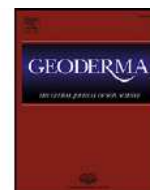




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Improved methodology to quantify the temperature sensitivity of the soil heterotrophic respiration in croplands



Emilie Delogu^{a,*}, Valérie Le Dantec^a, Patrick Mordelet^a, Eric Ceschia^a, Marc Aubinet^b,
Pauline Buysse^b, Elizabeth Pattey^c

^a Centre d'Etudes Spatiales de la Biosphère, CESBIO, Université de Toulouse, CNRS/UPS/CNES/IRD, 18 Av. Édouard Belin, 31401 Toulouse, France

^b Unit of Biosystem Physics, Gembloux Agro Bio-Tech (GxABT), University of Liège, Belgium

^c Agriculture and Agri-Food Canada, Ottawa Research and Development Centre, Ottawa, ON, Canada

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ABSTRACT

Soil heterotrophic respiration (R_H) is usually modeled using simple temperature dependence equations where the temperature sensitivity of R_H could vary for different soils and climate conditions. The temperature sensitivity is expressed as a function of the base rate of heterotrophic respiration ($R_H - 0$) and the respiration change rate over a 10 °C temperature shift (Q_{10}). A methodology was developed to better quantify these two parameters, and was validated using seven contrasting year-site soil respiration datasets collected in wheat fields. The data were acquired using soil respiration chambers and eddy flux towers in three mid-latitude European sites and one North American site. The first step consisted in parameterizing and initializing a semi-mechanistic process-based model then validating the prediction performance using 2/3 of the datasets. The coefficient of determinations between the predictions and the observations of daily soil respiration (R_s) was 0.71 and was 0.73 for its heterotrophic component (R_H). The second step consisted in using the daily semi-mechanistic model predictions of R_H for each growing season and site to calibrate a simple empirical model describing R_H response to soil temperature and water content. It was shown with the contrasting years-sites that coherent results were only obtained when a common average Q_{10} value was determined prior to fit the base rate of heterotrophic respiration coefficient. Using a common Q_{10} value of 2.2 provided more stable $R_H - 0$ for each site over time. It reflected the strong relationship between the $R_H - 0$ and the slow decomposing C in the first 30-cm soil layer. The simple empirical model, which was validated using 1/3 of the data, explained between 42% and 92% of the variability of R_H over the different sites.

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1. Introduction

The soil CO₂ efflux (R_S) is a major component of terrestrial ecosystems CO₂ emissions (Ryan and Law, 2005). Because crops cover about one third of the European land surface (FAOSTAT, 2010), the exchanges between crops and atmosphere are a major driver of annual atmospheric CO₂ fluctuations. Accurate understanding of the mechanisms that govern R_S response to climate change is essential for forecasting future changes in the terrestrial carbon balance (Buchmann, 2000; Ryan and Law, 2005). Soil respiration is the result of the production of CO₂ by root respiration including the rhizosphere (autotrophic respiration, R_A) and by microbial activity related to the decomposition of soil organic matter (heterotrophic respiration, R_H). The mean annual contribution of R_H to R_S was estimated from 45% to 70% from long-term experiments over different crops (Moureaux et al., 2006; Moyano et al., 2007; Shi et al., 2006; Zhang et al., 2013). These estimates highlight the

importance of understanding the factors controlling the decomposition processes and the associated CO₂ production. Studying R_H is essential for crops, as agricultural soils have been reported to lose large amount of carbon (Janssens et al., 2003; Smith, 2004), which results in increasing atmospheric CO₂ concentration. With regard to climate change and to increasing temperature, CO₂ emissions due to heterotrophic respiration may become more important (Davidson and Janssens, 2006). Moreover, the recently introduced carbon sequestration program for agriculture, named "4 per 1000", which aims to adapt agricultural practices with the goal of storing carbon more efficiently in the soil justify the necessity to better quantify soil fluxes components and to better understand their response to climate variations and to agricultural management.

Studies on the contribution of heterotrophic source are difficult to carry out because of the uncertainty involved in separating experimentally root respiration fluxes (R_{Ab} , belowground autotrophic respiration) from R_H in the field (Mäkiranta et al., 2008; Moyano et al., 2007; Subke et al., 2006). Thus most of previous studies used models to estimate the heterotrophic contribution to R_S . Most of the models used for simulating

* Corresponding author.

E-mail address: emilie.delogu@gmail.com (E. Delogu).

soil organic matter (SOM) decomposition partition SOM into several pools according to their potential decomposition rates, reflecting the mean residence time of carbon compounds in the soil profile. Kinetics of SOM decomposition is calculated as a combination of SOM quality (i.e., inherent stability of carbon compounds) and the environmental constraints (i.e., soil texture, soil moisture and temperature). The two well-known semi-mechanistic models CENTURY (Parton et al., 1987, 1988) and ROTH-C (Coleman and Jenkinson, 1995) use at least five pools. They include two compartments of plant material in the litter layer and three pools into the mineral soil (active, slow, and passive) with residence time varying from a few months to several hundreds of years. Previous studies have shown that these models successfully simulate the long-term dynamics of carbon stocks in soils of different ecosystems and also in the case of land use change (Kelly et al., 1997; Smith et al., 1997). However, these models remain difficult to implement, especially when developed for the daily time scale (Parton et al., 1998) as they require to document a lot of input parameters and to define initial conditions. Modeling soil respiration at the daily time scale is essential to understand the impact of climate variations and management practices on soil CO₂ fluxes.

The common approach to predict soil CO₂ fluxes at the daily time scale consists in expressing soil respiration flux as an exponential function of soil temperature. The temperature sensitivity is calculated using a Q₁₀ temperature coefficient which represents the respiration change rate over a 10 °C temperature shift. Lloyd and Taylor (1994) concluded that the Q₁₀ model is not well-suited for fitting soil CO₂ fluxes over a wide range of temperature. They suggested the use of an Arrhenius-type equation because it takes into account the varying temperature sensitivity of soil respiration. Their conclusion was made using measurements from various ecosystems. However, Q₁₀ is usually determined at local scale and requires dataset from a specific experimentation or field campaign. Values found in literature vary widely among different ecosystems (Raich and Schlesinger, 1992). This variability is mainly associated to a difference in the proportion of resistant against easily degradable (labile) carbon pools. Moreover, small but significant ranges of Q₁₀ variation are reported even for the same type of land use: for wheat crops, the Q₁₀ coefficient varies from 1.9 to 2.5 (Moyano et al., 2007; Shi et al., 2006; Suleau et al., 2011). As the complex organic substrate is assumed to be similar to the plant litter, these differences among sites could be attributed to either an effect of the soil texture in the protection against the decomposition (clay content), or to an effect of soil water content and/or soil temperature range due to the climate conditions. Seasonal variations of Q₁₀ associated with the soil temperature range were previously reported and discussed by Del Grosso et al. (2005), Janssens and Pilegaard (2003), Qi and Xu (2001), and Tjoelker et al. (2001). However, it remains unclear whether the Q₁₀ variability either reflects actual difference in the temperature sensitivity of the SOM decomposition or is a mathematical effect caused by adjusting the coefficients of the equation. The determination of the statistical parameters is often performed simultaneously for both Q₁₀ and the base rate of heterotrophic respiration (R_{H-0} defined at 0 °C) which makes the coefficients interpretation difficult. This model adjustment approach does not follow the basic assumptions found in most semi-mechanistic SOM models, where sensitivity to temperature is considered constant and identical for all carbon pools and independent of ecosystem types and climate zones.

Moreover, the conceptual difference between the temperature sensitivity of soil CO₂ efflux (i.e., the efflux Q₁₀) and the temperature sensitivity of soil CO₂ production (i.e., the production Q₁₀) needs to be explored. As the production sensitivity of R_H corresponds to the absolute change in the decomposition rates (in SOM models) with respect to a change in soil temperature, several environmental constraints on respiration could modulate the production temperature sensitivity resulting in an efflux temperature sensitivity corresponding to the observed temperature response of soil CO₂ efflux (Davidson et al., 2006).

In this study, we compared the daily outputs of R_S and its heterotrophic component from a semi-mechanistic model in wheat cultivated land pertaining to different soil and climate conditions to several datasets acquired on wheat in four contrasting mid-latitude regions (issued from three European sites and one North American site). Following their validation, the R_H outputs of the semi-mechanistic SOM model were used as continuous datasets to calibrate the coefficients of a simple model combining temperature and water content sensitivity by either (1) allowing the two coefficients (i.e., R_{H-0} and Q₁₀) to vary or (2) assuming a constant temperature sensitivity. Our objectives were (1) to quantify the change of the base rate of heterotrophic respiration (R_{H-0}) and the respiration change rate over a 10 °C temperature shift (Q₁₀) in response to temperature and water content and to incorporate them in a simple equation describing the heterotrophic respiration (R_H) and (2) to verify whether the temperature sensitivity of R_H varies over different soils and climatic conditions. We also verified the magnitude of the difference between CO₂ production and CO₂ surface efflux temperature sensitivities and we investigated the change in R_{H-0} rates between sites according to the quantity and/or quality of soil organic carbon.

2. Material and methods

2.1. Semi-mechanistic modeling approach

In the semi-mechanistic SOM model, R_S was calculated as the sum of R_H and R_{Ab} (belowground autotrophic respiration).

2.1.1. Heterotrophic source

The soil organic carbon sub-model (SOC) used to simulate the dynamic of heterotrophic respiration is based on the soil organic matter (SOM) sub-model of CENTURY (Parton et al., 1987). The original version developed by Parton et al. (1987) has been successfully adapted at a daily time step (i.e., DAYCENT) over different ecosystems (Del Grosso et al., 2005; Epron et al., 2001).

Soil organic carbon is divided into three major components including active, slow and passive soil carbon. The “active” pool includes live soil microbes plus microbial products; the “slow” one includes mainly resistant plant material (lignin-derived material). The passive material is very resistant to decomposition, i.e., physically and chemically stabilized SOM. The model also includes a surface microbial pool, which is associated with decomposing surface litter (mainly leaf litter). Carbon flows between these pools are controlled by decomposition rate (Table 1) and microbial respiration loss parameters (Fig. 1), both of which are a function of soil texture, soil temperature and soil water content.

In this soil model, all the fractions are located in the soil vertical profile (Fig. 1). The soil is divided into four layers according to the vertical distribution of carbon content and soil texture, and crop management (i.e., depth of plowing): a surface layer, a superficial soil layer (from surface to 15 cm depth) and two deeper soil layers (from 15 to 30 cm and from 30 to 45 cm). No carbon migration is assumed between the superficial and the deep soil layers. The “slow

Table 1
Maximum decomposition rate (K, day⁻¹) of the soil organic matter for each C pools of the semi-mechanistic model (Parton et al., 1988).

Pool	K
Soil metabolic fraction	5.07 × 10 ⁻²
Surface metabolic fraction	4.05 × 10 ⁻²
Soil active C	2.00 × 10 ⁻²
Surface active C	1.64 × 10 ⁻²
Soil structural fraction	1.34 × 10 ⁻²
Surface structural fraction	1.07 × 10 ⁻²
Slow C	5.48 × 10 ⁻⁴
Passive C	1.23 × 10 ⁻⁵

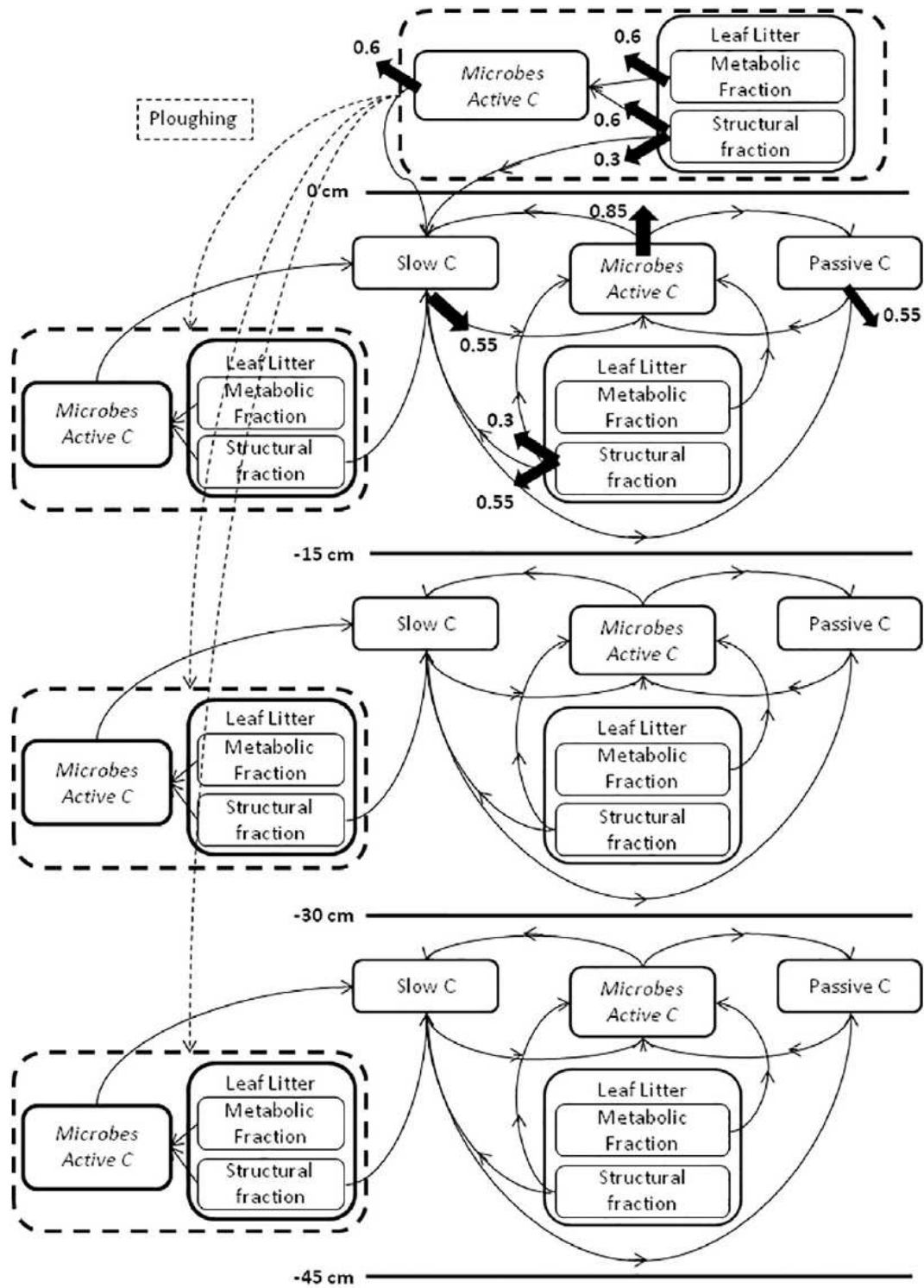


Fig. 1. Schematic diagram representing the distribution of carbon fractions in the semi-mechanistic model. The soil profile is divided into four layers: a surface layer, a superficial soil layer (0–15 cm) and two deeper soil layers (15–30 cm and 30–45 cm). Additional compartments considered for taking into account the burial of crop litter after plowing, are surrounded by dotted lines. Partitioning coefficients of carbon flow between sinks are indicated in bold black close to each large black arrow.

pool” of the superficial layer, however, is supplied with the organic carbon coming from both the structural fraction and the active SOC of the surface layer. Three compartments, i.e., structural fraction, metabolic fraction and microbial pool related to leaf litter were added to each soil layer to account for the burial of the crop litter after plowing (Fig. 1). The impact of manure fertilization was not accounted for in the model.

For the different pools (i), carbon decomposition rate (dC/dt), i.e., the output flow, is estimated using a first-order kinetic equation, as follows:

$$\frac{dC}{dt_{i,j}} = K_{i,j} \times F_{i,j} \times A_{w,j} \times A_{T,j} \times C_{i,j}$$

where j is the soil layer where the considered carbon pool i is located. K is the maximum decomposition rate, C the carbon content. F depends on soil textural properties of the considered j layer for the soil active and slow carbon pools; it depends on lignin content (LIGN) of leaves or fine roots for the litter structural material:

$$F_{(j)} = e^{(-3 \times \text{LIGN})}$$

F value is 1 for the other carbon pools.

The potential decomposition rate is proportional to constraint functions of soil moisture (A_w) and soil temperature (A_T), varying between 0 (maximal stress) to 1 (optimum conditions for C decomposition). The original equations were adapted to cultivated soils in temperate climate area. Based on previous studies (Izaurre et al., 2006; La Scala et al., 2003; Pietikäinen et al., 2005), the temperature optimum was readjusted to a more suitable range for the studied sites, having $A_T = 1$ for a soil temperature (T_s) range of 20–30 °C. Then A_T varied with soil temperature following a bell-shape relationship. The Q_{10} value was set to 2.3 at about 15 °C (Hartley et al., 2007; Kutsch and Kappen, 1997; Suleau et al., 2011), on the part of the curve that can be fitted with an exponential function ($T_s < 20$ °C).

$$A_{T(j)} = \left(\frac{45 - T_{s(j)}}{45 - 20} \right)^{2.5} \times e^{1.25 \times \left(1 - \left(\frac{45 - T_{s(j)}}{45 - 20} \right)^{2.5} \right)} \quad (1)$$

The effect of soil moisture on soil carbon decomposition (A_w) was modified according to Bréchet et al. (2017), to take into account the effect of soil saturation which occurred after heavy rainfall in the spring.

$$\text{When } \theta_{s(j)} < \theta_{fc(j)} \quad A_{w(j)} = \frac{1}{1 + 30 \times e^{-8.5 \times \frac{\theta_{s(j)} - \theta_{\min(j)}}{\theta_{fc(j)} - \theta_{\min(j)}}}} \quad (2)$$

$$\text{When } \theta_{s(j)} > \theta_{fc(j)} \quad A_w = -7.84 \times \left(\frac{\theta_{s(j)} - \theta_{\min(j)}}{\theta_{fc(j)} - \theta_{\min(j)}} \right)^2 + 15.84 \times \frac{\theta_{s(j)} - \theta_{\min(j)}}{\theta_{fc(j)} - \theta_{\min(j)}} - 7 \quad (3)$$

where $\theta_{fc(j)}$ is the value of soil water content (SWC) at field capacity, $\theta_{\min(j)}$ is the minimum value of SWC and $\theta_{s(j)}$ is the daily value of SWC of the considered layer j .

In this model, all C decomposition flows among pools are assumed to be associated with microbial activity and thus microbial respiration occurs for each flow. Depending on the pools, the fraction of CO_2 losses ranged from 30 to 85% of dC/dt (Parton et al., 1988, Fig. 1). R_H is calculated as the sum of all these sources of CO_2 fluxes.

Detailed descriptions of this SOC model could be found in Dufrêne et al. (2005) and Epron et al. (1999) and original equations of the lignin and texture effects (F) are given in Parton et al. (1988).

The original version of CENTURY was adapted for cultivated soils and agricultural management practices were included. In the soil model, all fractions were present in the soil vertical profile, which was divided into the following four layers: a surface layer, a superficial soil layer (from surface to 15 cm depth) and two deeper soil layers (from 15 to 30 cm and from 30 cm to 45 cm). The migration of carbon between the soil layers was not accounted for. Three compartments, i.e., structural fraction, metabolic fraction and microbial pool related to leaf litter were added to each soil layer to account for the burial of the crop litter after plowing (Fig. 1).

2.1.2. Root respiration

Daily R_{Ab} is calculated as the sum of growth respiration (R_{growth}) and maintenance respiration (R_{maint}), of roots.

The growth component depends on both root biomass growth (ΔBr) and construction cost of roots (Co_{cons}). The construction cost is equal to

1.3 g C g^{-1} C as suggested by Penning de Vries (1975a, 1975b) and Penning de Vries et al. (1974), based on the biochemical composition of the organ.

$$R_{\text{growth}} = (\text{Co}_{\text{cons}} - 1) \times \Delta Br \quad (4)$$

Maintenance respiration is calculated from a respiratory cost (Co_{resp}) according to protein turnover and assuming an exponential relationship to account for soil temperature dependence (Ryan, 1991), with $Q_{10} = 3$ (Bingham and Wu, 2011).

$$R_{\text{maint}} = \text{Co}_{\text{resp}} \times Q_{10}^{(T_s - T_{\text{ref}})/10} \quad (5)$$

Co_{resp} depends on the nitrogen content of the root biomass (Table 2) and it represents the rate of maintenance of the root respiration at a reference temperature ($T_{\text{ref}} = 10$ °C).

$$\text{Co}_{\text{resp}} = Br \times R_{\text{MN}} \times N_r \quad (6)$$

where Br is the dry biomass of the fine roots (g), N_r is the root nitrogen content (g N g^{-1} dry root biomass) and R_{MN} is the respiration rate (g N $^{-1}$), equal to 1.06 mmol CO_2 g^{-1} N h^{-1} (Ryan, 1991).

Simulation of root phenology, essential for the calculation of R_{growth} and R_{maint} , depends on the seasonal dynamics of the root to shoot ratio (R/S) (Baret et al., 1992; Barraclough and Leigh, 1984; Bolinder et al., 1997; Kätterer et al., 1993; Siddique et al., 1990). The R/S ratio dynamics varies with the growing degree-day using two different equations according to winter or spring wheat. Then R/S ratio varies from 0.7 at the beginning of the growing season to 0.1 at the stage of maximal development for spring wheat and between 1.2 and 0.1 for winter wheat.

The R_{Ab} module had the same three layers of soil as the R_H module. The vertical distribution of the root biomass was assumed to be constant through the whole season, with 60% located within the first 15 cm, 25% between 15 and 30 cm and 15% between 30 and 45 cm for wheat (Bolinder et al., 1997; Germida and Walley, 1996). For each layer, daily root mortality was equal to 3% of the predicted root biomass (Steingrobe et al., 2001). The plant residues made of dying roots and crop residues at harvest supplied both corresponding metabolic and structural pools of the leaf litter and root litter in the heterotrophic module (Fig. 1).

2.2. Experimental sites description

The four agricultural sites are located in mid-latitude (temperate) zone: Lamasquère and Auradé in Midi-Pyrénées region in France, Loncée in the Namur province in Belgium, and Ottawa in Ontario province, in Canada. All the soil types are luvisols (FAO classification), with different clay content, carbon content and management (Table 3).

2.3. Field measurements

2.3.1. Soil respiration flux chambers

Closed dynamic chambers coupled to an infrared $\text{CO}_2/\text{H}_2\text{O}$ analyzer were used to measure soil CO_2 fluxes at plot scale. Depending on sites, different types of automated or manual systems were installed (Table 4).

Four home-made automated closed dynamic chambers (20-cm diameter, 15-cm height) were used at Loncée (Suleau et al., 2011) in 2007. Soil respiration flux measurements from an automated chamber LI-8100A (LICOR Lincoln, Nebraska) were collected at Ottawa in 2007 and 2011 in addition to manual survey chambers. The soil respiration flux was measured every 30 min in Loncée and Ottawa.

In France, soil respiration data were acquired with manual closed dynamic chambers (SRC1 PP systems) in 2007 and 2009 at Lamasquère and in 2006 and 2008 at Auradé.

Table 2

Semi-mechanistic model parameters values and sources. Same values were used for spring wheat and winter wheat. DM is the dry matter.

Parameter		Unit	Value	Source	
Plant biochemistry					
Leaf lignin content		% DM	5	Laboratory analyze	
Leaf cellulose content		% DM	33	Van Soest method	
Leaf hemicelluloses content		% DM	31		
Root lignin content		% DM	17		
Root cellulose content		% DM	30		
Root hemicelluloses content		% DM	29		
Root N content (growing period)		g N g DM ⁻¹	0.018	Measurements with an elementary analyzer	
Root N content (maximal development stage)		g N g DM ⁻¹	0.09		
Root N content (senescence period)		g N g DM ⁻¹	0.07		
Soil					
Quantity of carbon [\pm standard deviation]	Lamothe	0 cm to –15 cm	2.0 kg \pm 0.1 kg	Granulometric analyses 5 fractions without decarbonation	
		–15 cm to –30 cm	1.0 kg \pm 0.0 kg		
		–30 cm to –45 cm	1.1 kg \pm 0.1 kg		
	Auradé	0 cm to –15 cm	1.8 kg \pm 0.1 kg		
		–15 cm to –30 cm	1.8 kg \pm 0.1 kg		
	Lonzée	–30 cm to –45 cm	0.6 kg \pm 0.2 kg		
		0 cm to –15 cm	2.3 kg \pm 0.2 kg		
		–15 cm to –30 cm	2.3 kg \pm 0.2 kg		
	Ottawa	–30 cm to –45 cm	0.9 kg \pm 0.1 kg		
		0 cm to –15 cm	3.9 kg \pm 0.2 kg		
		–15 cm to –30 cm	3.9 kg \pm 0.2 kg		
	–30 cm to –45 cm	2.8 kg \pm 0.1 kg			
	Belowground Autotrophic Respiration (R_{Ab})				
	Construction coefficient		mol CO ₂ g C ⁻¹ h ⁻¹	10.6 \times 10 ⁻⁴	Ryan (1991)
	Maintenance coefficient		g C g C ⁻¹	1.3	Agren and Axelsson (1980), Bréchet (2009)
Root Maintenance Q_{10}			3	Bingham and Wu (2011)	
Optimum temperature for microbial activity		°C	10		
Roots mortality rate		%	3	Steingrobe et al. (2001)	
Heterotrophic Respiration (R_H)					
Decomposition Q_{10}			2.3	Hartley et al. (2007), Kutsch and Kappen (1997), Suleau et al., (2011)	
Optimum temperature for microbial activity		°C	between 20 and 30	La Scala et al. (2003), Pietikäinen et al. (2005), Izaurralde et al. (2006)	
Initial content of active pool		% of total SOC	3	Parton et al. (1988)	
Initial content of slow pool		% of total SOC	44	Parton et al. (1988)	
Initial content of passive pool		% of total SOC	53	Parton et al. (1988)	

At each site, measurements were performed in the field during the growing seasons (winter wheat or spring wheat), providing total soil respiration fluxes ($R_s = R_{Ab} + R_H$) and during bare fallow periods or in root exclusion zones (REZ), providing heterotrophic respiration fluxes (R_H) (Table 4). On each site, the daily mean of R_s or R_H were estimated from the average of the whole measurements.

2.3.2. Eddy flux towers

Half-hourly CO₂ fluxes were measured continuously at the field scale using the eddy covariance technique during bare soil periods in Lamasquère, Auradé (Béziat et al., 2009), Lonzée (Moureaux et al., 2006), and Ottawa (Pattey et al., 2006). The measured CO₂ fluxes

were filtered and aggregated to quantify daily Net Ecosystem Exchange (NEE), which was assumed to be representative of the heterotrophic soil respiration efflux at field scale after harvest and prior to crop emergence, in absence of significant weed regrowth. In Lamasquère, NEE fluxes could not be used after harvest because of plant regrowth observed during July and August 2007. The field-scale NEE data were used to complete the period of observation to validate the soil respiration models and to verify the consistency of the models performance from small to large scale (i.e., m² to ha).

Moreover, the continuous 30-min CO₂ effluxes were also measured in the field during the growing season using the eddy covariance technique, to calculate the Total Ecosystem Respiration (TER). The eddy

Table 3

Experimental sites location, soil and climate conditions, and management practices.

	Lamasquère	Auradé	Lonzée	Ottawa
Latitude	43°49'N	43°54'N	50°33'N	45°18'N
Longitude	01°23'E	01°10'E	4°44'E	75°45'W
Mean annual temperature [°C]	13.1	13.3	9.1	6.3
Annual precipitation [mm]	615	671	771	914
Soil type	Gleyic luvisol	Luvisol	Luvisol	Luvisol
Soil texture [% silt; % clay]	34; 54	47; 32	75; 20	49; 31
Organic C in [kg m ⁻² \pm standard deviation] (0–15 cm depth)	2.0 \pm 0.1	1.8 \pm 0.1	2.3 \pm 0.2	3.9 \pm 0.2
Soil moisture at field capacity (θ_{fc}) %	40	35	31	34
Soil moisture at wilting point (θ_{min}) %	27	15	10	11
Crop rotation ^a	WW/M	WW/SF/WW/R	WW/P/WW/SuB	SW/M/SW/C
Tillage ^b	CT or NIT	CT or NIT	NIT	CT
Fertilization	Organic/mineral	Mineral	Organic/mineral	Mineral
References	(Béziat et al., 2009)	(Béziat et al., 2009)	(Moureaux et al., 2006)	(Jégo et al., 2010)

^a WW, winter wheat, M, maize, SF, Sunflower, R, rapeseed, SW, spring wheat, P, potatoes, SuB, SugarBeet, C canola.

^b CT, conventional tillage, NIT, noninversion tillage.

Table 4

Description of the measuring systems used at each site, sampling frequency and number of measurement days of soil CO₂ fluxes to quantify R_H, either on bare soil or on root exclusion zones, and R_S on cultivated soil at each experimental site.

	Lamasquère	Auradé	Lonzée	Ottawa	
R_H					
Bare soil					
Measurement technique	Eddy covariance	Eddy covariance	–	1 automated chamber	Eddy covariance
Measurement time step	30 min	30 min	–	30 min	30 min
Number of measurement days	38	12	–	56	211
Root exclusion zones					
Measurement technique	1 manual chamber	1 manual chamber	4 automated chambers	–	–
Measurement time step	1/week	1/week	30 min	–	–
Number of measurement days	32	12	104	–	–
R_S (R_H + R_{Ab})					
Measurement technique	1 manual chamber	1 manual chamber	4 automated chambers	1 automated chamber	2 manual chambers
Measurement time step	1/week	1/week	30 min	30 min	1/week
Number of measurement days	34	12	112	141	23

covariance flux data were corrected and filtered to remove the data associated with low turbulence periods and lack of stationarity (Béziat et al., 2009; Moureaux et al., 2006; Pattey et al., 2006). TER was parameterized as a function of temperature adjusted on night-time measurements. This equation was then applied to get an estimation of total ecosystem respiration during daytime at half-hourly time step. Night-time measurements were added to the diurnal estimates to calculate daily TER.

2.3.3. Auxiliary measurements

Soil temperature and soil moisture were both continuously monitored at 5 cm, 10 cm, 20 cm and 50 cm depth in Ottawa and Lonzée, at 5 cm, 10 cm, 30 cm et 60 cm depth in Auradé and 5 cm, 10 cm, 30 cm and 100 cm in Lamasquère. Measurements were recorded at the meteorological station and close to the automated chambers in Lonzée and Ottawa. Daily averages were used as input variables in the model.

During the growing season, shoot dry biomass of wheat was measured every two to three weeks. A linear interpolation between field campaigns was used to get an estimation of shoot biomass for each day. This value was used to calculate the daily root dry biomass using the corresponding R/S ratio.

2.4. Modeling approach: computation, validation and analysis

2.4.1. Semi-mechanistic model parameterization and initialization

The input variables of the model are the soil temperature and the soil water content measured in the three layers (from surface to 15 cm depth, from 15 to 30 cm and from 30 to 45 cm). In addition to these environmental variables, shoot biomass measurements were carried out to estimate daily root biomass using the root to shoot equations.

Numerous input parameters, listed as follows, are required to initialize the semi-mechanistic model:

- Biochemical composition of plants and cultural residues
- Soil texture (Table 3)
- Soil hydrologic properties (θ_{fc} and θ_{min} , Table 3)
- The construction and maintenance costs of roots
- The temperature sensibility of the different modeled processes
- The quantity of carbon contained in the soil profile and its distribution among the different pools

No calibration was performed to adjust the various parameters. The values were selected either from literature or from laboratory measurements (Table 2).

The initial distribution of SOC among the different pools in each layer evolves over time according to the different carbon inputs, their quality

and quantity and their relative decomposition rates. Management practices (residues plowing) also alters the carbon allocation among pools.

In a first step, the SOC distribution among the different pools is defined according to the first version of CENTURY (Parton et al., 1987, 1988) for each layers:

- Active Pool: 3% of the layer SOC
- Slow Pool: 44% of the layer SOC
- Passive Pool: 53% of the layer SOC

In a second step, the actual initial values of soil carbon content in each pool of the R_H model at each site were estimated under the equilibrium-state assumption. The 'spin-up-run' method was applied. It consisted to use the "R_H-R_{Ab}" coupled model to simulate temporal dynamics of SOC over 20 years using the same annual dataset in term of crop management and climate, repeated 20 times to obtain "stable" SOC partition of each pool, which were used as initial conditions for the simulations (Table 5).

2.4.2. Semi-mechanistic model validation

After parameterizing and initializing all carbon pools at each site (Table 5), outputs of R_H and R_S of the coupled "R_H-R_{Ab}" model were

Table 5

soil organic C content (g C m⁻²) in the three soil layers for each pool used in the semi-mechanistic model resulting from the 20 years simulation using the same forcing measured generic one-year climatic dataset for each site. All metabolic fractions were initially set to zero because of their high decomposition rate (i.e., maximum residence time in the soil of 6 months).

Description	Lamasquère	Auradé	Lonzée	Ottawa
0–15 cm layer				
Structural fraction of root litter	38	55	59	45
Metabolic fraction of root litter	0	0	0	0
Microbial biomass	54	51	18	60
Slow pool	784	887	969	1277
Passive pool	1047	807	1164	2505
15–30 cm layer				
Structural fraction of root litter	10	26	35	16
Metabolic fraction of root litter	0	0	0	0
Microbial biomass	20	32	75	38
Slow pool	309	684	686	930
Passive pool	669	1129	1524	2947
30–45 cm layer				
Structural fraction of root litter	6	11	18	9
Metabolic fraction of root litter	0	0	0	0
Microbial biomass	14	12	49	27
Slow pool	236	213	312	659
Passive pool	848	369	524	2178

compared for each site to soil CO₂ fluxes measured at Lamasquère (2007), Auradé (2008), Lonzeé (2007) and Ottawa (2007 and 2011) on bare soil and on cultivated wheat fields. The coefficients of determination (R^2) between model outputs and measurements (Table 4) were calculated on the five years for R_H and for R_S to assess for the reliability of the semi-mechanistic model outputs. Once validated, these outputs were compared to TER measurements for analyzing soil contribution in the various experimental sites.

2.4.3. Analyzing R_H response to both temperature and water content using a simple empirical model

The continuous R_H outputs simulated with the semi-mechanistic model at the daily time scale of the various sites were merged in a large dataset to calibrate a simple empirical model (Fig. 2), which expressed R_H as a function of soil temperature and relative soil moisture. This was done by using a non-linear function varying from 0 for the minimum relative soil moisture corresponding to wilting point, to 1 at field capacity.

$$R_H = a \times e^{b \times Ts} \times A_w \quad (7)$$

The coefficient “ a ” represents a reference heterotrophic respiration rate (R_{H-0} i.e., standardized at 0 °C and at field capacity, in $g C m^{-2} d^{-1}$) and coefficient “ b ” expresses the R_H sensitivity to temperature. Q_{10} is then defined as:

$$Q_{10} = e^{b \times 10} \quad (8)$$

The effect of soil moisture was modeled with the same equation than in the semi-mechanistic model to focus on temperature sensitive processes and on the difference between production and efflux Q_{10} .

Both coefficients (a and b) were adjusted for each site, using a non-linear regression to minimize the Root Mean Square Error (RMSE) between datasets (continuous semi-mechanistic outputs at the daily time scale) and modeled values (empirical) of R_H . For this purpose, only two third of the dataset were randomly selected and used to adjust R_{H-0} and Q_{10} over each site (Fig. 2). The one third remaining data was

then used to verify the performance of the empirical model for each site using RMSE and the coefficient of determination (R^2). This procedure was performed 50 times (i.e., 50 random selections splitting dataset of each site in two third adjustment data and one third validation data). Then, these 50 random selections and non-linear regressions were used to evaluate and ensure the robustness of the adjustment of the empirical model and calculate the standard deviation of each coefficient (a and b) and validation statistics (RMSE and R^2) at each site. Only the mean values of each coefficient and validation statistics were reported. Furthermore, the temperature sensitivity of R_H was assumed to be constant at each site and temperature range. Thus the same procedure was applied using a constant value of Q_{10} .

3. Results

3.1. Validation of the semi-mechanistic model

Fig. 3 illustrates the performance of the semi-mechanistic model compared to the measurements from the four sites. The predictions were in good agreement with the observations with regard to the high pedodiversity of the various sites, and the large climatic discrepancies. High values of R^2 were obtained on the three European sites for R_H (i.e., 0.89 at Lamasquère, 0.66 at Auradé and 0.79 at Lonzeé) and for R_S (i.e., 0.72 at Lamasquère, 0.69 at Auradé, 0.86 at Lonzeé). The lowest R^2 values were obtained for the Canadian site (0.59 for R_H and 0.55 for R_S), most likely because of N source which was organic in 2007 (dairy slurry) and synthetic in 2011. The organic N application tended to generate more spatial soil respiration variations than the synthetic N, as illustrated in Fig. 4 by comparing soil respiration data using closed chambers and eddy flux towers (for R_H mainly). Although the measurements were relatively well correlated, a wider dispersion was observed for the data collected using the chambers representing local emissions ($<1 m^2$) especially in 2007 compared to the consistency of the data measured the larger scale (ha range) with the flux towers. The soil CO₂ fluxes measured in May 2007 followed a dairy slurry application were very high up to $8 g C m^{-2} d^{-1}$. These high soil respiration rates ($>5 g C m^{-2} d^{-1}$) could not be well simulated by the model, which

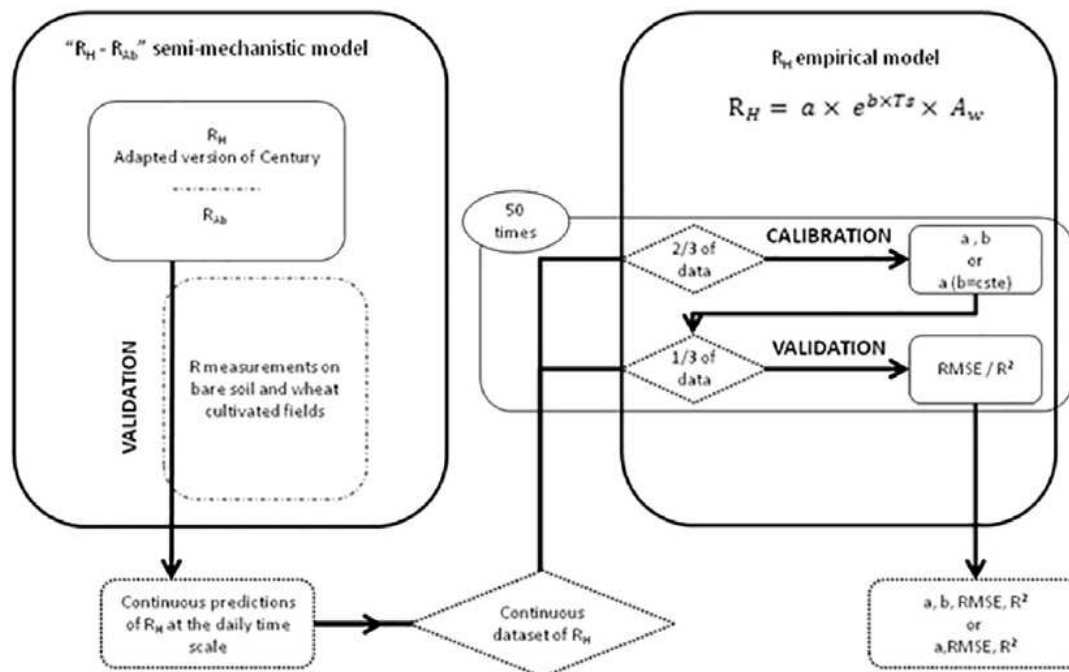


Fig. 2. Schematic diagram representing the procedure of the calibration/validation of the empirical model $R_H = a \times e^{b \times Ts} \times A_w$ where “ a ” represents a reference heterotrophic respiration rate, “ b ” expresses the R_H sensitivity to temperature and A_w is the effect of soil moisture on soil carbon decomposition. R_H is the heterotrophic respiration and $R_{S,b}$ is the belowground autotrophic respiration.

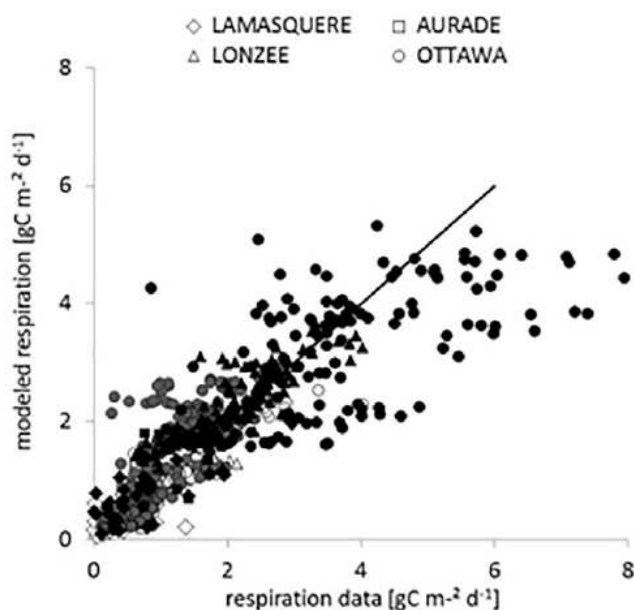


Fig. 3. Daily semi-mechanistic simulations of soil respiration fluxes compared to soil respiration measurements, on the four sites. Open symbols = Heterotrophic Respiration (R_H) chambers measurements over bare soil or Root exclusion zones (REZ); grey symbols = measured Net Ecosystem Exchange (NEE) over bare soil; black symbols = total soil respiration fluxes (R_H + belowground Autotrophic Respiration (R_{Ab})) measured using manual and automated chambers over the growing season.

reached $4.8 \text{ g C m}^{-2} \text{ d}^{-1}$ as a maximum value, because manure management was not accounted for in the model (e.g., addition of organic matter, impact on soil moisture and microorganisms). Since no significant impact on input soil temperature and moisture could be detected following the manure application (data not shown), the model did not predict the high flux values associated with this practice, which only affected relatively short period (18 days out of 251).

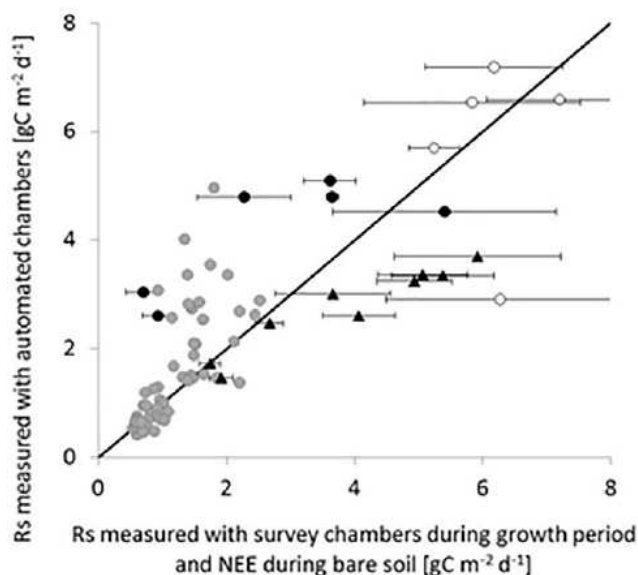


Fig. 4. Soil respiration fluxes measurements from the automated chamber compared to manual survey chambers (during growing season, black open and close symbols) and Net Ecosystem Exchange (NEE) measurements (over bare soil, grey symbols) at the Ottawa site in 2007 (circles) and in 2011 (triangles). Error bars correspond to the standard deviation and represent the spatial variability measured using the manual survey chambers. Open symbols = measurements following the manure application in 2007.

The proportion of the predicted heterotrophic contribution to soil CO_2 fluxes over the season illustrates the model's ability to capture major discrepancies among the sites (Fig. 5). Indeed, the model predicted that two third of R_S were produced by the soil organic matter decomposition processes for the winter wheat sites. For spring wheat, the model estimated that R_S was the dominant contribution (about 65% to 69%) to TER (Fig. 5, grey boxes) and that heterotrophic sources contributed by about 50% to R_S , which is significantly lower than proportions found in the 3 European sites (66%).

3.2. Temperature sensitivity

The semi-mechanistic Q_{10} was calculated using Eq. (1) on the portion of the curve that could be fitted with an exponential function ($T_S < 20^\circ \text{C}$), taking the temperature range of each site into account. The Q_{10} coefficient varied widely (from 3.8 to 2.5) and was strongly linearly related to the mean temperature of each dataset: an increase in temperature resulted in a decrease of sensitivity. This negative correlation was already documented and used to explain the seasonal variability of respiration processes in relation to temperature (Chen and Tian, 2005; Janssens and Pilegaard, 2003; Kirschbaum, 1995; Peng et al., 2009). For instance, this significant negative correlation could be related to changing soil temperature conditions over the different sites.

The coefficient values ("a" and "b" from Eq. (7)) were adjusted in order to minimize the RMSE between mechanistic model outputs considered as the dataset and empirically simulated values of R_H . The empirical model (Eq. (7)) was adjusted using T_S measured at 5-cm depth and a weighted θ_s calculated at 5-cm, 10-cm and 20-cm depth measurements in order to obtain robust $R_H - 0$ and Q_{10} adjustment especially on the datasets characterized by a long dry period such as in Ottawa 2011 (from DOY 186 to 271). Then, the empirical model explained between 38% and 91% of the variability of R_H for all the sites (Table 6). The procedure consisting of splitting randomly the dataset of each site in two third for data calibration and one third for data validation was repeated 50 times in order to ensure that no outranged data would lead to divergent coefficients ($R_H - 0$ or Q_{10}). An independent validation was performed for the individual calibrations. The very low standard deviation of each mean calibrated coefficient ($R_H - 0$ and Q_{10}) and validation statistics (RMSE and R^2) calculated over the 50 random samples confirmed the robustness of the equation. The range of adjusted Q_{10} values was large among sites (Table 6) but consistent with Q_{10} varying from 2 to 3 reported in previous studies over cultivated bare soils (Kutsch and Kappen, 1997; Moyano et al., 2007; Suleau et al., 2011).

Moreover, a linear relationship was obtained between $R_H - 0$ and Q_{10} (Fig. 6) showing a potential compensation between the two coefficients due to the curve-fitting procedure as both were adjusted

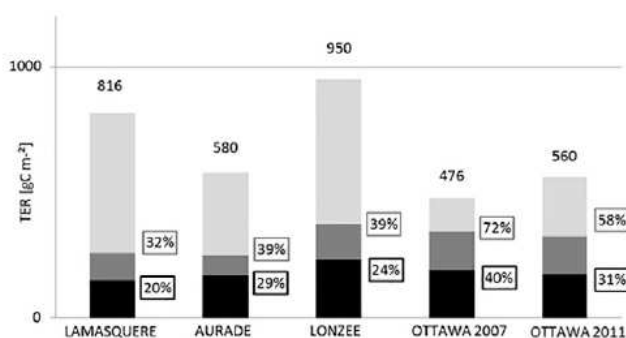


Fig. 5. Cumulative contributions of Heterotrophic Respiration (R_H) (black), belowground Autotrophic Respiration (R_{Ab}) (dark grey) and aboveground Autotrophic Respiration (R_{Aa}) (light grey) to Total Ecosystem Respiration (TER) predicted by the model over the growing season (from January 1st to harvest (August) for winter wheat (Lamasquère, Auradé and Lonzeé) and from sowing (May) to harvest (September) for spring wheat (Ottawa)). The relative contribution of R_H /TER is indicated as % in black boxes and of R_S /TER as % in grey boxes.

Table 6

Adjusted coefficients Q_{10} and R_{H-0} ($\text{g C m}^{-2} \text{d}^{-1}$) of the empirical model. Average soil temperature measured at 5-cm depth and corresponding semi-mechanistic Q_{10} (calculated as the respiration change rate over a 10°C temperature shift around the average temperature on dataset) are provided. RMSE and R^2 represent the validation statistics and StD is the standard deviation of the coefficients over the 50 regressions fitted on 50 randomly selected datasets.

Abbreviations in first row refer to the site and the cultural year studied. LAM07 = Lamasquière/year 2007. AUR = Auradé, LON = Loncée, OTT = Ottawa.

	LAM07	LAM09	AUR06	AUR08	LON07	OTT07	OTT11
Average Temperature on dataset ($^\circ\text{C}$)	12.1	10.7	10.3	13.1	11.9	13.8	11.9
Q_{10} - semi-mec. model	3.1	3.6	3.8	2.7	3.2	2.5	3.2
Empirical							
Q_{10} (StD)	2.3 (0.1)	2.7 (0.3)	3.0 (0.2)	1.7 (0.1)	2.1 (0.2)	2.5 (0.4)	1.6 (0.4)
R_{H-0} ($\text{g C m}^{-2} \text{d}^{-1}$)	0.22 (0.01)	0.15 (0.01)	0.22 (0.03)	0.51 (0.02)	0.31 (0.01)	0.36 (0.24)	0.61 (0.05)
RMSE (StD) ($\text{g C m}^{-2} \text{d}^{-1}$)	0.18 (0.01)	0.16 (0.01)	0.11 (0.02)	0.12 (0.02)	0.17 (0.01)	0.23 (0.11)	0.66 (0.07)
R^2 (StD) ($\text{g C m}^{-2} \text{d}^{-1}$)	0.53 (0.01)	0.67 (0.04)	0.91 (0.05)	0.87 (0.02)	0.74 (0.02)	0.82 (0.21)	0.38 (0.07)

simultaneously. It was expected that R_{H-0} should be constant between two years for a same site, except possibly at Ottawa because of the organic vs synthetic N application between the two years. Knowing that the management practices, the soil quality, the soil temperature and moisture ranges were quite similar at Auradé (Fig. 6) for the two years, the different R_{H-0} values are highly questionable. The effects of temperature and of other biochemical activities might interfere with the determination of the Q_{10} coefficient. To examine this hypothesis, the model coefficients were adjusted at each site assuming a constant empirical Q_{10} for all sites and years. A preliminary sensitivity study was performed where several adjustments were performed using constant Q_{10} values ranging between 1.6 and 2.4 by steps of 0.1, centred on the standard value of Q_{10} equal to 2 (Kätterer et al., 1998) (results not shown). The best statistical results between outputs of the empirical model and the 1/3 remaining validation data for each site were obtained for a Q_{10} value of 2.2, which was consistent with values previously reported (Kutsch and Kappen, 1997; Moyano et al., 2007; Suleau et al., 2011). By setting Q_{10} value equals to 2.2 for each site, similar RMSE and R^2 values were obtained compared to the original results (Table 7). Statistical results were not improved by fixing Q_{10} value to 2.2, although, the variability of R_{H-0} was more consistent. Indeed, R_{H-0} appeared to be very close for one identical site even over different study years (0.18 and 0.20 $\text{g C m}^{-2} \text{d}^{-1}$ in 2007 and 2009 at Lamasquière, 0.33 and 0.32 $\text{g C m}^{-2} \text{d}^{-1}$ in 2006 and 2008 at Auradé, 0.39 and 0.33 $\text{g C m}^{-2} \text{d}^{-1}$ in 2007 and 2011 at Ottawa). Furthermore, given the hypothesis that temperature sensitivity was constant for all sites, Fig. 7 shows the strong relationship between R_{H-0} and the “slow” decomposing carbon (i.e., with a mean residence time of

20 years) of the first 30-cm layer of soil. This result highlights the influence of the moderate-time residence carbon content on the reference heterotrophic respiration rate.

4. Discussion

4.1. Separating respiration sources

The contributions of R_H estimated with the semi-mechanistic model to soil respiration are in agreement with estimates from long-term experimentations carried out in winter wheat (Moureaux et al., 2006; Moyano et al., 2007; Shi et al., 2006; Zhang et al., 2013). The difference in carbon budget between the European and the Canadian sites can be partly explained by the length of the growing season, which is about 8 months for winter wheat and only 4 months for spring wheat. Moreover, the Canadian spring wheat is a short season cultivar, which has a high growth rate, especially towards late spring as observed by monitoring the fast stem elongation in 2007 and 2011 in Ottawa (data not shown) (Equiza et al., 2001). Consequently, according to Eq. (4), the model simulated a high root growth respiration associated to this stage, leading to a strong estimated contribution of R_{Ab} to TER. Moreover, Table 5 shows the higher quantity of carbon observed in the passive pool at the Ottawa site (from 2.1 to 2.9 kg C m^{-2}) compared to the three European soils (maximum of 1.5 kg C m^{-2} in the 15–30 cm layer at Loncée). This soil organic carbon fraction corresponds in the model to a complex molecular substrate with a high residence time in soil. Its low decomposition rate induces limited associated heterotrophic fluxes and then weaker influence of R_H in R_S compared to soil with high active (and slow) carbon content. This high proportion of “passive” carbon predicted by the model is mainly caused by strong environmental constraints (very low winter temperatures over a long period with presence of snow) rather than the quality of different residues since it is a similar crop (wheat) through the experimental sites.

4.2. Production vs efflux Q_{10}

The semi-mechanistic model predicted quite well the heterotrophic soil CO_2 efflux for a large range of SOC quality resulting from contrasting soil texture and climate constraints. In this model, as in most semi-mechanistic models, the sensitivity to temperature is assumed to be the same for all pools and substrate complexity. This assumption violates the kinetic theory of the Arrhenius model, which states that complex molecular substrates with high activation energies should have higher temperature sensitivities. This unresolved issue is still investigated. Several authors (Davidson and Janssens, 2006; Davidson et al., 2006; Knorr et al., 2005) concluded that recalcitrant pools are more sensitive to temperature compared to the labile ones, while others (Conant et al., 2008, 2011; Hartley et al., 2007; Reichstein, 2005) challenged this conclusion. They argue that substrate complexity is not the most important factor for temperature sensitivity (Thiessen et al., 2013). These contradictory results are explained by the fundamental importance to distinguish absolute (change of the respiration for a given

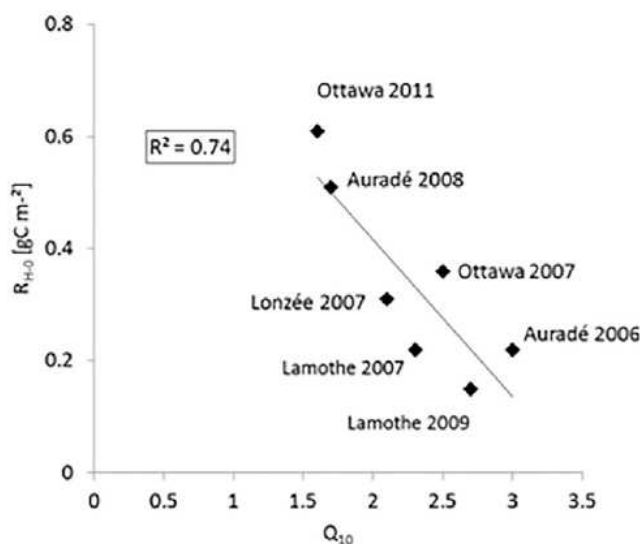


Fig. 6. Relationship between the reference heterotrophic respiration rate (R_{H-0} i.e., standardized at 0°C and at field capacity, in $\text{g C m}^{-2} \text{d}^{-1}$) and the R_H sensitivity to temperature Q_{10} ($Q_{10} = e^{b \times 10}$) both calibrated for the 6 study years.

Table 7

Calibration values of R_{H-0} obtained on each site and year for a common constant Q_{10} value equal to 2.2. RMSE and R^2 illustrate the validation statistics and StD is the standard deviation of coefficients of the 50 random samples.

Abbreviations in first row refer to the site and the cultural year studied. LAM07 = Lamasquère/year 2007. AUR = Auradé, LON = Lonzée, OTT = Ottawa.

	LAM07	LAM09	AUR06	AUR08	LON07	OTT07	OTT11
Q_{10}	2.2	2.2	2.2	2.2	2.2	2.2	2.2
R_{H-0} (StD)	0.18 (0.01)	0.20 (0.01)	0.33 (0.01)	0.32 (0.01)	0.29 (0.00)	0.39 (0.01)	0.33 (0.04)
RMSE (StD)	0.18 (0.01)	0.17 (0.01)	0.15 (0.01)	0.16 (0.01)	0.18 (0.02)	0.21 (0.01)	0.73 (0.04)
R^2 (StD)	0.51 (0.05)	0.71 (0.04)	0.87 (0.03)	0.81 (0.03)	0.73 (0.04)	0.92 (0.02)	0.42 (0.05)

unit change in temperature) and relative (change relative to the actual value of the measure respiration) sensitivities to understand the role of temperature on the decomposition of organic matter of different qualities (Sierra, 2012). Most of the studies compared relative and absolute sensitivity indistinctly (Sierra, 2012). Actually, this question is relatively difficult to elucidate as the commonly used Q_{10} apply only for relative changes in decomposition rates. In our study, a conceptual difference exists between the efflux Q_{10} corresponding to the observed temperature response of soil CO_2 efflux and the Q_{10} of CO_2 production. In other words, the efflux sensitivity corresponds to the production sensitivity modulated by environmental constraints. The fact that the values of the efflux Q_{10} (empirical) are lower than the production Q_{10} coefficients of the semi-mechanistic model (Table 6) might be due to the influence of several environmental constraints, which could induce several temperature-sensitive processes, interfering with the production temperature sensitivity of substrate decomposition (Davidson and Janssens, 2006). Moreover, in addition to temperature and litter quality, physical factors as transport of CO_2 produced into the soil up to the atmosphere, which are not studied here, could lead to discrepancies between production and efflux and explain the differences between efflux Q_{10} and production Q_{10} .

4.3. R_{H-0} , Q_{10} and substrate quality

Davidson and Janssens (2006) suggest that differences in substrate quality and quantity could contribute to a large variability in Q_{10} . Assuming a constant efflux Q_{10} value provides the opportunity to disentangle the confounding effects of temperature and substrate quality for different environmental constraints. This assumption, means that temperature sensitivity of R_H is independent of the complexity of the carbon substrate, and allowed to correctly predict R_H for a wide range of climate and soil types. The strong relationship observed between R_{H-0} and the “slow” decomposing carbon for a constant Q_{10} is

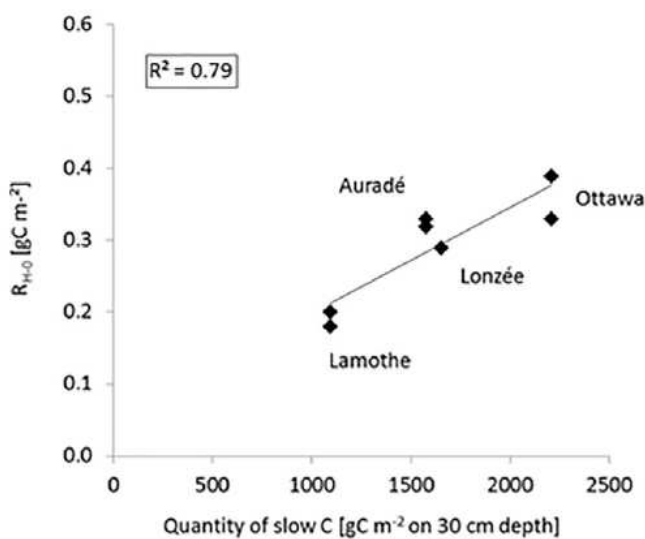


Fig. 7. Comparison of calibrated R_{H-0} values obtained using a Q_{10} coefficient of 2.2 according to the quantity of slow decomposed C in the first 30 cm of the soil.

consistent with previous studies that demonstrated a direct relationship between substrate quantity and heterotrophic CO_2 emissions (Jacinthe et al., 2002; Liu et al., 2006; Vinther et al., 2004) and with several previous laboratory experimentations (Fang et al., 2005; Reichstein, 2005). However, because these are short-term studies, the temperature response of old and resistant or protected carbon pools (i.e., high residence time) cannot be quantified, while its role in the carbon sequestration could be major in the context of global warming.

4.4. Usefulness and limitations of the modeling approach

The semi-mechanistic model is a useful tool to predict soil autotrophic and heterotrophic respiration at the daily time scale among multiple sites as it can easily be parameterized for any site. That model cannot be used in order to predict soil efflux at a shorter time scale as it does not take into account fast but relevant processes such as pulses of CO_2 following a rainfall. Nevertheless, the initialization of the C content in each pool is a crucial step to obtain relevant predictions. As the partition of soil organic carbon between the different pools is a theoretical approach, the different fractions of carbon could not be easily measured. As a consequence, huge assumptions are made to initialize the model in our study, such as reaching a stable C partition among the different pools after 20 years. Moreover, the analyze of R_H response to soil water content and temperature using a simple empirical model showed that the range of values of the site-specific parameter, R_{H-0} , varied as a linear function of the “slow” carbon pool amount. Only a few easily available data (soil temperature, soil water content and soil CO_2 efflux from bare soil) are needed to calibrate R_{H-0} for a specific site. This parameter could then be used as a proxy for the theoretical carbon distribution in order to initialize the semi-mechanistic model.

5. Conclusion

Our approach consisted to simplify R_H modeling using a Q_{10} -type equation adjusted using the continuous outputs of a mechanistic model. The use of the simple modeling approach demonstrated that assuming a constant value of the efflux temperature sensitivity over the entire growing season for all sites provided good predictions of R_H in absence of soil moisture deficit. It showed that the range of values of R_{H-0} between sites varied as a linear function of the “slow” carbon pool content. Our understanding of soil respiration improved way beyond Q_{10} because the variations in efflux Q_{10} could be explained by the impact of substrate allocation. However, since the partition of soil organic carbon is only a theoretical approach for modeling, the partition is not easy to verify experimentally. Existing models provide satisfactory annual predictions of CO_2 emissions and C turnover but using them for predicting the impact of future climate scenarios is highly questionable and uncertain. The next step to the study will consist in using different SOM pools defined according to the quantifiable carbon substrates in the field directly in the model.

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Appendix A. Detailed description of the model equations for transfers of organic matter that occur among pools

(1) Structural fraction of leaf litter pool

$$dC_{1j} = -K_{1j} \times F_{1j} \times A_{wj} \times A_{Tj} \times C_{1j}$$

(2) Structural fraction of soil litter pool

$$dC_{2,j} = -K_{2,j} \times F_{2,j} \times A_{wj} \times A_{Tj} \times C_{2,j}$$

(3) Soil active pool

$$dC_{3,j} = A_{wj} \times A_{Tj} \times (K_{2,j} \times F_{2,j} \times C_{2,j} + K_{6,j} \times C_{6,j} + K_{8,j} \times C_{8,j} + K_{7,j} \times F_{7,j} \times C_{7,j} - K_{3,j} \times F_{3,j} \times C_{3,j})$$

(4) Litter active pool

$$dC_{4,j} = A_{wj} \times A_{Tj} \times (K_{1j} \times F_{1j} \times C_{1j} + K_{5j} \times C_{5j} - K_{4j} \times C_{4j})$$

(5) Metabolic fraction of leaf litter pool

$$dC_{5j} = -K_{5j} \times F_{5j} \times A_{wj} \times A_{Tj} \times C_{5j}$$

(6) Metabolic fraction of soil litter pool

$$dC_{6,j} = -K_{6,j} \times F_{6,j} \times A_{wj} \times A_{Tj} \times C_{6,j}$$

(7) Soil slow pool

$$dC_{7,j} = A_{wj} \times A_{Tj} \times (K_{1j} \times F_{1j} \times C_{1j} + K_{2j} \times F_{2j} \times C_{2j} + K_{4j} \times C_{4j} + K_{3,j} \times F_{3,j} \times C_{3,j} - K_{7,j} \times C_{7,j})$$

(8) Soil Passive pool

$$dC_{8,j} = A_{wj} \times A_{Tj} \times (K_{7,j} \times F_{7,j} \times C_{7,j} + K_{3,j} \times F_{3,j} \times C_{3,j} - K_{8,j} \times C_{8,j})$$

where j is the soil layer where the considered carbon pool i is located, K is the maximum decomposition rate, C the carbon content, F depends on soil textural properties of the considered j layer for the soil active and

slow carbon, pools; it depends on lignin content (LIGN) of leaves or fine roots for the litter structural material,

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