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Procedia Environmental Sciences 19 (2013) 96 – 105

Procedia Environmental Sciences

Four Decades of Progress in Monitoring and Modeling of Processes in the Soil-Plant-Atmosphere System: Applications and Challenges

Modelling the functional role of microorganisms in the daily exchanges of carbon between atmosphere, plants and soil

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Abstract

There has been considerable research on organic carbon (OC) stocks in the upper layer of the soil but it has focused on semi-mechanistic predictions of OC stocks in the long term rather than on microbial processes acting on OC transformations. Published data lack of reference concerning the modelling of the short-term exchanges between atmosphere, plants, rhizobia and other microorganisms of soil. We think it is because the mechanistic role of microorganisms is poorly considered in most of the existing models. Compartmental theory is the most used to model the complex system of OC forms, with linear or no-linear propositions. Sometimes, the models did not consider explicitly an active microbial compartment and were often over parameterized. In contrast, the MOMOS proposition defined linearly the functional role of microorganisms with only a no-linear term linked to microbial respiration. It uses only 7 kinetic parameters having a clear ecological definition and being related to climate (all parameters), soil texture or pH (microbial respiration), and biological properties of debris inputs (enzymatic breakdown of plant debris and microbial mortality). The 3 other parameters (rates of humus stabilisation and enzyme assimilation of labile and stable humus) were found linked only to climate, suggesting that quality of humified materials should be more constant than OC forms from living materials. In coupling with soil water and production modules, the model emerges as a new theoretical basis to describe the life cycle and its applications to agro-ecology and global change.

Selection and/or peer-review under responsibility of the Scientific Committee of the conference

Keywords: Modelling ; Carbon ; soil ; plant; organic matter

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1878-0296
Selection and/or peer-review under responsibility of the Scientific Committee of the Conference
doi:10.1016/j.proenv.2013.06.011

1. Introduction

More of 200 models have been proposed in the last decades to describe part or whole C cycle in soils [1]. But the proposed models were often over-parameterized, included parameters not always linked to environmental conditions, and generally did not consider the real functional role of microorganisms. This presentation aims to present the genesis of the MOMOS model which is centred on microbial functioning and appears very sensitive to meteorological, edaphic and biological conditions. In contrast with other published propositions which need long term comparisons to quantify significant C transfer between soils and atmosphere, our experimental work aimed to answer to 2 questions: (i) could MOMOS predict the daily evolution at short term of leaving and dead forms of organic carbon in complex systems, (ii) could we couple the equations of OC decomposition with different equations of OC production and propose a new theory for agro-ecology and global change**.**

2. Material and methods

2.1. The MOMOS equation system

It 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:

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

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:

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

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 [2,3], 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 [2]. $f(\theta)$ is the function of the soil water content normalised to the water holding capacity (*WHC*) of the soil [2]:

$$f(\theta) = \mathrm{MIN}\left(\frac{\theta}{WHC}, 1\right) \qquad (3)$$

The soil water content (θ) was predicted using the SAHEL model [4], 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 **A** and vector **x** for the model are:

$$\mathbf{A} = \begin{bmatrix} -k_{\mathrm{VL}} & 0 & 0 & 0 & 0 \\ 0 & -k_{\mathrm{VS}} & 0 & 0 & 0 \\ k_{\mathrm{VL}} & k_{\mathrm{VS}} & -\left(q_{CO_2} + k_{\mathrm{MB}}\right) & k_{\mathrm{HL}} & k_{\mathrm{HS}} \\ 0 & 0 & k_{\mathrm{MB}} & -\left(k_{\mathrm{HL}} + k_{\mathrm{HS}}\right) & 0 \\ 0 & 0 & 0 & k_{\mathrm{HLS}} & -k_{\mathrm{HS}} \end{bmatrix} \quad \text{and}$$

$$\mathbf{x} = \begin{bmatrix} x_{\mathrm{VL}} \\ x_{\mathrm{VS}} \\ x_{\mathrm{MB}} \\ x_{\mathrm{HL}} \\ x_{\mathrm{HS}} \end{bmatrix} \qquad (4)$$

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

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

where $q_{\mathrm{CO_2}}$ is the metabolic quotient of the microbial biomass:

$$q_{\mathrm{CO_2}} = k_{resp} \frac{x_{MB}}{C^0_{\mathrm{MB}}} \qquad (6)$$

where C^0_{MB} 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 ($F_{0\text{-}20}$) by the transfer function using the two sites used for calibrating the model plus the six sites used for validating the model [2]:

$$k_{resp} = -\,0.0008\, F_{0\text{-}20} + 0.062 \qquad (7)$$

Alternately another transfer function linking k_{resp} to soil pH can be used [2]. 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 14) [5]. 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 d^{-1},
- optimum rate of enzymatic digestion of stable humus k_{HS} = 0.00005 d^{-1},
- optimum rate of chemical stabilisation from labile humus to stable humus k_{HLS} = 0.0003 d^{-1}.

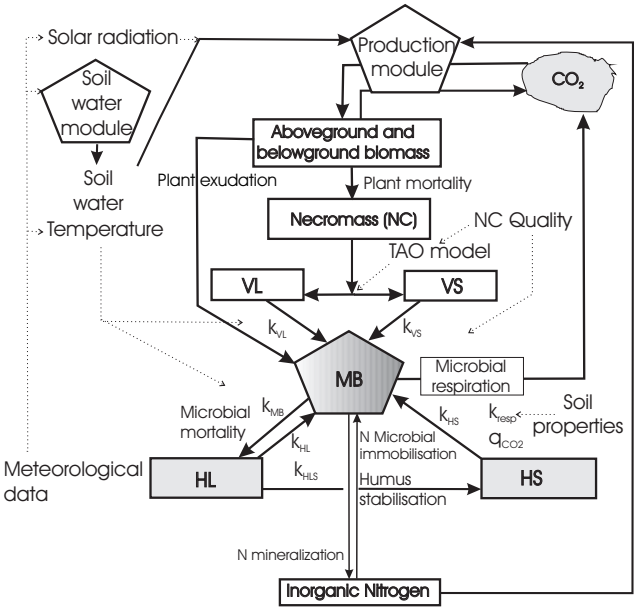

Fig. 1 – The MOMOS model, coupled with soil water and production modules: MB is microbial biomass, VL and VS are the labile and stable debris of vegetal origin entering the soil, HL and HS are the labile and stable humus fractions, k_{VL}, k_{VS}, k_{HL}, and k_{HS} are the daily rates of enzymatic breakdown of VL, VS, HL, and HS, respectively, k_{MB} is the daily rate of microbial mortality, k_{resp} is the daily rate of microbial respiration, q_{CO2} is the MB respiratory quotient and k_{HLS} is the daily rate of humus stabilisation

2.2. 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 ^{14}C 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:

$$\dot{\mathbf{x}} = f(T) f(\theta)\, \mathbf{A}\, \mathbf{x} \tag{8}$$

$$\mathbf{x} = \begin{bmatrix} x_{VL}^{0} \\ x_{VS}^{0} \\ 0 \\ 0 \\ 0 \end{bmatrix} \tag{9}$$

2.3. Formulation for C evolutions in agro-ecosystems

The previously defined matrix **A** and its relationships with climate, soil texture (Equation 7) and quality of organic inputs were preserved. So, 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:

$$\dot{\mathbf{x}} = f(T)f(\theta)\ \mathbf{A}\ \mathbf{x} + \sum_{j=1}^{5} \mathbf{B}j \qquad (10)$$

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 [6] used in calibration experiment [7,8],
- roots, shoots and symbiotic nodules in the Mauguio intercropped system [9]:
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 [6] was used; for wheat-fababean intercropping, another production module was defined [9];

qualitative estimate of necromass to divide each input into labile and stable fractions in the MOMOS decomposition processes.

2.4. 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 [3,10-12]. The model has since been validated on tropical materials [13], 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 model [10]:

$$C_o = 7.18\ C_{OM} + 0.14\ Lig/N_{OM} - 3.84 \qquad (11)$$

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 $C_o \leq 0$: $P'_L = 0.35\ fsol + 2.2\ N_{OM} - 0.01\ Lig/N_{OM,}$ 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} *(12)*

where fsol = 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 (Fig. 1), 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 [5]:

k_{VL}= MAX(0.65 - 0.0019 η_{NC}, 0.1) *(13)*

k_{VS} = MAX(0.0037-0.000026 η_{NC},0.00005) *(13')*

An increase of η_{NC} was also found to increase the rate of microbial mortality [8]:

k_{MB} = MIN(0.42 + 0.0012 η_{NC}, 0.8) *(14)*

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.

2.5. Data collection for calibration and validation

^{14}C and ^{15}N 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 ^{14}C and ^{15}N and ^{14}C and ^{15}N 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.

2.6. 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 [14]. 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 [15]. 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 kc = 0.45 [16].

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 µg 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 µmol 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 [9].

3. Some results

3.1. MOMOS validation

MOMOS allowed to adequately predict total and microbial ^{14}C dynamics 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 [17,18]. Furthermore, k_{resp} was the only parameter found bond to soil properties, demonstrating that the function of microbial respiration alone was soil dependent. Overall, this study demonstrated that climate, together with basic soil properties as texture and pH, were the main drivers of soil respiration and 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.

3.2. Short term microbial exchanges in fallow systems

Both parameter values calibrated on ^{14}C and total C input from roots estimated with the fallow production model FAPROM [6] has been used to predict carbon evolution [8] in the Bolivian puna (Fig. 2). The model enabled to explain the observed values of total-C as the sum of the predicted values of (i) evolution of initial total-C, (ii) evolution predicted by FAPROM of total carbon deposited by roots during the experiment and by MOMOS for remaining amount of the deposited C.

It validated another time the MOMOS structure: parameters obtained with ^{14}C tracer enabled to predict total-C using additional carbon input from root. This result described the turnover of C brought from photosynthesis in fallow systems and enabled to propose a new modelling tool to predict in situ the C input from root. The other methods study the transfer of labelled CO_2-C from leaves to roots in controlled conditions; conversely the proposed tool uses the model previously calibrated by ^{14}C tracer experiment to quantify the inputs of ^{12}C from leaves to roots in field conditions.

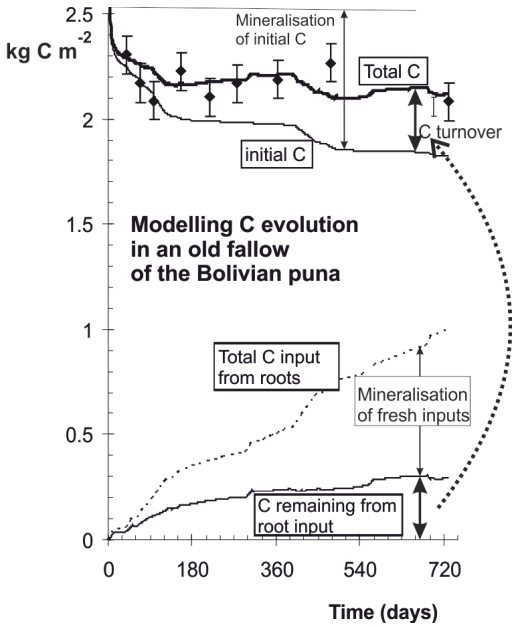

Fig. 2. Modelling of the turnover of carbon in a fallow plot of the Bolivian puna [6]

3.3. Short term microbial exchange in complex agro-systems

Another C production module was written [9] in place of Faprom [6] to describe the growth of plant organs in cereal legume intercropping and another time associated to the MOMOS schemes (Fig. 1); This module assumed that plant growth was also controlled by the climate correction factor used for microbial functioning (equation 1), and by aerial C of cereals and legumes. The production was allocated to plant organs and nodules for symbiotic N fixation by partition coefficients and time functions. Other parameters and time functions regulated shoot and root mortalities and root respirations. The MOMOS model, associated to the equation system calculated from ^{14}C experiments, and then coupled with this particular physiological module of plant growth in a cereal-legume system emerges as a new tool to quantify physiological parameters as growth rates, shoot and root mortalities and root respirations, which are of prime importance in agronomy and environmental studies, and difficult to estimate by other methods.

Fig. 3a reproduces the measured and daily predicted values of microbial OC during one year of cereal-legume intercropping. It illustrates the growth of microorganisms associated to plant growth and OC brought to soil from the part lost from photosynthesis.

Fig. 3b shows that the sum of predicted C from the mortality of plant roots and shoots, which provide the C substrates for microbial growth, was greater than the daily total CO_2-C respired by microorganisms and plant roots over the whole cultivation period. The total C input increased again at harvest where 80%

of leaf and stem material was modelled as falling to become litter, in addition to decomposition of the remaining shoots and roots by natural mortality. This showed that the intercropping was a sink of OC during all the cultivation period and became a source of OC about two months after the harvest, but during a period where all processes were slowed by the winter conditions. The increase of measured and predicted total OC during the intercropping season was not significant, as in other modelling studies which need long term situations to detect effect of land use change on net OC sequestration or mineralisation. But total OC is not the only variable of interest; MOMOS modelled most of carbon compartments as almost stable except labile humus of microbial origin which was found increasing during the plant growth. From this study, microbial metabolites represent the short term reserve for microbial activity and available fertilizing elements, possibly a key for ecological intensification

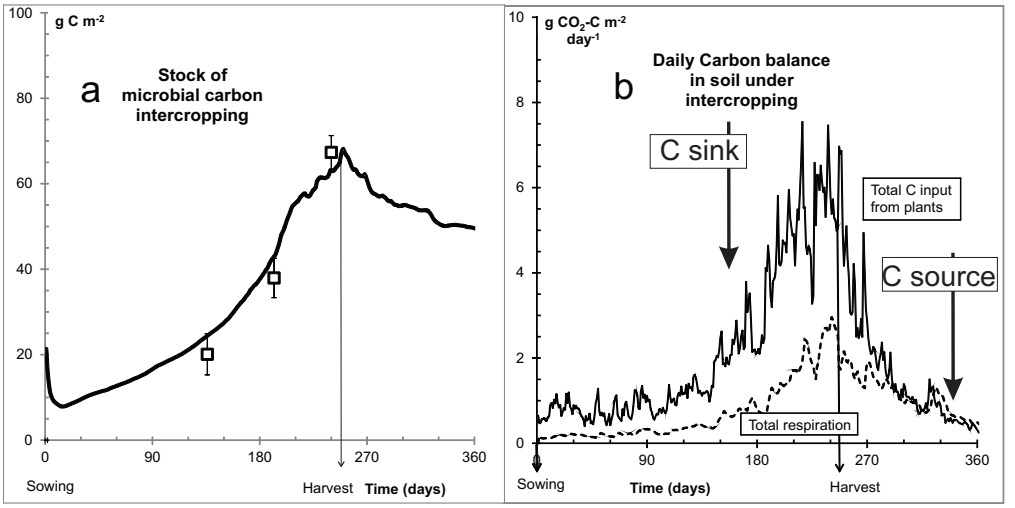

Fig. 3. a) measured and modelled daily evolution of the microbial C stocks during the growth of durum wheat and faba bean in intercropped plots; b) modelled evolution of total C inputs and outputs in soil during intercropping. [9].

3.4. Modelling the key role of microorganisms

MOMOS 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. The equation system respects the principle of parsimony (Ockham's razor) since it uses only seven kinetic parameters all linked to climate (equation 1), and additionally linked to the quality of organic inputs (equations 12-14), and soil texture (equation 7). Proposed initially to predict the evolution of ^{14}C tracer in two ecosystems [7], it was then validated in six other contrasted ecosystems of the tropical area [2]. It has been successfully used to quantify the turnover of OC in Andean fallow ecosystems [19] and to regulate the daily exchanges of C between plant organs, nodule rhizobia, microorganisms and atmosphere in cereal legume intercropping in Mediterranean conditions [9]. In coupling with soil water and production modules, the MOMOS equation system emerges as a new theory for agro-ecology and global change.

Acknowledgements

This work was part of international programs Tropandes (EU), Ecos-Nord (France-Venezuela), and Fabatropimed (Agropolis Fondation of Montpellier, *France*). The authors thank Lina Sarmiento, ULA, Venezuela, and Jean-Jacques Drevon (UMR Eco&sols, Supagro, Cirad, Inra, IRD, http://www.montpellier.inra.fr/ecosols), coordinators of the programs.

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