

Modelling carbon turnover through the microbial biomass in soil

H. Ibrahim^{a,*}, N. Brahim^a, A. Hatira^a

^aU.R. 04/UR/10-02 Research Unit of Pedology, Department of Geology, Faculty of Sciences of Tunis, El Manar University, 2092 Tunis, Tunisia.

Abstract

There are three main ways to model the evolution of organic matters: (i) the multi-agent models which try to reconstitute the interaction mechanisms at particle scale, (ii) mathematical theories which try to consider evolution as a continuum, and (iii) compartmental theories which include linear and no linear models and try to split the complex components of organic matter in more homogeneous pools, which exchange organic matters between them in the solid phase and with the external gaseous and liquid phases. Many proposed models did not consider explicitly an active microbial compartment and were possibly over parameterized. In contrast, the MOMOS based on microbial biomass. Results showed proximity between measured and predicted values of carbon content in plant organs, soil and microbial biomass. Field respiration measurements which included respiration of active roots were found to be quite higher than predicted microbial heterotrophic respiration. Model predictions indicated higher microbial C content and higher microbial respiration activity in wheat parcels than in faba bean. Microbial biomass and microbial activity responded quickly to changes in environmental conditions such as soil moisture levels and inputs of plant necromass.

Keywords: Modelling ; Carbon ; Soil; Organic matter.

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1. The modelling approaches in exchanges soil-plant-atmosphere

Description of Carbon and Nitrogen Cycles: Interactions in the soil

Carbon and Nitrogen are elements found in the basic structure of all life forms, they are cycled through the atmosphere, biosphere, hydrosphere and soil through a multitude of biological, chemical and physical processes. A large part of organic carbon of terrestrial ecosystems and the main part of organic nitrogen are found in plant residues and soil organic matter. This means that the soil is an extremely important place of storage and exchange of these elements.

* Corresponding author. Tel.: +21699284163; Fax: +21671408885.
E-mail address: brahim_hatem@yahoo.fr.

Atmospheric carbon enters living forms through plant photosynthetic activity. Plants take in carbon dioxide to create complex carbohydrates that then move into the soil and its microorganisms through root exudates and plant mortality. Microorganisms work on decomposing this organic matter, part of which is easily decomposable, or labile, and part of which remains for a long time as stable organic matter in the soil (becoming a carbon reservoir). The action of these microorganisms converts this organic matter into humus, ammonia and nitrates, available phosphates and micronutrients; which in turn increase the fertility of the soil stimulating plant growth. Simultaneously, root and microbial respiration release CO₂ back into the atmosphere.

Microorganisms also play an essential role in the nitrogen cycle. Atmospheric nitrogen (N₂) cannot be directly used by plants and therefore passes first through nitrogen-fixing bacteria found in the soil, or in symbiotic relationships on root nodules of leguminous plants. These bacteria, through an energetically costly process, convert N₂ to ammonia (NH₃) and ammonium (NH₄) available for plant growth. The action of soil decomposers also breaks down the amino acids and proteins of dead organic matter into ammonium. Then, NH₄ can be further oxidised into nitrates by nitrifying bacteria in the soil, these nitrates are available for plant use and for use by denitrifying bacteria that release N₂ or nitrous oxides back into the atmosphere.

Carbon and nitrogen cycles are closely linked, for this reason the C/N ratio is an important piece of data to collect. Soil microbes are C limited; they depend on plant organic matter as their source of carbon. They tend to have a low C/N ratio which means a large demand for nitrogen per unit of carbon. If plant litter C/N ratios are too high, or higher than 30:1, microorganisms will compete strongly with plants for N liberated during decomposition thus reducing the availability of this N pool to the plants. (Lukac and Godbold, 2011)

Carbon and Nitrogen biogeochemical cycles: Models

Through modern-day agricultural practices, humans have heavily impacted the earth's carbon and nitrogen biogeochemical cycles. The fundamental discovery of Liebig in last XIX century of absorption of inorganic forms of fertilizers by plant roots has induced extensive synthesis of ammonia from N₂ and H₂, despite its high energetic cost. This resulted in high increases of crop yield, but current systems have reached limitations and possible inversions from many environmental problems. Nitrogen inputs to terrestrial systems have doubled with careless use of inorganic fertilizers and the cultivation of N-fixing crops (Vitousek et al. 1997). Nitrogen losses from cultivated systems, leading to excess nitrogen within natural ecosystems have caused major environmental problems. Among these are soil acidification (the ammonium ion created with the addition of N fertilizers is a proton donor), eutrophication and surface water toxicity (resulting from nitrate lixiviation) and greenhouse gas release (like N₂O production during nitrification/denitrification processes or the increase of CO₂ from the respiration of a microbial community unlimited by N stocks) (Gardner & Drinkwater, 2009). Corresponding decrease of the C reservoir can cause other environmental problems such as soil compaction, the decrease of physical fertility, or increase of erosion.

Developing models that closely represent the flow of these elements through the ecosystem can be used as a tool to help evaluate the sustainability of agricultural practices, and guide choices to more suitable forms of crop management. Numerous field studies have shown that crop management practices can either

enhance or diminish quantities of soil C and N, in addition to altering microbial biodiversity over time (Kucharik et al, 2001).

A wide range of models, of different levels of complexity exist to describe soil carbon and nitrogen dynamics. The soil is an extremely heterogeneous environment, and models have to take into account this heterogeneity across different spatial (from the micrometer to thousands of kilometres) and temporal scales (from hours to centuries) (Manzoni and Porporato, 2009). At the moment, there is no universal model that ‘works’ under all conditions.

Most models describing carbon and nitrogen dynamics deal with long-term predictions. However short-term models are important as a tool to address challenges such as achieving high levels of soil organic matter (that increase soil fertility) while keeping concentrations of inorganic nitrogen relatively low during time periods when leaching is at its peak (Petersen et al.). The practical aspect of these models is that they might help to time mineral and organic fertilizer inputs, and other agricultural practices. In the context of current debates on climate change, models can also be used to determine if particular systems are sources or sinks of carbon, and perhaps provide insight into how to maximise carbon sequestration.

1.1. Multi-agent systems

These computational ways simulate the interactions between agents of real system knowing only few of their basic properties [2]. Attempts had been made to approaches the soil organic systems by simulating the behaviour of decomposing agents and particles of organic substrates [3]. Different living agents were considered like microorganisms in the MIOR model [4] or earthworm in the SWORM model [5]. The difficulties are to define the number and properties of the agents as soils contain a broad panel of decomposing agents and available substrates. So at this time the simulations concern small samples and extrapolations to large areas remain hazardous.

1.2. Using continuous mathematical theories

A mathematical theory attributed a continuous evolution of the quality of organic materials entering the soil [6]. The method was used to study isotope discrimination during decomposition of organic matter [7] and combined with ¹⁵N labelling experiments [8] but is questionable concerning sources of soil organic matters which are not originated of only one organic source which could change continuously, but from plant debris, microbial debris, microbial synthesis, or chemical condensations.

1.3. Using compartment mathematical theories

The theory of compartmental modelling is based on fractionation of the complex system in various compartments more homogeneous in terms of quality and decomposition kinetic, and to program exchanges, inputs and outputs between these compartments and the environment [9, 10, 11, 12, 13]. Two types could be defined: (i) the linear models, in which the decrease of each compartment is modelled only as a function of its carbon content, (ii) the no linear models in which the compartment decrease is modelled both as a function of its contents and of those of the microbial decomposers.

Multiple scenarios can be defined to take into account the advances in knowledge of the various organic pools and reactions. Three risks must be avoided: (i) to complicate excessively the relational or flow diagrams and the associated equation system, (ii) to over parameterize the model, (iii) to choose a relational diagram poorly coherent with the ecological knowledge.

Two examples of flow diagrams of widely used compartment models are shown Fig.1. The Roth-C model (Fig.1a) was proposed initially to describe the organic evolution of the experimental site of Rothamsted integrating many data available for over a century [14]. It was a first attempt to consider simultaneous

evolution of five organic compartments: decomposable and resistant plant materials (DPM and RPM in Fig.1a), microbial biomass (BIO), humified materials (HUM), and inert organic matter (IOM). This model needed four kinetic constants regulating the decomposition of DPM, RPM, BIO and HUM which could be the most easily linked to climate conditions by analogy with chemical or microbial laws. The other parameters concerned fractionation of flows. Fractionation of plant materials into RPM and RPM, like estimations of IOM can be based on chemical and biochemical properties of organic materials, but parameters of fractionation of flows into BIO and HUM are more difficult to quantify and to associate to environmental conditions. But the sensitivity analyses showed the importance of these parameters on model outputs [15], indicating that these outputs should be poorly related to environmental conditions. Another question concerned the place of BIO in this type of model, which is the same of that of HUM, and not really at the centre of the organic evolutions.

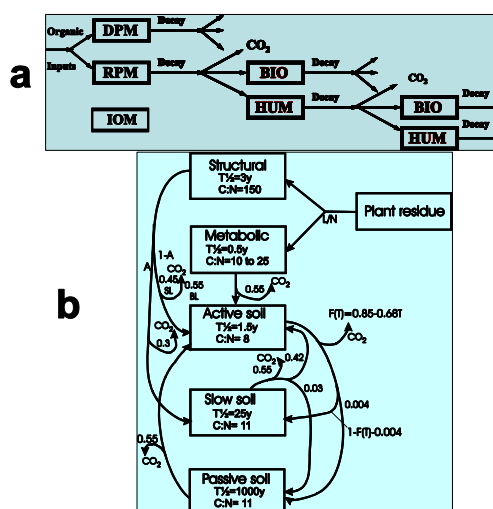


Figure 1 - Examples of flow diagrams of two currently used compartment models of decomposition, a) The Roth-C model [16], b) the century model [17]

The century model (Fig.1b) included also five compartments: metabolic and structural which could be analogous to DPM and RPM of Roth-C (Fig.1a), active soil could be analogous to BIO with an increased functional role comparatively to Roth-C since most of SOM transit in active soil Fig.1a. But a half-life of 0.5 y seemed great relatively to basic knowledge about microbial populations. Slow and passive soils could be compared to HUM and IOM of Roth-C Fig.1a. Century (Fig.1b) was not already mentioned in the comparative study¹⁵ since it could appeared over-parameterized compared to Roth-C (Fig.1a). A number of parameters greater than the number of the experimental points enable to adjust all observations but was not significant from a statistical point of view. At the 5 kinetic constants regulating the decrease of each compartment Century added 8 partition parameters (constant values given in arrow splits in Fig.1b regulating the inputs in each compartment and sometimes called efficiency factors, as they could traduce the C consumed in CO₂ as energy source to synthetize the C compounds of a given compartment. A problem was that these values were given as constants not linked to environmental conditions, while sensitivity analysis shows model responses sometimes very dependant to slow fluctuations of the given constant values.

2. Material and methods

2.1. Modelling the key role of microorganisms

MOMOS (Modelling Organic transformations by Micro-Organisms of Soil, Fig.2) was the first proposition to put the microbial compartment at the centre of the exchanges and associated it to linear equations of microbial assimilations and microbial mortality, and only a no linear one for microbial respiration. MOMOS respects the principle of parsimony (Ockham's razor) since it uses only seven kinetic parameters all linked to climate, and additionally linked to the quality of organic inputs [18], and soil texture [19]. It has been proposed to predict the evolution of ^{14}C tracer in two ecosystems [15]. Then it was validated (Fig.3) in six other contrasted ecosystems of the tropical area [20]. It has been successfully used to quantify the turnover of OC in Andean fallow ecosystems [21] and to regulate the daily exchanges of C between plant organs, nodule rhizobia, microorganisms and atmosphere in cereal legume intercropping in Mediterranean conditions [22].

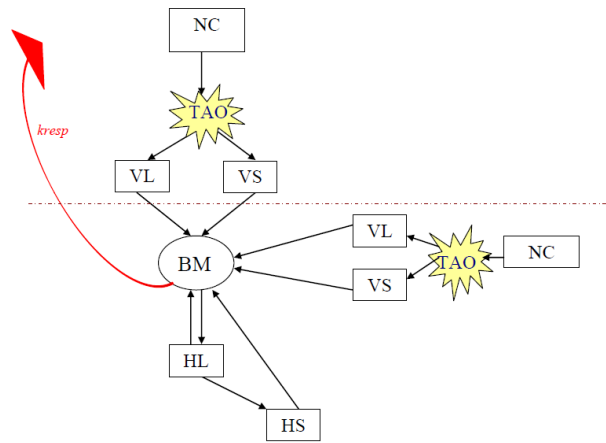


Figure 2 – The MOMOS model, coupled with soil water model and production module: MB is microbial biomass, VL and VS are the labile and stable debris of vegetal origin entering the soil, HL and HS are the labile and stable humus fractions, VL, VS, HL, and HS, respectively, k_{resp} is the daily rate of microbial respiration

2.2. The MOMOS equation system

MOMOS is based on the functional ecology of soil microbial biomass (MB) which increases by enzymatic assimilation of labile and stable vegetal necromass (VL and VS) and labile and stable humus (HL and HS) and decreases by microbial respiration and mortality. The only process which is assumed to be more chemical than biological is humus stabilisation from HL to HS. MOMOS is parameterised only by seven first order rate constants (dimension day^{-1}). Unlike other multi-compartment models, MOMOS does not use flow-partitioning coefficients (efficiency factors), that are usually specified as not depending on climate variables in other models. All MOMOS parameters depend on soil moisture content (θ) and temperature (T) and the model is probably one of the more sensitive to climate change as shown in the general equation:

$$\dot{\mathbf{x}} = f(T)f(\theta)\mathbf{A}\mathbf{x} + \mathbf{B} \quad (1)$$

where \mathbf{x} is the vector of the state variables (C content of compartments), $\dot{\mathbf{x}}$ is the vector of the derivatives of \mathbf{x} (day^{-1}), \mathbf{A} is the matrix of the model parameters, \mathbf{B} is a vector determining the external C input. $f(T)$ is an exponential function of temperature:

$$f(T) = Q_{10}^{(T-T_{opt})/10} \quad (2)$$

where T is the soil temperature (0-30 cm layer) assumed to be the same as the air temperature, T_{opt} is the optimum decomposition temperature fixed at 28°C, a temperature often taken as the optimum for decomposition[20,23], Q_{10} is the difference in rate for a temperature increase of 10°C, fixed at 2.2, the value found when the model was validated[20]. $f(\theta)$ is the function of the soil water content normalised to the water holding capacity (WHC) of the soil[20].

The soil water content (θ) was predicted using the SAHEL model, based on meteorological data near the experimental plots. The minimal data can include only air temperature, rainfall, but the precision is better if they include also solar radiation, wind speed and water vapour pressure, for accurate determination of potential evapotranspiration by the FAO Penman-Monteith method.

Matrix \mathbf{A} and vector \mathbf{x} for the model are:

$$\mathbf{x} = \begin{bmatrix} x_{VL} \\ x_{VS} \\ x_{MB} \\ x_{HL} \\ x_{HS} \end{bmatrix} \quad (3)$$

After each incubation period, the total C decrease by microbial respiration \dot{c} for the five compartments is:

$$\dot{C} = \sum_{i=1}^5 \dot{x}_{i,C} = -f(T)f(\theta) q_{CO_2} x_{C,MB} \quad (4)$$

where q_{CO_2} is the metabolic quotient of the microbial biomass

where C_{MB}^0 is an estimate of the biomass at steady state, k_{resp} is the respiration coefficient (day^{-1}) adjusted to the 0-20 μm soil textural fraction (F_{0-20}) by the transfer function using the two sites used for calibrating the model plus the six sites used for validating the model[20]:

$$k_{resp} = -0.0008 F_{0-20} + 0.062 \quad (5)$$

Alternately another transfer function linking k_{resp} to soil pH can be used [20]. The optimal rates of enzymatic digestion of labile (k_{VL}) and stable (k_{VS}) plant materials (equations 17 and 17'), and the optimal rate of microbial mortality (k_{MB}) are linked to the type of organic inputs (equation 18)[18]. The values in optimum pedoclimatic conditions ($f(T) = f(\theta) = 1$) for the other MOMOS parameters remained unchanged from the previous MOMOS calibration and validation experiments:

- optimum rate of enzymatic digestion of labile humus $k_{HL} = 0.05 \text{ d}^{-1}$,
- optimum rate of enzymatic digestion of stable humus $k_{HS} = 0.00005 \text{ d}^{-1}$,
- optimum rate of chemical stabilisation from labile humus to stable humus $k_{HLS} = 0.0003 \text{ d}^{-1}$.

2.3. Formulation for isotopic tracers

Previous studies using isotopic tracers defined the matrix **A** in equation 1 as the initial values of the vector **x** were known (from the rate of ¹⁴C accumulation and the types of labelled materials that were added) and all values of vector **B** = 0 (no inputs of labelled C from plants). Equations 1 and 4 became:

$$\dot{\mathbf{x}} = f(T)f(\theta) \mathbf{A} \mathbf{x} \quad (6)$$

$$\mathbf{x} = \begin{bmatrix} x_{VL}^0 \\ x_{VS}^0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad (7)$$

2.4. Formulation for C evolutions in agro-ecosystems

The previously defined matrix **A** and its relationships with climate, soil texture and quality of organic inputs were preserved. So, and it was only necessary to estimate the initial values for the vector **x** and the daily inputs from necromass C (NC) for the vector **B** in the 5 compartments comprising the debris of plant shoots, plant roots and if necessary root exudation or symbiotic nodules. Equation 1 became:

$$\dot{\mathbf{x}} = f(T)f(\theta) \mathbf{A} \mathbf{x} + \sum_{j=1}^5 \mathbf{B}_j \quad (8)$$

Where the subscript *j* indicated each plant organ in each study:

- shoots, root debris and root exudates of five plants chosen as typical of fallow implantation in high altitude systems of Bolivian puna and Venezuelan paramo [24] used in calibration experiment[15,25],
- roots, shoots and nodules of symbiotic N fixation in the Mauguio intercropped system [22]:

The elements of **B_j** were estimated in two stages:

- quantitative estimate of necromass input from each plant part by a production module adapted at each ecosystem; for Andean ecosystems the fallow production model FAPROM[24] was used; for wheat-fababean intercropping, another production module was defined[22];
- qualitative estimate of necromass to divide each input into labile and stable fractions in the MOMOS decomposition processes (see below).

2.5. Modelling the quality of necromass entering the soil

The TAO (Transformation of Added Organic materials) model was designed to describe the transformation of carbon and nitrogen from organic amendments and fertilisers in soils from temperate areas in controlled laboratory conditions[23,26-28]. The model has since been validated on tropical materials[29], and the TAO-C version describing carbon transformations, was designed to estimate the fractions of labile and stable necromass that are then used for the ‘microbial biomass’ compartments of MOMOS. TAO-C is a parallel three-compartment model using only two parameters (very labile (*P_L*) and stable (*P_S*) fractions of OM) to predict C mineralisation.

Basing *P_L* and *P_S* on biochemical data first required the OM to be classified using a criterion based on principal component analysis of the OM data set used to calibrate the model²⁶:

$$C_o = 7.18 C_{OM} + 0.14 Lig/N_{OM} - 3.84 \quad (9)$$

where C, N, Lig express carbon, nitrogen, and lignin content in g g⁻¹ of OM, respectively.

OM with negative C_o values was mainly N-rich materials such as organic fertilisers or materials of animal origin. OM with positive C_o values was mainly ligneous material originating from plants. The following formulae were then used to calculate P'_L and P_S depending on the sign of C_o .

If $C_o \leq 0$: $P'_L = 0.35 f_{sol} + 2.2 N_{OM} - 0.01 Lig/N_{OM}$, and $P_S = 3.60 Lig$

If $C_o > 0$: $P'_L = 0.099 flab + 0.14 Hem$, and $P_S = 1.61 Lig + 0.62 Ash_{OM}$ (10)

where $f_{sol} = Sol/(Sol + Hem + Cel + Lig)$, $flab = (Sol + Hem)/(Sol + Hem + Cel + Lig)$, N_{OM} was total nitrogen in OM and Sol, Hem, Cel, Lig and Ash_{OM} were OM mass fractions obtained by fibre fractionation. This study in field conditions simplified the TAO organisation of plant debris compartments. Only two compartments, labile VL and stable VS vegetal necromass (figure 2), are considered in MOMOS, VL being the sum of very labile and intermediary resistant TAO compartments, VS being the stable TAO compartment.

Another factor which determines decomposition in MOMOS is η_{NC} , the C:N ratio of input necromass NC from each plant organ. An increase of η_{NC} was modelled as decreasing the assimilation rates of labile (k_{VL}) and stable (k_{VS}) NC compartments [18]:

$$k_{VL} = MAX(0.65 - 0.0019 \eta_{NC}, 0.1) \quad (11)$$

$$k_{VS} = MAX(0.0037 - 0.000026 \eta_{NC}, 0.00005) \quad (12)$$

An increase of η_{NC} was also found to increase the rate of microbial mortality²⁵:

$$k_{MB} = MIN(0.42 + 0.0012 \eta_{NC}, 0.8) \quad (13)$$

Equations 13 and 13' were applied separately to each of the five NC inputs, while η_{NC} in equation 14 was calculated each day by the model from the sums of C and N of the inputs materials entering MB.

2.6. Data collection for calibration and validation

¹⁴C and ¹⁵N labeled straw was mixed with soils, from the top 0–10 cm layer at each of the sites, in 14×15 cm porous bags. The top part of the bags had a 1 mm mesh to allow the passage of plant roots and mesofauna and the mesh of the bottom part was 0.1 mm to minimize losses by gravity. 40 bags containing the labeled straw and soil were buried 5 cm deep along four parallel lines in each experimental plot (10 samples at different times × 4 replicates for each sample at each site, making a total of 240 soil bags). On each sampling date, one bag from each line of the four lines at each site was selected at random to measure soil water content, total ¹⁴C and ¹⁵N and ¹⁴C and ¹⁵N in the microbial biomass and inorganic N stock. The soil bags were left in the soil for 18 months at the two lowest sites (A(65) and A(165)) 24 months at A(780), 31 months at A(1800) and 38 months at the two highest sites (A(3400) and A(3968)). The first samples were taken one month after setting up the experiment and the sampling interval increased with time to 6 months at the end of the experiment for the highest sites. After collection, the soil bags were stored refrigerated for no more than three days before analysis.

2.7. Data collection for C evolution in agro-systems

Four whole plants of each species were collected from each plot (4 replicates) at each sampling occasion during plant growth. At the same time, two replicates of soil samples from the 0-5 cm and 25-30 cm layers were collected in 500 mL stainless steel cylinders from each plot. These samples were used to determine the soil moisture and bulk density.

The near-root soil was collected from the field and preserved in iceboxes for microbial biomass (MB) determination (4 plots×4 modalities×4 replicates). These samples were then homogenised and crushed without drying and passed through a 4×4 mm grid sieve in the laboratory [30]. The coarse and fine fractions were weighed and the fine fraction was kept without drying at 4°C. MB determination was carried out within two days after sampling.

The soil MB carbon was determined by fumigation-extraction [31]. A fresh soil sub-sample equivalent to 10 g dry soil was fumigated with alcohol free chloroform for 18 h. The fumigated sample and a similar control soil sample were shaken with 30 mL of a 0.5 mol K_2SO_4 L^{-1} aqueous solution for 45 minutes, centrifuged for 10 min and sterilised by filtration on a 0.2 μm membrane syringe. The liquid filtrates were stored in sterile plastic tubes at 4°C before C analysis in aqueous phase (Shimadzu TOC- V_{CSH} analyser). The soil microbial C concentration (MB-cC) was calculated as the difference between the total organic C of the extracts of fumigated soils with destroyed organisms and extracts from the control soils, divided by a factor $k_c = 0.45$ [32].

The roots and shoots were separated, the roots were washed in water, the root nodules were separated manually and the grains were separated from the shoots. All parts were dried at 60°C for 2 days and weighed again when dry. For subsequent C analysis, samples of each part were grouped and ground to 0.2 mm in a steel planetary ball mill.

A dry combustion elemental analyser (NA2000, Fisons Instruments) was used for C analysis of the soil and plant parts. The soil CO_3 -C was subtracted if necessary from the soil total C to give the soil OC. All C concentrations (total-cC in $mg\ g^{-1}$, MB-cC in $\mu g\ mL^{-1}$) were converted to carbon stock ($g\ C\ m^{-2}$) on the 0-30 cm layer, using bulk density, coarse fraction and moisture for soil data, and plant density for plant data.

The CO_2 -C fluxes from the soil surface were measured in the field for six replicates per plot using a LI-COR 8100 system and 8.7 cm high PVC cylinders with 10 cm internal diameter, which were buried leaving 2-3 cm above the soil surface. The exact heights between the soil surface and the tops of the cylinders were measured for the flux calculation. The flux in $\mu mol\ CO_2\ C\ m^{-2}\ s^{-1}$ was multiplied by 1.0368 to obtain the daily flux in $g\ CO_2\ C\ m^{-2}\ day^{-1}$ and corrected if necessary in case of very hot surface temperature in summer[22].

3. Some results

3.1. MOMOS validation

MOMOS allowed to adequately predict total and microbial ^{14}C dynamics (figure 3) during the decomposition of a standard plant material in six extremely contrasting tropical environments using only one parameter specific to each site (k_{resp}) instead of the two or three site specific parameters necessary in previous analysis using the same database to predict only total ^{14}C by two exponential models [33,34]. Furthermore, k_{resp} was the only parameter found related to soil properties, demonstrating that the function of microbial respiration alone was site dependent. Overall, this study demonstrated that climate, together with basic soil properties as texture and pH, were the main drivers of soil organic matter dynamics when a large range of conditions are considered. Other specific soil characteristics, as the composition of soil microbial communities seemed to be of secondary importance.

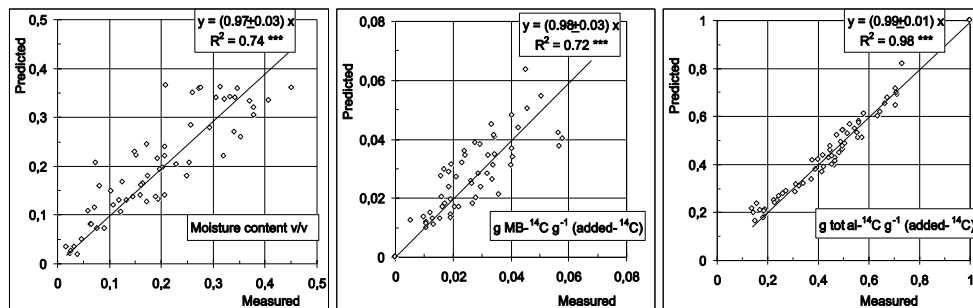


Figure 3 – Validation of the MOMOS model, predicted vs measured values of soil water, soil microbial ^{14}C and total ^{14}C in 6 contrasted ecosystems of an altitudinal gradient between 60 and 4000 m altitude, 10 sampling occasions, 4 replicates [20]

3.2. Short term microbial exchanges in fallow systems

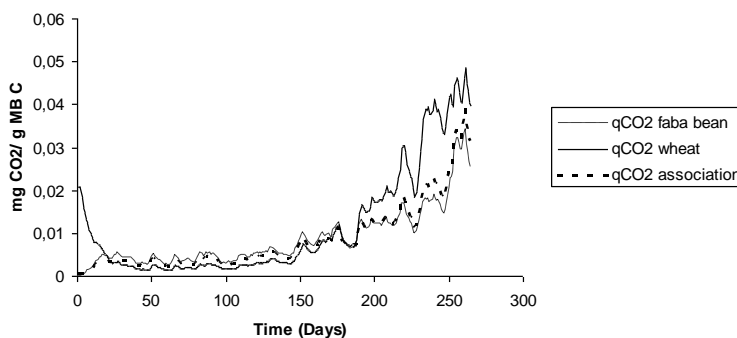


Figure 4-Metabolic quotient, qCO₂, in faba bean, wheat, and faba bean-wheat parcels

Soil respiration is composed of both autotrophic respiration (plant roots) and heterotrophic respiration (soil microorganisms). Field measurements did not separate these two components. Predicted values estimated only the heterotrophic component. It is therefore to be expected that measured values for microbial respiration be higher than predicted values. The last measure of soil respiration was taken ten days after harvest time, when root respiration can be considered minimal, and this value is the one that comes closest to MOMOS predictions (Fig.4).

Total Soil Carbon and the net Carbon balance

Plotting microbial respiration against total plant input of C allows us to form an idea of if the agrosystem in question has a tendency to act as source or sink of carbon. Microbial respiration represents the exit of C from the system, and plant material necromass is the entrance. It can be observed in (Fig.5) that carbon input is higher than output through microbial respiration and it can be inferred that all three of the studied modes of culture act as carbon sinks.

However in this case, we have also noted that stable humus decreases slightly over time as the labile pool increases. As stable forms of C are transformed to labile it leads to question the durability of the system. Though it seems to stock carbon in the short term (of one cultural cycle) the behaviour of this system remains to be studied when plant input is reduced (for example during the winter).

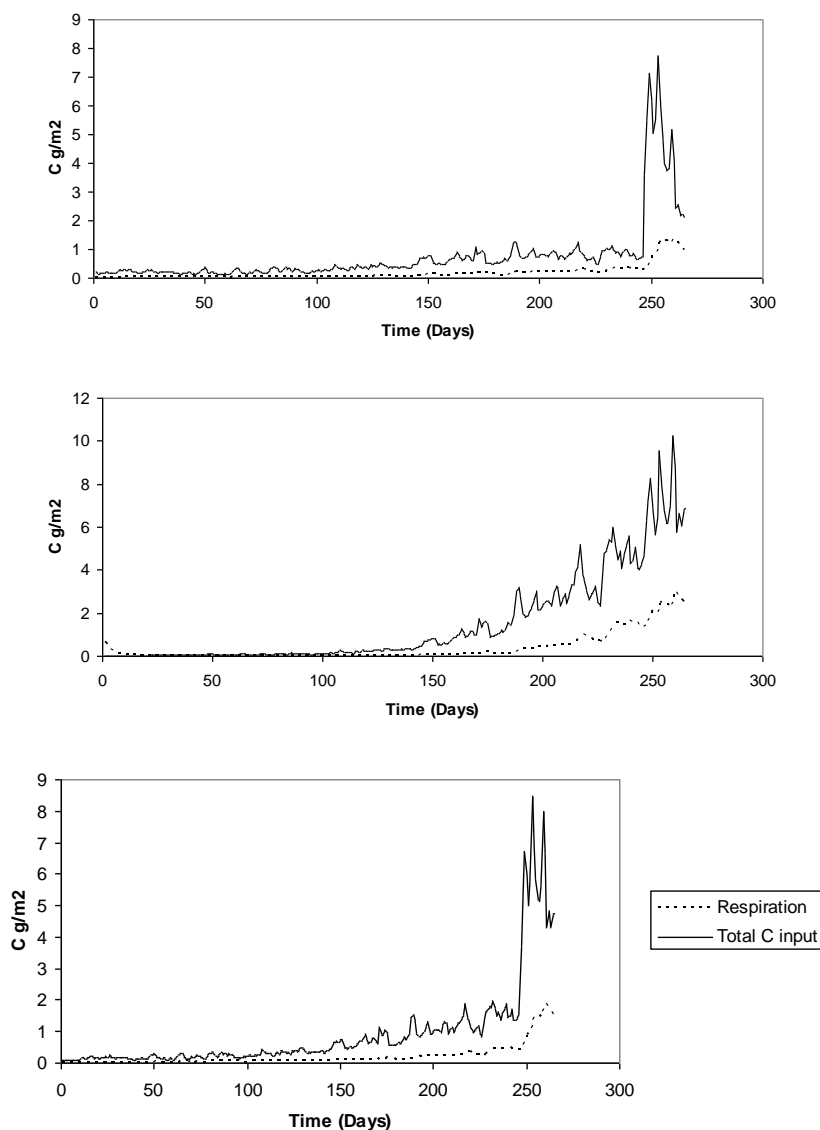


Figure 5 The carbon balance; total carbon input from plants and carbon output from microbial respiration in faba bean (top), wheat (middle) and associated (bottom) parcels.

3. Conclusion

The work realised was a first step in applying MOMOS to a complex system. Comparing model predictions to a whole range of field collected data gave overall encouraging results which showed that the model is able to simulate carbon transformations and movement from plant to soil to atmosphere based on the parameters that were previously defined under controlled conditions for its calibration.

This internship touched upon a wide range of factors that play a role in the carbon cycle, and observations of patterns, relationships and trends lead to questions for eventual further study:

- ❖ How can nodules be incorporated into the MOMOS plant production module as a factor stimulating plant growth?
- ❖ What are the factors that could lead to an observed increase in microbial biomass of wheat parcels as opposed to faba beans?
- ❖ What is the contribution of heterotrophic respiration to total soil respiration?

The difficulties encountered in this internship regarding crop health can serve as a basis for reflection for further study into the application of MOMOS to complex systems.

References

- [1] Manzoni S, and Porporato A. Soil carbon and nitrogen mineralization: Theory and models across scales. *Soil Biology & Biochemistry* 2009; **41**: 1355-1379.
- [2] Treuil JP, Drogoul A, Zucker JD. *Modélisation et simulation à base d'agents*. Dunod, Paris ; 2008.
- [3] Marilleau N, Cambier C, Drogoul A, Chotte J L, Perrier E, Blanchart E. Multiscale MAS modelling to simulate the soil environment. *Application to soil ecology, Simulation, Modelling, Practice and Theory* 2008; **16**:736-745.
- [4] Cambier C, Bousso M, Masse D, Perrier E. A new, offer versus demand, modelling approach to assess the impact of micro-organisms spatio-temporal population dynamics on soil organic matter decomposition rates. *Ecological Modelling* 2007 ;**209**:301-313.
- [5] Blanchart E, Marilleau N, Chotte J L, Drogoul A, Perrier E, Cambier C. SWORM: an agent-based model to simulate the effect of earthworms on soil structure. *European Journal of Soil Science* 2009;**60**: 13-21.
- [6] Agren G I, Bosatta E. Quality: A bridge between theory and experiment in soil organic matter studies. *Oikos* 1996 ;**76**:522-528.
- [7] Agren GI, Bosatta E, Balesdent J. Isotope discrimination during decomposition of organic matter: A theoretical analysis, *Soil Science Society of America Journal* 1996; **60**: 1121-1126.
- [8] d'Annunzio R., Zeller B, Nicolas M, Dhôte JF, Saint-Andre L. Decomposition of European beech (*Fagus sylvatica*) litter: Combining quality theory and 15N labelling experiments. *Soil Biology & Biochemistry* 2008;**40** : 322-333.
- [9] Auger P, Lett C, Poggiale JC. *Modélisation mathématique en écologie, Sciences sup. Mathématiques appliquées pour le master*, edited by: IRD, Dunod, 2010
- [10] Coquillard P, Hill DRC. *Modélisation et simulation d'écosystèmes. Des modèles déterministes aux simulations à événements discrets*, Ecologie, Masson 1997.
- [11] Anderson DH. *Compartmental modeling and tracer kinetics. Lectures notes in biomathematics*, edited by: Levin, S., Springer, Berlin, Heidelberg, New-York, Tokyo, 1983.
- [12] Jolivet E. *Introduction aux modèles mathématiques en biologie*, edited by: INRA, A. s. e. a., Masson, Paris, New-York, Mexico, 151 p., 1983.
- [13] Pielou EC. *An introduction to mathematical ecology*, Wiley Interscience, 1969.
- [14] Jenkinson D S, Rayner JH. The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science* 1977; **123**:298-303.
- [15] Pansu M, Bottner P, Sarmiento L, Metselaar K. Comparison of five soil organic matter decomposition models using data from a 14C and 15N labeling field experiment. *Global Biogeochemical Cycles* 2004;**18**:
- [16] Jenkinson D S. The turnover of organic carbon and nitrogen in soil. *Phil. Trans. R. Soc. Lond* 1990;**329**:361-368.
- [17] Parton WJ, Schimel D S, Cole CV, Ojima DS. Analysis of factors controlling soil organic matter levels in great plains grasslands. *Soil Science Society of America Journal* 1987;**51**:1173-1179.
- [18] Bottner P et al. Factors controlling decomposition of soil organic matter in fallow systems of the high tropical Andes: a field simulation approach using 14C and 15N labelled plant material. *Soil Biology & Biochemistry* 2006;**38**:2162-2177.
- [19] Pansu M, Sarmiento L, Metselaar K, Hervé D, Bottner P. Modelling the transformations and sequestration of soil organic matter in two contrasting ecosystems of the Andes. *European Journal of Soil Science* 2007;**58**: 775 - 785.
- [20] Pansu M. et al. Modeling Organic transformations by Micro-Organisms of Soils in six contrasting ecosystems: validation of the MOMOS model. *Global Biogeochemical Cycles* 2010;**24**:

- [21] Pansu M, Bottner P, Sarmiento L. Micro-Organismes et Matière Organique du Sol (modèle MOMOS) : bilan de 20 ans de modélisation basée sur le traçage isotopique in situ. *Etude et Gestion des Sols* 2009;**16**:213-232.
- [22] Ibrahim H et al. The daily exchange of carbon between living organisms, the soil and the atmosphere, Submitted, 2013.
- [23] Thuriès L, Pansu M, Feller C, Herrmann P, Rémy J.C. Kinetics of added organic matter decomposition in a Mediterranean sandy soil. *Soil Biology & Biochemistry* 2001;**33**: 997-1010.
- [24] Martineau Y, Saugier B. A process-based model of old field succession linking ecosystem and community ecology. *Ecological Modelling* 2007;**204**:399-419.
- [25] Pansu M, Martineau Y, Saugier B. A modelling method to quantify in situ the input of carbon from roots and the resulting C turnover in soil. *Plant and Soil* 2009;**317**:103-120
- [26] Thuriès L, Pansu M, Larré-Larrouy M.C, Feller C. Biochemical composition and mineralization kinetics of organic inputs in a sandy soil. *Soil Biology & Biochemistry* 2002;**34**: 239-250.
- [27] Pansu M, Thuriès L. Kinetics of C and N mineralization, N immobilization and N volatilization of organic inputs in soil. *Soil Biology & Biochemistry* 2003;**35**: 37-48.
- [28] Pansu M, Thuriès L, Larré-Larrouy M.C, Bottner P. Predicting N transformations from organic inputs in soil in relation to incubation time and biochemical composition. *Soil Biology & Biochemistry* 2003;**35**:353-363.
- [29] Kaboré W.T, Pansu M, Hien E, Houot S, Zombré N.P, Masse D.. Usefulness of TAO model to predict and manage the transformation in soil of carbon and nitrogen forms from West-Africa urban solid wastes. *Waste management* 2011;**31**: 154-167.
- [30] Pansu M, Gautheyrou J. *Handbook of soil analysis - Mineralogical, organic and inorganic methods*. Springer, 2006.
- [31] Brookes P.C, Kragt J.F, Powlson D.S, Jenkinson D.S. Chloroform fumigation and the release of soil nitrogen : the effects of fumigation time and temperature. *Soil Biology & Biochemistry* 1985;**17**: 831-835.
- [32] Joergensen R.G. The fumigation-extraction method to estimate soil microbial biomass: Calibration of the k(EC) value. *Soil Biology & Biochemistry* 1996;**28**: 25-31.
- [33] Coûteaux M.M, Sarmiento L, Bottner P, Acevedo D, Thiéry J.M . Decomposition of standard plant material along an altitudinal transect (65-3968 m) in the tropical Andes. *Soil Biol. Biochem.* 2002;**34**:69-78.
- [34] Braakhekke WG, De Bruijn A.M.G. Modelling decomposition of standard plant material along and altitudinal gradient: a re-analysis of data of Coûteaux et al (2002). *Soil Biol. Biochem.*, 2007;**39**: 99-105.