Towards a representation of priming on soil carbon decomposition in the global land biosphere model ORCHIDEE (version 1.9.5.2).

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Abstract

Priming of soil carbon decomposition encompasses different processes through which the decomposition of native (already present) soil organic matter is amplified through the addition of new organic matter, with new inputs typically being more labile than the native soil organic matter. Evidence for priming comes from laboratory and field experiments, but to date there is no estimate of its impact at global scale and under the current anthropogenic perturbation of the carbon cycle. Current soil carbon decomposition models do not include priming mechanisms, thereby introducing uncertainty when extrapolating short-term local observations to ecosystem and regional to global scale. In this study we present a simple conceptual model of decomposition priming, called PRIM, able to reproduce laboratory (incubation) and field (litter manipulation) priming experiments. Parameters for this model were first optimized against data from 20 soil incubation experiments using a Bayesian framework. The optimized parameter values were evaluated against another set of soil incubation data independent from the ones used for calibration and the PRIM model reproduced the soil incubations data better than the original, CENTURY-type soil decomposition model, whose decomposition equations are based only on first order kinetics. We then compared the PRIM model and the standard first order decay model incorporated into the global land biosphere model ORCHIDEE. A test of both models was performed at ecosystem scale using litter manipulation experiments from 5 sites. Although both versions were equally able to reproduce observed decay rates of litter, only ORCHIDEE-PRIM could simulate the observed priming (R^2=0.54) in cases where litter was added or removed. This result suggests that a conceptually simple and numerically tractable representation of priming adapted to global models is able to capture the sign and magnitude of the priming of litter and soil organic matter.

Keywords: soil carbon decomposition, global land biosphere model, priming effect, climate change.

1. Introduction

Soils are the largest reservoir of organic carbon (C) on land, holding three times as much as plant biomass globally (MEA, 2005). The dynamics of long-term soil organic matter formation (Schmidt et al., 2011) and its decomposition on time scales of future climate change (Jones et al. 2003) both remain poorly understood. The lack of a mechanistic understanding of soil carbon dynamics on time scales going from years to centuries induces important differences in the future projections of the global land carbon storage among global land biosphere models (Todd-Brown et al., 2013).

Different conceptual models have been proposed to explain empirical data on soil carbon decomposition, mainly incubation experiments (Wutzler and Reichstein, 2008; Manzoni and Porporato, 2009). Those conceptual models are usually calibrated to fit data (i.e. measurements of stock evolution or fluxes) from experiments on soil incubation, and on time scales going from hours to days (Panikov and Sizova, 1996; Blagodatsky and Richter 1998). It was shown by Wutzler and Reichstein (2008) that conceptual decomposition models accounting for interactions between labile and more recalcitrant microbial-related carbon, often called “priming effects”, could better fit data from incubation experiments acquired over periods of about 100 days.

The conceptual models of soil carbon decomposition encapsulated in global land biosphere models usually ignore interactions between labile and recalcitrant carbon. All global land biosphere models part of the Earth System Models used for IPCC climate projections are based on donor-pool dominant transfer and first order decay (Luo et al. 2015). Many of those global land biosphere models have soil carbon modules derived from the CENTURY (Parton et al., 1988) and RothC (Coleman and Jenkinson, 1999) models, in which the first order decay rates of different pools are modulated by soil temperature and moisture, as well as by soil texture (Friedlingstein et al., 2006).

Although the conceptual models with priming showed a more realistic behavior than first order decay models when applied to short term incubation data, one may still wonder if priming significantly influences the dynamics of soil carbon on time scales ranging from years to decades, and at large spatial scales. On the one hand, incorporating priming in a global land biosphere model has the disadvantage of introducing new parameters that are difficult to constrain and of generating a more complex - but unproven - dynamical behavior than the first order decay models. On the other hand, if the performances of first order decay models are not satisfactory at the large scale, structural changes of soil carbon models are needed and must be carefully tested.

The current situation with first-order decay dynamics in global land biosphere is that out of the 11 Earth System models used for the IPCC-AR5 CMIP5 simulations and benchmarked by Todd-Brown et al., (2013) against a global soil organic carbon (SOC) map, only six succeeded in representing the total mean C stocks at the global scale, but all failed to reproduce the spatial heterogeneity of SOC stocks as well as the SOC distribution under different vegetation cover (Todd-Brown et al., 2013). Possible causes of model failure include both errors in model structure but also errors in the different parameters controlling soil carbon dynamics. The optimization of the parameters of a first order decay model against a global SOC map could only partly reduce regional discrepancies with observations, with the optimized model explaining only 41% of the global variability of SOC (Hararuk et al., 2014). On the other hand, the use of a structurally different model that accounted for microbial biomass was shown to produce a rather realistic large-scale SOC variability, but very different soil carbon dynamics in response to future climate change (Wieder et al., 2013). This illustrates that model structure matters a lot for the simulation of the current distribution of soil carbon and its future evolution in response to climate and CO_2 changes.

Discrepancies between global land biosphere model predictions and observations are partially due to models lacking key mechanisms controlling SOC dynamics (Schmidt et al.,

91 2011). One example is the interactions with the N cycle. The majority of the ESMs used for
92 the IPCC-AR5 CMIP5 Earth System simulations did not represent explicitly the nitrogen
93 cycle, but the two ESMs with an explicit nitrogen cycle did not result either in a better
94 simulations of current SOC (Todd-Brown et al., 2013). Another example is the role of
95 microorganisms. The first order kinetics used in most models obviates the role that microbial
96 decomposers are known to play in controlling SOC mineralization (Cleveland et al., 2007;
97 Garcia-Pausas and Paterson 2011), but their activities is controlled by physical and chemical
98 drivers (Kemmit et al., 2008). Therefore, ESMs have significant gaps in reproducing the
99 mechanisms related to microbial dynamics such as priming (see definition below), the object
100 of this study.

101 Soil C priming is defined as a modification of SOC decomposition rates when fresh
102 organic C (FOC) is added (Kuzyakov et al., 2000). Priming is almost ubiquitously observed in
103 ecosystem studies where organic matter inputs are altered in laboratory incubations (reviewed
104 by Blagodatskaya and Kuzyakov 2008) or directly on the field (Boone et al., 1998; Borken et
105 al., 2002; Chemidlin-Prévost-Bouré et al., 2010; Subke et al., 2004; Sulzman et al., 2005;
106 Xiao et al., 2015). Priming can occasionally be negative but most commonly has a stimulative
107 effect on the decomposition of organic matter that decomposes. Several mechanisms may be
108 involved in controlling priming (Fontaine et al., 2003; Blagodatskaya and Kuzyakov 2008,
109 Guenet et al., 2010b), and conceptual models of priming can have substantial number of
110 parameters making their parameterization quite complex at large scales (Wutzler and
111 Reichstein, 2013). Wutzler and Reichstein (2008) proposed conceptual models summarized
112 into different equations to introduce priming without using too many parameters, but in all
113 cases an explicit representation of microbial biomass was required. Recently, Guenet et al.,
114 (2013a) modified the equation proposed by Wutzler and Reichstein (2008) to represent
115 priming without an explicit representation of microbial biomass, assuming that microbial
116 biomass is always at equilibrium with FOC. This assumption is suitable for being

incorporated into ESMs since it adds only one more free parameter compared to the first order kinetic models. This priming scheme was incorporated into the global land biosphere model ORCHIDEE, with the priming parameters statistically calibrated to reproduce the same equilibrium state (in terms of C stocks, after spin up of the model) than the standard version based on CENTURY (Guenet et al., 2013b). Despite its calibration ensuring the same initial state of SOC for England and Wales, the version of ORCHIDEE with priming resulted in a loss of SOC during the late 20th Century, in better agreement with inventory data (Bellamy et al., 2005) than the standard version which produced a continuous SOC gain. In that study, however, the parameters of the priming model were not based on observations but tuned instead to equilibrium SOC values. The objectives of this study are therefore:

- To derive optimal parameter values of a priming model (PRIM) with C inputs forced by data by using a Bayesian method (Tarantola, 1987) with priors and data from 20 different soil incubations.
- To introduce the calibrated PRIM model into the ORCHIDEE ecosystem model version AR5 and evaluate the new version ORCHIDEE-PRIM against independent *in situ* litter manipulation experiments at ecosystem scale.
- To assess if the priming model significantly improves the simulation of SOC mineralization compared to the standard first order decay model used in ORCHIDEE, on time scales of months to years.

2. Materials and Methods

The material and methods section is summarized in Fig. 1.

2.1 Models presentation

2.1.1 Soil carbon priming model PRIM

To represent priming, we used the ORCHIDEE soil decomposition module, which is based on the carbon-related modules of CENTURY (Parton et al., 1988). It has three carbon pools (active, slow and passive) and two litter pools (metabolic and structural). SOC decomposition is modulated by soil temperature and moisture functions. Active SOC decomposition is further modulated by a clay function. These functions are the same as in CENTURY but they are driven by soil physical variables calculated at a daily time step by the soil physics of ORCHIDEE (Krinner et al., 2005). The transfers among pools are described using the CENTURY equations with similar parameters (Parton et al., 1988). In the PRIM model, we replaced the CENTURY decomposition equations by those developed by Guenet et al. (2013a) to simulate a priming effect:

$$(1)\ \frac{dSOC_{Active}}{dt} = I - k_{SOC_{Active}} \times SOC \times (1 - e^{-c \times (Litter\_C)}) \times \theta \times \tau \times \gamma$$

$$(2)\ \frac{dSOC_{Slow}}{dt} = I - k_{SOC_{Slow}} \times SOC \times (1 - e^{-c \times (Litter\_C + SOC_{Active})}) \times \theta \times \tau$$

$$(3)\ \frac{dSOC_{Passive}}{dt} = I - k_{SOC_{Passive}} \times SOC \times (1 - e^{-c \times (Litter\_C + SOC_{Active} + SOC_{Slow})}) \times \theta \times \tau$$

with I being the input of C into the pool considered, k_{SOC} the SOC decomposition rate for the active, the slow and the passive pool, $Litter\_C$, the sum of all the litter pools of the model. θ, τ, and γ are the soil moisture function, the temperature function and the clay function modulating decomposition, respectively. c is a parameter controlling the impact of the fresh organic carbon (FOC) pool on the SOC mineralization rate. Here, we considered that FOC represents all the carbon from pools more labile than the pool being affected as shown in equation (1) to (3). Therefore, FOC is only litter for the active SOC pool, but for the slow SOC pool, FOC is the sum of the litter and the active SOC pool. Finally, for the passive SOC

pool, FOC is the litter and the active and slow carbon pools. The decomposition of the first donor litter pool is described using first order kinetics (4):

$$(4)\ \frac{dLitter\_C}{dt} = I - k_{Litter\_C} \times Litter\_C \times \theta \times \tau$$

In the Wutzler and Reichstein (2008) equation, the SOC mineralization was described by:

$$(5)\ \frac{dSOC}{dt} = I - k_{SOC} \times SOC \times (1 - e^{-c \times MB})$$

with *MB* being the microbial biomass. Unlike Wutzler and Reichstein (2008), our model does not explicitly simulate *MB* but assumes that MB equilibrates with FOC thus the relationship between MB and FOC is linear. Consequently, we represent priming using a direct relationship between FOC and SOC mineralization. Finally, the moisture, temperature and clay functions are described by equation (6), (7) and (8), respectively with *soil_moisture* in m^3 H_2O m^{-3} of soil, *soil_temperature* in Kelvin and *clay* in %wt :

$$(6)\ \theta = \max(0.25, \min(1, -1.1 \times soil\_moisture^2 + 2.4 \times soil\_moisture + 0.29))$$

$$(7)\ \tau = \exp(0.69 \times (soil\_temperature - 303)/10)$$

$$(8)\ \gamma = 1 - 0.75 \times clay$$

2.1.2 ORCHIDEE and ORCHIDEE-PRIM

ORCHIDEE is a process-based global land biosphere model that calculates the fluxes of CO_2, H_2O, and heat between the terrestrial land and the atmosphere. The time step of the model is 1/2-hour, and the variations of H_2O and C pools are calculated on a daily basis. The model has been evaluated at different scales (sites, regions, globes) and under different climates from the tropics to northern boreal zones (Krinner et al., 2005; Ciais et al., 2005;

185 Santaren et al., 2007; Piao et al., 2006). ORCHIDEE results from the coupling of three
186 different sub-models. The first one is called SVAT SECHIBA and describes soil water budget
187 and turbulent fluxes of energy and water between the atmosphere and the biosphere
188 (Ducoudré et al., 1993; de Rosnay and Polcher, 1998). The second one is derived from the
189 dynamic global vegetation model LPJ (Sitch et al., 2003) and deals with vegetation dynamics
190 (fire, sapling establishment, light competition, tree mortality, and climatic criteria for the
191 introduction or elimination of plant functional types). The last, called STOMATE (Saclay
192 Toulouse Orsay Model for the Analysis of Terrestrial Ecosystems) deals with phenology and
193 carbon dynamics of the terrestrial biosphere. Twelve plant functional types (PFT) are used to
194 classify the vegetation. Each PFT dynamic is controlled by similar set of governing equations
195 but using different parameter values. Only the leafy season onset and offset, are PFT-specific
196 (Krinner et al., 2005).

197 The simulation of SOC in ORCHIDEE version is based on CENTURY (Parton et al.,
198 1988) as described above. No vertical description of the SOC is included in the ORCHIDEE
199 version used here. In ORCHIDEE-PRIM we replaced CENTURY by the PRIM model
200 described in section 2.1.1.

201

202 ## 2.2 Data description

203 ### 2.2.1 Incubation experiments to calibrate the priming model

204 We optimized the PRIM parameters and the ORCHIDEE soil module parameters
205 using data from soil incubation experiments where FOC was added and the priming effect
206 was measured by comparing a control study without FOC with a perturbation study with FOC
207 (table 1). The data come from 20 incubations (from nine studies) of duration going from one
208 week to 10 months. The incubated soil samples have very different characteristics (table 1)
209 and came from different ecosystems (grassland, cropland, broadleaf forest, needleleaf forest,

210 savannah). However, the great majority of the data used to optimize the model were obtained
211 from temperate soils. In the incubation experiments, added FOC was labeled with ^{13}C or ^{14}C
212 and therefore the respired CO_2 fluxes coming from either SOC already present before the
213 FOC amendments or from the FOC induced priming of SOC pools was estimated separately.
214 We used only incubations performed during at least 7 days to eliminate all studies that
215 potentially observed apparent priming effects. Apparent priming is a replacement of the ^{12}C in
216 microbial biomass with labeled carbon isotopes, a short- term artifact due to the amendment
217 of labeled material to an unlabelled soil (Blagodatskaya and Kuzyakov, 2008). Moreover, we
218 used only studies that reported cumulative respired CO_2 fluxes in order to optimize the
219 priming parameters against the extra CO_2 fluxes obtained at the end of the experiment and not
220 those resulting from short-term priming dynamics, since cumulative mineralization integrates
221 the different processes occurring during incubation. Finally, several treatments might be
222 performed in the studies used to optimize the model (different soils, different types and
223 amount of FOC). When the treatments performed differed on aspects reproducible by the
224 model (amounts of FOC added, different clay content in the soils used, etc.) we considered all
225 the treatments. In the opposite case we averaged the results of the different treatments to
226 perform the optimization except in case where the treatments clearly impact the results
227 without the possibility to reproduce the experimental design with the model (addition of
228 mineral N for instance).

229 We also use the control incubations without FOC amendments to evaluate both
230 models. We extracted data from the figures of original publications (Table 1) using
231 GraphClick version 3.0 . Several input variables are needed to run the soil model, as described
232 in section 2.1.1. When data were not available from the surveyed publications, we obtained
233 them from the databases normally used for running ORCHIDEE, except for the C:N ratio of
234 FOC and for clay content where data came from Rodal et al., (1960) and from USDA
235 (http://soils.usda.gov/technical/classification/osd/index.html.), respectively. The three

carbon pools of CENTURY are not measurable (Six et al., 2002), so we cannot estimate how much C of in each pool is present in the incubated samples. To calculate the distribution of C among the three pools of the model we ran ORCHIDEE until equilibrium was reached at the sites where soil samples were taken and calculated the percentage of each pool.

2.2.2 Incubation data used for evaluation of the priming model

A first evaluation of the soil carbon model with and without priming is performed at the scale of soil samples against independent data from the large database of soil incubations (300 in total) published by Moyano et al., (2012). Within this database we selected the experiments where all the inputs necessary to run the two soil carbon models were available (clay, content, moisture, temperature, SOC content at the beginning of the incubation) and where cumulative mineralization or mineralization rates associated to the time step between two measurements were reported. We removed all the studies without information on the location since geographical coordinates are necessary to run ORCHIDEE and thus estimate the initial fraction of each pool. We selected only data coming from experiments without important soil manipulation (e.g. compaction, litter amendments). The model evaluation was performed against a set of 164 independent incubation experiments.

2.2.3 Ecosystem-level data used for evaluation of the priming model

A second evaluation of the ORCHIDEE-PRIM model was performed at ecosystem scale against observations of four litter manipulation experiments (Boone et al., 1998; Chemidlin-Prévost-Bouré et al., 2010; Subke et al., 2004; Sulzman et al., 2005) and one compost amendment experiment (Borken et al., 2002). In the litter experiments, two treatments and a control are generally performed. The treatments are total exclusion of above ground litter using nets to prevent fresh litter from falling onto the soil, often transplanting the collected fresh litter to create a second treatment with doubled aboveground litter inputs (Boone et al., 1998; Chemidlin-Prévost-Bouré et al., 2010; Sulzman et al., 2005). For the compost

amendment experiment by Borken et al. (2002), 1.4 kg C m^{-2} (and a zero-addition control) of compost was added to the soil. These studies are presented in table 3. When information about soil clay content was not available in the original study, we extracted it from Zobler (1986). The data measured at field scale are the soil CO_2 efflux including the heterotrophic respiration but also root respiration in the same flux without clear separation of the two components.

2.3 Optimization procedure

For PRIM, the 6 parameters optimized are turnover rate (k_{SOC}) and priming parameters c for each of the three pools (table 2). For the ORCHIDEE soil module, only the three k_{SOC} values are optimized. The same parameters are optimized against the priming incubations dataset described in 2.2.1. Since optimizations were performed using soil incubations data obtained at optimal temperature and soil moisture, we did not optimize the parameters related to the eq. (6) and (7) because the range of observations was quite limited. Optimization was performed in the framework of the Bayesian inversion method with priors (Tarantola, 1987) as described by Santaren et al., (2007) using assimilating all data streams in the same cost function. Assuming that all uncertainties follow Gaussian distributions (parameter error, measurement error, model error), the optimized parameters correspond to a set minimizing the following quadratic cost function:

$$(9)\quad J(\mathbf{x}) = \frac{1}{2}\left[\left(\mathbf{y}-\mathbf{H}(\mathbf{x})\right)^{t}\mathbf{R}^{-1}\left(\mathbf{y}-\mathbf{H}(\mathbf{x})\right)+\left(\mathbf{x}-\mathbf{x_b}\right)^{t}\mathbf{P}_{b}^{-1}\left(\mathbf{x}-\mathbf{x_b}\right)\right]$$

The cost function defined by equation (9) contains both the mismatch between model outputs and observed data, and the mismatch between optimized parameters and the prior values. The mismatch is weighted by errors of each quantity. **x** is the of unknown parameters vector, $\mathbf{x_b}$ the prior values, **y** the observations vector and **H(x)** the model outputs. $\mathbf{P}_b$ is the

285 prior parameter error variances/covariances, and **R** contains the observational error
286 variances/covariances which represents both measurement uncertainty and model uncertainty.

287 To minimize the cost function, we used a gradient-based iterative algorithm, called L-
288 BFGS-B (Zhu et al., 1995). A range of values for all the parameters is prescribed by called L-
289 BFGS-B. At each iteration, the cost function J(**x**) gradient is calculated, with respect to the six
290 parameters. When J(**x**) is minimized, using a classic finite difference method, we further
291 calculated the posterior error covariance matrix on the parameters $\mathbf{P}_a$ from the prior error
292 covariance matrices and the Jacobian of the model at the minimum of the cost function, using
293 the linearity assumption (Tarantola, 1987). When error correlations are close to 1 it suggests
294 that the observations do not permit to clearly separate the effect of two parameters.

295 The model **H**(**x**) is non linear and therefore the approach to minimize the cost function
296 is sensitive to potential local minima. We get around by performing 30 optimizations with
297 different sets of prior parameter randomly distributed within their variation range. We then
298 used the case providing the lowest cost function. This approach reduces drastically the
299 sensitivity to potential local minima as illustrated in Santaren et al. (2014).

300 We defined the prior ranges of decomposition rates using literature data (Parton et al.,
301 1988; Gignoux et al., 2001). However, only two studies already estimated the *c* parameter
302 before (Guenet et al, 2013a, Guenet et al., 2013b), its prior value is therefore considered as
303 non-informative and we set a large error on the prior (50%). As for the variance of the model-
304 data mismatch term in the cost function of equation (9), note that with our formalism this
305 error should include both the model error (for instance the model capability to represent the
306 measurement) and the measurement error. Given that the error on the measurements was
307 difficult to estimate precisely for each study, we fixed it to 5% of the mean observed CO_2 flux
308 assuming that all incubation data were independent. At its minimum, J(**x**) should be close to

309 half the number of observations (reduced χ^2 of one). We assumed that all errors (the
310 observations and on the a priori parameters) are uncorrelated.

311

312 ## 2.4 Simulations protocol

313 ### 2.4.1 Simulation protocol for the soil priming model PRIM

314 Simulations were performed for each incubation experiment presented in 2.2.1 (table
315 1) as well as for the evaluation sites in 2.2.2. The simulations of the stand-alone PRIM carbon
316 model (i.e. unplugged from the ORCHIDEE full ecosystem model) were run at a daily time
317 step using FOC inputs from table 1 or from the Moyano et al., (2012) database. No spin-up
318 was performed. We started the simulation by prescribing to the soil carbon models with and
319 without priming an initial amount of SOC equal to that measured in the study considered,
320 distributed among active, slow and passive pools as explained in section 2.2.1 At each time
321 step we increment the cumulative heterotrophic respiration coming from SOC mineralization,
322 so that this cumulative simulated CO_2 flux can be compared to data from the end of the
323 incubation experiment. Simulations were performed using R 3.0.2.

324

325 ### 2.4.2 Simulation protocol for ORCHIDEE-PRIM and ORCHIDEE

326 We ran ORCHIDEE and ORCHIDEE-PRIM at each litter manipulation site presented
327 in table 3 using. 6 hourly climate data obtained from the combination of two existing datasets:
328 the Climate Research Unit (CRU) (Mitchell et al. 2004) and the National Centers for
329 Environmental Prediction (NCEP) (Kalnay et al., 1996). Both models were run using the first
330 ten years of the climate forcing (1901-1909) repeated in a loop, and an atmospheric CO_2 value
331 corresponding to the year 1901. When the simulated relative yearly change of the SOC stock
332 was less than 0.01%, we considered that SOC equilibrium was reached. Once pre-industrial
333 equilibrium was reached in each grid point, we run transient simulations from 1901 until the

beginning of the manipulation experiment assuming no land use change driven by reconstructed climate and observed CO_2. Then when the simulation reached the year at which the litter manipulation experiment began, we modified the input of above-ground litter in the same proportion than in the actual manipulation experiments, Finally, we ran the model for each treatment during a period corresponding to duration of each experiment.

2.5 Model evaluation

The model evaluation was performed in two steps. First, we evaluated separately PRIM and the standard first order decay model with their optimized parameters, as stand alone decomposition models, i.e. unplugged from the ORCHIDEE ecosystem model. To evaluate the stand-alone soil models, we used incubation data coming from Moyano et al., (2012) as described in 2.2.2. Secondly, we evaluated ORCHIDEE and ORCHIDEE-PRIM, against litter manipulation experiments (see 2.2.3).

To compare model outputs with data we used different metrics. First a linear mixed effect model with intercept value forced to zero using model outputs as the variable to explain, and data as the fixed effect and the study where data came from as random effect. This approach aimed to take into account the fact that incubations performed within the same study are not independent because they were performed and analyzed by the same team. The linear-mixed effect model gives the slope of the relationship as output. A slope close to one indicates that the model reproduces the data well. Then, we used the Normalized Standard Deviation (*NSD*) or ratio of model to observed standard deviations ; *NSD* = 1 means that the model perfectly reproduces the observed standard deviations across experiments:

$$NSD = \frac{\sqrt{\frac{1}{n} \times \sum_{i=1}^{n} (x_i - \bar{x})^2}}{\sqrt{\frac{1}{n} \times \sum_{i=1}^{n} (o_i - \bar{o})^2}} \quad (10)$$

where x refers to the model value, o to the observed value and n the number of samples. Finally, we compared model performance using the Bayesian Information Criterion (*BIC*) to take into account that the PRIM soil model has three more priming parameters (one per pool) than the standard model:

$$BIC = \log(MSD) \times n + \log(n) \times p \quad (11)$$

with *MSD* being the mean squared deviation derived from equation (12), n the number of data used to evaluate the model, and p the number of parameters of the soil model.

$$MSD = \frac{\sum (m - o)^2}{n} \quad (12)$$

with o the observed values, m the values calculated by the model and n the number of observations. The lowest is the BIC the better the model is.

3. Results

3.1 Optimized parameters of the priming model

The parameters obtained after optimization using incubation data described in section 2.2.1 are given in Table 2. The turnover times ranged from a few months (0.30 ± 0.15 year) for the active pool to 462.0 ± 233.8 years for the passive pool, the slow pool being intermediate with 1.12 ± 0.01 years. The priming parameters indicated a decreasing sensitivity with increasing turnover time. The parameter c values were 493.7 ± 246.8, 194.0± 97.0 and 136.5 ± 68.3 for the active, slow and passive pools, respectively. Errors correspond to the estimates from the linear assumption at the minimum of J(x). For both, the correlation between parameters was low (data not shown).

After optimization, both models with and without priming parameterization were able to reproduce the cumulative mineralization measured in the different incubations where FOC was added well (Fig. 2, top panel). The slope of the linear regression between optimized model output and incubation measurements was 1.13 for PRIM and 0.93 for the ORCHIDEE

soil module. The NSD value (1.80 and 1.52 for PRIM and the standard soil module, respectively) showed that the models overestimated the variance after optimization. When both models were evaluated against the same incubation experiments but without FOM addition, the PRIM model slightly over-estimated accumulated mineralization (Fig. 2 middle panel), as indicated by the value of the slope (1.05). Nevertheless, it performed better than the standard soil module, which underestimated the soil mineralization as indicated by the value of the slope (0.72). The PRIM soil model reproduced quite well the observed priming effect (section 2.2.1) as shown in Fig. 2 (lower panel) with a slope value (1.07). PRIM largely overestimated however the variance of data as indicated by the NSD value (3.14). As expected, the standard soil module was totally unable to reproduce priming (Fig. 2, lower panel).

3.2 Standard soil module vs. PRIM against incubations data

To evaluate the performance of PRIM we tested it against data from soil incubation experiments independent from those used for optimization (see section 2.2.2). We did the same with the standard soil module (Fig. 3). The standard soil module tended to overestimate accumulated mineralization as indicated by a slope value of 1.32 and to underestimate the cross-experiments variance by more than 50% (NSD=0.44). PRIM performed slightly better, but underestimated accumulated mineralization (slope 0.80). The optimized PRIM underestimated the variance by 29%, but the NSD value (0.71) was closer to 1 compared to the standard model. Using the BIC index, which takes into account the higher number of parameters of PRIM, this model still performed better (BIC values of 546.2 vs. 347.4 for standard and PRIM, respectively).

3.3 ORCHIDEE vs. ORCHIDEE-PRIM comparison using *in situ* datasets

When tested at ecosystem-level against litter manipulation experiments, 4 studies x 3 treatments and 1 study with 2 treatments. Both ORCHIDEE and ORCHIDEE-PRIM performed generally well to reproduce the soil CO_2 efflux (Fig. 4). Generally, both versions showed similar performance as indicated by the values of slopes and NSD presented in table 4. The mean slopes are 0.98 for ORCHIDEE-PRIM against 0.97 for ORCHIDEE, and the mean NSD are 1.26 and 1.27, respectively. It must be noted that slope values were generally lower for the treatments excluding litter compared to control and double litter inputs (Table 4). No particular differences of the NSD values were observed between the different litter input regimes. Nevertheless, the BIC index was always higher for ORCHIDEE-PRIM because three more parameters were used by this version compared to ORCHIDEE.

ORCHIDEE-PRIM was able to reproduce the priming observed defined as the difference of CO_2 efflux coming from SOC only with or without litter (Fig. 5), but tended to underestimate its intensity as indicated by the slope value lower than one (0.55). The variance between experiments calculated for priming was overestimated as shown by the NSD value of 1.29. It must be noted that priming was not calculated for ORCHIDEE since the structure of its soil decomposition model does not include a priming mechanisms.

4. Discussion

4.1 PRIM in the context of other soil priming conceptual models

Priming is a complex phenomenon controlled by several mechanisms, such as N mining by microbial communities with different growth strategies, competition between microbial groups for substrate, energy limitations, etc. (Kuzyakov et al., 200; Fontaine et al., 2003; Guenet et al., 2010b). Priming may have important consequences on the feedbacks between climate and C cycle (Schmidt et al., 2011) and it is therefore crucial to better quantify the C fluxes due to priming, especially at large scale (i.e, continental to global). Several models have been developed to describe soil C mineralization with a representation of priming (Gignoux et al., 2001; Fontaine and Barot, 2005; Neill and Gignoux, 2006; Moorhead

and Sinsabaugh, 2006; Wutzler and Reichstein, 2008; Neill and Guenet, 2010; Blagodatsky et al., 2010) and such models generally succeeded at reproducing short-term data, mainly incubation. However, to our knowledge, they have never been tested in a range of contrasted situations (different soil types, different FOC amount and chemical composition, different temperature and soil moisture, etc.). Here, we used most of the available incubation data respecting the criteria described in the material and method section. Moreover, previous priming models all needed a high number of parameters compared to PRIM. For these two reasons, the conceptual soil models accounting for soil priming were thus far not included in global land biosphere models (Wutzler and Reichstein, 2008) and very few studies of soil priming at global scale have been performed (Foereid et al., 2014). Here, using a simple scheme with only three additional parameters than the standard soil module of ORCHIDEE, we were able to reproduce priming but also soil mineralization data coming from very different incubation studies performed with different soils at different temperature and moisture, with different time length, etc. The PRIM soil model, which is a microbial steady-state model, might not be able to reproduce short-term response to abrupt change of FOC inputs but with negligible bias over the long term (Wutzler and Reichstein 2013). However, it might have similar performances than more complex models to reproduce long-term trends of FOC inputs (Wutzler and Reichstein 2013). PRIM performed better than the standard soil module to reproduce soil incubation data used to optimize, but it must be noted that the BIC values indicate that the improvement observed with PRIM may be simply due to a higher number of parameters. Nevertheless, when using independent soil incubations data from the one used to optimize the model the improvement is quite clear with BIC values much lower with PRIM than with the standard soil module (347.4 and 546.2, respectively). Furthermore, PRIM was not able to fully catch the observed variability of priming. As discussed above, priming is a complex phenomenon resulting from the interactions of different mechanisms that we summarized in a very simple equation. Therefore, PRIM is probably good in representing a general trends but not all the complexity of the phenomenon. Nevertheless, the

458 use of the PRIM soil model seems justified since it increases only slightly the number of
459 parameter of a global land biosphere model and since the parameter values were obtained
460 after optimization on data coming from incubations performed in a range of soils and
461 conditions (different soil types, different ecosystems, different temperatures, different
462 moistures, different amount and type of FOC amended, etc.).
463
464 **4.2** ORCHIDEE vs. ORCHIDEE-PRIM
465 **4.2.1** Cross sites evaluation
466 ORCHIDEE-PRIM exhibited similar performance than ORCHIDEE when simulating
467 litter manipulation experiments. It must be noted that both versions share the same scheme for
468 primary production (controlling soil C input by litter), soil temperature and moisture function.
469 The similar performance obtained by the two versions may be due to a model bias for these
470 quantities as well as poorly constrained site histories and climate forcing errors. Since primary
471 production is the main driver of the C input into the soil, the soil CO_2 efflux calculated by the
472 models was largely driven by the capacity of the model to reproduce the observed primary
473 production. In particular, both models largely underestimated the soil CO_2 efflux when litter
474 was removed (Table 4), but obtained good results when litter was kept or when litter was
475 added. This suggests that both models performed quite well when reproducing soil CO_2
476 efflux, but this was due to bias compensation, meaning that the fraction of CO_2 coming from
477 soil mineralization and root respiration was underestimated and the fraction of CO_2 coming
478 from litter mineralization was overestimated. Moreover, the modification of the litter cover
479 may change the soil humidity and temperature and these effects were not represented in the
480 models.
481 Finally, the use of microbial steady state model like ORCHIDEE-PRIM present some
482 advantages compared to explicit microbial models. Wieder et al., (2015) identified several
483 challenges related to the incorporation of explicit microbial models in ESMs. In particular, it

needs much more parameter than the classical approach. With ORCHIDEE-PRIM these difficulty is resolved since we only add three more parameters.

5. Conclusion

Regarding the several processes that may lead to priming, the satisfactory performance of ORCHIDEE-PRIM compared to observations from both laboratory incubation and field litter manipulation experiments suggests that the simple PRIM conceptual model simulates well the magnitude of observed priming. Consequently, ORCHIDEE-PRIM has the potential to quantify the impact of priming on the soil C cycle at large scales. Nevertheless, ORCHIDEE-PRIM underestimates the priming intensity as shown by the slope value (0.55), indicating that the model still misses important mechanisms explaining the observations. In particular, N availability is an important driver of priming, inducing higher priming when N availability is reduced (Fontaine et al., 2004; Blagodatskaya et al., 2007). The role of N in the priming intensity as well as the extra N mineralization induced by priming and its effect on primary production may represent the next addition to the soil representation in a land surface model by adding a control on the *c* parameter depending on the mineral N availability and on the C:N ratio of the considered pool. Nevertheless, some detailed information on the N dynamic in priming effect experiments would be necessary to do so and very few authors reported the impact of priming effect on N dynamic after FOC additions.

Code availability

For ORCHIDEE, the main part of the code was written by Krinner et al., (2005). The version used here is the 1.9.5.2 version. In this version, compared to the one presented in Krinner et al., (2005), the albedo representation was improved (Hourdin et al., pers. com.), a

routing scheme controlling the flux of water from land surface to the ocean was added (Ngo-Duc et al., 2007) and the dynamic of vegetation was modified (Viovy et al., pers. com.). Furthermore, since 2005 the code has been parallelized. A detailed documentation and the code can be provided upon request to the corresponding author.

ORCHIDEE-PRIM is derived from ORCHIDEE with the modifications presented in the section 2.1.2. A detailed description can be found in Guenet et al., (2013). The code is available upon request to the corresponding author.

518 References

519 Bell, J., Smith, J., Bailey, V., Bolton, H., 2003. Priming effect and C storage in semi-arid no-
520 till spring crop rotations. Biology and Fertility of Soils 37, 237–244.

521 Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., Kirk, G.J.D., 2005. Carbon losses
522 from all soils across England and Wales 1978-2003. Nature 437, 245–8.
523 Blagodatsky, S.A., Richter, O., 1998. Microbial growth in soil and nitrogen turnover: a
524 theoretical model considering the activity state of microorganisms. Soil Biology &
525 Biochemistry 30, 1743–1755.
526 Blagodatsky, S., Blagodatskaya, E., Yuyukina, T., Kuzyakov, Y., 2010. Model of apparent
527 and real priming effects: Linking microbial activity with soil organic matter
528 decomposition. Soil Biology and Biochemistry.

529 Blagodatskaya, E.V., Blagodatsky, S.A., Anderson, T.-H., Kuzyakov, Y., 2007: Priming
530 effects in chernozem induced by glucose and N in relation to microbial growth
531 strategies. Applied Soil Ecology 37, 95-105.
532 Blagodatskaya, E., Kuzyakov, Y., 2008. Mechanisms of real and apparent priming effects and
533 their dependence on soil microbial biomass and community structure: critical review.
534 Biology and Fertility of Soils 45, 115–131.
535 Boone, R., Nadelhoffer, K., Canary, J., 1998. Roots exert a strong influence on the
536 temperature sensitivity of soil respiration. Nature 396, 570–572.

537 Borken, W., Muhs, A., 2002. Application of compost in spruce forests: effects on soil
538 respiration, basal respiration and microbial biomass. Forest Ecology and Management
539 159, 49–58.

540 Chemidlin Prévost-Bouré, N., Soudani, K., Damesin, C., Berveiller, D., Lata, J.-C., Dufrêne,
541 E., 2010. Increase in aboveground fresh litter quantity over-stimulates soil respiration in
542 a temperate deciduous forest. Applied Soil Ecology 46, 26–34.

543 Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M.,
544 Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend,
545 A.D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A.,
546 Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M.,
547 Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J.,
548 Schulze, E.D., Vesala, T., Valentini, R.: Europe-wide reduction in primary
549 productivity caused by the heat and drought in 2003. Nature 437,529–533, 2005.
550 Cleveland CC, Nemergut DR, Schmidt SK, Townsend AR (2007) Increases in soil respiration
551 following labile carbon additions linked to rapid shifts in soil microbial community
552 composition. Biogeochemistry 82: 229-240

553 Coleman, K. and Jenkinson, D. S.: RothC-26.3, A Model for the Turnover of Carbon in Soil:
554 Model Description and User's Guide. Lawes Agric. Trust, Harpenden, UK, 1999.
555 Conde, E., Cardenas, M., Poncemendoza, a, Lunaguido, M., Cruzmondragon, C., Dendooven,
556 L., 2005. The impacts of inorganic nitrogen application on mineralization of C-labelled
557 maize and glucose, and on priming effect in saline alkaline soil. Soil Biology and
558 Biochemistry 37, 681–691.

559 De Nobili, M., Contin, M., Mondini, C., 2001. Soil microbial biomass is triggered into
560 activity by trace amounts of substrate. Soil biology and 33, 1163–1170.

561 de Rosnay, P., Polcher, J.: Modeling root water uptake in a complex land surface scheme
562 coupled to a GCM. Hydrology and Earth System Sciences 2, 239–256, 1998.
563 Ducoudré, N. I., Laval, K., Perrier, A.: SECHIBA, a new set of parameterizations of the
564 hydrologic exchanges at the land-atmosphere interface within theLMDatmospheric
565 general circulation model. Journal of Climate, 6, 248–273, 1993.
566 Falchini, L., Naumova, N., Kuikman, P.J., Bloem, J., Nannipieri, P., 2003. CO2 evolution and
567 denaturing gradient gel electrophoresis profiles of bacterial communities in soil

following addition of low molecular weight substrates to simulate root exudation. Soil Biology and Biochemistry 35, 775–782.

FAO/IIASA/ISRIC/ISSCAS/JRC, 2012. *Harmonized World Soil Database (version 1.2)*. FAO, Rome, Italy and IIASA, Laxenburg, Austria.

Foereid, B., Ward, D.S., Mahowald, N., Paterson, E., Lehmann, J., 2014. The sensitivity of carbon turnover in the Community Land Model to modified assumptions about soil processes. Earth System Dynamics 5, 211–221.

Fontaine, S., Mariotti, A., Abbadie, L., 2003. The priming effect of organic matter: a question of microbial competition? Soil Biology and Biochemistry 35, 837–843.

Fontaine, S., Bardoux, G., Benest, D., 2004. Mechanisms of the priming effect in a savannah soil amended with cellulose. Soil Science Society of America Journal 125–131.

Fontaine, S., Bardoux, G., Abbadie, L., Mariotti, A., 2004. Carbon input to soil may decrease soil carbon content. Ecology Letters 7, 314–320.

Fontaine, S., Barot, S., 2005. Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. Ecology Letters 8, 1075–1087.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnit- zler, K. G., Schnur, R., Strassmann, K.,Weaver, A. J., Yoshikawa, C., and Zeng, N. : Climate- carbon cycle feedback analysis: results from the C4MIP model intercomparison. J. Climate, 19, 3337–3353, 2006.

Garcia-Pausas, J., Paterson, E., 2011. Microbial community abundance and structure are determinants of soil organic matter mineralisation in the presence of labile carbon. Soil Biology and Biochemistry 43, 1705–1713.

592 Gignoux, J., House, J., Hall, D., Masse, D., Nacro, H.B., Abbadie, L., 2001. Design and test
593 of a generic cohort model of soil organic matter decomposition: the SOMKO model.
594 Global Ecology and Biogeography 10, 639–660.
595 Guenet, B., Neill, C., Bardoux, G., Abbadie, L., 2010. Is there a linear relationship between
596 priming effect intensity and the amount of organic matter input? Applied Soil Ecology.

597 Guenet, B., Danger, M., Abbadie, L., Lacroix, G., 2010b. Priming effect: bridging the gap
598 between terrestrial and aquatic ecology. Ecology 91, 2850–2861.

599 Guenet, B., Juarez, S., Bardoux, G., Luc, A., Claire, C., 2012. Evidence that stable C is as
600 vulnerable to priming effect as is more labile C in soil. Soil Biology and Biochemistry
601 43–48.

602 Guenet, B., Eglin, T., Vasilyeva, N., Peylin, P., Ciais, P., Chenu, C.: The relative importance
603 of decomposition and transport mechanisms in accounting for soil organic carbon
604 profiles.. Biogeosciences 10, 2379-2392, 2013a.

605 Guenet, B., E Moyano, F., Vuichard, N., Kirk, G.J.D., Bellamy, P.H., Zaehle, S., Ciais, P.,
606 2013b. Can we model observed soil carbon changes from a dense inventory? A case
607 study over england and wales using three version of orchidee ecosystem model (AR5,
608 AR5-PRIM and O-CN). Geoscientific Model Development Discussions 6, 3655–3680.
609 Hamer, U., Marschner, B., 2005. Priming effects in different soil types induced by fructose,
610 alanine, oxalic acid and catechol additions. Soil Biology & Biochemistry 37, 445–454.

611 Hararuk, O., Xia, J., Luo, Y., 2014. Evaluation and improvement of a global land model
612 against soil carbon data using a Bayesian Markov chain Monte Carlo method. Journal of
613 Geophysical Research: Biogeosciences 119, 403–417.
614 Jones, C.D., Cox, P., Huntingford, C.: Uncertainty in climate–carbon-cycle projections
615 associated with the sensitivity of soil respiration to temperature. Tellus B 55, 642–
616 648, 2003.

617 Kalnay et al.,The NCEP/NCAR 40-year reanalysis project, Bull. Amer. Meteor. Soc., 77,
618 437-470, 1996.
619 Kemmitt, S.J., Lanyon, C. V, Waite, I.S., Wen, Q., Addiscott, T.M., Bird, N.R.A., O'donnell,
620 A.G., Brookes, P.C., 2008. Mineralization of native soil organic matter is not regulated
621 by the size, activity or composition of the soil microbial biomass - a new perspective.
622 Soil Biology & Biochemistry 40, 61–73.
623 Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P.,
624 Ciais, P., Sitch, S., Prentice, I.C.: A dynamic global vegetation model for studies of
625 the coupled atmosphere-biosphere system. Global Biogeochemical Cycles 19,
626 GB1015, 2005
627 Kuzyakov, Y., Friedel, J.K., Stahr, K.: Review of mechanisms and quantification of priming
628 effects. Soil Biology & Biochemistry 32, 1485-1498, 2000.
629 Luo, Y., Ahlström, A., Allison, S.D., Batjes, N.H., Brovkin, V., Carvalhais, N., Chappell, A.,
630 Ciais, P., Davidson, E.A., Finzi, A., Georgiou, K., Guenet, B., Hararuk, O., Harden,
631 J.W., He, Y., Hopkins, F., Jiang, L., Koven, C., Jackson, R.B., Jones, C.D., Lara, M.J.,
632 Liang, J., McGuire, D., Parton, W., Peng, C., Randerson, J.T., Salazar, A., Sierra, C.A.,
633 Smith, M.J., Tian, H., Todd-Brown, K.E.O., Torn, M., van Groenigen, K.J., Wang,
634 Y.P., West, T.O., Wei, Y., Wieder, W.R., Xia, J., Xu, X., Xu, X., Zhou, T.: Towards
635 More Realistic Projections of Soil Carbon Dynamics by Earth System Models.
636 Global Biogeochemical Cycles 12, DOI:10.1002/2015GB005239, 2015.
637 Manzoni, S., Porporato, A., 2009. Soil carbon and nitrogen mineralization: Theory and
638 models across scales. Soil Biology and Biochemistry 41, 1355–1379.
639 MEA, Millennium Ecosystem Assessment-Nutrient Cycling. World Resource Institute,
640 Washington DC (2005).
641 Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M., New, M.: A Comprehensive Set of
642 High-Resolution Grids of Monthly Climate for Europe and the Globe: The Observed

643 Record (1901–2000) and 16 Scenarios (2001–2100), 33 pp., Tyndall Center for
644 Climate Change Research, University of East Anglia, Norwich, U. K, 2004.
645 Moorhead, D.L., Sinsabaugh, R.L.: A theoretical model of litter decay and microbial
646 interaction. Ecological Monographs 76, 151-174, 2006.
647 Moyano, F.E., Vasilyeva, N., Bouckaert, L., Cook, F., Craine, J., Curiel Yuste, J., Don, a.,
648 Epron, D., Formanek, P., Franzluebbers, a., Ilstedt, U., Kätterer, T., Orchard, V.,
649 Reichstein, M., Rey, a., Ruamps, L., Subke, J. -a., Thomsen, I.K., Chenu, C., 2012. The
650 moisture response of soil heterotrophic respiration: interaction with soil properties.
651 Biogeosciences 9, 1173–1182.
652 Neill, C., Gignoux, J., 2006. Soil organic matter decomposition driven by microbial growth: a
653 simple model for a complex network of interactions. Soil Biology and Biochemistry 38,
654 803–811.
655 Neill, C., Guenet, B., 2010. Comparing two mechanistic formalisms for soil organic matter
656 dynamics: A test with in vitro priming effect observations. Soil Biology and
657 Biochemistry 42, 1212–1221.

658 Panikov, N.S., Sizova, M.V., 1996. A kinetic method for estimating the biomass of microbial
659 functional groups in soil. Journal of Microbiological Methods 24, 219–230.
660 Parton,W.J., Stewart, J.W.B., and Cole, C.V.: Dynamics of C, N, P and S in grassland soils - a
661 model. Biogeochemistry, 5, 109–131, 1988.
662 Piao, S.L., Friedlingstein, P., Ciais, P., Zhou, L., Chen, A.: Effect of climate and CO_2 changes
663 on the greening of the Northern Hemisphere over the past two decades. Geophysical
664 Research Letters 33, L23402, 2006.

665 J. I. Rodale and staff, Complete Book of Composting, Rodale Books, 1960

666 Santaren, D., Peylin, P., Viovy, N., and Ciais, P.: Optimizing a process-based ecosystem
667 model with eddy-covariance flux measurements: A pine forest in southern France,

668 Global Bio- geochem. Cy., 21, GB2013, doi:10.1029/2006GB002834, 2007.
669 Santaren, D., P., P., Bacour, C., Ciais, P., Longdoz, B., 2014. Ecosystem model optimization
670 using in-situ flux observations : benefit of monte-carlo vs . variational schemes and
671 analyses of the year-to-year model performances. Biogeosciences 11, 7137–7158.
672
673 Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I., Kleber,
674 M., Kögel-Knabner, I., Lehmann, J., Manning, D.C., Nannipieri, P., Rasse, D.P.,
675 Weiner, S., Trumbore, S.E.: Persistence of soil organic matter as an ecosystem
676 property. Nature 478, 49-56, 2011.
677 Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P.,
678 Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., Woodward, F.I. : Evaluation
679 of the terrestrial carbon cycle, future plant geography and climate-carbon cycle
680 feedbacks using five Dynamic Global Vegetation Models (DGVMs). Global Change
681 Biology 14, 2015–2039, 2008.

682 Six, J., Conant, R., Paul, E., Paustian, K., 2002. Stabilization mechanisms of soil organic
683 matter: Implications for C-saturation of soils. Plant and Soil 241, 155–176.
684 Subke, J.-A., Hahn, V., Battipaglia, G., Linder, S., Buchmann, N., Cotrufo, M.F., 2004.
685 Feedback interactions between needle litter decomposition and rhizosphere activity.
686 Oecologia 139, 551–9.

687 Sulzman, E.W., Brant, J.B., Bowden, R.D., Lajtha, K., 2005. Contribution of aboveground
688 litter, belowground litter, and rhizosphere respiration to total soil CO2 efflux in an old
689 growth coniferous forest. Biogeochemistry 73, 231–256.

690 Tarantola, A.: Inverse Problem Theory: Methods of Data Fitting and Model Parameter
691 Estimation, Elsevier Science Ltd., 630 pp., 1987.

692 Todd-Brown, K.E.O., Randerson, J.T., Post, W.M., Hoffman, F.M., Tarnocai, C., Schuur, E.
693 a. G., Allison, S.D., 2013. Causes of variation in soil carbon simulations from CMIP5
694 Earth system models and comparison with observations. Biogeosciences 10, 1717–1736.
695 Wieder, W.R., Bonan, G.B., Allison, S.D., 2013. Global soil carbon projections are improved
696 by modelling microbial processes. Nature Climate Change 3, 1–4.
697
698 Wutzler, T., and Reichstein, M. : Colimitation of decomposition by substrate and
699 decomposers- a comparison of model formulations. Biogeosciences, 5, 749-759,
700 2008.
701 Wutzler, T., Reichstein, M., 2013. Priming and substrate quality interactions in soil organic
702 matter models. Biogeosciences 10, 2089–2103.
703 Xiao, C., Guenet, B., Zhou, Y., Su, J., Janssens, I. a., 2015. Priming of soil organic matter
704 decomposition scales linearly with microbial biomass response to litter input in steppe
705 vegetation. Oikos 124,649:647.
706 Zobler, L.: A World Soil File for Global Climate Modeling. Technical Mem- orandum 87802.
707 NASA Goddard Institute for Space Studies (GISS), New York, NY, 1986.
708 Zhu, C., Byrd, R. H., Lu, P., and Nocedal, J.: A limited memory algorithm for bound
709 constrained optimisation, SIAM J. Sci. Stat. Comput., 16, 1190–1208, 1995.
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712

713 Figure legends

714 Figure 1: Summarizing scheme of the methods

715 Figure 2: Scatter plot between data and the PRIM model outputs for the incubations with FOC
716 amendment (a), without FOC amendment (b) and for priming effect (c). The dataset used here
717 are the similar to those used for optimization (a) or are the control incubations (b) and are
718 described in section (2.2.1). Red lines indicate the 1:1 line. Different symbol indicate different
719 studies.

720 Figure 3: Scatter plot between independent data from optimization (dataset describes in
721 section 2.2.2) and the soil module of ORCHIDEE outputs (a) or between data and the PRIM
722 model outputs (b). Red lines indicate the 1:1 line.

723 Figure 4: Soil CO_2 efflux calculated by ORCHIDEE on the left side and by ORCHIDEE-
724 PRIM on the right side for the data coming from Boone et al., (1998) (a), from Borken et al.,
725 (2002) (b), from Chemidlin-Prévost-Bourré et al., (2010) (c), from Subke et al., (2004) (d)
726 and from Sulzman et al., (2005) (e). Red lines indicate the 1:1 line, black, dashed and dotted
727 lines correspond to control, litter exclusion and litter amendment situations respectively.

728 Figure 5: Scatter plot between the priming effect measured and the priming effect calculated
729 by ORCHIDEE-PRIM. Red line indicate the 1:1 line and different symbol indicate different
730 studies.

731

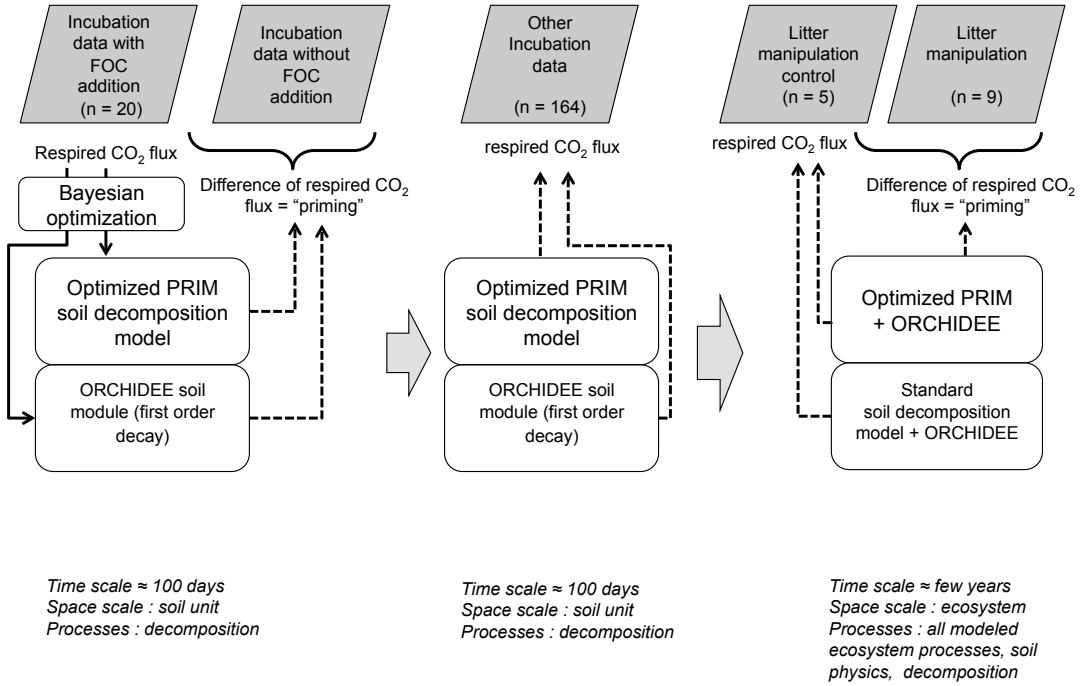
Incubation data with FOC addition (n = 20)
Incubation data without FOC addition
Respired CO_2 flux
Bayesian optimization
Difference of respired CO_2 flux = "priming"
Optimized PRIM soil decomposition model
ORCHIDEE soil module (first order decay)
Time scale ≈ 100 days
Space scale : soil unit
Processes : decomposition
Other Incubation data (n = 164)
respired CO_2 flux
Optimized PRIM soil decomposition model
ORCHIDEE soil module (first order decay)
Time scale ≈ 100 days
Space scale : soil unit
Processes : decomposition
Litter manipulation control (n = 5)
Litter manipulation (n = 9)
respired CO_2 flux
Difference of respired CO_2 flux = "priming"
Optimized PRIM + ORCHIDEE
Standard soil decomposition model + ORCHIDEE
Time scale ≈ few years
Space scale : ecosystem
Processes : all modeled ecosystem processes, soil physics, decomposition

Figure 1

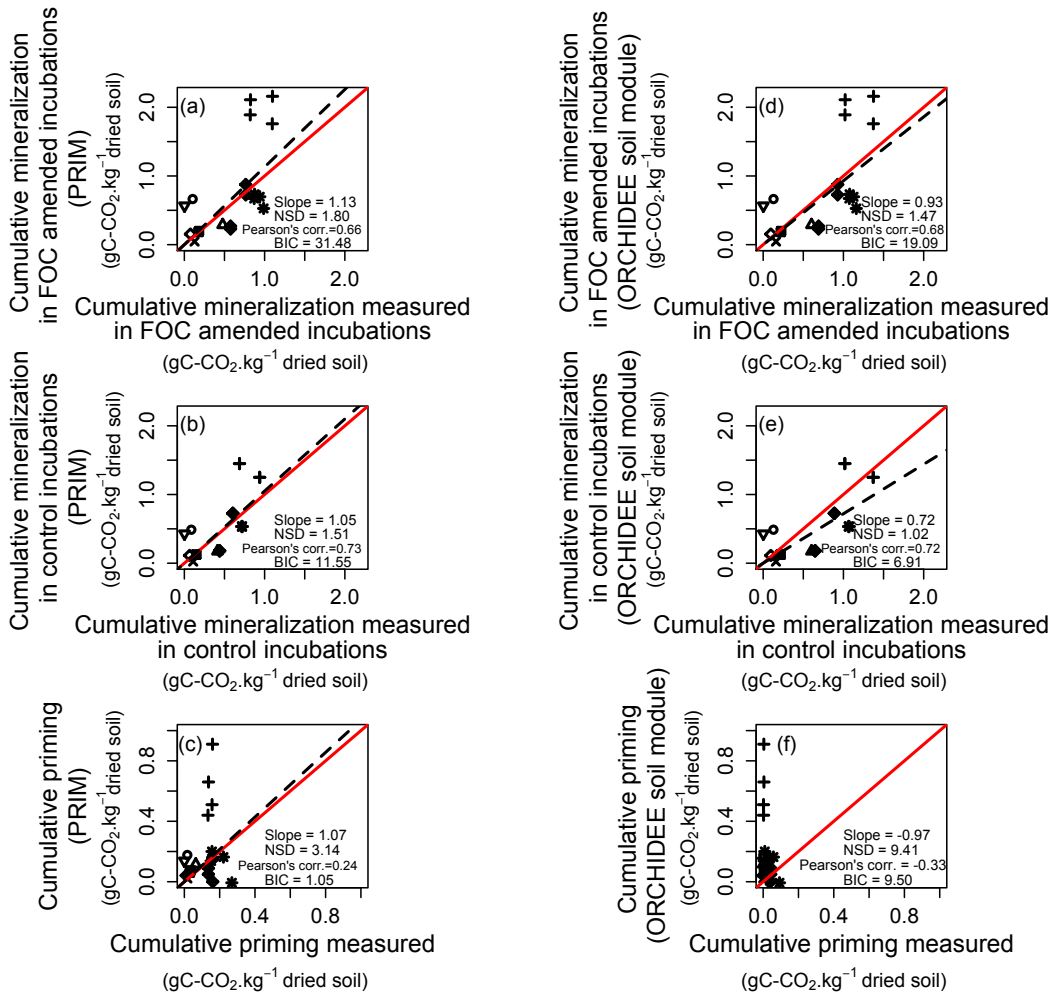
(a)
Slope = 1.13
NSD = 1.80
Pearson's corr.=0.66
BIC = 31.48
Cumulative mineralization in FOC amended incubations (PRIM) (gC-CO2.kg-1 dried soil)
Cumulative mineralization measured in FOC amended incubations (gC-CO2.kg-1 dried soil)
(b)
Slope = 1.05
NSD = 1.51
Pearson's corr.=0.73
BIC = 11.55
Cumulative mineralization in control incubations (PRIM) (gC-CO2.kg-1 dried soil)
Cumulative mineralization measured in control incubations (gC-CO2.kg-1 dried soil)
(c)
Slope = 1.07
NSD = 3.14
Pearson's corr.=0.24
BIC = 1.05
Cumulative priming (PRIM) (gC-CO2.kg-1 dried soil)
Cumulative priming measured (gC-CO2.kg-1 dried soil)
(d)
Slope = 0.93
NSD = 1.47
Pearson's corr.=0.68
BIC = 19.09
Cumulative mineralization in FOC amended incubations (ORCHIDEE soil module) (gC-CO2.kg-1 dried soil)
Cumulative mineralization measured in FOC amended incubations (gC-CO2.kg-1 dried soil)
(e)
Slope = 0.72
NSD = 1.02
Pearson's corr.=0.72
BIC = 6.91
Cumulative mineralization in control incubations (ORCHIDEE soil module) (gC-CO2.kg-1 dried soil)
Cumulative mineralization measured in control incubations (gC-CO2.kg-1 dried soil)
(f)
Slope = -0.97
NSD = 9.41
Pearson's corr. = -0.33
BIC = 9.50
Cumulative priming (ORCHIDEE soil module) (gC-CO2.kg-1 dried soil)
Cumulative priming measured (gC-CO2.kg-1 dried soil)

Figure 2

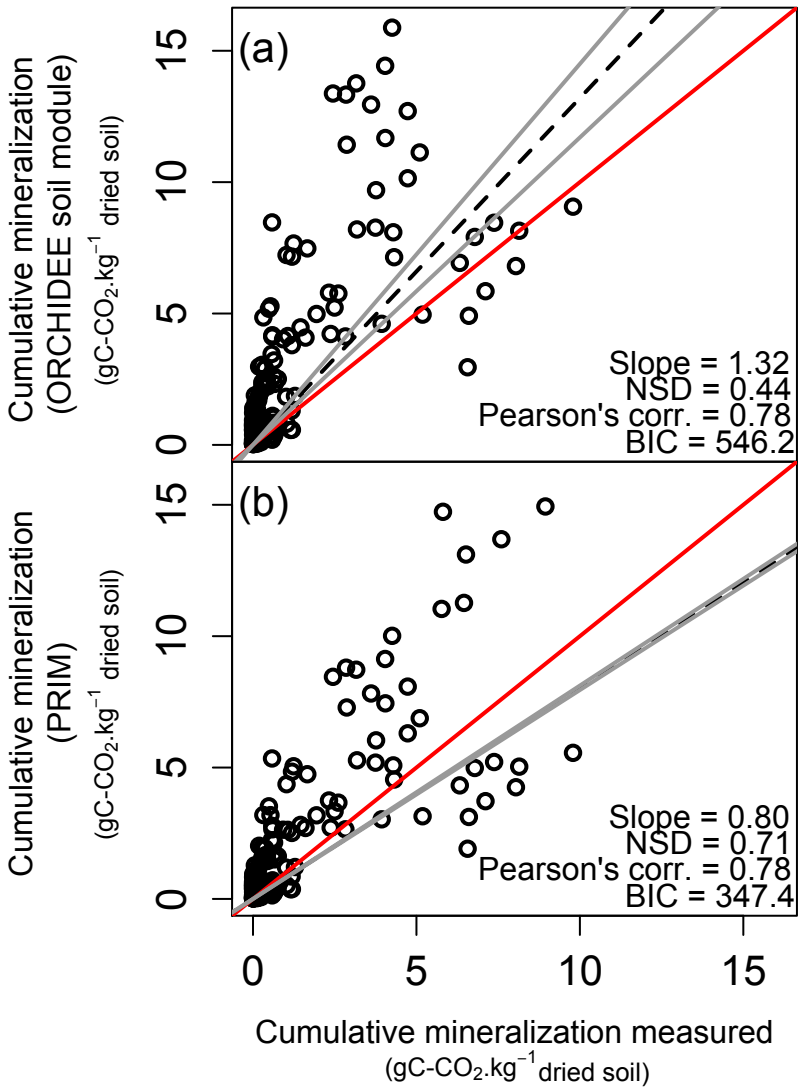
(a)
Slope = 1.32
NSD = 0.44
Pearson's corr. = 0.78
BIC = 546.2
(b)
Slope = 0.80
NSD = 0.71
Pearson's corr. = 0.78
BIC = 347.4
Cumulative mineralization (ORCHIDEE soil module)
(gC-CO2.kg-1 dried soil)
Cumulative mineralization (PRIM)
(gC-CO2.kg-1 dried soil)
Cumulative mineralization measured
(gC-CO2.kg-1 dried soil)
0
5
10
15

Figure 3

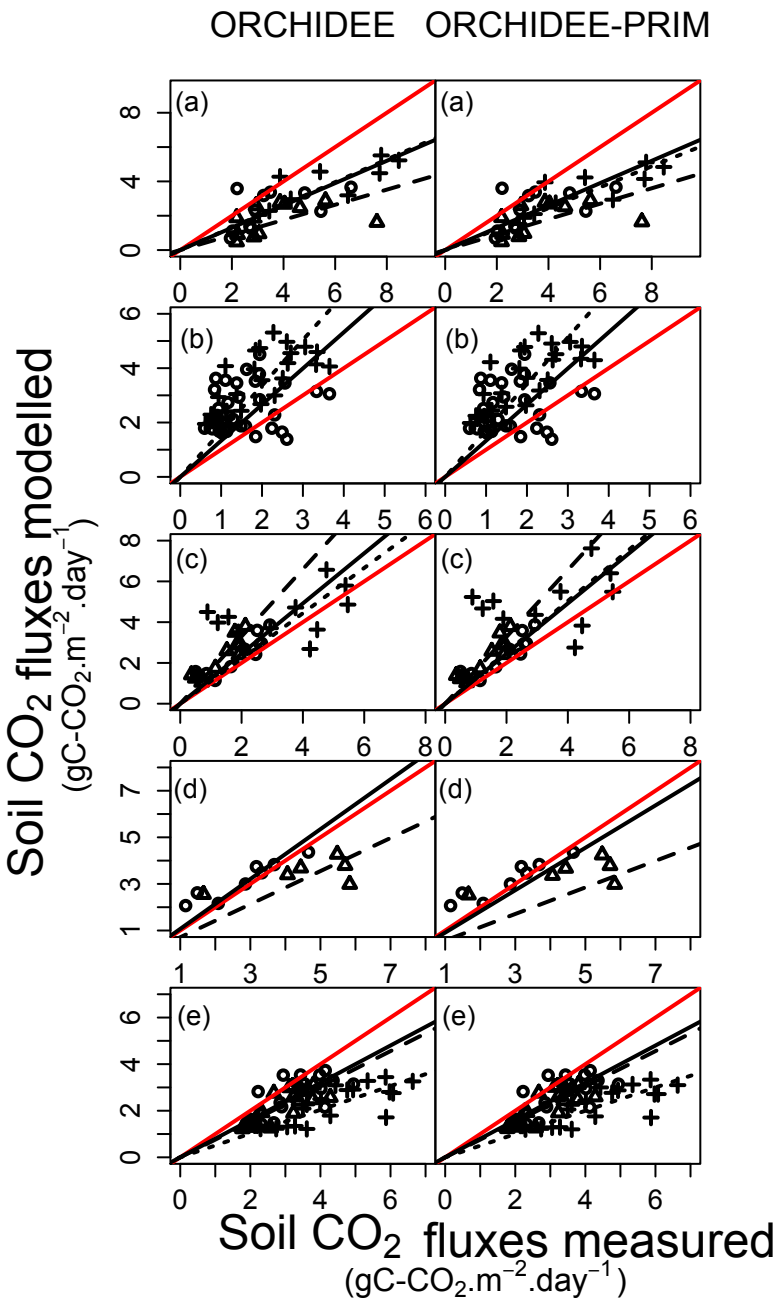
ORCHIDEE
ORCHIDEE-PRIM
(a)
(b)
(c)
(d)
(e)
Soil CO_2 fluxes modelled
($gC\text{-}CO_2.m^{-2}.day^{-1}$)
Soil CO_2 fluxes measured
($gC\text{-}CO_2.m^{-2}.day^{-1}$)

Figure 4

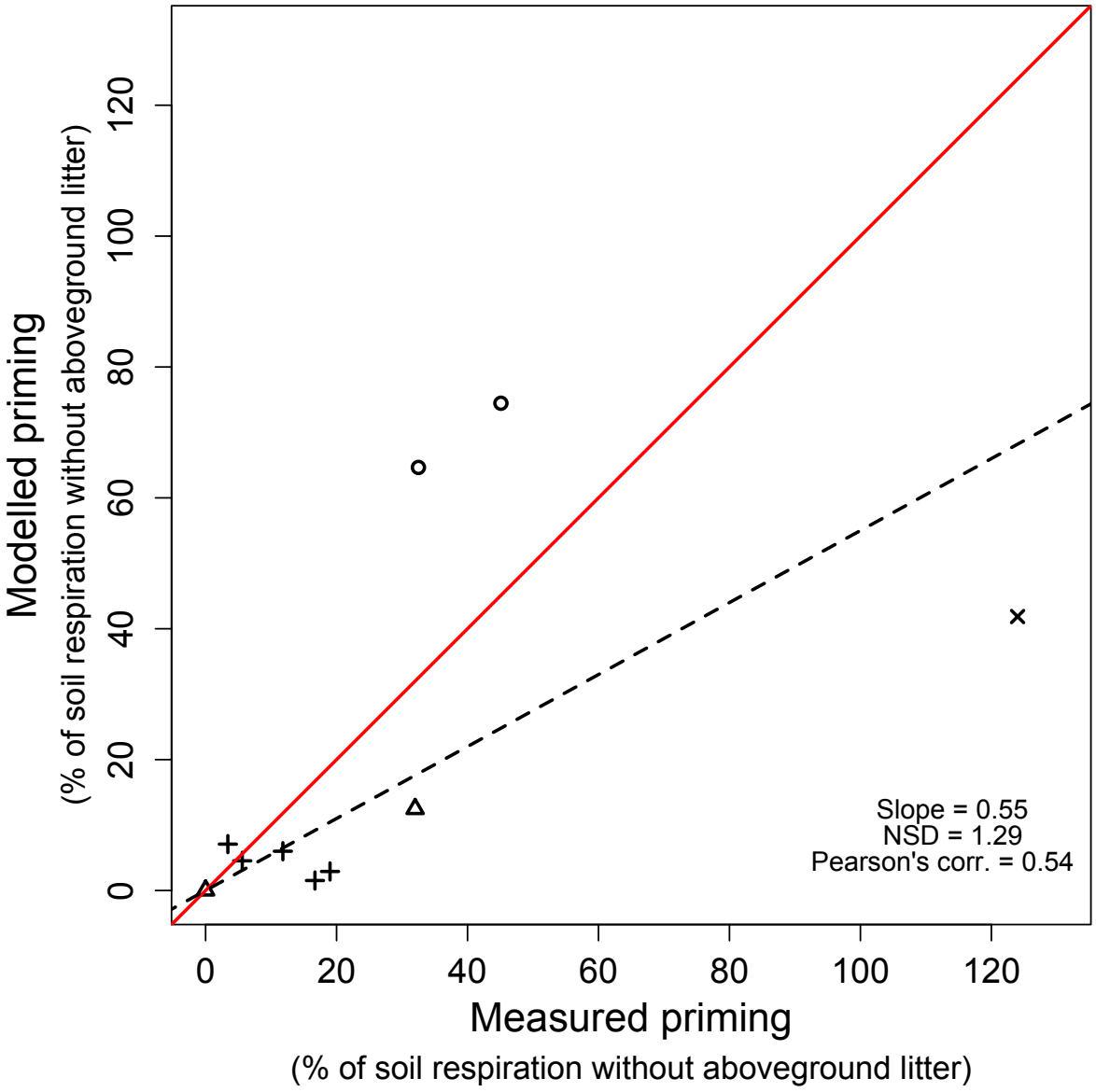
Modelled priming
(% of soil respiration without aboveground litter)
0
20
40
60
80
100
120
Measured priming
(% of soil respiration without aboveground litter)
Slope = 0.55
NSD = 1.29
Pearson's corr. = 0.54

Figure 5

Table 1: Description of the studies used to optimize the model parameters

Study	Incubations	Study site	FOC types	Amount of FOC amended (g C kg^{-1} dry soil)	Lignin:C ratio of FOC	C:N ratio of FOC	Soil clay content (%)	Temperature (K)	Moisture (% of Field Capacity)	Incubation length (days)	SOC content (g C kg^{-1} dry soil)
Bell et al., (2003)	Experience 1 averaged over the 4 soils tested	Ralston, Washington State, USA	Wheat straw	1.54	0.22*	128*	0.08	298.15	0.2	31	10.1
Blagodatskaya et al., (2007)	GL treatment	Ramon, Voronezh region, Russia	Glucose	0.0487	0	0	0.2*	295.15	0.6	14	50
Conde et al., (2005)	Soil A+ Maize	Former lake Texcoco in the valley of Mexico City (Mexico)	Maize	1	0.575	39.8	0.22	295.15	0.55	28	53
	Soil A + Glucose	former lake Texcoco in the valley of Mexico City (Mexico)	Glucose	1	0	0	0.22	295.15	0.55	28	53
	Soil B + Maize	former lake Texcoco in the valley of Mexico City (Mexico)	Maize	1	0.575	39.8	0.054	295.15	0.55	28	38.8
	Soil B + Glucose	former lake Texcoco in the valley of Mexico City (Mexico)	Glucose	1	0	0	0.054	295.15	0.55	28	38.8
De Nobili et al., (2001)	Experiment 1 with Soil 2	Rothamsted experimental station, UK	Cellulose	1	0	0	0.24	298.15	0.5	11	14.8
Falchini et al., (2003)	Average over the tree treatments	Grassland in Tuscany, Italy	Oxalix acid/ Glutamic acid/ Glucose	0.1815	0	0	0.14	298.15	0.5	7	16.6
Fontaine et al., (2004)	Only one incubation	Lamto experimental station, Ivory Coast	Cellulose	0.495	0	0	0.1	231.15	0.032	70	10.5

Guenet et al., (2010)	S1 without N amendment	La cage experimental station, France	Wheat Straw	1.5	0.22*	44	0.167	293.15	0.17	80	10.4
	S2 without N amendment	La cage experimental station, France	Wheat Straw	2.2	0.22*	44	0.167	293.15	0.17	80	10.4
	S3 without N amendment	La cage experimental station, France	Wheat Straw	3.2	0.22*	44	0.167	293.15	0.17	80	10.4
Guenet et al., (2012)	Arable soil with high cellulose input	Closeaux experimental station, France	Cellulose	5	0	0	0.167	293.15	0.19	209	19.9
	Arable soil with high wheat straw input	Closeaux experimental station, France	Wheat Straw	5	0.22*	98	0.167	293.15	0.19	209	19.9
	Arable soil with low cellulose input	Closeaux experimental station, France	Cellulose	0.5	0	0	0.167	293.15	0.19	209	19.9
	Arable soil with low wheat straw input	Closeaux experimental station, France	Wheat Straw	0.5	0.22*	98	0.167	293.15	0.19	209	19.9
Harmer & Marschner (2005)	Dystric cambisol (A horizon) + Alanine	Steigerwald, Baviaria, Germany	Alanine	13.3	0	3	0.14	293.15	0.6	26	44
	Dystric cambisol (A horizon)+ Fructose	Steigerwald, Baviaria, Germany	Fructose	13.3	0	0	0.14	293.15	0.6	26	44
	Haplic podzol (EA horizon) + Alanine	Fichtelgebirge, Baviaria, Germany	Alanine	13.3	0	3	0.104	293.15	0.6	26	32
	Haplic podzol (EA horizon) + Fructose	Fichtelgebirge, Baviaria, Germany	Fructose	13.3	0	0	0.104	293.15	0.6	26	32

*estimated values

Table 2: Model parameters summary for PRIM and the ORCHIDEE soil module

Model parameter	Meaning	SOC pools	Prior range	Posterior modes ± s.d. (prior modes) for PRIM	Posterior modes ± s.d. (prior modes) for the ORCHIDEE soil module
k_{SOC}	Turnover rate of SOM (d)	Active	10^{-3}-0.5	0.30 ±0.15 (0.31)	0.43 ±0.22 (0.43)
		Slow	0.5-5	1.12 ±0.01 (4.51)	0.50 ±0.09 (2.39)
		Passive	5-500	462.0 ± 233.8 (467.55)	40.17 ± 22.19 (44.39)
c	Influence of the FOM carbon pool in the SOM mineralization (priming parameter)	Active	2.10^{-4}-500	493.7 ± 246.8 (493.7)	NA
		Slow	2.10^{-4}-500	194.0 ± 97.0 (194.0)	NA
		Passive	2.10^{-4}-500	136.5 ± 68.3 (136.5)	NA

Table 3: Description of the studies used to evaluate the model

Study	Treatments performed	Ecosystems	Sites Names (Coordinates)	Treatment performed in:	CO_2 monitored between:	Soil clay content (%)	Soil silt content (%)	Soil sand content (%)
Boone et al., (1998)	No litter/Double litter/ Control	Deciduous forest	Harvard forest, Petersham, Massachusetts, USA (42°30' N,72°12' W)	January 1990	June 1994-June 1995	25*	30*	45*
Borken et al. (2002)	Compost amendment/ Control	Needleleaf forest	Solling, Norway (51°46'N, 9°34'E)	August 1997	September 1997-December 1999	3	23	74
Chemidlin-Prévost-Bouré et al., (2010)	No litter/Double litter/ Control	Deciduous forest	Barbeau National Forest, France (48°29'N,02°47'E)	March 2006	May 2006-March 2007	19.3	38.8	41.9
Subke et al., (2004)	Double litter/ Control	Needleleaf forest	Wetzstein, Thüringisches Schiefergebirge, Germany (50°30′N 11°10′E)	April 2002	April 2002(three weeks after treatment) - October 2002	70*	18*	12*
Sulzman et al., (2005)	No litter/Double litter/ Control	Needleleaf forest	H.J. Andrews Experimental Forest, Oregon, USA (44°15'N, 122°10'W)	January 1997	July 2001-December 2003	25*	30*	45*

*estimated values

Table 4: Model performances for each evaluation sites

		Boone et al., (1998)				**Borken et al., (2002)**			**Chemidlin-Prévost-Bouré et al., (2010)**				**Subke et al., (2004)**			**Sulzman et al., (2005)**			
		All data	No litter	Control	Double litter	All data	Compost	Control	All data	No litter	Control	Double litter	All data	No litter	Control	All data	No litter	Control	Double litter
ORCHIDEE	slope	0.56	0.45	0.65	0.66	0.65	1.68	1.33	0.55	1.65	1.23	1.11	0.48	0.72	1.07	0.60	0.77	0.80	0.51
	NSD	1.43	1.86	1.37	1.48	0.77	0.79	0.87	1.03	0.70	0.97	1.56	1.85	1.65	1.41	1.53	1.10	1.08	1.68
	BIC	103.4	57.9	49.3	53.8	116.8	84.0	74.9	73.1	39.4	29.1	52.2	45.9	38.3	24.3	109.9	39.9	42.4	78.3
ORCHIDEE-PRIM	slope	0.55	0.45	0.65	0.61	0.67	1.71	1.33	0.54	1.64	1.23	1.26	0.48	0.71	1.07	0.58	0.76	0.80	0.50
	NSD	1.53	1.85	1.37	1.59	0.77	0.79	0.86	0.86	0.70	0.97	1.30	1.86	1.66	1.41	1.55	1.10	1.09	1.76
	BIC	116.3	64.9	56.5	63.46	131.1	95.9	85. 0	96.1	46.2	36.3	65.1	54.3	44.6	30.5	124.1	48.2	51.3	88.1

Table 5: Correlation between optimized parameters

		Active	Slow	Passive	Active	Slow	Passive
k_{soc}	Active	1.00	0.00	0.00	0.00	0.00	0.00
	Slow	0.00	1.00	-0.02	0.00	0.00	0.00
	Passive	0.00	-0.02	1.00	0.00	0.00	0.00
c	Active	0.00	0.00	0.00	1.00	0.00	0.00
	Slow	0.00	0.00	0.00	0.00	1.00	0.00
	Passive	0.00	0.00	0.00	0.00	0.00	1.00