19 *Model description*

20 To simulate soil organic matter (SOM) decomposition, we used the Century model (Parton

21 and others 1987) adapted for application to forest ecosystems (Epron and others 2001).

22 Briefly, the model includes above- and below-ground litter pools (excluding coarse woody

23 debris) and three soil organic C pools (active, passive, and slow; Table 2); their potential

24 decomposition rates *i* are calculated as:

1

2 $$\frac{dC_i}{dt}(j) = K_i(j) \times T_i(j) \times Aw(j) \times At(j) \times C_i(j) \tag{1}$$

3

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

5 is the maximum decomposition rate and T_i the soil texture reducing factor affecting the

6 decomposition of pool *i* (Table 2); Aw is the soil water content reducing factor, which

7 accounts for the reduction in decomposition at low soil water content, and At is the

8 corresponding soil temperature reducing factor. A full description of the model and C pools is

9 given in Parton and others (1987).

10 In the model, the litter decomposition rates are determined by the structural fraction. The

11 organic C of fresh plant litter is partitioned into metabolic (*Fm*) and structural fractions (*Fs* =

12 1-*Fm*) based on the lignin to nitrogen (L:N) ratio. The L:N ratio of leaf litter was derived from

13 45 tree species growing at our study site (mean 33.8 ± 13.3; Hättenschwiler and others 2008)

14 and from the fine roots analysis of the five tree species mentioned above (mean 33.6 ± 6.7).

15 Accordingly, the values of *Fm* used in the model were 31.2% and 33.3% for leaf- and root

16 litter, respectively.

17 We modified the soil water content reducing factor (Aw) to better account for tropical

18 conditions, where heavy rainfall can result in sudden, transitory waterlogging. Soil water

19 content was expressed relative to field capacity (SWCr), such that SWCr is > 1 when the soil

20 is waterlogged. We calculated the impact of soil water content on decomposition rates from

21 the relationship between SR_H and SWCr measured during a two-week period when SWCr was

22 continuously > 1. The relationship was described by a second-order polynomial equation (Eq.

23 2), which we added to the original function for SWCr > 1 in the model (Appendix B2, Fig.

24 B2). Consequently, the soil water reducing factor (Aw) was calculated as:

1

2
$$
Aw = \begin{cases} \dfrac{1}{(1 + 30 \times e^{(-8.5 \times SWCr))}}, \text{ if SWCr} < 1 \\ \\ -5.8289 \times SWCr^2 + 10.191 \times SWCr - 3.3575, \text{ if SWCr} > 1 \end{cases}
$$
(2)

5

6 *Model parameterization*

7 For our study, the Century model included a three-layer soil profile: surface organic layer,

8 superficial soil (0 - 15 cm), and deep soil (15 - 30 cm) layers. For the mineral soil layers, we

9 used mean values of soil C and clay content from the soil pit to initialize the model.

10 All model runs used a 1-day time step and corresponding daily means of air temperature and

11 soil temperature. The fresh C input from aboveground litter was calculated assuming a C

12 content of 49.5% dry mass (Hättenschwiler and others 2008) and litterfall remained constant

13 between each monthly collection (Fig. 1). The daily C input from root litter was estimated as

14 the product of root biomass and turnover rates given by Gill and Jackson (2000; Table 3),

15 assuming a root C content of 48% dry mass. For model validation, we used the daily means of

16 SR_{TP} measurements for each trenched plot from May 2006 to August 2007.

17

18 *Model initialization and validation*

19 The model initialization process was performed under the equilibrium-state assumption (*i.e.*

20 the measured C stock represents the equilibrium stock). The size of each initial C pool in the

21 model was generated with the 'spin-up-run' method, which simulates the C content of each

22 pool using constant mean annual parameters until an equilibrium state is reached (Smith and

23 others 2005). For our study, we used a spin-up run of 20 years and a standard

24 parameterization based on the mean values of leaf- and root litter mass and chemical

1 composition. The initialization was based on (1) the vertical distribution of soil C content

2 from the soil pit at the study site and the relative proportions of each C pool reported by

3 Motavalli and others (1994) and Wang and others (2002); (2) the residence times of soil C

4 pools according to Waelbroeck (1995); and (3) the vertical distribution of the microbial

5 biomass at the study site (Table 2).

6 The first model validation compared simulated SR_H to SR_{TP} measured *in situ* using the

7 standard parameterization and the corresponding measurements of soil water content in the

8 trenched plots. We performed the validation with and without the modified equation for Aw

9 to ascertain whether accounting for transient waterlogging improved the performance of the

10 Century model in wet tropical conditions. We also tested whether the model could reproduce

11 the effects of trenching during plot establishment by comparing simulations using standard

12 root litter inputs (*i.e.* simulated SR_H) to simulations with an initial single large pulse of dead

13 roots (*i.e.* simulated SR_{TP}).

14 The second model validation compared the simulated values of root C during decomposition

15 with the values measured *in situ* in the litterbag study, using the fine root chemistry of each of

16 the four species to parameterize the model.

17 Statistical comparisons between measured and simulated values were performed using the

18 linear regression procedure in SAS 9.1 (Statistical Analysis Systems, SAS Institute Inc., Cary,

19 NC, USA).

20

21 *Modelling the influence of plant traits on SR_H*

22 We conducted three sensitivity analyses to explore how changes in litter traits would affect

23 simulated SR_H dynamics. The first test successively examined individual parameters of litter

24 quantity and quality (Table 3) to identify potential variables that may account for spatial

1   variation in annual SR_H. We assessed the effect size of changes to input parameters on SR_H by

2   dividing the total range of measured values for each parameter into five equal ranges and

3   using these to incrementally increase the parameter values. The second test estimated the

4   variation in model outputs due to species-specific parameterizations.

5   The sensitivity index (*I*) for each parameter or group of parameters of the two previous tests

6   was calculated as the proportional difference between SR_H estimated using the changed

7   parameter values and SR_H estimated using the standard parameterization. Thus, for a given

8   parameter, $I = 0$ indicates that a change in the parameter values has no influence on simulated

9   SR_H compared to the standard parameterization. To differentiate between short-term and

10   longer-term effects of litter inputs on soil C dynamics, we used model runs of 1 and 20 years.

11   Finally, to evaluate the model's ability to estimate spatial variation in SR_H at the study site, we

12   used 4000 model runs created from random selections of the measured parameters within

13   their ranges of variation (*i.e.* soil water content, leaf- and root litter mass, and leaf- and root

14   litter chemistry) to simulate the maximum expected range of spatial variation in a highly

15   diverse tropical forest.

16   **Results**

17   **Field measurements**

18   *Plant litter, microbial biomass and soil properties*

19   Average litter production in the Paracou experimental forest in 2006 and 2007 was 3.7 and

20   3.6 Mg C ha^{-1} yr^{-1} (1.01 and 0.98 g C m^{-2} d^{-1}), respectively. Carbon inputs from litterfall

21   varied notably throughout the year with a distinct peak at the beginning of the dry season

22   (~2.00 g C m^{-2} d^{-1} in August 2006 and September 2007) and the lower values the following

23   three months (~0.50 g C m^{-2} d^{-1}; Fig. 1).

1   Root biomass at 0 - 15 cm depth (858 and 424 g m^{-2} for fine and medium roots, respectively)

2   accounted for *c.* 74% of the root biomass at 0 - 30 cm depth (1742 g m^{-2}). Soil C content at

3   our study site decreased exponentially with depth, from 13.84 kg C m^{-2} at 0 - 15 cm to 3.05 kg

4   C m^{-2} at 15 - 30 cm. Soil microbial biomass C was 2.4% of the total soil organic C at 0 - 15

5   cm and 0.4% at 15 - 30 cm depth. Soil clay content increased moderately from 33.2% to

6   41.4% with depth, whereas the sand content decreased (Table 3).

7

8   *Litter chemistry and root decomposition*

9   The five studied tree species varied widely in their leaf- and root- litter chemistry, particularly

10   in lignin content (Table 1). Leaf litter lignin content ranged from 18.2% dry mass in *Platonia*

11   to 44.4% in *Dicorynia* with an average of 31.4% across all species. The L:N ratio of the leaf

12   litter varied by a factor of 2.7 among the five species, whereby *Carapa* and *Dicorynia* had the

13   highest L:N ratios and *Platonia* had the lowest. Similarly, the lignin content of fine root litter

14   ranged from 20.1% dry mass in *Platonia* to 44.5% in *Carapa* and fine root L:N ratios varied

15   by a factor of 1.6. The highest L:N ratio was measured in fine roots of *Eperua* followed by

16   *Carapa, Dicorynia, Symphonia,* and *Platonia* (Table 1). The proportion of lignin in total

17   structural C was generally lower for leaf litter (30 - 59%) compared to fine roots (44 - 63%;

18   Table 1).

19   Mass loss during the first six months of root decomposition for the four measured species

20   mirrored root L:N ratios, whereby *Eperua* had the lowest mass loss followed by *Dicorynia*

21   and *Carapa*, and *Symphonia* had the highest mass loss. After twelve months, mass loss was

22   notably greater in *Symphonia* compared to the other three species. Across all species, the

23   proportion of fine root mass remaining was 76 ± 7% after six months and 58 ±5 % after

24   twelve months (Fig. 2).

25

1   *Soil respiration*

2   Total SR in the control plots during the entire study period was higher and less variable

3   (mean: 3.46 g C m^{-2} d^{-1}, coefficient of variation (CV): 19%) than heterotrophic soil respiration

4   measured in the trenched plots (*i.e.* including the respiration related to the decomposition of

5   roots killed during trenching (SR$_{TP}$); mean: 3.18 g C m^{-2} d^{-1}, CV: 26%).

6   Three different periods of SR$_{TP}$ were identified by visual examination (Fig. 3): the

7   'establishment period' corresponded to three months immediately following plot establishment

8   where SR$_{TP}$ (4.50 ± 0.44 g C m^{-2} d^{-1}) was higher than total SR (3.71 ± 0.66 g C m^{-2} d^{-1}). The

9   second period encompassed *c.* three months during the dry season in which SR$_{TP}$ was 3.35 ±

10   0.43 g C m^{-2} d^{-1} and *c.* 95% of total SR. Finally, the third 'main period' corresponded to *c.*

11   seven-months during which mean SR$_{TP}$ was 2.66 ± 0.49 g C m^{-2} d^{-1}, which was equivalent to

12   81% of total SR.

13

14   **Model performance and validation tests**

15   Initial validation tests of the Century model using data from the field experiments and the

16   relevant literature (summarised in Tables 2 and 3), showed that the modified equation for the

17   soil water content reducing factor (Aw; Eq. 2) significantly improved the correlation between

18   simulated and measured values ($R^2 = 0.86$ compared to $R^2 = 0.63$, $n = 222$; Appendix B2, Fig.

19   B2b). Hence, we used the modified equation for all subsequent model runs and tests.

20   Our simulations accounting for the large root litter input during trenching showed that the

21   accuracy of the model in simulating SR$_{TP}$ varied among the three distinct periods described

22   from the field measurements above (Fig. 3). During the initial three-month after trenching,

23   simulated SR$_{TP}$ (mean: 4.87 ± 0.22 g C m^{-2} d^{-1}) was generally higher and less variable

24   compared to measured SR$_{TP}$ (4.50 ±0.44 g C m^{-2} d^{-1}). During the subsequent dry season,

1   simulated SR_{TP} (mean: 3.92 ± 0.40 g C m^{-2} d^{-1}) was slightly but consistently higher than

2   measured values (3.35 ± 0.43 g C m^{-2} d^{-1}). However, during the main seven-month period,

3   there was a strong correlation between simulated and measured SR_{TP} (R^2 = 0.86; Appendix

4   B2), which also had very similar mean values (simulated SR_{TP} 2.73 ± 0.47 g C m^{-2} d^{-1};

5   measured SR_{TP} 2.66 ± 0.49 g C m^{-2} d^{-1}; Fig. 3). When we used standard inputs of root litter to

6   simulate SR_H during the main seven-month period, we observed a slightly weaker correlation

7   between simulated SR_H and measured SR_{TP} (R^2 = 0.76; Appendix B2, Fig. B2c).

8   The model performed well in simulating mass loss during the decomposition of fine roots

9   (Fig. 2). Using species-specific parameterizations (Table 1) for the four tree species,

10   simulated decomposition after six months and twelve months of decomposition (73 ± 6% and

11   57 ± 8% mass remaining, respectively) were consistent with measured values (76 ± 7% and

12   58 ± 5%, respectively; R^2 = 0.83, n = 8).

13

14   **Relative influence of litter traits on decomposition processes and SR_H**

15   The sensitivity indices (I) calculated to test the influence of litter traits on SR_H varied between

16   0.2 and 56.4 (Fig. 4) with a greater range of variation for the 20-year model run than the 1-

17   year run. Of all tested parameters, leaf- and root litter mass and lignin contents (M_{Leaf}, M_{Root},

18   L_{Leaf} and L_{Root}) had the highest sensitivity indices, but their relative influence on SR_H changed

19   between 1-year and 20-year model runs (Fig. 4a, b). After 1 year, L_{Leaf} had the greatest

20   influence on annual SR_H (I = 27.4; Fig. 4a), followed by L_{Root} and M_{Leaf} (I = 26.1 and 19.8,

21   respectively). After 20 years, a new equilibrium was reached and M_{Leaf} had the greatest

22   influence on annual SR_H (I = 43.3; Fig. 4b), followed by M_{Root} (I = 29.8), whereas L_{Leaf} and

23   L_{Root} had almost no effect (I = 2.0 and 1.0, respectively).

1   Similarly, simulations using data from individual tree species to parameterize the model runs

2   (Table 1; Fig. 4c, d) showed effects of species-specific litter traits on annual SR_H only in the

3   1-year model run, whereby parameters from species characterised by low L:N and L:Cs ratios

4   (*Platonia* and *Symphonia)*, produced higher annual SR_H than species with higher L:N and

5   L:Cs ratios (*Eperua*, *Carapa* and *Dicorynia*; Table 1).

6   The final sensitivity analysis used 4000 model scenarios obtained by complete randomization

7   of the parameters to simulate spatial heterogeneity of SR_H. Although the mean simulated daily

8   values of SR_H were in good agreement with measured SR_H, the standard deviation was

9   consistently lower in the model simulations compared to the field measurements, indicating

10   that other parameters contribute to the variation in SR_H over small spatial scales (Fig. 5).

11

Discussion

Root decomposition

14   The importance of leaf litter traits, especially lignin content and L:N ratios, in controlling

15   decomposition processes is well established (Meentemeyer 1978; Mellilo and others 1982;

16   Cornwell and others 2008) but most studies of litter decomposition have focussed on leaf

17   litter because root decomposition studies are notoriously difficult to conduct (Vogt and others

18   1996). We show that, among the four tree species of the decomposition experiment, the

19   relatively large range in fine root lignin concentrations (31.4 - 44.5%) explained much of the

20   variation in root decomposition rates: mass loss at six months was related to L:N ratios and

21   mass loss at twelve months was greatest in the species with the lowest root lignin content

22   (Fig. 2; Table 1). The twelve-month mass loss of fine roots for the four species was similar to

23   the range reported for a study in subtropical China (Lin and others 2010) but was much lower

1   than the mass loss measured in Puerto Rico (Bloomfield and others 1993), which most likely

2   reflects the higher lignin content of the roots in our study.

3   The high diversity of tropical trees and current lack of data on plant tissue chemistry for the

4   majority of tropical species make it extremely difficult to quantify the effect of above- and

5   belowground litter traits on tropical soil C dynamics. Nevertheless, fine root mortality and

6   decomposition represents a large flux of C and nutrients into the soil (*c.* 50% of the C in the

7   top 10 cm of mineral soil; Silver and others 2000), and we were able to accurately simulate

8   root decomposition rates in Century using species-specific data on lignin, nitrogen and

9   structural carbon content (Fig. 2) without accounting for other factors that are though to

10   control root decomposition processes (*e.g.* pH, soil nutrient availability and the dynamics of

11   microbial decomposers) (Swift and others 1979).

12

13   **Measured and simulated soil CO_2 efflux**

14   We estimated that respiration in the trenched plots (SR_{TP}) was 80% of total soil respiration

15   measured in control plots (SR) during the wet season in 2006 and 2007, which is remarkably

16   similar to a previous estimate for lowland tropical forest (Sayer and Tanner 2010). Our

17   estimate is based on the main seven-month period of the study because decomposition of cut

18   roots can influence soil CO_2 efflux for several weeks up to months after trenching (Uchida

19   and others 1998; Sayer and Tanner 2010). Accordingly, we measured higher respiration in

20   trenched plots compared to the controls for the first three months of the study. Soil water

21   content was higher in the trenched plots compared to the control plots, particularly during the

22   dry season (*i.e.* 13% and 26% in control and trenched plots, respectively; data not shown).

23   Consequently, SR_{TP} was equivalent to ~95% of total SR for during the three-month dry

24   season. A study in lowland tropical forest in Panama reported a similar pattern of disturbance

1 after trenching and high respiration rates in trenched plots during the dry season, which was

2 attributed to greater soil water content in trenched plots (Sayer and Tanner 2010).

3 Our model provided a good simulation of SR_{TP} during the main seven-month period when we

4 accounted for the decomposition of roots killed by trenching (Fig. 3) and the simulation was

5 improved with the modified equation for Aw to account for waterlogging, which can

6 drastically decrease SOM decomposition rates (Trumbore 1997). The heavy rains that occur

7 frequently in the wet tropics can strongly reduce, and even temporarily halt, soil respiration

8 within a short period of time by saturating soil pores and limiting gas diffusion (Linn and

9 Doran 1984; Sotta and others 2004). The original Century model did not account for changes

10 in soil CO_2 efflux during a rapid increase in soil water content and consequently

11 overestimated SR_H for water-saturated soils.

12 It is noteworthy that the simulations of SR_{TP} were inaccurate during the initial establishment

13 period. Although we accounted for the dead root biomass in the trenched plots, simulated

14 SR_{TP} was still higher and also less variable than measured SR_{TP} for the three months

15 following trenching (Fig. 3, period 1). This discrepancy is most likely because Century's

16 decomposition dynamics are described by a single-phase first order kinetic function (Smith

17 and others 1997) and are based on assumptions of steady-state conditions in which root

18 turnover occurs constantly and gradually, whereas trenching constitutes a major disturbance.

19 Large, sudden inputs of fresh organic matter can also alter microbial activity and dynamics,

20 which are not accounted for in the model. Furthermore, the early stages of decomposition in

21 tropical forests can be particularly rapid, as frequent and heavy rains cause substantial

22 leaching of soluble compounds (Swift and others 1979; Couteaux and others 1995) and hence

23 simulations could underestimate the initial stages of decomposition and then overestimate the

24 amount of C remaining in the soil during the following months. In our study, simulated SR_H

25 was representative of *in situ* measurements six months after plot establishment, which

1   coincides with the start of main study period identified by the comparison of trenched and

2   control plots in the field; this demonstrates that Century performs well under steady-state

3   conditions but is not currently able to model strong disturbances.

4

5   **Shift in predominant drivers of SR_H over time**

6   Our sensitivity analyses demonstrate the influence of litter quality on rates of SR_H in the short

7   term (1-year model runs). The simulations parameterized using litter traits of individual tree

8   species showed that modelled rates of SR_H were higher for species with lower leaf- and root

9   litter L:N ratios, which reflects the rapid decomposition and turnover of C in high-quality

10   plant material (Berg 1986; Prescott 2000). However, the mass of plant litter was the most

11   important predictor of SR_H in the 20-year model run, whereas litter chemistry had almost no

12   influence. This can at least partly be attributed to the change in the relative contribution of

13   different soil C pools to SR_H over time in the Century model. The turnover of the active C

14   pool is determined by the metabolic fraction of organic matter during decomposition whereas

15   the structural fraction of plant material is assumed to go directly to the slow C pool (Parton

16   and others 1987). The size of the slow C pool increases with the duration of the model run

17   and as a result, SR_H derived from the slow C pool also increases. Litter manipulation

18   experiments in different forest ecosystems have emphasized the predominant role of litter

19   mass on soil C cycling (Sayer 2006; Liu and others 2009; Sayer and others 2011). Our

20   findings emphasised the role of litter chemistry in the short-term decomposition dynamics but

21   also highlighted the importance of litter quantity in regulating longer-term soil C dynamics.

22   Nonetheless, litter quality is likely to play an indirect role in SR_H over decadal times scales by

23   influencing the transfer of C to the slow pool (Berg and McClaugherty 2008; Grandy and

24   Neff 2008).

1

2 **Spatial variation in SR$_H$**

3 We tested whether we could use the Century model to simulate spatial variation in SR$_H$ by

4 running 4000 different model scenarios in which random combinations of measured plant

5 traits represented small-scale differences in the quality of litter inputs in highly diverse

6 tropical forests. Even though our *in situ* measurements probably underestimated the full range

7 of variation in the studied parameters, the simulated standard deviation was still lower than

8 measured values (Fig. 5), which shows that the model was only able to capture part of the

9 spatial heterogeneity in SR$_H$ observed at our study site. Arguably, Century was not developed

10 to model spatial variation and capturing the full extent of small-scale spatial heterogeneity is

11 thus unfeasible, especially in highly diverse tropical forests. However, although we included

12 species-specific data for litter chemistry, we used mean rates of litterfall across the site, which

13 does not account for the large differences in leafing phenology and root turnover rates among

14 tree species. Consequently, it could be possible to improve simulations of spatial

15 heterogeneity by incorporating information on species-specific litter production. Given the

16 strong evidence for species-specific effects on SR and soil C storage (Bréchet and others

17 2009; Potvin and others 2011), this possibility merits further investigation because the ability

18 to model variation in SR as a function of specific plant traits would allow us to simulate soil C

19 dynamics in response to changes in tree species composition *e.g.* following anthropogenic

20 disturbance.

21

22 **Conclusions**

23 We assessed the influence of plant traits on SR$_H$ in a lowland tropical forest and provide

24 insights into the role of litter quality in the variability of SR$_H$. By using field measurements to

1   test and parameterize the Century model, we demonstrated that data on specific plant traits

2   can be used to improve simulations of SR_H. Although litter quality was important for SR_H

3   linked to short-term decomposition dynamics, litter quantity was more important for

4   determining SR_H under steady-state conditions. In future, additional data such as species-

5   specific patterns of litterfall could allow us to model soil C dynamics and soil C storage in

6   response to changes in tree diversity, *e.g.* during secondary succession and may also improve

7   simulations of spatial heterogeneity in SR_H.

8

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18

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16

1 **Table 1** Chemical composition (in % of dry mass for lignin, L; nitrogen, N; structural carbon,

2 Cs) of fine root and leaf litter of five tropical tree species present in the study site (*i.e.* a 0.5 ha

3 area) in the Paracou experimental forest, French Guiana; where *n* is the number of individuals

4 per species among 277 trees, L is the lignin content, N is the nitrogen content, L:N is the ratio

5 of lignin to nitrogen, and L:Cs is the ratio of lignin to structural carbon for leaf- and root litter.

Species	*n*	Leaf				Fine root (< 2mm)			
		L_{Leaf}	N_{Leaf}	$L{:}N_{Leaf}$	$L{:}Cs_{Leaf}$	L_{Rf}	N_{Rf}	$L{:}N_{Rf}$	$L{:}Cs_{Rf}$
Carapa procera	6	37.60	1.10	34.90	0.54	44.50	1.20	37.10	0.60
Dicorynia guianensis	2	44.40	1.30	34.70	0.59	44.00	1.30	33.80	0.57
Eperua falcata	5	34.10	1.20	27.90	0.52	41.80	1.00	42.70	0.63
Platonia insignis	1	18.20	1.40	12.80	0.30	20.10	0.80	26.10	0.45
Symphonia spI	3	22.50	1.10	19.70	0.34	31.40	1.10	28.50	0.44

6

7

Table 2 Values of the coefficients describing the soil organic C distribution based on *in situ* measurements in the Paracou study site or existing literature. There were used to estimate the soil organic C pools (%) used in the Century model for the initial conditions before initialization and projections after 20-year simulation using the 2006 climate data from the Paracou experimental forest, French Guiana. Both structural and metabolic fractions of leaf litter were calculated from the C content of leaf litterfall of 2 years (2004 - 2005). For the other parameters, values were calculated from the total C content (for each soil layer separately for active C).

Symbol	Description	Coefficient	Values of the soil organic C pools before initialization (%, in corresponding soil layer)			Values of the soil organic C pools after 20-year simulation (%, in corresponding soil layer)		
			Surface	0 - 15 cm	0 - 30 cm	Surface	0 - 15 cm	0 - 30 cm
Fs_{Leaf}	Structural fraction	$1 - Fm$ [a]	59.8	-	-	92.3	-	-
Fm_{Leaf}	Metabolic fraction	0.32 [a]	28.6	-	-	2.4	-	-
$Active\ C_{surf}$	Soil surface microbial biomass C	0.53×10^{-2} [b]	11.6	-	-	5.3	-	-
Fs_{Root}	Structural fraction of root litter	19×10^{-3} [c]		1.9	1.9		3.8	4.8
Fm_{Root}	Metabolic fraction of root litter	0.032×10^{-3} [c]		3×10^{-3}	3×10^{-3}		0.1	0.1
$Active\ C$	Soil microbial biomass C	1.1×10^{-2} [a] / 1.12×10^{-2} [a]		1.1	1.1		0.8	0.8
$Slow\ C$	Slow C	37.72×10^{-2} [b]		37.3	37.3		26.4	20.0
$Passive\ C$	Passive C	60.36×10^{-2} [b]		59.7	59.7		68.9	74.3

[a] Paracou experimental forest, French Guiana; this study

[b] Luquillo experimental forest, Puerto Rico; Wang and others (2002)

[c] Manaus forest, Brazil; Motavalli and others (1994)

1   **Table 3** Parameters and their ranges (where available) for the quantity and quality of root and

2   leaf litter and soil characteristics. Except in Gill and Jackson (2000), all studies were carried

3   on in our site.

Symbol	Description	Units	Value	Reference
L_{Leaf}	Leaf litter lignin content of 45 tree species	%	35.00 (18.20; 56.00)	Hättenschwiler and others (2008)
N_{Leaf}	Leaf litter nitrogen content of 45 tree species	%	1.09 (0.68; 2.00)	Hättenschwiler and others (2008)
Cs_{Leaf}	Leaf litter structural carbon content of 45 tree species	%	69.00 (50.00; 120.00)	Hättenschwiler and others (2008)
$L:Cs_{Leaf}$	Leaf litter L:Cs ratio		0.51	Hättenschwiler 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 and others (2008)
L_{Rf}	Fine root lignin content of 16 tree species	%	35.00 (20.10; 46.20)	This study
N_{Rf}	Fine root nitrogen content of 16 tree species	%	0.91 (0.56; 1.43)	This study
Cs_{Rf}	Fine root structural carbon content of 16 tree species	%	69.00 (44.00; 81.00)	This study
$L:Cs_{Rf}$	Fine root L:Cs ratio		0.5₁	This study
M_{Rf} , 0 - 15 cm	Fine root (< 2 mm) production from 5 soil samples	g C m^{-2} d^{-1}	0.90 (0.56; 1.33)	This study
M_{Rf} , 15 - 30 cm	Fine root (< 2 mm) production from 5 soil samples	g C m^{-2} d^{-1}	0.30 (0.19; 0.41)	This study
M_{Rc}, 0 - 15 cm	Medium root (> 2 mm) production from 5 soil samples	g C m^{-2} d^{-1}	0.14 (0.13; 0.15)	This study
M_{Rc}, 15 - 30 cm	Medium root (> 2 mm) production from 5 soil samples	g C m^{-2} d^{-1}	0.03 (0.01; 0.06)	This study
T_{Rf}	Fine root (< 2 mm) turnover	%	80.00	Gill and Jackson (2000)
T_{Root}	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

1

1 **Figure captions**

2 **Fig. 1** Seasonal variation in C input from aboveground fine litter production during 2006 and

3 2007 at the study plot in the Paracou experimental forest, French Guiana, calculated from

4 litter traps.

5

6 **Fig. 2** Comparison of measured (solid symbols) and simulated (open symbols) dry mass

7 remaining during the decomposition of fine roots of four tropical tree species (*Carapa*

8 *procera*, *Dicorynia guianensis*, *Eperua falcata*, *Symphonia spI*) in the Paracou experimental

9 forest, French Guiana; the simulations in the Century model used species-specific parameters

10 of root chemical composition; bars indicate ± standard deviation for n = 9 per species.

11

12 **Fig. 3** Mean seasonal variation of heterotrophic soil CO_2 efflux (SR_{TP}) measured in trenched

13 plots (black line) in the Paracou experimental forest, French Guiana, and simulated SR_{TP} (*i.e.*

14 with an initial single large pulse of dead roots; grey line) from the Century model; dashed and

15 dotted lines represent the maximum and minimum measured values, respectively. Three

16 distinct periods defined by visual examination of the temporal course of SR_{TP} were: 1) the

17 three-month period after plot establishment; 2) the subsequent three-month dry-season; and 3)

18 the seven-month main study period.

19

20 **Fig. 4** Sensitivity indexes (*I*) for the influence of individual plant trait parameters (a and b)

21 and, from Table 1, species-specific groups of parameters (b and d) on SR_H simulated by the

22 Century model in 1-year and 20-year model runs, where L_{Leaf}, L_{Rf} are the lignin contents,

23 N_{Leaf}, N_{Rf} are the nitrogen contents, Cs_{Leaf}, Cs_{Rf} are the total structural carbon contents and

24 M_{Leaf}, M_{Rf} are the mass of leaf- and fine root litter, respectively.

1

2   **Fig. 5** Comparison between measured and simulated values of SR_H for randomly selected sets

3   of parameter values (soil water content, leaf- and fine root litter mass, and leaf- and root litter

4   chemistry) with equilibrium conditions obtained after 20-year simulation in the Century

5   model. The dashed black lines represent the maximum and minimum values of measured

6   SR_H; the dark grey line and grey vertical bars represent the mean and standard deviations,

7   respectively, from 4000 model runs.

8

1

2

3 **Fig. 1**

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38

Fig. 2

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2

3　**Fig. 3**

4

40

After 1 year

a)

After 20 years

b)

c)

d)
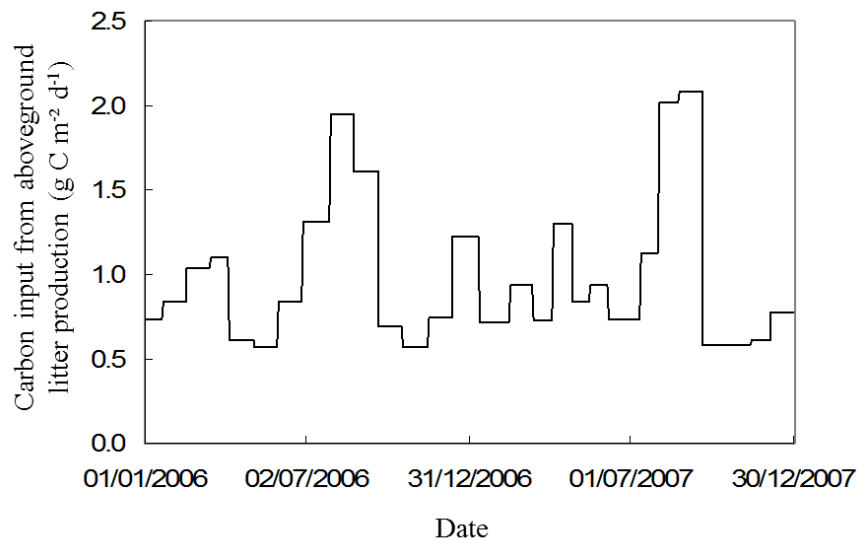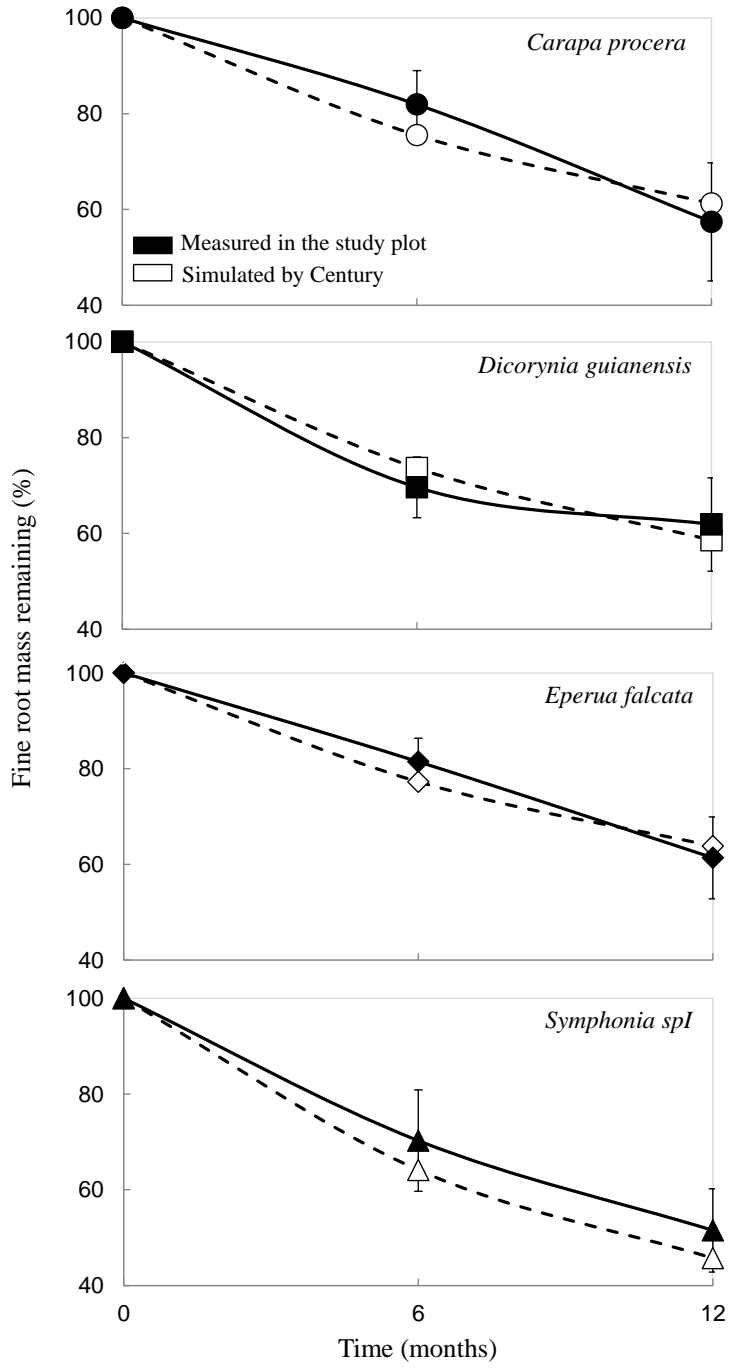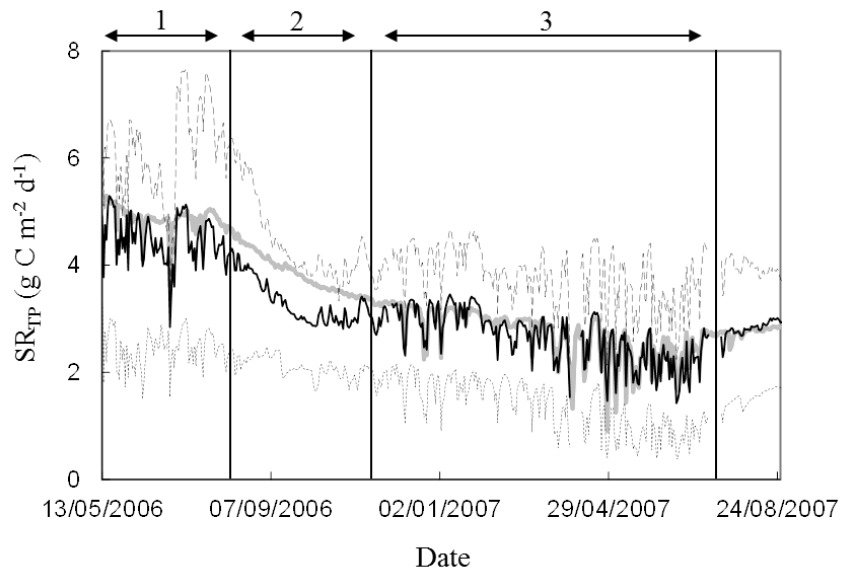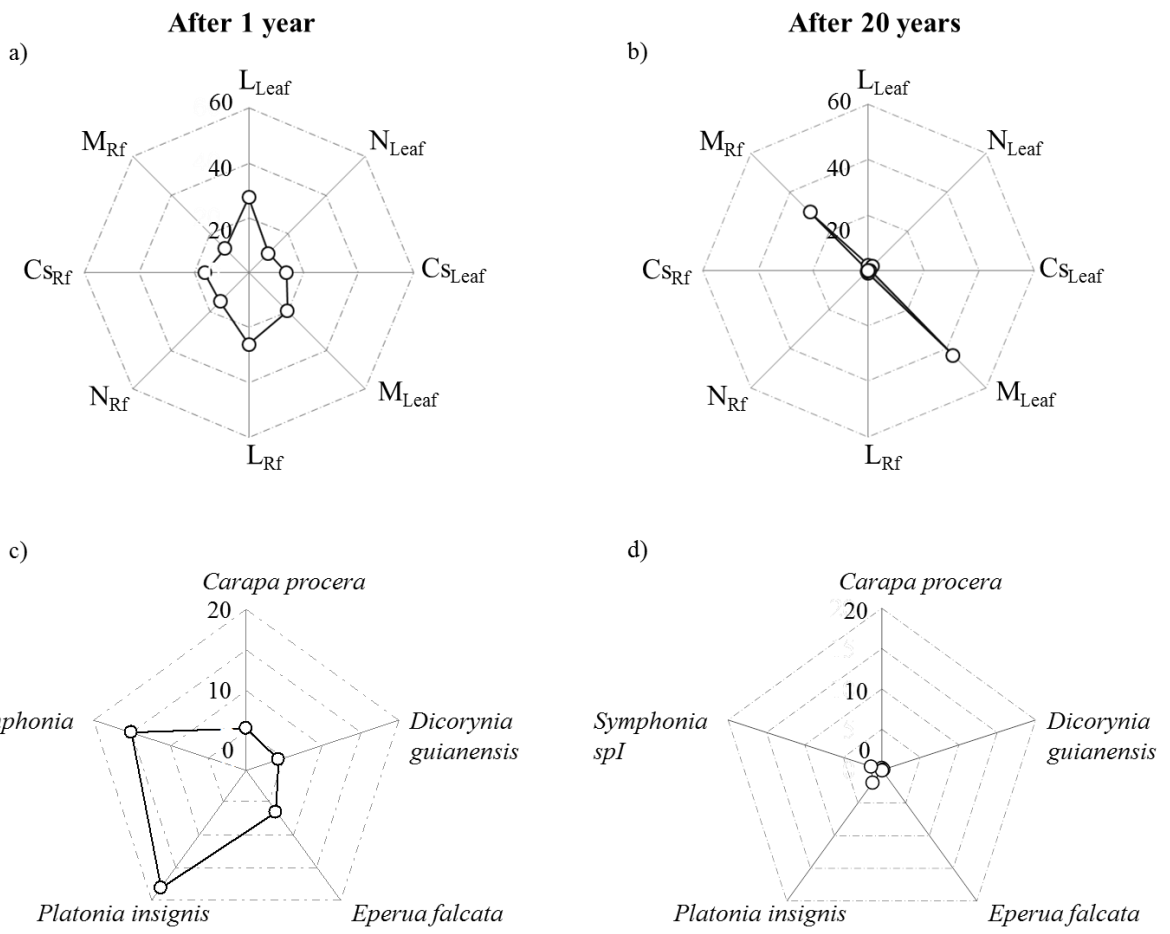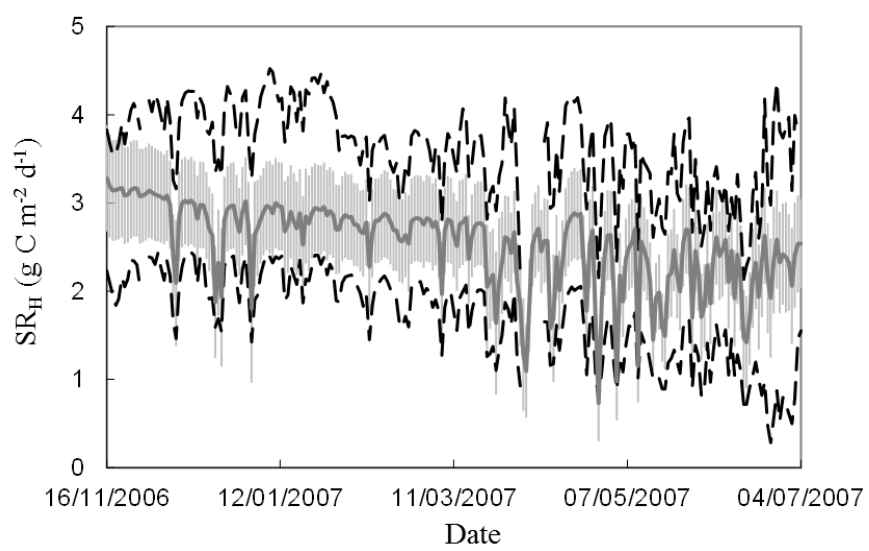
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2   **Fig. 4**

1
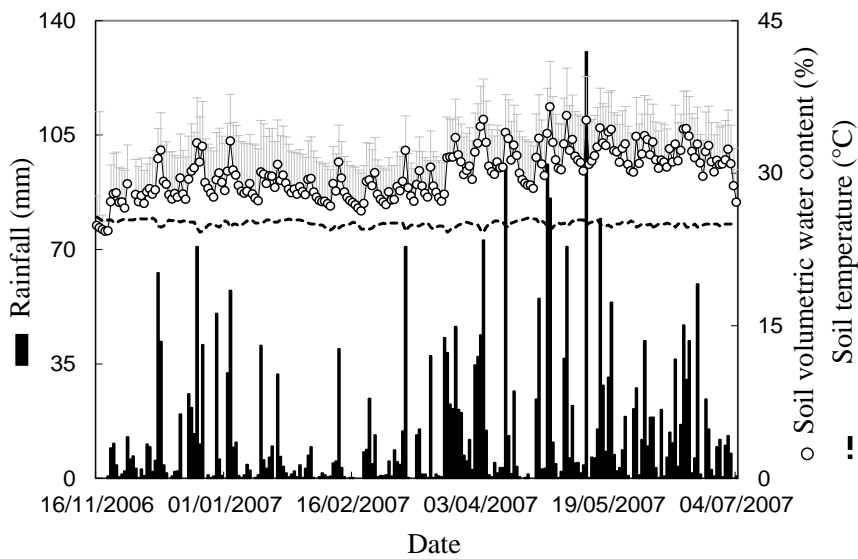
2 **Fig. 5**

3

1   **Supplementary data**

2

3   **Appendix A1**

4

5

6   **Fig. A1** Seasonal pattern of daily mean rainfall (filled bars), mean soil volumetric water

7   content (open circles) at 5 cm depth and mean soil temperature (dashed line) at 3 cm depth

8   recorded between 16/11/2006 and 04/07/2007 at the Guyaflux site in the Paracou

9   experimental forest, French Guiana. For soil water content means and standard errors are

10 given for $n = 4$.

11

1

2 **Appendix B2**

3
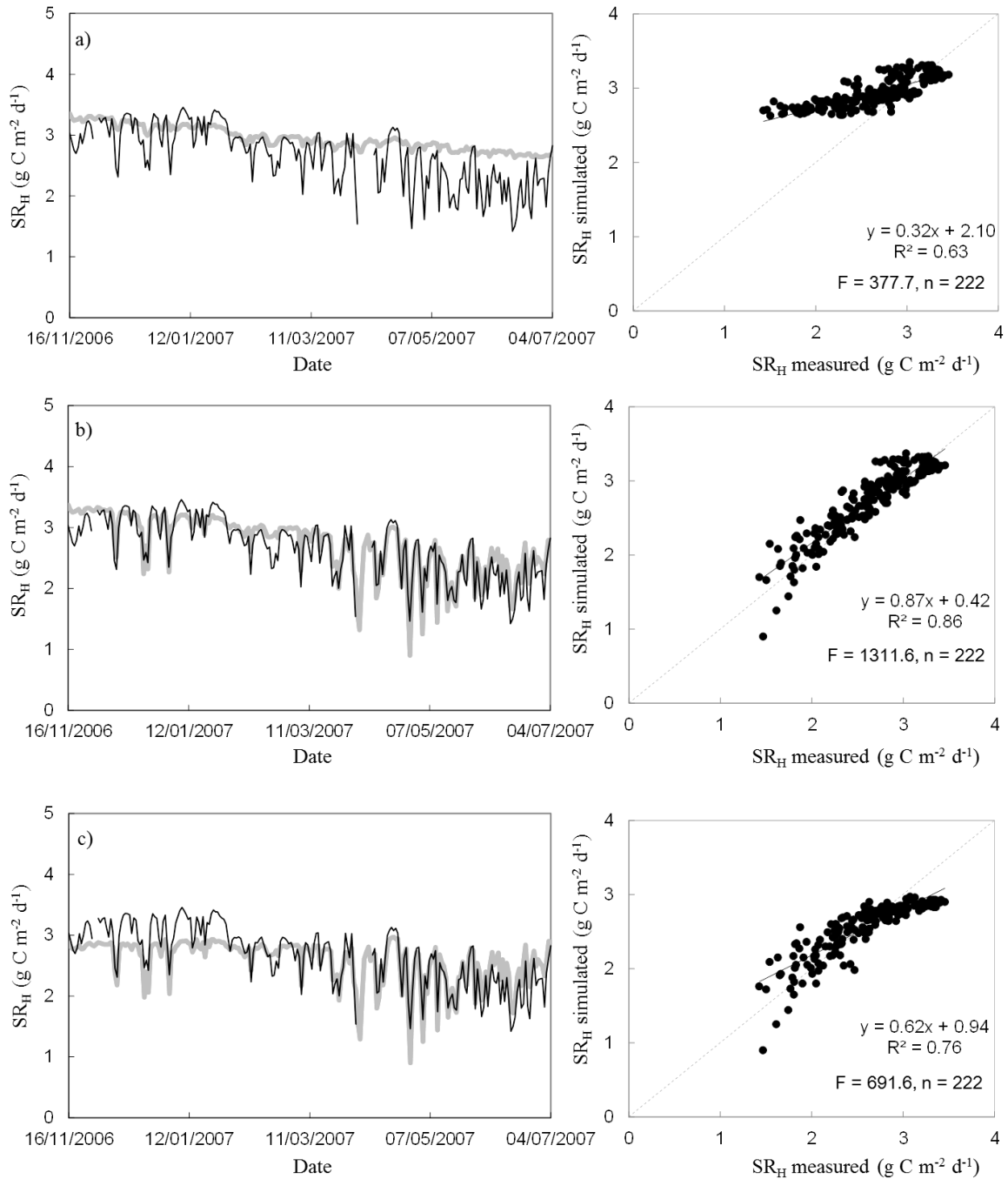
4
5 **Fig. B2** Seasonal course of soil CO_2 efflux measured in the trenched plots in the Paracou

6 experimental forest, French Guiana (black line), and simulated by the model Century (SR_H,

7 grey line) over a seven-month period (left hand panel) and the correlation between measured

1   mean and simulated values of SR_H (right hand panels). Simulations were done, with standard

2   parameterization (*i.e.* average parameter values), using a) the original formulation of the soil

3   water content reduction factor (A_w), b) and c) with the modified version of Aw accounting for

4   transitory waterlogging events. The additional dead root mass (also referred as "pulse of dead

5   root") brought by trenching was a) and b) taken into account or c) ignored. The latter was

6   used thereafter for the sensitivity analyses.

7