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MODELISATION DES CYCLES C ET N DANS LES SYSTEMES SOLS-CEREALES-LEGUMINEUSES

Soutenue le 28 Novembre 2013 devant le jury composé de :

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Résumé

A l'interface des échanges sol-plante-atmosphère, la couche supérieure du sol contient la plus grande réserve de carbone organique (Corg) et d'azote (N) potentiellement disponible pour la croissance des plantes, elle joue un rôle fondamental dans la nutrition et l'équilibre de la planète.
Dans les sols Tunisiens, une première quantification de N, faisant suite à celle de Corg, nous a permis de mettre en évidence une fragilité des réserves, et la nécessité de managements préservatifs des terres et des pratiques agricoles. Nous nous sommes alors rapprochés des nombreuses études de modélisation des variations de stocks de Corg et N suite à des changements d'usage. Cependant, la majorité des références publiées concernait les évolutions globales à moyen ou plus long terme (de plusieurs années à plusieurs décades) et manquaient de précision sur la prédiction mécaniste des transferts journaliers entre les plantes, les compartiments du sol et l'atmosphère. Selon nous et d'autres auteurs, ces études ne prenaient pas suffisamment en compte le rôle crucial des micro-organismes dans les échanges. Ceci nous a orientés vers le modèle MOMOS centré sur l'écologie fonctionnelle de la biomasse microbienne (BM), avec des paramètres pour sa croissance, sa mortalité, et sa respiration étroitement liés aux conditions climatiques, édaphiques, et culturales.
L'objectif était d'étudier à court terme les cycles Corg et N dans les systèmes complexes de production céréalière intensifiés par couplage avec des légumineuses à graines fixatrices d'azote en milieu méditerranéen. Il comportait deux défis : (i) coupler les équations de décomposition avec des modules d'eau du sol, et de production végétale vers un nouvel outil pour l'agro-écologie et le changement global (ii) faire tourner l'ensemble en milieu méditerranéen calcaire, avec des équations proposées et validées en milieu tropical acide.
Le dispositif agronomique comportait des associations comparées à des rotations blé dur-féverole en culture biologique sans fertilisation depuis treize ans. Les simulations ont été trouvées en bonne concordance avec les données mesurées et celles de la littérature. Croissances végétales et fonctionnement microbien apparaissent prédits par les mêmes fonctions climatiques et co-limités par la température en hiver et l'humidité en été. Dans les parcelles expérimentales peu fertiles, la plus grande part de Corg photo synthétisé était modélisée comme allouée aux racines et perdue pour les parties aériennes et le rendement des récoltes. Ces pertes étaient simulées vers la respiration de croissance des racines de céréales, probablement pour la recherche des nutriments, et la mortalité des racines de légumineuses alimentant la croissance des décomposeurs et peut-être des symbiotes fixateurs d'azote. Au total, le système de culture associée était modélisé comme un puits de plus 4 Mg Corg ha^{-1} durant la saison culturale, mais uniquement dans Corg labile d'origine microbienne. Ce compartiment était aussi simulé comme la principale réserve de N potentiellement disponible pour les organismes vivants, très supérieure à celle des micro-organismes, elle-même supérieure à celle de la céréale et égale à celle de la légumineuse. La modélisation des échanges microbiens avec N minéral montrait une immobilisation nette d'azote juste compensée par la fixation symbiotique. Elle a permis de mieux comprendre les flux de Corg et N entre atmosphère, légumineuse, micro-organismes et céréale et de proposer des solutions agronomiques pour l'amélioration des systèmes de culture en association ou rotation.

Mots clés : Modélisation cycle biogéochimique, Carbone, Azote, Sol, Tunisie, France.

ABSTRACT

At the interface of soil-plant-atmosphere exchanges, the top layer of soil contains the largest part of organic carbon (Corg) and nitrogen (N) potentially available for plant growth; this soil layer plays a fundamental role in nutrition and equilibrium of earth.

In Tunisians soils, a first quantification of N, following that of Corg, has allowed us to highlight the fragility of the reserves, and the need of conservation managements of lands and improvement of agricultural practices.

Many studies of literature data try to model the changes of Corg and N stocks due to land use changes. However, most of the published references concern overall trends at medium or longer term (several years to several decades) and lack of precision in mechanistic prediction of daily transfers between plants, soil compartments and the atmosphere. Conjointly with other authors we think that the published studies do not take sufficient account of the crucial role of microorganisms in the exchange modelling. This directed us to the MOMOS model centered on the functional ecology of microbial biomass (MB), with parameters for growth, mortality and respiration of MB, closely related to climate, soil conditions and the quality of organic inputs.

Our objective was to study the Corg and N cycles during a cropping season in complex cereal-legume systems for intensification by symbiotic N fixation in the Mediterranean environment. It included two challenges: (i) to couple the equations of decomposition with a model of soil water and modules of quantitative and qualitative vegetal production toward a new tool for agro-ecology and the global change (ii) to run this tool in Mediterranean calcareous conditions, with equations proposed and validated in tropical acid areas.

The agronomic experiment included an intercropping of durum wheat and faba bean compared with pure cropping both managed in organic farming without any fertilizer addition during the last thirteen years. The model predicted ecophysiological parameters in accordance with published references and simulated accurately the measured data. Plant growth and the microbial functioning appear linked to the same climate equations and co-limited by temperature in winter and availability of water in summer. In these unfertile plots, the largest part of Corg photo-synthesized was modelled as allocated to roots and lost for the aerial parts and grain yields. These losses were simulated mainly (i) to increase root respiration of cereal, probably as energy source for root growth in order to find nutrients, and (ii) to increase the mortality of legume roots as energy source for the growth of decomposers and perhaps the growth of symbiotes for fixation of atmospheric N. Overall, the intercropping system was modeled as a sink of over 4 Mg ha^{-1} of Corg during the growing season, but only in the compartment labile of microbial origin. This compartment was also simulated as the main reserve of N potentially available for living organisms, much higher than N stock of microorganisms, which is itself higher than N stored in the cereal and similar to N stored in the legume. The modeling of microbial exchange with inorganic N showed a net immobilization of N just compensated by the symbiotic fixation. It helped to better understand the flows of Corg and N between atmosphere, legume, microorganisms and cereal, and to propose solutions for improving agricultural cropping systems in combination or rotation.

Keywords: Modeling, biogeochemical cycle, Carbon, Nitrogen, Soil, Tunisia, France.

نمذجة دورات الكربون والنيتروجين في التربة وعلاقتها بزراعة الحبوب/البقول

ملخص

عند مستوى التبادل ما بين التربة-النباتات-الغلاف الجوي، تحتوي الطبقة العلوية من التربة على معظم المخزون من الكربون العضوي والنيتروجين والتي بالإمكان أن تستعمل من طرف النباتات لنموها، كما تلعب أيضا دورا هاما في الغذاء والتوازن على سطح الأرض.
في تربة البلاد التونسية التعداد الأولي لمخزون النيتروجين والذي سبق بتعداد لمخزون الكربون العضوي، مكننا من استنتاج هشاشة المخزون العضوي وضرورة المحافظة على الأراضي الزراعية وطرق الزراعة.
ولهذا الغرض اعتمدنا على عديد الدراسات التي تعتمد على نمذجة تغير مخزون الكربون العضوي والنيتروجين إثر تغيير استعمالات الأرض. ولكن أغلبية الدراسات المنشورة تطرقت إلى التطورات الجملية على مستوى متوسط أو بعيد المدى (عديد السنوات أو عديد عشرات السنين) وتنقصهم الدقة في التوقع في التبادلات الميكانيكية اليومية ما بين النباتات، التربة والغلاف الجوي.
حسب تقديرنا كما هو الشأن لدى بعض الباحثين الآخرين، تلك الدراسات لا تأخذ بالقدر الكافي أهمية الكائنات الحية الدقيقة المتواجدة بالتربة في التبادلات اليومية. وهذا ما من شأنه أن وجهنا إلى العمل بنموذج MOMOS الذي ترتكز عليه هذه الأطروحة والذي يرتكز على بيئة الكائنات الحية الدقيقة مع بعض المعلومات التابعة لها على غرار نموها، موتها، وخاصة تنفسها المرتبط بالظروف المناخية، الغذائية، والزراعية.
وكان الهدف هو دراسة الكربون العضوي والنيتروجين داخل الأراضي ذات الأنظمة المعقدة التي يتداول فيها على زراعة الحبوب بطريقة مكثفة والمقترنة بالبقوليات ذات الحب المثبتة للنيتروجين في تربة منطقة البحر الأبيض المتوسط. وتشتمل هذه الدراسة على تحديين إثنين: (1) إقتران معادلات التحلل مع وحدات ماء التربة، الإنتاج النباتي، وصولا إلى وسائل جديدة في الفلاحة البيئية والتغيرات المناخية. (2) تدوير النموذج وسط محيط بيئي متوسطي غني بالكلس، مع معادلات مقترحة ومعدلة في محيط استوائي حامض.
يتألف الجهاز الفلاحي للتجربة من خلال الزراعات المتداولة والمزدوجة حبوب/بقول في ظروف بيولوجية بدون إضافة الأسمدة لمدة ثلاثة عشرة سنة. النتائج المتحصل عليها عبر النموذج تتماشى مع ما هو متحصل عليه عبر التجارب والتحاليل، كذلك نفس النتيجة بالنسبة لتطور النباتات وعمل الكائنات الدقيقة، ولكن يمكن أن تكون محدودة بالعوامل المناخية، كالحرارة في فصل الشتاء والرطوبة في فصل الصيف. في الحقول التجريبية قليلة الخصوبة، الأغلبية في الكربون العضوي المتحصل عليه عبر التركيب الضوئي قمنا بنمذجته على أساس أنه معطى للجذور وتخسره النبتة عبر أجهزتها الفضائية وعبر المحصول.
هذه الخسائر حاكيناها نحو التنفس ونمو الجذور للحبوب، وموت الجذور للبقوليات يغذي الكائنات الحية الدقيقة المثبتة للنيتروجين.
إجمالا، كانت منظومة الزراعة المتداولة تمثل بئرا للكربون بقيمة تتجاوز 4 مغ من الكربون العضوي في الهكتار الواحد، ولكن فقط بالنسبة للكربون العضوي المتحرك الذي مصدره الميكروبات والكائنات الحية الدقيقة. هذا القسم كان أيضا أثناء المحاكاة يعتبر أهم مصدر لمخزون النيتروجين المتاحة للكائنات الحية، والذي يتجاوز كثيرا ما يلزم الكائنات المجهرية، والتي بدورها تتجاوز ماهو متاح من الحبوب والذي يضاهي ما هو متاح من البقول. أن نمذجة التبادل ما بين بكتيريات التربة والنيتروجين المعدني يبين تثبيتا واضحا للنيتروجين معوض عن طريق التثبيت التكافلي. وقد ساهم ذلك في فهم التدفق للكربون العضوي والنيتروجين ما بين البقوليات، الكائنات الدقيقة المجهرية والحبوب، ومكننا من إقتراح حلول زراعية لتحسين نظم الزراعة المتداولة والمزدوجة.

كلمات مفاتيح: نمذجة الدورة البيوجيوكيميائية، الكربون، النيتروجين، التربة، تونس، فرنسا.

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Fig.7 a- the measured values (open squares with 95% confidence intervals) and the predicted C stock in nodules for symbiotic N fixation (left axis, continuous line for intercropping, dashed lines for pure faba bean cropping) and the predicted nodular respiration (right axis, continuous line for intercropping, dashed line for pure cropping), b- the predicted relationships between shoot C and nodule C of faba bean in intercropping (continuous line) and in monoculture (dashed line)

Figures chapitre 5:

Fig. 1 Flow diagram of N exchanges between plant organs and microorganisms in the MOMOS model.

Fig. 2 Flows of organic N directed by microorganisms: a) predicted and measured values with 95% confidence intervals of soil total N, and predicted N in plant debris and labile and stable humified compartments, b) daily exchange of N between microorganisms, plant debris and labile humus, c) daily balance of input and output of organic N in microorganisms.

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INTRODUCTION GENERALE

Introduction générale

La couche la plus externe de la croûte terrestre couramment appelée « *pédosphère* » est le résultat de l'interaction des quatre grands compartiments du globe, à savoir la lithosphère, l'hydrosphère, l'atmosphère et la biosphère (Calvet, 2003 ; Duchoufour, 2001). De ce fait, les sols représentent une exclusivité de la planète Terre, ils représentent un foyer pour de nombreux organismes et le lieu d'innombrables transformations biogéochimiques et de processus de transferts (Bonneau et Souchier, 1994). En outre, les sols stockent de nombreuses substances qui sont essentielles pour maintenir la vie humaine et les processus des écosystèmes. Par conséquent, les sols ont été au centre de la recherche depuis plus d'un siècle, la science du sol appelée « *Pédologie* » a des liens profonds avec la géodynamique externe, l'écologie, l'agriculture et la conservation de la nature (Aubert et Boulaine, 1980).

Les changements d'usage des terres apparaissent responsables d'une part non négligeable estimée à 20-30% de l'augmentation des gaz à effet de serre liée au

réchauffement climatique (GIEC, 2007). Ils entraînent également un abaissement de la durabilité des systèmes de cultures annuelles ou arboricoles par diminution des réserves organiques, ainsi que des pertes dans l'aquifère préjudiciables à l'alimentation et à la santé. La connaissance précise et la capacité de pouvoir modéliser les flux de carbone (C) apportés par photosynthèse, transmis au sol par exsudation racinaire et mortalité végétale, puis restitués à l'atmosphère par respiration microbienne ou partiellement accumulés dans le sol par métabolisation microbienne, apparaissent une priorité de la recherche environnementale et agronomique (Schlesinger et Andrews 2000 ; GIEC, 2007). La végétation fournit des débris végétaux qui constituent une litière sur la surface du sol. Dans les sols agricoles, ces débris végétaux et les débris racinaires correspondent aux résidus de culture. Ils sont dégradés sous l'action de la faune et de la microflore du sol (bactéries et champignons). La matière organique est contrôlée par les microorganismes hétérotrophes qui assurent le recyclage des nutriments et stabilisent une partie des composés en matières plus récalcitrantes, les humus. Leurs besoins métaboliques règlent la stœchiométrie à l'intérieur de leurs cellules et les transformations qu'ils réalisent : décomposition, minéralisation et humification. Une information sur la qualité de la matière organique et son aptitude à la biodégradation est donnée par le rapport C/N, ce rapport est généralement utilisé pour expliquer les flux d'échange et la richesse en carbone et azote organique qui en découle. Ce concept est repris dans de nombreux modèles voués à la décomposition des matières organiques du sol (MOS).

La modélisation est indispensable pour étudier la dynamique du carbone et de l'azote dans le sol. De nombreux modèles compartimentaux de décomposition des matières organiques ont été élaborés, parmi lesquels on peut classer des modèles linéaires et des modèles non linéaires. Dans les premiers, les flux de sortie d'un compartiment sont liés uniquement au contenu de ce compartiment selon une cinétique d'ordre 1, dans la littérature le plus grand nombre de modèles de décomposition sont de ce type, on peut citer Century (Parton et al., 1987), Daisy (Hansen et al., 1991), DNDC (Li et al., 1997), CO2Fix (Masera et al., 2003), STICS (Brisson et al., 1998), Roth-C (Jenkinson et al., 1987), NCsoil (Molina et al., 1983). Les

composés organiques des litières et MOS sont assimilés à des pools homogènes et indépendants de carbone et d'azote. Les taux de sortie sont spécifiques aux pools. Ils correspondent à une vitesse maximale dans les conditions physico-chimiques optimales pour l'activité des microorganismes. Dans le cas des pools de litières les taux peuvent être déterminés par la nature biochimique (Century, DNDC, NCSoil, CO2Fix, Daisy) et/ou par le type ou la taille des débris (CO2Fix, STICS). Ils sont modulés par des fonctions de limitation traduisant le ralentissement de l'activité des microorganismes par: les conditions climatiques (température et humidité), parfois par la protection des molécules organiques par les argiles (Daisy, Roth-C, DNDC,…), teneur de l'N inorganique (Candy de Franko et al., 1997), teneur de lignine (Century). Le flux de respiration est affecté par ces fonctions de limitations, par contre celui de minéralisation nette d'azote ne l'est pas en général. Le traitement de ces deux flux est particulier et varie d'un modèle à l'autre. La respiration est proportionnelle à la biomasse microbienne les modèles considèrent généralement une perte de CO_2 liée à chaque flux de décomposition, la minéralisation de l'azote étant liée au rapport C/N. Les microorganismes minéralisent de l'N en excès par rapport à sa teneur en C, ou prélève sous forme inorganique la dose nécessaire de l'N en défaut. Enfin, certains modèles prévoient des flux de stabilisation d'origine non biologique. Dans Century, DNDC, Daisy ou NCsoil des humus « récents » sont lentement transférés vers un compartiment d'humus plus stables. Dans Century et Daisy, les composés végétaux les plus récalcitrants peuvent gagner les pools d'humus sans transformation microbienne préalable.

Les modèles non linéaires s'écartent de cette conception classique. La sortie de chaque compartiment est proportionnelle à la fois à son contenu et à la croissance des décomposeurs ou de leurs enzymes. Les microorganismes produisent des enzymes extracellulaires qui dégradent la matière organique. Les microorganismes absorberaient le carbone dissous par les enzymes, induisant de ce fait, une voie indirecte entre la biomasse microbienne et la matière organique du sol (Schimel et Weintraub 2002).

Dans les dernières décennies, plus de 200 modèles avec des niveaux de complexité distincts ont été développés pour décrire des processus biogéochimiques dans le sol.

La plupart sont basés sur la cinétique et les taux stœchiométriques qui forcent les éléments cycliques au sein du sol, les nutriments, et les échanges de carbone avec la végétation et l'atmosphère.

Parmi ceux-ci, MOMOS (Pansu et al., 2010) sur lequel cette thèse s'est penchée, est un modèle de décomposition conçu de manière à limiter les paramètres à des taux de décroissance des compartiments qui ont pu être ajustés grâce à des expériences d'incubation avec traçage isotopique (Pansu et al., 2004 ; 2007 ; 2010). Nous avons émis l'hypothèse que des exercices de modélisation prédictive pourraient donner des renseignements fondamentaux dans la dynamique des agrosystèmes complexes. MOMOS est proche des modèles linéaires dans sa structure. Cependant seule l'expression de la respiration microbienne est non-linéaire : elle est fonction du pool de biomasse microbienne au carré. Cette particularité rend le flux de respiration très sensible aux apports et aux conditions climatiques pour un niveau de biomasse microbienne relativement constant.

Il s'agit d'un modèle, couplé C-N, piloté par les microorganismes, et régi par des paramètres tous liés aux conditions de température et d'humidité, le rendant apte à simuler les impacts liés au changement climatique. Il définit une écologie fonctionnelle de la biomasse microbienne, en la munissant de lois de respiration, de mortalité et d'assimilation des autres compartiments organiques. Cette particularité permet d'apprécier au plus près la séquestration de C et N dans les compartiments labiles et stables d'origine microbienne, et la durabilité des systèmes. Parallèlement aux liens entre climats et fonctions microbiennes, des liaisons MOMOS sont aussi proposées avec la qualité et la forme des apports, et avec les propriétés des sols.

Le travail de thèse s'inscrit dans le contexte de maintien et restauration de la fertilité des sols dans des systèmes méditerranéens de cultures céréalières. L'outil agronomique de base s'appuie sur des associations ou rotations de céréales avec des légumineuses fixatrices d'azote, généralement à graines. Ces systèmes existent déjà localement, mais leurs pratiques de gestion méritent d'être améliorées, particulièrement en ce qui concerne les types d'associations plante-plante et plante microorganismes, et la sélection de génotypes plus performants pour contrer les limitations de la fixation d'azote dues à des déficiences en phosphore. Le but est de

maximiser les flux de carbone et d'azote de l'atmosphère vers les plantes et le sol, et au contraire de minimiser les pertes gazeuses de carbone et d'azote depuis le sol vers l'atmosphère.

Cette étude découlait de la nécessité d'améliorer les fonctions de pédotransfert au niveau des sols argileux et sableux tunisiens et d'évaluer les relations de l'azote (N) de ces réserves organiques avec les propriétés du sol. Des systèmes à faible restitution organique sont susceptibles d'appauvrir dangereusement les faibles réserves en C et N des sols tunisiens. Les modèles mécanistes constituent un outil pour répondre à plusieurs questions pertinentes concernant la dynamique de l'azote et du carbone dans les sols méditerranéens (sols de Mauguio en France). Ils peuvent permettre par exemple de distinguer les compartiments d'origine végétale généralement situés dans des fractions grossières du sol, ou d'origine microbienne plutôt situés dans les fractions plus fines.

La modélisation des échanges de C et N entre l'atmosphère, les plantes, les microorganismes et le sol était le but ultime de notre travail.

Les travaux de cette thèse s'organisent autour de cinq chapitres :

- le chapitre I est une synthèse bibliographique qui positionne la thèse dans son contexte global ;
- le chapitre II traite les modèles de la séquestration de l'azote du sol dans les zones arides explorées avec des fonctions de pédotransfert et des analyses Bayésiennes ;
- le chapitre III est consacré à la modélisation du rôle fonctionnel des micro-organismes dans les échanges journaliers du carbone entre l'atmosphère, les plantes et le sol ;
- le chapitre IV traite l'échange journalier du carbone dans le système : organismes vivants-sol-atmosphère ;
- et le chapitre V traite L'échange journalier de l'azote dans le système : organismes vivants-sol-atmosphère.

Le mémoire s'achève par une conclusion générale reprenant les principaux résultats de la thèse.

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CHAPITRE I

SYNTHESE BIBLIOGRAPHIQUE ET POSITIONNEMENT DU SUJET DANS SON CONTEXTE, OBJECTIFS DE L'ETUDE

INTRODUCTION

Le carbone (C) et l'azote (N) sont avec l'hydrogène et l'oxygène, les deux éléments constitutifs de la vie sur Terre. Le carbone est à la base des trois grandes familles de nutriments (glucides, lipides et protéines) et l'azote est la composante fondamentale des protéines (dont les enzymes) et des acides nucléiques. Les formes organiques de C et N propres aux matériaux vivants puis morts sont donc à l'origine par mortalité des molécules des Matières Organiques des Sols (MOS).

Les formes inorganiques de C et N sont présents dans tous les écosystèmes terrestres. Dans l'atmosphère, le carbone est présent sous forme de dioxyde de carbone (CO_2), ainsi que sous d'autres formes de gaz carbonés en quantités infimes comme le méthane (CH_4) et le monoxyde de carbone (CO). Dans la lithosphère, le C est un constituant majeur des roches carbonatées. Les carbonates sont aussi présents sous forme dissoute dans les océans et eaux douces. Les flux de carbone entre les quatre grands compartiments terrestres (atmosphère, hydrosphère, biosphère et lithosphère) déterminent le cycle global du carbone (Schimel, 1995). Les flux dominants de ce cycle sont ceux les échanges entre le CO_2 de l'atmosphère, les molécules organiques de la biosphère (sols, végétaux et animaux) et les carbonates de l'hydrosphère (Raich et Schlesinger, 1992).

Environ 98% de l'azote sur Terre se trouve dans la partie solide de la Terre : les roches, les sols et les sédiments. Le reste se déplace dans un cycle dynamique impliquant l'atmosphère, l'hydrosphère (les océans, les mers, les lacs et les cours d'eau) et la biosphère. L'azote dans l'atmosphère existe principalement sous forme d'azote moléculaire (N_2), qui constitue à lui seul 78% des gaz de l'atmosphère. Le reste est sous forme de traces (ammoniac gazeux, protoxyde d'azote, acide nitrique et, particules de nitrate, et l'azote organique). Les composés atmosphériques d'azote rejoignent les sols et les eaux par des dépôts humides et secs. Au cours du cycle de l'azote, les molécules sont transformées à travers de nombreux processus biogéochimiques, pour la plupart de type redox. Dans l'hydrosphère, l'azote existe sous forme organique ou inorganique soluble.

Le cycle global de carbone est l'un des cycles les plus importants et complexes sur Terre, il influence directement plusieurs systèmes physiques et biologiques et il influence également les températures globales. L'intérêt de la communauté internationale pour le cycle global du carbone s'est accru considérablement au cours des deux dernières décennies en raison du réchauffement climatique lié à la hausse des émissions anthropiques de CO_2 dans l'atmosphère.

Dès 1896, le chimiste suédois Svante August Arrhenius (1859-1927) a souligné l'importance de l'effet de CO_2 atmosphérique sur la température globale de la Terre, ainsi que la modification de la température terrestre qui suivrait l'augmentation de la concentration de CO_2 atmosphérique. Cependant, ce sujet de recherche était peu considéré jusqu'en 1958, lorsque les mesures en continu des concentrations atmosphériques de CO_2 ont été initiées à Mauna Loa à Hawaï par le scientifique américain Charles David Keeling (1928-2005). Toutefois, le véritable élan de la recherche sur le cycle de C a commencé en 1980 par les indices fournis par les mesures effectuées sur les sédiments océaniques, puis sur les carottes glaciaires. Les carottes de glace de la station russe de Vostok, en Antarctique, ont montré que les concentrations atmosphériques en CO_2 étaient beaucoup plus faibles dans les périodes glaciaires par rapport à l'époque contemporaine (Petit et al., 1999). Ces résultats ont poussé la communauté scientifique à se concentrer sur les conséquences possibles des émissions anthropiques de CO_2.

La concentration en CO_2 atmosphérique a augmenté de 117,6 ppm au cours des 260 dernières années (d'environ 275 ppm à l'ère préindustrielle en 1750 (Denman et al., 2007) à 392,6 ppm en 2010 (Blasing, 2010)). Cette progression est principalement due aux activités humaines, impliquant l'utilisation des combustibles fossiles, la fabrication de ciments, les changements d'utilisation des terres et la déforestation. Les travaux du GIEC, (2007) prévoient une augmentation de la température moyenne de 2 à 6°C et avec des perturbations climatiques se traduisant par phénomènes météorologiques extrêmes (inondation et/ou sécheresse) plus fréquents et de graves implications pour les écosystèmes.

Outre le CO_2, d'autres gaz à effet de serre (GES) comme le méthane (CH_4), l'oxyde nitreux (N_2O) et l'oxyde nitrique (NO) contribuent au réchauffement global. La concentration moyenne mondiale de CH_4 a plus que doublé entre l'ère préindustrielle : de 700 ppb en 1750 (GIEC, 2007) à 1758 ppb en 2010 (Blasing, 2010). Ces dernières années, le taux de croissance du CH_4 atmosphérique semble stagner, voire même diminuer, mais aucune tendance claire ne se dégage pour le futur (Forster et al., 2007). Les zones humides représentent environ 80% du total des émissions naturelles de CH_4 avec de petites contributions des océans, des forêts, des termites, des incendies et des combustibles fossiles (GIEC, 2007).

Le protoxyde d'azote N_2 (ou oxyde nitreux), contribue à hauteur de 6% à l'effet de serre anthropique (GIEC, 2007) avec une progression de 0,25% par an (de 270 ppb à l'époque préindustrielle à 324 ppb en 2010 (Blasing, 2010)). L'oxyde nitreux a une origine double, naturelle (les sols, les océans et l'oxydation du NH_3 atmosphérique) et anthropique. Les émissions anthropiques de N_2O proviennent de la combustion de la biomasse et de la dénitrification par les microorganismes dans les sols.

L'utilisation des hydrocarbures fossiles, les changements d'affectation des terres, la déforestation et la combustion de la biomasse sont les principales causes de la perturbation des cycles de C et d'N. Pendant les années 1990, la déforestation à l'échelle internationale a eu lieu à un taux d'environ 13 millions ha/an de 1990 à 2005. Le monde a perdu 3% de sa superficie forestière totale (FAO, 2007). La plupart du C stocké dans la biosphère terrestre (végétaux et sols) est associée à la forêt. Quand cette dernière est défrichée et/ou brûlée la plus grande partie du carbone est minéralisé sous forme de CO_2.

1. LES STOCKS DE CARBONE ET D'AZOTE DANS LES ECOSYSTEMES TERRESTRES

L'importance des échanges de C et d'N entre les sols et l'atmosphère ne réside pas seulement dans leur implication dans le réchauffement global, mais aussi dans leur rôle dans la qualité et le rendement des sols.

Le carbone et l'azote constituent 95% de la masse de la biosphère terrestre et sont deux des six principaux éléments chimiques (C, H, O, N, P, S) constituants les tissus vivants. Le carbone est perpétuellement absorbé, libéré, et recyclé par une série de processus biologiques et chimiques, naturels et anthropiques. Le processus de photosynthèse chez les plantes détermine leur croissance. Lorsque les résidus végétaux et racinaires se décomposent, le carbone qu'ils contiennent se transforme en partie en CO_2 (minéralisation) et composés formant la matière organique du sol (MOS) par les processus d'humification. La nature et la quantité de MOS conditionne la qualité du sol. L'azote est le facteur limitant de la croissance des plantes dans la plupart des écosystèmes.

L'intérêt récent porté aux sols en ce qui concerne les cycles globaux de C et d'N provient de leurs fortes capacités à stocker le carbone et l'azote.

1.1 LES FORMES ET LES QUANTITES DE CARBONE ET D'AZOTE SUR LA TERRE

1.1.1 Le carbone

a) Les composés du carbone

Il y a plus d'un million de composés carbonés dont plusieurs milliers sont nécessaires pour la vie sur Terre. Le carbone sous sa forme élémentaire est connu sous ses formes amorphes, graphite et diamant. Les atomes de carbone peuvent changer leur état d'oxydation de +IV à -IV. Les composés carbonés les plus abondants (dioxyde de carbone et carbonates) sont des formes oxydées (+IV). Dans la lithosphère, les carbonates sont présent sous la forme de $CaCO_3$, $Ca/Mg\ (CO_3)_2$ et $FeCO_3$ principalement. Dans les eaux, les carbonates existent sous les formes H_2CO_3, HCO_3^-

et CO_3^{2-}. Dans l'atmosphère, le carbone de monoxyde de carbone (CO) est à l'état d'oxydation +II le méthane (CH_4) constitue la forme la plus réduite (-IV).
Parmi les sept isotopes du carbone (^{10}C, ^{11}C, ^{12}C, ^{13}C, ^{14}C, ^{15}C, ^{16}C), deux (^{12}C et ^{13}C) sont stables et cinq (^{10}C, ^{11}C, ^{14}C, ^{15}C, ^{16}C) sont radioactifs à temps de demi-vie variant entre 0,74 siècle pour le (^{16}C) et 5726 années pour le (^{14}C) (Holmen, 2000). Le ^{12}C est l'isotope le plus abondant sur Terre, il constitue à lui seul 99% du C des écosystèmes. La variation isotopique constitue un outil important pour le calcul des flux de C entre les différents réservoirs de carbone. Les différences dans la composition isotopique du C sont causées soit par le fractionnement isotopique (par exemple l'absorption préférentielle ^{12}C par les plantes) ou par la désintégration radioactive dans la haute atmosphère (formation de ^{14}C). En conséquence, la teneur en radiocarbone du matériel végétal ou du sol dépend du taux d'échange avec l'atmosphère. Les réservoirs de carbone avec un âge géologique élevé (10^3-10^5 ans pour le lignite, 10^6-10^9 ans pour la houille et les roches carbonatées) sont dépourvus de radiocarbone parce que leurs temps de séjour est plus long que le temps de demi-vie du ^{14}C.

b) Les formes de carbone dans les sols

Le carbone dans le sol existe sous les deux formes, organique (carbone organique du sol: COS) et inorganique (carbone minéral du sol). Le carbone total est défini comme étant la somme des deux formes. Le carbone organique du sol comprend les substances humiques. Une partie peut être colmatée à l'intérieur du charbon et des phytolithes (Parr et Sullivan, 2005; Drees et al., 1989; Mulholland et Prior, 1993).

Le carbone inorganique dans le sol se trouve principalement dans les minéraux carbonatés, comme les carbonates de calcium ($CaCO_3$) et la dolomie ($CaMg(CO_3)_2$). Les grandes concentrations de carbonates sont typiques des sols, qui se sont développés sur des matériaux parentaux calcaires et sous des climats aride ou semi-aride FAO, (1998). La teneur en C des carbonates est un critère de différenciation des sols calcaires des autres unités de sols selon la classification FAO/UNESCO (1974). Les charbons et phytolithes constituent d'autres formes de C inorganique.

c) Le stock de carbone à l'échelle mondiale

La Terre contient environ 10^8 Pg (1 Pg = petagramme = 10^{15} g = 1 milliard de tonnes) de carbone (Schlesinger, 1997). La pédosphère est le plus grand réservoir de carbone organique à la surface de la Terre, son stock est estimé à environ 1500 jusqu'à 2000 Gt C (Gt C : Gigatonnes de carbone = 10^9 tonnes de carbone = 1 Pg C) sur la profondeur d'un mètre (Eswaran et al., 1993; Batjes,1996; GIEC, 2001 et 2007), c'est-à-dire plus de deux fois la quantité de carbone stockée dans l'atmosphère sous la forme de CO_2 et trois fois la quantité stockée dans la végétation (tableau 1).

La somme des stocks actifs auprès de la surface de la Terre (C dans les sols et les végétaux) est d'environ 3×10^3 Gt C. L'hydrosphère (océans et mers) contient environ 50 fois plus de carbone que l'atmosphère. Les sols, la végétation, les océans et l'atmosphère sont liés par les échanges de dioxyde de carbone et sont donc les plus importants pour le cycle global du carbone. Le tableau 1 en résume le stock dans chaque réservoir.

Tableau 1 Les différents stocks de carbone à l'échelle mondiale

Réservoir	**Pg C ou Gt C**	**Source**
Atmosphère	8×10^2	Schimel et al., (1995)
	$7{,}5 \times 10^2$	GIEC, (2007)
Sédiments terrestres (y compris les sols)		
Composés organiques	$1{,}56 \times 10^7$	Des Marais et al., (1992)
Carbonates	$6{,}5 \times 10^7$	Li, (1972)
Sols		
Matière organique du sol	$1{,}5 \times 10^3$	Batjes, (1996)
Carbonates du sol	$7{,}2 \times 10^2$	Sombroek et al., (1993)
	$6{,}95 \times 10^2$	Batjes, (1997)
Végétation	$5\text{-}7 \times 10^2$	Houghton et Skole (1990) Melillo et al., (1990) Sombroek, (1990) Schimel et al., (1995) GIEC, (2007)
Carbone des hydrocarbures fossiles		
Charbon	4×10^3	Lal, (2000)
Gaz	5×10^2	Lal, (2000)
Pétrole	5×10^2	Lal, (2000)
Océans	$3{,}8 \times 10^4$	Schimel et al., (1995)

1.1.2 L'AZOTE

a) Les composés de l'azote

Dans la nature, l''azote existe dans de nombreuses formes avec un état d'oxydation entre +V et -III (+V: HNO_3, +IV: NO_2, +III: HNO_2, +II: NO, +I: N_2O, 0: N_2, -III: NH_3, NH_4^+) (Jaffe, 2000). De nombreux composés d'azote contiennent aussi du carbone (C), de l'hydrogène (H) et/ou de l'oxygène (O). Lorsque l'N est lié au C ou à l'H, l'état d'oxydation de l'azote est négatif, car l'N est plus électronégatif que le C ou l'H. Par contre, lorsqu'il est lié à l'oxygène, il a un état d'oxydation positif (Nieder et Benbi, 2008).

b) Les formes d'azote dans le sol

L'azote dans le sol est principalement stocké sous sa forme organique (azote organique du sol : NOS). Les sols à texture très fine stockent environ 90% de l'azote stocké dans la matière organique. Le reste est représenté par de l'ammonium fixé aux minéraux de type illite ou vermiculite (6 à 12%), et d'azote minéral dissous (NO_3^- et NH_4^+ : 1 à 3%), disponible pour les plantes (Benbi et Richter, 2003). Dans les sols à texture grossière ayant peu de capacité à immobiliser ou adsorber NH_4^+ dans les minéraux argileux, la proportion d'azote organique est supérieure à 97%, et la fraction inorganique varie de 1 à 3% (Baldock et Nelson, 2000). À l'échelle globale, la fraction d'azote organique peut représenter jusqu'à 95% de l'azote total du sol (Söderlund et Svensson, 1976). Le rapport C/N de la MOS dépend de la composition chimique de la restitution végétale. La connaissance des teneurs en C et en N permet le calcul de ce rapport. Ce rapport C/N est largement utilisé pour caractériser et classer les types de matières organiques contenues dans un sol, il permet d'estimer de façon très grossière la rapidité de minéralisation de l'azote. Plus le rapport C/N est élevé, moins l'azote est rapidement disponible.

Tableau 2 Le stock mondial d'azote

Réservoir	Tg N	Source
Atmosphère	$3,9 \times 10^{12}$	Schlesinger, (1997)
La biomasse terrestre	$3,5 \times 10^{3}$	Schlesinger, (1997)
La biomasse végétale	$1,0 \times 10^{3}$	Davidson, (1994)
La biomasse microbienne	$2,0 \times 10^{3}$	Davidson, (1994)
La matière organique du sol	$1,33 \times 10^{5}$	Batjes, (1997)
La lithosphere	$1,64 \times 10^{11}$	Pierzynski et al., (2000)
Les roches ignées (croûte et manteau)	$1,63 \times 10^{11}$	Pierzynski et al., (2000)
Les sédiments (l'azote fossile)	$4,50 \times 10^{8}$	Pierzynski et al., (2000)
Le noyau de la Terre	$1,30 \times 10^{8}$	Pierzynski et al., (2000)
Le charbon	$1,00 \times 10^{5}$	Pierzynski et al., (2000)
Hydrosphere (oceans, estuaries, lacs, rivières)	$2,30 \times 10^{7}$	Pierzynski et al., (2000)
Les sediments océaniques	$5,40 \times 10^{5}$	Pierzynski et al., (2000)

c) Le stock d'azote à l'échelle mondiale

La terre contient $3,9 \times 10^{12}$ Tg d'azote (1 Tg = Téragramme = 10^{12} g = 1 million de tonnes), l'atmosphère constitue le plus grand réservoir d'azote (tableau 2). Le stock d'azote organique du sol est inférieur au stock atmosphérique mais plus grand que celui de la biomasse et de la surface des océans (Nieder et Benbi, 2008).

1.2 LE CARBONE ET L'AZOTE DANS LES SOLS

Les stocks de carbone et d'azote organique du sol sont difficiles à quantifier pour plusieurs raisons. La variabilité spatiale des sols, les mesures limitées de certaines variables telles que la densité apparente, l'absence de données relatives à la fraction grossière, ainsi que l'effet de confusion de la végétation et des changements d'utilisation des terres sont à l'origine des différences d'estimation (Nieder et al., 2003) résumées dans le tableau 3.

Pour ce qui est des stocks, aujourd'hui, une valeur d'environ 1500 Gt est communément admise pour le carbone, ainsi qu'une valeur d'environ 100 Gt pour l'azote pour une profondeur de 0-100 cm.

Tableau 3 Historique des différentes estimations des stocks de C et N dans le sol à l'échelle planétaire sur 0-100 cm

Stock de carbone en Pg	**Source**
700	Bolin, (1970)
1392	Bazilevich, (1974)
1080	Baes et al., (1977)
2946	Bohn, (1978)
2070	Ajtay et al., (1979)
1395	Post et al., (1982)
1515	Schlesinger, (1984)
1500	Woodwell (1984), Eswaran et al., (1993); Watson et al., (1995); Batjes, (1996, 1997), GIEC, (2007)
3200 (0-300 cm)	Jobaggy et Jackson (2000)
Stock d'azote en Pg	**Source**
92-117	Zinke et al., (1984)
95	Post et al., (1982)
100	Davidson (1994)
96	Eswaran et al., (1995)
133	Batjes, (1997)

2. LE CYCLE GLOBAL DU CARBONE

2.1 ECHANGE DE DIOXYDE DE CARBONE ENTRE BIOSPHERE ET ATMOSPHERE

Les écosystèmes terrestres renferment de grandes quantités de carbone, et entre l'atmosphère, les végétaux et les sols il y a un échange rapide de gaz carbonique (CO_2). Les flux dominants du cycle global du carbone sont ceux qui relient le CO_2 dans l'atmosphère à la biomasse primaire et aux océans (Figure 1).

La production primaire nette (PPN) globale correspond aux taux de respiration annuelle, elle est estimée à 60 Pg CO_2-C/an. Le réservoir atmosphérique correspond à environ 750 Pg CO_2-C et le temps de séjour moyen de CO_2 dans l'atmosphère est d'environ 5,3 ans. La concentration actuelle de CO_2 atmosphérique est de 398,58 ppm (mesure effectuée à Mauna Loa en juin 2013) (http://co2now.org/) avec une augmentation annuelle d'environ 0,4% causée principalement par l'utilisation des combustibles fossiles. L'absorption annuelle par les océans (92 Pg C) est légèrement supérieure à celle de son dégagement vers l'atmosphère (90 Pg C).

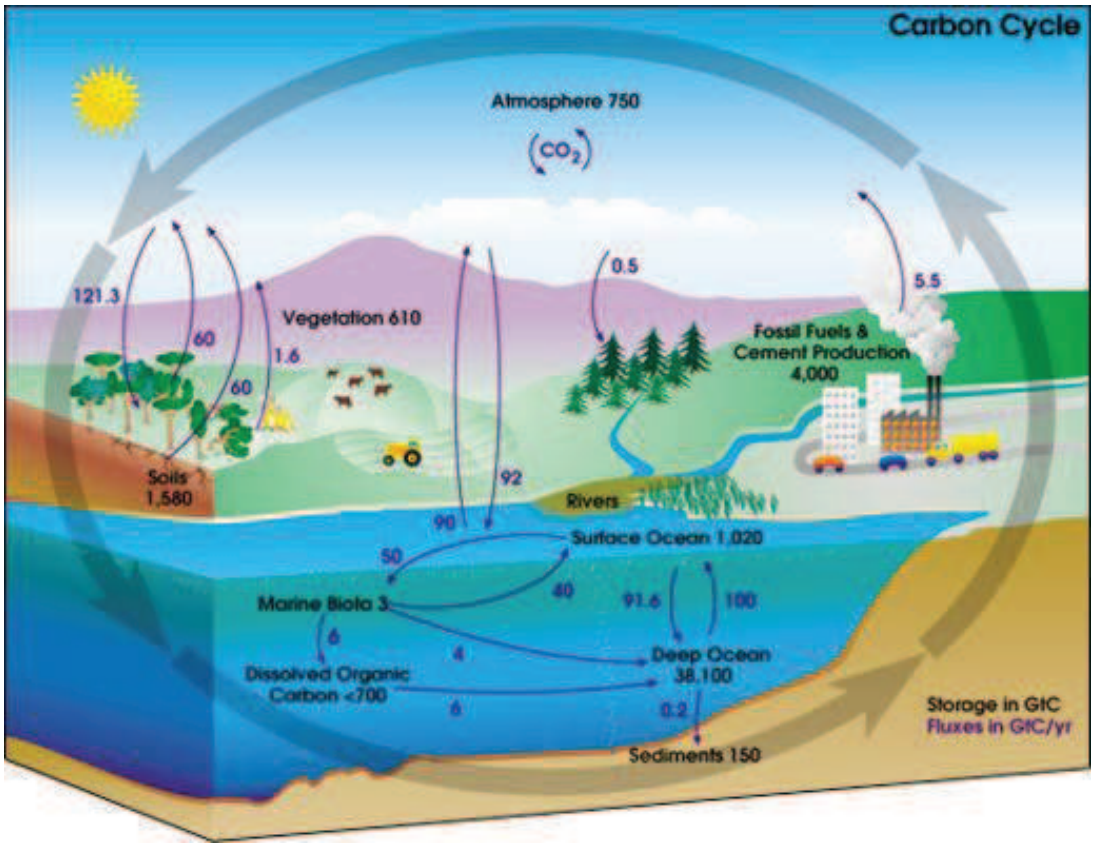


Figure 1 Le cycle global du carbone (NASA, 2007 http://www.nasa.gov/centers/langley/news/researchernews/rn_carboncycle_prt.htm)

Ce puits océanique d'environ 2 Pg C/an est relativement faible en comparaison avec les flux globaux. Les concentrations de CO_2 dans l'atmosphère varient selon un cycle saisonnier. Les enregistrements continus des oscillations saisonnières de CO_2 ont commencé en 1958 à Mauna Loa sur une montagne volcanique (altitude: 3400 m) sur l'île de Hawaii (Pales et Keeling, 1965) et dans la même année au pôle Sud par Keeling et al. (1976). Tous les enregistrements en continu montrent un pic de CO_2 en fin d'hiver et un minimum en fin d'été. Pendant l'été, dans les deux hémisphères il y a une fixation nette de carbone par la photosynthèse qui dépasse la respiration. Pendant le reste de l'année, la respiration totale dépasse la photosynthèse (Bolin et Keeling, 1963).

2.2. PROCESSUS AEROBIES

La photosynthèse: la photosynthèse par l'énergie du rayonnement solaire, elle permet à une plante en présence de l'eau, de capter le CO_2 de l'atmosphère afin de synthétiser des glucides. La photosynthèse utilise la radiation solaire visible (400 à 700 nm) qui représente environ 50% de la radiation solaire globale (USDA, 2013).

De cette fraction, environ 85% de l'énergie solaire est absorbé par les feuilles, mais cette valeur peut varier considérablement selon leur structure et leur âge. Enfin, de la quantité de lumière absorbée par la feuille, seulement 5% sert à la photosynthèse alors que le reste est perdu sous forme de chaleur (Salisbury et Ross, 1978).

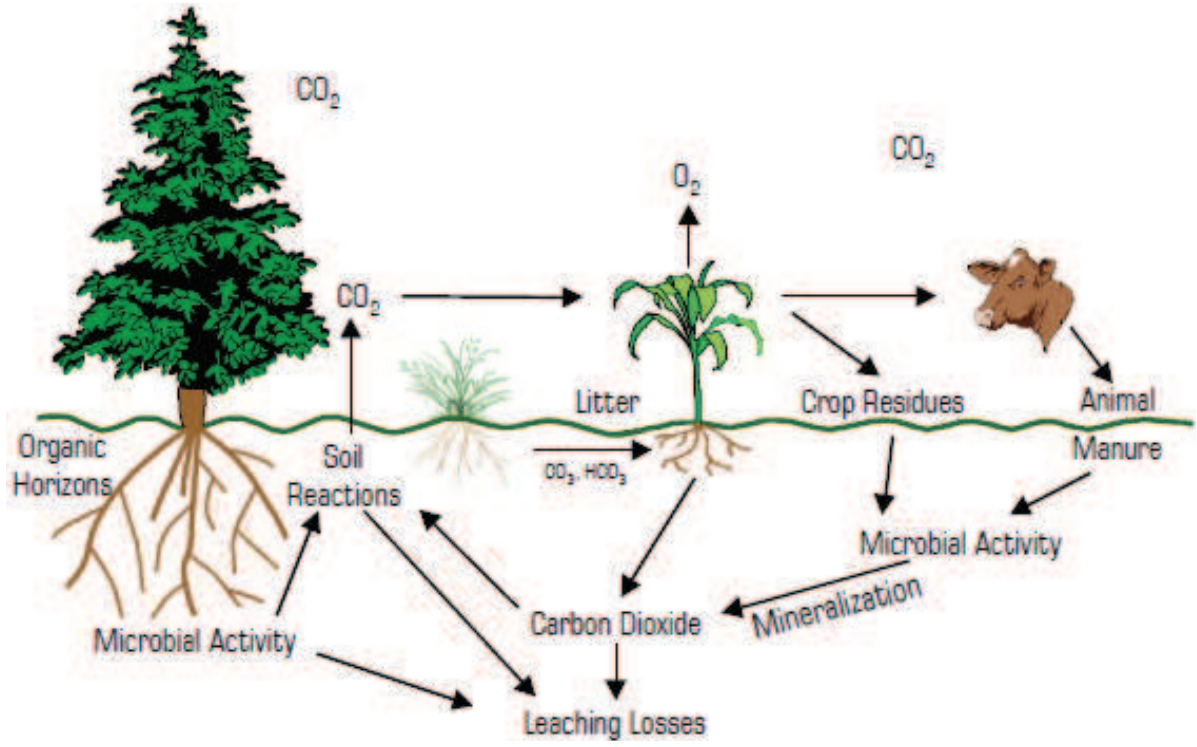


Figure 2 Le cycle de carbone dans le sol (USDA, 2013 : http://www.usda.gov/wps/portal/usda/usdahome)

La majorité du processus de la photosynthèse se fait dans le feuillage, mais il s'en fait aussi (très peu) dans les tiges, les branches (Waring et Schlesinger, 1985; Kozlowski et al., 1991), l'écorce, les cotylédons, les bourgeons et les fruits (Kozlowski et al., 1991).

L'équation chimique qui décrit la photosynthèse est :

$nCO_2 + 2nH_2O$ + lumière $\longrightarrow$ $(CH_2O)n + n/2\ O_2$ (Salisbury et Ross, 1978).

Cette réaction couvre deux phases distinctes de réactions : une phase photochimique, dite "phase claire", de capture de l'énergie solaire, et une phase biochimique, dite "phase sombre", de synthèse de composés organiques (Demeyer et al, 1981).

La respiration : elle est sous deux formes :

- *La photorespiration* ou respiration à la lumière est due à une concurrence entre le CO_2 et l'O_2 qui cherchent tous deux à se fixer sur le ribulose-1,5-diphosphate (RuDP : enzyme de fixation de carbone atmosphérique). Ce mécanisme se traduit par une consommation d'oxygène accompagnée d'un rejet de dioxyde de carbone et réduit donc l'efficacité de la photosynthèse (Maisongrande, 1996).
- *La respiration métabolique* a pour but de subvenir aux besoins métaboliques des plantes, en fournissant l'énergie nécessaire pour assurer les différents flux de matières et leur transformation au sein du végétal. Chimiquement, elle consiste à transférer l'énergie contenue dans les substrats glucidiques dans le but de la restituer sous forme d'ATP (Glycolyse, Cycle de Krebs, Voie des pentoses phosphates). Cette énergie est alors mise à la disposition des processus de maintenance et de croissance qui opèrent de jour comme de nuit (USDA, 2013).

2.3. PROCESSUS ANAEROBIES

Les transferts du carbone dans les sols se font par l'apport de débris organiques, l'exsudation dans la rhizosphère et le relargage gazeux par respiration et volatilisation (Schimann, 2005).

La fermentation : En milieu anaérobie, des processus de fermentation peuvent se produire ; ils se caractérisent par l'utilisation de substrats organiques comme accepteurs d'électrons par des microorganismes anaérobies ou anaérobies facultatifs (Madigou, 2005).

La méthanogènese **:** Lors de sa transformation, une partie de la matière organique est dégradée en CO_2 et une autre est changée en produits organiques intermédiaires. Ceux-ci sont susceptibles d'être utilisés par les bactéries méthanogènes (anaérobies

strictes) pour aboutir à la formation de CH_4. Celui-ci peut être réoxydé par les méthanotrophes (microaérobies) ou méthanogènes pour redonner du dioxyde de carbone libéré vers l'atmosphère (Madigou, 2005). Les processus anaerobies sont peu présents dans les sols méditerranéens généralement bien aérés.

3. LE CYCLE DE L'AZOTE

L'azote circule selon un cycle biogéochimique au cours duquel il passe sous des formes organiques et minérales (Jego, 2008). La plupart des transformations d'azote impliquent l'oxydation ou la réduction de l'atome d'azote par les deux moyens biologiques et physicochimiques (Figure 3). Dans l'atmosphère, l'azote existe principalement sous forme de N_2 qui correspond à 78% des gaz atmosphériques. La transformation de N_2 en d'autres formes nécessite de l'énergie pour briser la liaison N=N.

L'azote est présent dans le sol sous plusieurs formes. L'azote organique constitue la principale forme de stockage dans un sol agricole, essentiellement depuis les forme d'enzymes et de protéines. Il existe sous forme d'ions comme les nitrates, les nitrites et l'ammonium, qui en dehors de périodes d'apport d'engrais ne représentent généralement que quelques dizaines de kilogramme par hectare, et comme gaz (ex : NH_3, N_2O, N_2). Dans le système sol-plante-atmosphère, le cycle de l'azote comporte un grand nombre de transformations, il s'agit de processus en grande partie de nature biologique et dans une moindre mesure physico-chimique, agissant parfois de façons concurrentes et dont l'intensité dépendrait à la fois des conditions du milieu, des apports de matière organique, et des pratiques agricoles (Nicolardot et al., 1996).

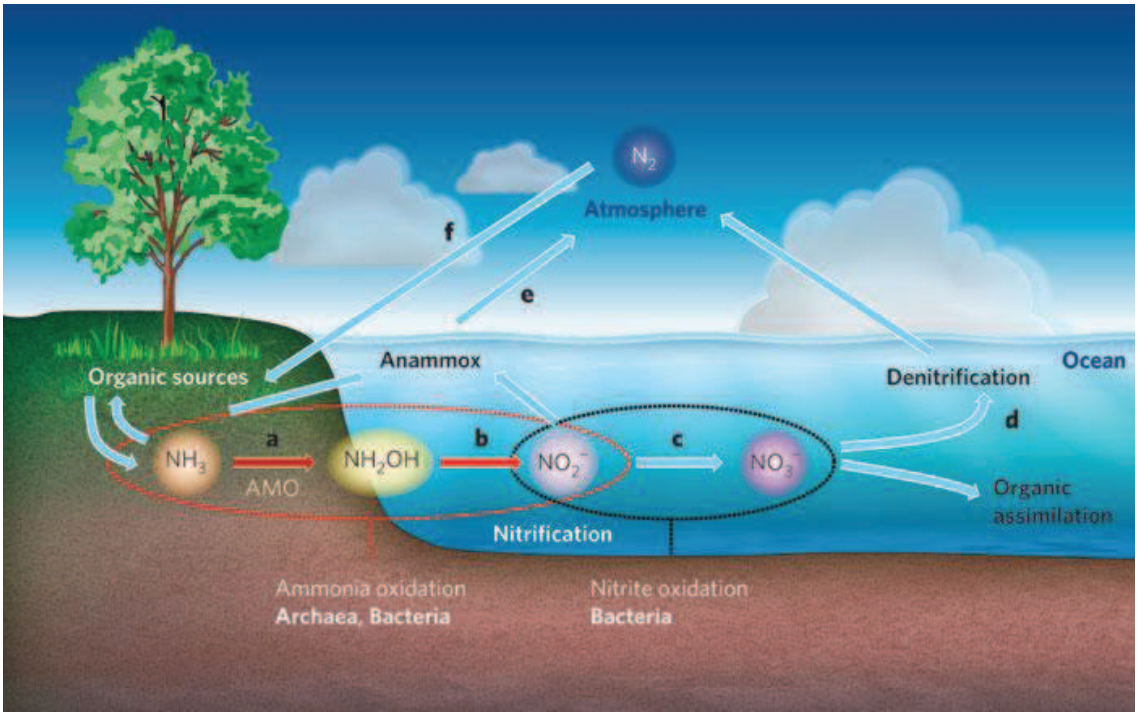


Figure 3 Le cycle global d'azote (Schleper, 2008)

L'oxydation de l'ammoniac est la première étape de la nitrification, le processus dans lequel l'ammoniac (NH_3, d'origine organique) est oxydé en ions nitrate (NO_3^-). La nitrification se produit sur terre et dans les océans. Le processus ne peut être réalisé que par certaines bactéries, mais récemment certaines Archées (Crénarchées) ont été trouvées capables d'oxyder de l'ammoniac, et contient des gènes de mono-oxygénase de l'ammoniac (AMO, l'enzyme clé impliquée dans l'oxydation de l'ammoniac). **a**, AMO convertit l'ammoniac en hydroxylamine (NH_2OH). **b**, l'hydroxylamine est converti par les mêmes micro-organismes en ions nitrites (NO_2^-), une protéine qui catalyse ce processus n'a pas encore été trouvée chez les archées. **c**, autres bactéries spécialisées complètent la nitrification en convertissant les ions nitrites en ions nitrates. **d**, Le nitrate est alors soit assimilé à la matière organique ou dénitrifié par d'autres micro-organismes pour produire de l'azote, qui s'échappe dans l'atmosphère sous forme de N_2. **e**, Les bactéries de type « Anammox» peuvent aussi convertir les ions nitrites en azote et en ammoniac. **f**, l'azote est fixé principalement par des bactéries spécialisées en la production d'ammoniac. Cela peut être incorporé dans la matière organique, ou oxydé au fur et à mesure que le cycle continue.

3.1. LA FIXATION BIOLOGIQUE DE L'AZOTE

La fixation biologique de l'azote est le processus biochimique le plus important après l'assimilation du CO_2. Elle assure la transformation du diazote en ammoniac (lui-même converti en ammonium). C'est l'ammonification. Seuls quelques microorganismes diazotrophes sont capables d'assurer ce processus, parmi lesquels on distingue les bactéries libres vivant dans le sol comme : les azotobacters, les cyanobactéries (algues bleu-vert), les rhizobactéries (bactéries symbiotiques vivant en association avec les légumineuses dans des structures racinaires ou caulinaires organisées appelées nodosités).

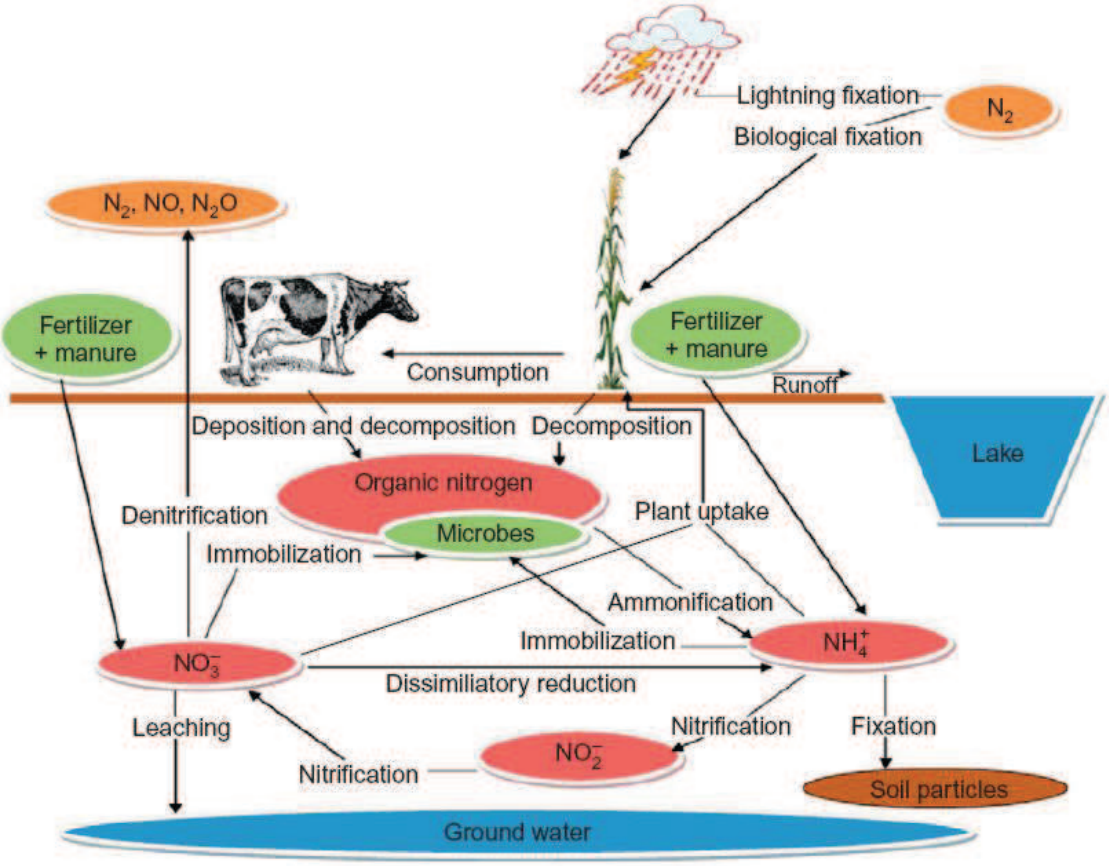
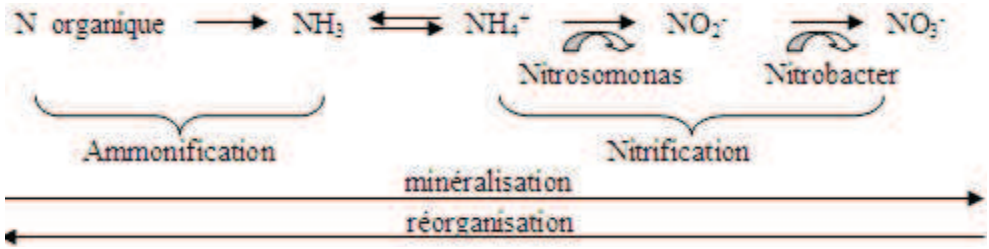


Figure 4 Illustration du cycle de l'azote dans le sol (Luce et al., 2011)

L'oxydation de l'ammonium en nitrites puis en nitrates (nitrification) est ensuite assurée par des bactéries. L'azote nitrique (NO_3^-) et l'ammonium (NH_4^+) sont très solubles (les nitrites NO_2^- représentent quant à eux une forme transitoire, étant en général directement réduits en nitrates dans le sol). Lorsque cet azote n'est pas utilisé par les plantes ou fixé par les bactéries, il est perdu par lessivage ou dénitrification (Aguesse, 1971).



3.2. L'ASSIMILATION DES NH_4^+ ET DES NO_3^-

L'assimilation est le processus biologique par lequel l'ammonium (NH_4^+) et ou les nitrates (NO_3^-) sont assimilés par les plantes, les animaux et les microorganismes pour former la matière organique. L'ammonium est la forme préférentiellement assimilée par les micro-organismes (bactéries et champignons) et les nitrates pour les plantes. Les concentrations en nitrates et en ammonium dans les sols sont très variables, allant de concentrations micromolaires à plusieurs millimolaires selon Marschner (1995).

2.2.1. L'AMMONIFICATION

Cette phase constitue la dégradation des protéines de tous les apports annuels provenant des végétaux et en moindre mesure d'animaux et de micro-organismes telluriques (Andreux et Monrozier, 1981). Ces microorganismes comprennent une très grande diversité d'espèces de bactéries, d'actinomycètes ou de champignons, de sorte que l'ammonification est un processus sans exigence écologique particulière puisque, quelles que soient les conditions de l'environnement, il se trouve presque toujours dans le sol des espèces microbiennes ammonifiantes adaptées à ces conditions (Dommergues, 1968).

2.2.2. LA NITRIFICATION

La nitrification est un ensemble de réactions microbiologiques complexes de nature autotrophe ou hétérotrophe qui consistent en l'oxydation de l'ammoniac en azote nitreux (nitritation ou nitrosation) et dans son oxydation ultérieure en azote nitrique (nitratation). Il existe deux types de nitrifications :

- *La nitrification autotrophe*: elle se fait par des bactéries nitrifiantes autotrophes de genres *Nitrosomonas* et *Nitrobacter* essentiellement. Ces bactéries présentent des exigences écologiques très strictes ; *in-vitro*, elles sont aérobies et neutrophiles ; mais, dans le sol, l'interaction de divers processus physico-chimiques et biologiques permet à ces bactéries de se développer à des pH moyens inférieurs à 6.0 ou même de 5.0.

- *La nitrification hétérotrophe*: elle existe dans le sol sous l'effet des microorganismes nitrificateurs hétérotrophes comme *Aspergillus flavus*, dont les exigences écologiques sont beaucoup moins strictes mais dont le rendement est bien inférieur (Dommergues, 1968).

2.2.3. DENITRIFICATION

La dénitrification représente les processus par lesquels les nitrates (et accessoirement les nitrites NO_2^-) sont réduits à l'état de produits gazeux (oxyde nitreux N_2O, azote moléculaire N_2), ainsi perdus pour le sol (Dommergues, 1968). Les conditions d'humidité élevée favorisent cette réduction. Le protoxyde d'azote (N_2O) est émis en général en même temps que N_2 en proportion très variables (Firestone et Davidson, 1989). La capacité dénitrifiante potentielle des sols est généralement très supérieure aux activités *in-situ* indiquant que le potentiel enzymatique est rarement le facteur limitant de ce processus microbien (Cellier et al., 1996). Ces processus apparaissent lorsque, se trouvant en anaérobiose, les microorganismes dénitrificateurs utilisent les nitrates comme accepteurs d'électrons à la place de l'oxygène qui fait défaut. Ce mécanisme respiratoire, dans lequel les nitrates remplacent le dioxygène, est également connu sous le nom de réduction dissimilatrice des nitrates ou encore respiration nitrate. Il y a donc deux autres types de processus de réduction des nitrates :

- La réduction dissimilatrice qui conduit à la formation de nitrites ;
- La réduction assimilatrice qui conduit à la formation d'ammonium, composé qui entre dans la constitution des protéines et autres constituants azotés des organismes vivants.

Ce sont évidemment les processus de dénitrification vraie aboutissant effectivement à la perte d'azote, qui présentent le plus d'enjeux agronomiques.

La chaîne des réactions de dénitrification se présente schématiquement comme suit (Dommergues, 1968):

$$NO_3^- \rightarrow 2NO_2^- \rightarrow 2NO \rightarrow N_2O \rightarrow \uparrow N_2$$

4. PERSPECTIVES HISTORIQUES DE LA MODELISATION DE LA DYNAMIQUE DE C ET N DANS LE SOL

La dynamique du carbone et de l'azote affecte directement la qualité et la productivité des sols. Elle été depuis longtemps un des objets de la science du sol. Avec l'amélioration de la méthodologie expérimentale, les scientifiques ont accumulé de précieux renseignements sur la dynamique du carbone et de l'azote du sol et ils ont amélioré la gestion agronomique des intrants (Shaffer and Ma, 2001; DeBusk et al., 2001). D'après la littérature, les modèles conceptuels des processus de C et N dans les sols sont toujours en cours de développement (Molina and Smith, 1998). Les premiers chercheurs se sont concentrés sur chaque processus prisindividuellement, mais n'avaient pas les outils et les connaissances nécessaires pour appréhender les interactions de processus multiples et traiter les sols comme un ensemble intégré. Les travaux sur les processus individuels gardent leur valeur aujourd'hui, mais des progrès récents dans la technologie informatique, les techniques de traçage, la télédétection, les procédures d'échantillonnage sur le terrain, et les méthodes d'analyse au laboratoire ont permis des améliorations significatives dans la connaissance des processus de C et N ainsi que leurs interactions (Shaffer et Ma, 2001; DeBusk et al, 2001). L'exemple classique d'un des premiers modèles traitant l'aspect cyclique du C et N par minéralisation potentielle de la MO est celui de Stanford et Smith (1972). Jenny (1941), Henin et Dupuis (1945), et Olson (1963) sont des exemples de travaux antérieurs sur la modélisation de la MO ne distinguant pas spécifiquement C et N du sol.

Parmi les plus grandes révolutions dans l'étude des cycles C et N du sol dans les 30 dernières années apparu le développement des modèles de simulation, et la liaison des processus avec l'écosystème. Ceci a été rendu possible par l'introduction des ordinateurs « *pédologies assistées par ordinateur* » avec des capacités de calcul et de mémoire suffisantes pour permettre la simulation des systèmes complets et intégrés de sols.

L'origine de la modélisation de la simulation par ordinateur de la dynamique du carbone et de l'azote dans les sols remonte au début des années 1970 avec les premiers modèles intégrés de *sol-système* rapporté aux travaux de Dutt et al., (1972) aux États-Unis et Beek et Frissel (1973) en Europe. Ces modèles sont les premiers à combiner les dynamiques de C et N et relient leur processus dans le système *sol-culture-nutriments* dans un modèle intégré.

À la fin des années 1970, d'autres modèles d'azote et de carbone des sols ont commencé à apparaître, comme le modèle de retour de flux (Shaffer et al., 1977), modèle d'azote de Tanji (Tanji et Gupta, 1978); et les modèles C et N réalisés par Hunt (1978), Watts et Hanks (1978) et Anderson (1979). Les approches intégrées observées dans ce groupe de modèles ont été développées plus tard et ont concerné les réservoirs de matière organique du sol dans le modèle PHOENIX (McGill et al., 1981), le modèle PAPRAN (Seligman et Van Keulen, 1981), et le modèle des cycles de C et N de Frissel et Van Veen's (1981).

En les années 1980, l'intérêt pour la modélisation de la gestion des intrants agricoles a fait un bond en raison des préoccupations environnementales, et plusieurs sous-modèles de carbone et d'azote du sol ont été développés dans les modèles tels que: Century (Parton et al., 1983), NCsoil (Molina et al., 1983), EPIC (Williams et Renard, 1985), ANIMO (Berghuijs van Dijk et al., 1985), et SOILN (Johnsson et al., 1987).

À la fin des années 1980 et jusqu'à la moitié des années 1990, plusieurs autres modèles sont apparus et les modèles précédents ont été améliorés. Des nouveaux modèles introduisent la dynamique de l'azote comme celui de Bergstrom et Johnsson (1988), le modèle de Kersebaum (1995), le modèle DAISY d'Hansen et al., (1990), le modèle Candy de Franko (1996), le modèle ECOSYS de Grant (1997), et le modèle ICBM de Kätterer et Andren (1997) ainsi que des versions améliorées de Century (Parton et Rasmussen, 1994), SOILN (Eckersten et al., 1996) et ANIMO (Groenendijk et Kroes, 1997).

5. MODELES DE DECOMPOSITION

La matière organique du sol (MOS) joue un rôle fondamental dans le maintien de la fertilité via ses effets sur les propriétés physiques, chimiques et biologiques des sols. L'importance des pools de MOS dépend des apports de matière organique (grâce aux résidus après récolte, au turnover des racines et des mycorhizes et aux exsudats racinaires), et des pertes de C, principalement via la respiration hétérotrophe due à la décomposition de la MOS.

De nombreux modèles compartimentaux de décomposition des matières organiques ont été élaborés, qu'on peut classer en:

i) Modèles linéaires : les flux de sortie d'un compartiment sont liés uniquement au contenu de ce compartiment selon une cinétique d'ordre 1. Dans la littérature le plus grand nombre de modèles de décomposition sont de ce type. On peut citer parmi les plus connus Century (Parton et al., 1987), Roth-C (Jenkinson et al., 1987), Daisy (Hansen et al., 1991) ; MOMOS-1 (Sallih et Pansu 1993 ; Pansu et al., 1998), DNDC (Li et al., 1996), NCsoil (Molina et al., 1983), STICS (Brisson et al., 1998), ou CO_2Fix (Masera et al., 2003).

Les composés organiques des litières et MOS sont assimilés à des pools homogènes et indépendants de carbone et d'azote. Les taux de transformation sont spécifiques aux pools. Ils correspondent à une vitesse maximale dans les conditions physico-chimiques optimales pour l'activité des microorganismes. Dans le cas des pools de litières, les taux peuvent être déterminés par la nature biochimique (Century, DNDC, NCSoil, CO_2Fix, Daisy) et /ou par le type ou la taille des débris (CO_2Fix, STICS). Ils sont modulés par des fonctions de limitation traduisant le ralentissement de l'activité des microorganismes par les conditions climatiques (température et humidité), parfois par la protection des molécules organiques par les argiles, teneur de N inorganique, la teneur de lignine. Le flux de respiration est affecté par ces fonctions de limitations, par contre celui de minéralisation nette d'azote ne l'est pas en général. Le traitement de ces deux flux est particulier et varie d'un modèle à l'autre. Dans ces modèles, la respiration n'est pas traitée comme un flux de transformation à part

entière et elle n'est pas proportionnelle à la biomasse microbienne. Elle est représentée par une fraction de perte des autres flux. La minéralisation de l'azote est par contre liée au rapport C/N du pool.

ii) Modèles non linéaires : la sortie de chaque compartiment est proportionnelle à la fois à son contenu et à la croissance des décomposeurs ou de leurs enzymes. Les microorganismes produisent des enzymes extracellulaires qui dégradent la matière organique. Les microorganismes absorbent le carbone dissous par les enzymes. De ce fait il y a une voie indirecte entre la biomasse microbienne et la matière organique du sol et donc une cinétique non linéaire.

Plus de 200 modèles mathématiques avec des niveaux de complexité distincts ont été développés pour décrire des processus biogéochimiques dans le sol. La plupart de ces modèles sont basés sur la cinétique et les taux stœchiométriques qui forcent les éléments cycliques au sein du sol, les nutriments, et les échanges de carbone avec la végétation et l'atmosphère (Manzoni et Porporato, 2009).

MOMOS a évolué depuis sa conception initiale vers un modèle de décomposition pouvant décrire au mieux l'écologie fonctionnelle de la biomasse microbienne. Il a été conçu de manière à limiter les paramètres principalement à des taux cinétiques de décomposition des compartiments qui ont pu être ajustés grâce à des expériences d'incubation avec traçage isotopique (Pansu et al., 2004 ; 2007 ; 2010). Aucune application à des systèmes complexes ouverts avec des flux réguliers n'a encore été publiée. Des exercices de modélisation prédictive peuvent donner des renseignements utiles dans la dynamique d'un écosystème complexe.

MOMOS est proche des modèles linéaires dans sa structure. Cependant seule l'expression de la respiration microbienne est non-linéaire : elle est une fonction quadratique du pool de biomasse microbienne au carré. Cette particularité rend le flux de respiration très sensible aux apports et aux conditions climatiques (teneur en eau et température) pour un niveau de biomasse microbienne relativement constant.

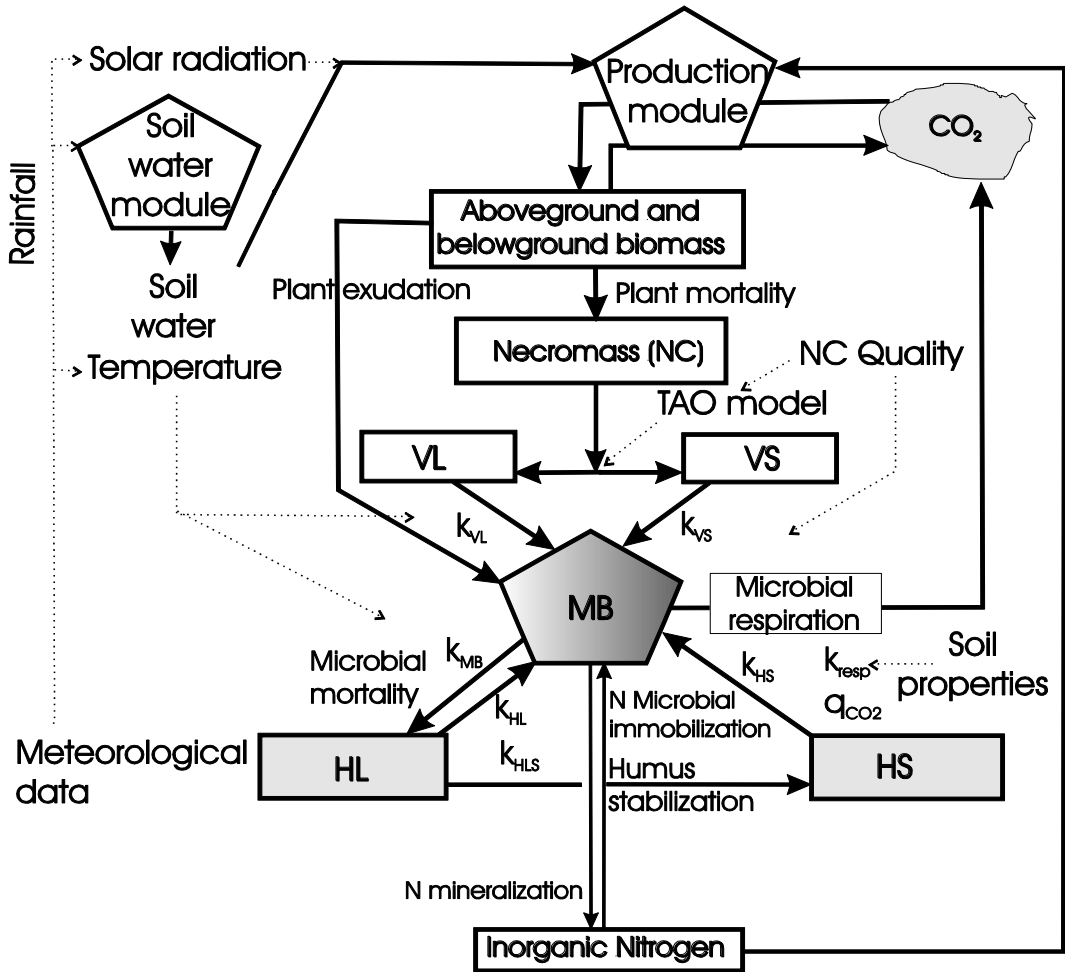


Figure 5 : Diagramme relationnel de la modélisation des transformations organiques par les microorganismes du sol MOMOS, (Pansu et al., 2010)

CONCLUSION

Les cycles du carbone et de l'azote sont essentiels à la vie et sont au cœur d'enjeux environnementaux et de production importants. De nombreuses transformations de C et de N se produisent dans le sol. A l'échelle globale, le sol est donc un compartiment clé où le carbone peut être stocké naturellement. A l'échelle de la parcelle, l'accumulation de C améliore les qualités physiques et chimiques du sol et la minéralisation/immobilisation de l'azote détermine les rendements agronomiques et les risques de lessivage.

Les transformations de C et de N dans les sols sont en grande partie assurées par des microorganismes. Ce sont donc ces microorganismes qui déterminent la cinétique de décomposition et qui sont responsables du couplage entre les dynamiques de C et N. Il existe plus de deux cents modèles traitant de la décomposition de la matière organique avec des différences dans les équations, les compartiments, les échelles de temps et d'espace. Parmi ceux-ci MOMOS a été retenu pour sa description du fonctionnement microbien du sol gérant les dynamiques de transformation des formes C et N. Sa structure mathématique et son échelle de temps permettent de simuler la sensibilité des flux de minéralisation aux conditions climatiques jour après jour et de lier l'évolution de la disponibilité de l'azote pour les plantes avec le rendement pour une saison de culture.

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CHAPITRE II
LES MODELES DE STOCK DE L'AZOTE DU SOL DANS LES ZONES ARIDES EXPLOREES AVEC DES FONCTIONS DE PEDOTRANSFERT ET DES ANALYSES BAYESIENNES

Ce chapitre correspond à l'article publié dans la revue internationale «*Research Journal of Applied Sciences, Engineering and Technology*» (In Press, Corrected Proof, Available online 30 August 2013) et qui s'intitule: "**Patterns of soil nitrogen sequestration in drylands explored with pedotransfer functions and Bayesian analysis"**

L'objectif de ce chapitre est d'examiner l'effet des différents facteurs physico-chimiques des sols sur le stock d'azote total au niveau des sols argileux et des sols sableux sous bioclimats semi-arides et arides méditerranéens, par l'étude des sols de Tunisie.

Résumé

L'évaluation des stocks de carbone organique et de l'azote total dans le sol, ainsi que la compréhension de leurs relations avec les caractéristiques du site est d'une importance majeure, que ce soit à l'échelle locale, régionale ou mondiale. L'amélioration des fonctions de pédotransfert améliore l'évaluation de ces stocks dans les sols. La bonne évaluation du stock et sa connaissance est un élément clé de la durabilité des agro-systèmes, en particulier dans les systèmes sensibles à l'érosion des zones arides et semi-arides méditerranéennes. Ce travail visait à étudier les relations entre les stocks d'azote total et les autres propriétés physico-chimiques des sols argileux et sableux de Tunisie, et pour ce faire, nous avons utilisé les fonctions de pédotransfert et la modélisation par les équations structurelles. Pour la modélisation des stocks d'azote total des sols tunisiens, deux bases de données ont été utilisées, elles étaient composées de 450 horizons de sols argileux et 602 horizons de sols sableux. Les modèles optimaux de stocks d'azote ont été donnés par deux fonctions importantes de pédotransfert: (i) pour les sols argileux avec une erreur standard de prédiction de 18,51 et *p-value* = 0,000 et (ii) pour les sols sableux avec une erreur standard de prédiction de 5,76 et *p-value* de 0,016. Ensuite, nous avons procédé à une analyse du cheminement en utilisant la modélisation par les équations structurelles et l'analyse bayésienne pour étudier simultanément les interactions entre les différentes composantes des propriétés du sol et leurs relations avec les stocks d'azote total. Les résultats montrent que, dans les deux types de sol, le stock d'azote total est toujours contrôlé de la même façon, il est fortement lié aux propriétés chimiques et la densité apparente plus qu'aux propriétés physiques. Les RMSEA *(Root Mean Squared Error of Approximation)* étaient respectivement 0,080 et 0,043 pour les modèles argileux et sableux, ce qui suggère que nos modèles sont bien ajustés et sont fiables.

Mots clés: Azote total, fonctions pédotransfert, analyse bayésienne, région méditerranéenne.

Patterns of soil nitrogen sequestration in drylands explored with pedotransfer functions and Bayesian analysis

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ABSTRACT:

The stock assessment of organic carbon and total nitrogen in the soil in addition to their relationships with site characteristics is of major importance whether at local, regional or global scale. The improvement of pedotransfer functions for these stocks evaluation in soils is a key for sustainability of agro-systems, especially in erodible systems of Mediterranean semi-arid areas. This work aimed to study relationships between total nitrogen stocks and other physico-chemical properties of clayey and sandy soils of Tunisian database, and to do this, we used pedotransfer functions and structural equations modeling. For modeling total nitrogen stocks, two Tunisian soil databases composed from 450 horizons of clayey soils and 602 horizons of sandy soils were used. The optimal models of nitrogen stocks were given by two significant pedotransfer functions: (i) that of clayey soils with a standard error of prediction of 18.51and associated p-value of 0.000 and (ii) that of sandy soils with a standard error of prediction of 5.76 and associated p-value of 0.016. Then, we perform a path analysis using structural equations modeling and Bayesian analysis to investigate simultaneously the interactions between the different components of the soil properties and their relationships with total nitrogen stocks. Results show that, in both soil types, the stock of total nitrogen is always controlled in the same way; it is significantly linked to chemical properties and bulk density more than by physical properties. The root mean square errors of the approximations were 0.080 and 0.043 for the clayey and sandy models, respectively.

***Keywords*:** Total nitrogen, pedotransfer functions, Bayesian analysis, Mediterranean region.

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INTRODUCTION

The importance of an understanding of the national levels of organic matter (OM) is reinforced by the statements of the Framework Convention of United Nations on Climate Change (UNFCCC) signed at Rio de Janeiro in 1992. In fact, the UNFCCC aims to stabilize greenhouse gas concentrations in the atmosphere at a level that limits adverse impacts on the global warming. Their Articles 3.3 and 3.4 describe the potential mechanisms which can reduce the emissions and the choice of activities that can increase terrestrial sinks (Smith, 2004). There are clear linkages between the United Nation Convention to Combat Desertification (UNCCD) and the UNFCCC. One of the most evident linkages concerns the soil organic matter (OM) status (Brahim *et al.,* 2012). The stabilization of increasing N_2O and CO_2 concentration in the atmosphere is the major ecological concern of the world (Mishra *et al.,* 2010). In fact, knowing the sequestration potential allows preserving the soil conservation, and especially helps strengthen the "wells function" of soil and to offset anthropogenic emission of greenhouse gases. Organic matter (OM), as transversal indicator, is a major determinant of soil fertility, water holding capacity, biological activity and is highly correlated to levels of above- and below-ground biodiversity. OM also influences structure, friability and aggregation of soil, which have major implications for its permeability and erodibility. The level of OM can, therefore, be a robust indicator of the degradation of a soil system (Brahim *et al.,* 2012). Soil OM is a key element of some terrestrial ecosystem, and any variation in its abundance and composition has significant effects on several of the processes that occur within the system (Batjes, 1996). The organic stock (carbon and nitrogen) is influenced by vegetation, soil types, climatic conditions, and topography (Bedison and Johnson, 2009). Vegetation is the main source of soil OM. For this reason, land uses are known to play a major role in organic stocks build up through organic matter input (Pandey *et al.,* 2010) in different depths (Batjes, 1996; Bernoux *et al.,* 2002; Brahim *et al.,* 2010), and bioclimatic zones into soils through the processes of soil aggregation (Brahim *et al.,* 2011a).

Global stocks of soil nitrogen are estimated at 133-140 Pg of N (1 Pg=10^{15} g) for the upper 100 cm (Batjes, 1996). In arid zones, soils are already poor to very poor in organic matter, and are naturally unstable and easily eroded. Though "azote", the French name for nitrogen given by Lavoisier, means "lifeless" and inert, this element is a major constituent of living organisms which catalyze key steps in biogeochemical cycling (Pansu *et al.,* 1997). Nitrogen is a remarkable element; the vegetative growth of plants (leaves, stems, and roots). The soil fertility is especially N dependent, the nitrogen problem is particularly crucial under arid soil conditions. As a result of a too low supply of total nitrogen, coupled with the relatively small fraction thereof which is rendered available by plants, nitrogen poverty with its various manifestations is one of the prominent problems of soil fertility in Tunisia and especially in soils of arid and semi-arid Northern Africa areas. Many of these soils are situated in regions of high winter rainfall (extreme northwest) and produce an abundant spring growth; hence their nitrogen-content, owing to the large supply of decaying OM, may compare very favorably with that of an average soil of the humid region. In the Maghreb arid soils, however, which receive only 350 mm of rain per year or less, it is quite usual to find concentrations of total nitrogen below 0.01% in the air-dried surface soil. To do this, starting from the arid climatic conditions and meager vegetation that influence this low rate of nitrogen in the soil, it remains to study the effect of soil type on the stock of this important and vital element. Nitrogen was predicted by different biochemical properties (Trasar-Cepeda *et al.,* 1998). The biochemical properties are also closely related to physical and especially chemical soil properties because of the dynamic and interactive nature of soil processes (Schoenholtz *et al.,* 2000).

Many efforts have been made in research on the status of organic stocks in the soil and improved procedures for interpreting results. In recent decades, simple or multiple regressions models or pedotransfer functions (PTFs) and the structural equations modeling (SEM) based on easily measurable soil properties are a suitable tool for the explanation. Studies of organic carbon stocks and total nitrogen in the Tunisian soils (Ibrahim *et al.,* 2009; Brahim *et al.,* 2011a) have determined the stocks in each soil type, the total stock in the country and finally mapped and compiled the

maps for the OC and TN. However, variables and factors affecting these stocks are well known, especially with regard to stock of total nitrogen. This work has two objectives: (i) to establish a model using PTFs based on different soil physical and chemical properties, in sandy and clayey soils from Tunisia, and (ii) to build models using SEM, in order to estimate the real variables except the soil cover in these drylands.

1. MATERIALS AND METHODS

1.1 STUDY AREA

Tunisia situated in Nord Africa and in south of Mediterranean Sea between the latitudes 32° and 38° North and between the longitudes 7° and 12° Est. It is located at the junction of the western and oriental Mediterranean and covering a surface of 164000 km², of which more than 67% are under semi-arid and arid climate and the rest are under sub-humid and humid climate (Figure 1). In spite of this small surface, nor the climate neither the vegetation are uniform. In fact, the geographical position and the general orientation of the topography are influenced at the North by the Mediterranean Sea and at the South by the Sahara. Concerning the Center, it is under the conjugated effect of these two elements. Even the dominance of calcareous rocks, geology consists of large range of type of rocks. It has for consequence an enormous variety of soils which can be regrouped in nine big classes (Brahim *et al.,* 2010). At the same time Mediterranean and Saharian country, Tunisia shows several soil resources that relates the importance of the climatic and morphological effects on its physiography. From North to South, the country shows remarkable variation in organic matter content, going from 20% in the humid and sub-humid bioclimatic stages with dense vegetation, until 0.3% in the arid and Saharian bioclimatic stages with skinny and little abundant vegetations, except of the oases where the contents are relatively raised due to the artificial organic contributions (Brahim *et al.,* 2011a). Pragmatically, the sampling is consisted of layer of soil, for the superficial slice 0-30cm depth.

Three main areas characterized the country:

(i) The northern zone has three sub-climates; the humid, the sub-humid and the semi-arid;

(ii) The center zone is characterized by the semi-arid and arid climates, limited at the north by the Dorsale (mountain range system) (1) and spreads until the line of Gafsa-Sfax (2);

(iii) The southern zone has an arid and Saharian climate, spreads from the south of the mounts of Gafsa until the confines of the Sahara (Fig. 1).

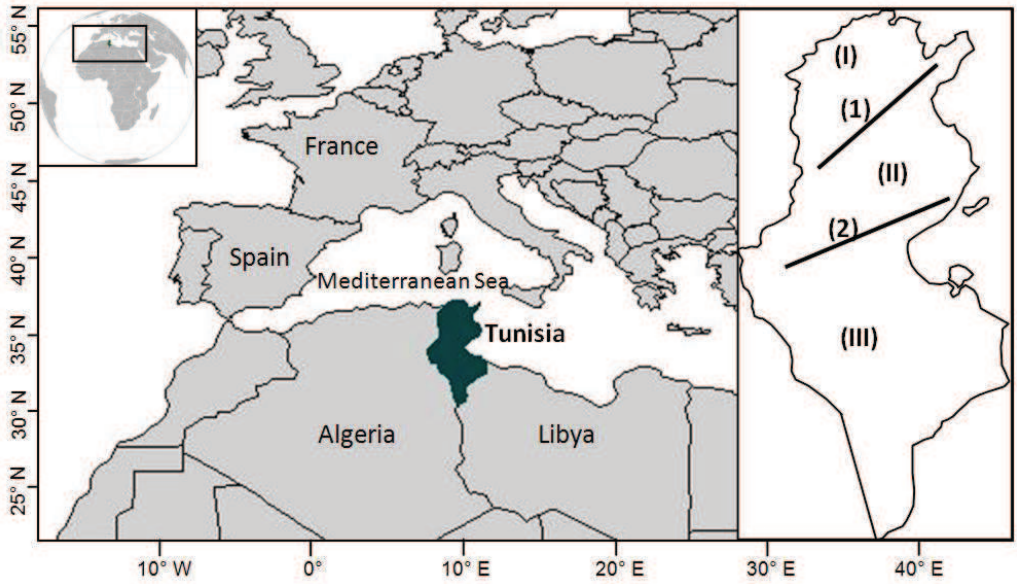


Fig. 1 Location of Tunisia in the Mediterranean Sea and localization of the bioclimatic zones: zone (I) zone (II) and zone (III); (1) Dorsale; (2) Gafsa-Sfax line

1.2 SOIL SAMPLING

Soils were sampled during the two years 2007-2009 in various climate and land use conditions. A total of 1052 soil samples were collected from 124 sampling sites, covering all types of land use. For modeling TN stocks, the samples were divided in two databases clayey and sandy soils including 450 and 602 soil horizons, respectively. At each site, samples were collected at 0-30 cm depths.

1.3 LABORATORY ANALYSIS

The samples were transported to the laboratory and a part of soil passing through the 2 mm sieve was used for analysis. The soil organic carbon content was determined by Walkley-Black method. The total nitrogen (TN) content was

determined by Kjeldahl digestion method. The soil pH was measured in distilled water with dry soil by a pH-meter. The soil bulk density (D_b) was determined as the dry weight per unit volume of soil core (cylinder method) after a 12 hours drying in an oven at 105°C. The granulometric fraction were calculated after soil dispersion with sodium hexametaphosphate (Robinson pipette method): clay (particle 0-2 µm), silt (fine and coarse 2-50 µm), and sand (fine and coarse; 50-2000 µm) are calculated in percent. Calcium carbonate ($CaCO_3$) content was determined by Bernard calcimeter method. All procedures used for the soil analysis are detailed in Pansu and Gautheyrou (2006).

1.4 DATA ANALYSIS

1.4.1 PEDOTRANSFER FUNCTIONS (PTFS) OR MULTIPLE LINEAR REGRESSIONS (MLR)

Predictive equations using simple or multiple regressions (also named Pedotransfer functions-PTFs) were generally developed within one specific soil unit (Arrouays and Pélissier, 1994) and/or for specific ecosystem (Dupouey *et al.,* 1997; Grigal *et al.,* 1989; Howard *et al.,* 1995, Wang *et al.,* 2012).

MLR constitutes an accurate tool to evaluate soil quality, since it generates a minimum data set of indicators. MLR have been successfully used by different authors to evaluate soil quality, being used in natural forest soils balanced with the overall environment (Trasar-Cepeda *et al.,* 1998) or in agriculture soils under different management (Lentzsh et al. 2005; Bernoux *et al.,* 1998; Brahim *et al.,* 2012). The objective of the present work is: firstly, to establish a models using MLR based on different soil physical and chemical properties, in different zones from Tunisia, so that we can searched equations ($N = \beta 0 + \beta 1\ X1 + \beta 2\ X2 + ... + \beta n\ Xn + \varepsilon$. where, N is the dependent variable and X1, X2,…. Xn the independent variables as well as the soil physical and chemical properties) for both groups of soils. Then, all the variables would be included simultaneously into single model in order to test the interactions between the independents variables as well as their contributions on the dependent variable.

The procedure used was a stepwise linear regression, which allowed independent variable to be individually added or deleted from the model at each step of the regression. The MLR method was used because it is a practical tool that furnishes direct quantitative results, and also because the data set was not adapted to spatial analysis such as geostatitics due to lacking or imprecise geographic coordinates.

In the linear regressions, only parameters with statistical significance at the 0.01 significance level were considered for computing predictive equations and reporting results. Standard error of the prediction (SEP) and percentage of variance explained, through R^2 values, were used as means to evaluate the reliability of the models. All the statistical analyses were conducted using the SPSS 16.0 software. The optimal models of nitrogen stocks are obtained by PTFs combined with principal component analysis (PCA) to eliminate multicollinearity among variables (Wang *et al.,* 2012).

1.4.2 STRUCTURAL EQUATION MODELING (SEM)

Structural equation modeling (SEM) is a statistical methodology that takes a confirmatory approach to the analysis of a structural theory bearing on some phenomenon. Typically, this theory represents "causal" processes that generate observations on multiple variables (Bentler, 1989, 1990, 1992). The structural equation modeling conveys that the causal processes under study are represented by a series of structural equations. And that these relations can be modeled. The model can then be tested statistically in a simultaneous analysis of the entire system of variables to determine to which it is consistent with the data.

Several aspects of SEM set it apart from the older generation of multivariate procedure (Fan *et al.,* 1999). First, as noted earlier, it takes a confirmatory, rather than an explanatory, approach to the data analysis (although aspects of the latter can be addressed). Furthermore, by demanding that the pattern of intervariable relations be specified *a priori*, SEM lends itself well to the analysis of data for inferential purpose. By contrast, most other multivariate procedures are essentially descriptive by nature, so that hypothesis testing is difficult, if not impossible. Second, although traditional

multivariate procedures are incapable of either assessing or correcting for measurement error, SEM provides explicit estimates of these error variance parameters (Byrne, 2009). All the statistical analyses were conducted using the Amos 4.0 software.

Table 1 show the variety of different fit indices used in structural equations modeling. To clarify things, stringent thresholds levels are inventoried in a column and Acceptable threshold levels for complex models in a second column. In the field of structural equation modeling, it is difficult to have stringent thresholds (Kenny and McCoach, 2003; Marsh *et al.,* 2004) this is why many authors (Table 1) gave the solution by acceptable threshold levels.

Table 1 Summary of indicative thresholds adjustment tests of SEM

Abréviation	Fit index	Stringent thresholds levels	Acceptable threshold levels for complex models	References
χ^2/df	Chi-square /Degrees of Freedom	< 2 or 3	< 5	Wheaton et al., (1977) ; Tabachnick and Fidell, (2007)
GFI	Goodness of Fit Index	> 0.9	> 0.95	Tabachnick and Fidell, (2007)
AGFI	Adjusted Goodness of Fit Index	> 0.8	> 0.95	Tabachnick and Fidell, (2007)
PGFI	Parsimony Goodness of Fit Index	< 0.5	> 0.9	Mulaik et al., (1989); Crowley and Fan, (1997)
NFI	Normed Fit Index	> 0.8	> 0.95	Bentler and Hu, (1999)
TLI	Bentler-Bonett non-normed fit index or NNFI	> 0.9	> 0.95	Sharma et al., (2005)
RFI	Relative Fit Index	> 0.9	> 0.8	Hu and Bentler, (1999)
IFI	Incremental Fit Index	> 0.9	> 0.8	Miles and Shevlin, (2007)
CFI	Comparative Fit Index	> 0.9	> 0.95	Hu and Bentler, (1999)
RMR	Root Mean Square Residual	< 0.05	< 0.08	Hu and Bentler, (1999)
RMSEA	Root Mean Square Error of Approximation	< 0.06 or 0.07	< 0.09 or 0.1	MacCallum et al., (1996) ; Steiger, (2007)

1.4.3 TUNISIAN SOIL ORGANIC STOCKS AND THEIR MAPS

For Tunisia, organic stocks were already calculated in previous studies. In fact, the TN stock (Ibrahim *et al.,* 2009) and the OC stock (Brahim *et al.,* 2011a) were calculated from 0-30 cm depth and maps of density were developed in this topic (Fig. 2). The methodology used by these authors is summarized as follows:

(i) Soil map: the soil map constructed by Belkhodja *et al.,* (1973) at the scale (1:500.000) is digitized. Nine main orders of soils were inventoried: Lithosols, Regosols, Cambisols, Vertisols, Kastanozems, Podzoluvisools, Luvisols, Solonchaks and Gleysols. The total number of soil map units was 34049.

(ii) Procedure for determining the individual SOC stocks and TN stocks: to estimate SOC or TN stocks, requires knowledge of the vertical distribution of OC in profiles. The way of calculating stocks for a given depth consists of summing SOC Stocks by layer determined as a product of D_b, OC concentration, and layer thickness. For an individual profile with n layers, we estimated the organic carbon stock by the following equation:

$$\text{Stock} = \sum_{i=1}^{n} [D_{bi} \times (\text{OC } or \text{ TN})_i \times D_i]$$

Where Stock is expressed in kg OC or TN/m^2, D_{bi} is the bulk density (Mg/m^3) of layer *i*, OC*i* or TN*i* is the proportion of organic carbon (g OC/g) and total nitrogen (g TN/g) in layer *i*, respectively. Di is the thickness of this layer (cm). Next step of calculation, SOC density or TN density of each great order was multiplied by its respective area to estimate SOC storage for each soil map units. Summation of individually of carbon of the nine great soil orders gave total carbon and nitrogen stock in Tunisia.

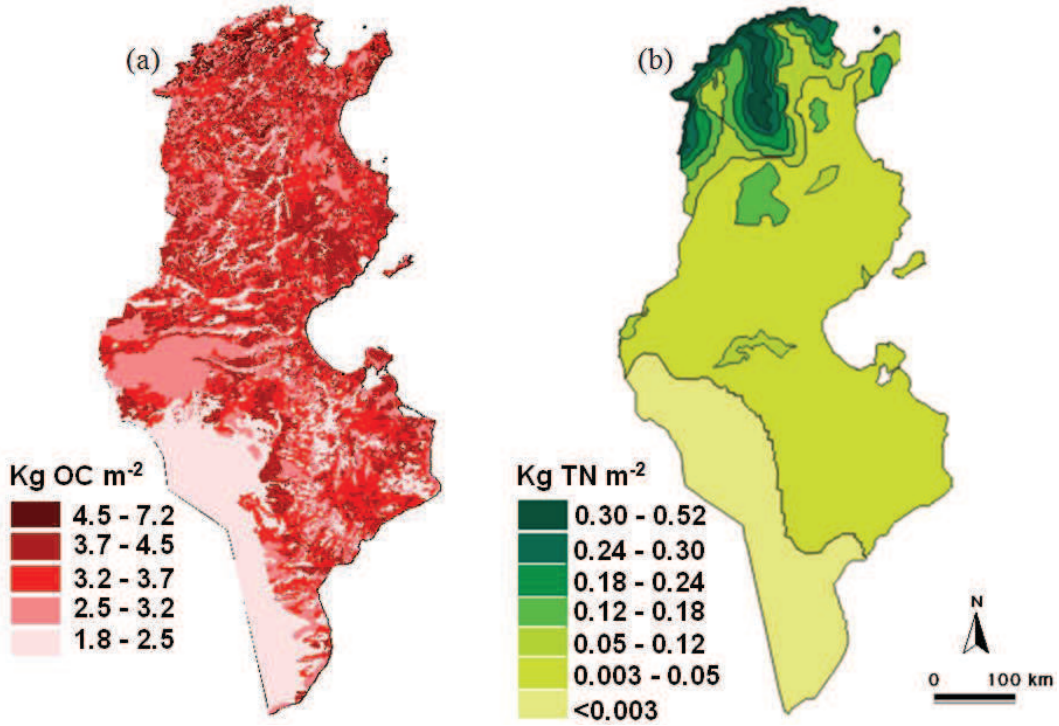


Fig. 2 Maps of Tunisian soil organic stocks in 0-30cm depth, (a) map of soil organic carbon stock (Brahim *et al.,* 2011a) and (b) map of soil total nitrogen stock (Ibrahim *et al.,* 2009)

2. RESULTS AND DISCUSSION

2.1 THE DATABASE OF TUNISIAN SOILS

This study used data from the Tunisian soils. For building of two models of TN stocks under clayey soils and sandy soils, two databases were used. The first was constructed from clayey soils, it was made of 170 soil profiles, corresponding to 450 soil horizons, the second was constructed from sandy soils it was made of 602 soil horizons, corresponding to 285 soil profiles. Descriptive statistics for all databases are reported in Table 2.

Table 2 Descriptive statistics for the two soil databases: clay and sand

	Clay	F-Silt	C-Silt	F-Sand	C-Sand	OC	pH	OM	D_b	$CaCO_3$	TN	OC/TN	TN Stock t/ha 0-30 cm depth
Database of clayey soils													
Valid case	450	450	450	450	450	450	450	450	450	450	450	450	450
Minimum	18.00	0.00	0.00	0.00	0.00	0.10	5.40	0.11	0.87	0.00	0.01	1.40	0.139
Maximum	81.40	51.00	30.10	30.60	38.00	6.40	9.62	11.00	1.80	85.80	2.79	75.00	179.28
Mean	45.77	22.84	12.18	12.25	7.32	1.19	7.90	2.05	1.50	15.09	0.24	11.81	8.80
Std. Deviation	12.33	9.87	7.17	7.16	6.91	0.92	0.66	1.63	0.14	17.10	0.45	6.03	19,11
Variance	151.91	97.39	51.41	51.29	47.78	0.86	0.44	2.65	0.02	292.55	0.20	36.37	365.07
Database of sandy soils													
Valid case	602	602	602	602	602	602	602	602	602	602	602	602	602
Minimum	0.00	0.00	0.00	0.00	0.10	0.06	4.90	0.01	0.63	0.00	0.00	0.00	0.10
Maximum	41.00	49.00	47.00	84.00	93.00	5.78	9.30	11.00	1.90	98.21	1.72	58.52	84.00
Mean	16.56	16.27	10.54	29.87	29.83	1.03	7.46	1.90	1.57	11.11	0.13	3.93	10.97
Std. Deviation	8.62	11.39	6.82	14.98	20.71	0.95	1.01	1.75	0.15	13.46	0.19	5.79	6.86
Variance	74.22	129.78	46.51	224.41	428.75	0.90	1.02	3.06	0.02	181.15	0.03	33.55	47.10

2.2 PEDOTRANSFER FUNCTIONS (PTFS) FOR ESTIMATING TN STOCKS

2.2.1 PTFS FOR CLAYEY SOILS

Multiple linear regression (MLR) analyses were carried out on all the data and subgroups according to soil types.

In the linear regressions, only parameters with statistical significance at the 0.01 significance level were considered for computing predictive equations and reporting results. Standard error of the estimate (SE) and percentage of variance explained, through R values, were used as means to evaluate the reliability of the models. The input variables were chosen either because they are known to influence TN stocks.

In order to group the different soil properties to the smallest possible subsets representing most of the original data set variation, PCA was performed and then these variables were summarized into four principal components with eigenvalue > 1, interpreting 68.47% of the total variance (Table 3).

The first and the most important component (PC1), explaining 25.65% of the variation, showed high factor loadings (> 0.50) for OC, OM, D_b and soil pH. The second component (PC2) loaded heavily on coarse silt and fine sand and explained 18.86% of the total variance. The third component (PC3) had high loadings for soil clay, fine silt contents, OC/TN and $CaCO_3$. The highly weighted variables in the fourth component (PC4) were coarse sand.

Table 4 shows the matrix of correlations between TN stock and soil properties. There are 13 variables in the matrix. The correlation coefficients show that a TN stock is significantly related to 5 variables (F-Silt, C-Silt, F-Sand, TN and OC/TN) at the 0.05 probability level.

Table 3 PCA results based on different clayey and sandy soil properties

Database	Clayey soils				Sandy soils				
Principal component	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC5
Eigenvalue	3.08	2.26	1.70	1.18	2.843	2.10	1.44	1.29	1.05
% total variance	25.65	18.86	14.15	9.80	23.69	17.54	11.96	10.74	8.77
Cumulative %	25.65	44.52	58.67	68.47	23.69	41.23	53.20	63.94	72.71
Factor loading									
Clay	0.45	-0.33	-0.54	0.40	0.04	0.61	-0.60	0.12	0.03
F-Silt	-0.29	-0.26	0.67	0.29	0.02	0.46	0.13	0.34	-0.04
C-Silt	-0.42	0.87	0.00	-0.02	0.02	0.66	-0.04	-0.27	-0.02
F-Sand	-0.43	0.87	0.00	-0.03	-0.09	0.27	0.88	0.00	-0.04
C-Sand	0.25	-0.18	-0.05	-0.90	-0.03	-0.92	-0.30	-0.02	0.00
OC	0.85	0.31	0.29	0.09	-0.19	-0.13	0.13	0.75	0.03
pH	-0.52	-0.33	0.09	0.20	0.93	0.06	-0.01	-0.09	-0.03
OM	0.85	0.32	0.30	0.09	0.93	0.09	-0.01	-0.10	-0.01
D_b	-0.78	-0.11	-0.04	-0.07	-0.66	0.16	0.49	0.19	0.06
TN	0.20	0.45	-0.28	0.16	0.35	0.10	-0.06	-0.11	-0.75
OC/TN	-0.06	0.03	0.59	0.08	0.19	0.04	-0.08	-0.08	0.86
$CaCO_3$	0,08	-0,11	0.59	-0.17	-0.09	0.06	-0.16	0.80	-0.01

Table 4 Bivariate correlation of TN stock with some clayey soil properties

	TN Stock	Clay	F-Silt	C-Silt	F-Sand	C-Sand	$CaCO_3$	D_b	pH	OM	OC	TN	OC/TN
TN Stock	1.000												
Clay	-0.027	1.000											
F-Silt	-0.140**	-0.426**	1.000										
C-Silt	0.233**	-0.415**	-0.154**	1.000									
F-Sand	0.221**	-0.416**	-0.156**	0.974**	1.000								
C-Sand	-0.034	-0.144**	-0.277**	-0.243**	-0.243**	1.000							
$CaCO_3$	-0.065	-0.125**	0.204**	-0.075	-0.076	0.099*	1.000						
D_b	0.011	-0.287**	0.196**	0.195**	0.218**	-0.133**	-0.050	1.000					
pH	-0.037	-0.059	0.232**	-0.029	-0.029	-0.122**	0.098*	0.321**	1.000				
OM	0.030	0.135**	-0.094*	-0.083*	-0.085*	0.077	0.150**	-0.599**	-0.424**	1.000			
OC	0.026	0.143**	-0.098*	-0.097*	-0.098*	0.084*	0.134**	-0.596**	-0.420**	0.993**	1.000		
TN	0.835**	0.049**	-0.166**	0.213**	0.193**	-0.041	-0.092*	-0.202**	-0.088*	0.194**	0.193**	1.000	
OC/TN	-0.195**	-0.167**	0.178**	0.058	0.061	-0.065	0.157**	-0.041	0.086*	0.064	0.074	-0.195**	1.000

** Correlation is significant at the 0.01 level.
* Correlation is significant at the 0.05 level.

Relationships of TN stock with soil properties were obtained by multiple regression analysis with the stepwise method using the PCA-derived subset of al variables using all the available parameters, the best MLR resulted in the following equation is:

TN stock = 6.494 ($\pm$2.854) + 0.577 C-Silt ($\pm$0.123) – 0.207 F-Silt ($\pm$0.09)
(R = 0.256; SE = 18.51; p = 0.000 < 0.05)

The regression equation were highly significant (p = 0.000) and relationships is given essentially by the two variables coarse silt and fine silt. Therefore we find that the stock of total nitrogen is explained by the *physical properties* (coarse and fine silt) and not by *chemical properties*.

2.2.2 PTFs FOR SANDY SOILS

We proceed in the same way as clay soils. PCA was performed and then these variables were summarized into five principal components with eigenvalue > 1, interpreting 72.71% of the total variance (Table 3).

The first component (PC1), explaining 23.69% of the variation, showed high factor loadings (> 0.50) for soil pH, OM and D_b. The second component (PC2) loaded heavily on coarse sand, coarse silt and clay and explained 17.54% of the total variance. The third component (PC3) had high loadings for fine sand and clay contents. The fourth component (PC4) had high factor loadings for $CaCO_3$ (0.80) and OC (0.75). The highly weighted variables in the fifth component (PC5) were TN and OC/TN.

Table 5 shows the matrix of correlations between TN stock and soil properties. There are 13 variables in the matrix. The correlation coefficients show that a TN stock at sandy soils is significantly related to 5 variables, where OM, TN and OC/TN at the 0.01 level of significance; and Coarse silt and OC at the 0.05 probability level.

Using all the available parameters, the best MLR resulted in the following equation:

TN stock = 3.044 ($\pm$0.433) + 0.84 C-Silt ($\pm$0.035)

(R = 0.099; SE = 5.76; p = 0.016 < 0.05)

Pedotransfer function is significant at p = 0.016 (< 0.05*) and relationships is given by the only coarse silt variable. Same with sandy soils, we come across the same result; the TN stock is explained first by the *physical properties* (coarse silt).

R is relatively low for both PTF equations. However, they are reliable by significant p and statistically are acceptable. We searched for PTF with physical properties (Clay, silt and sand) for two reasons: (i) when the nitrogen content was then the stock is estimated directly, and (ii) we have tried to determine the variable that controls the storage in such type's soils under arid and semi-arid zones.

Table 5 Bivariate correlation of TN stock with some sandy soil properties

	TN Stock	Clay	F-Silt	C-Silt	F-Sand	C-Sand	$CaCO_3$	D_b	pH	OM	OC	TN	OC/TN
TN Stock	1.000												
Clay	0.061	1.000											
F-Silt	0.019	0.123**	1.000										
C-Silt	0.099*	0.150**	0.065	1.000									
F-Sand	-0.032	-0.266**	0.138**	0.012	1.000								
C-Sand	-0.039	-0.430**	-0.382**	-0.520	-0.552**	1.000							
$CaCO_3$	-0.005	0.129**	0.113**	-0.082**	-0.063	-0.034	1.000						
D_b	-0.071	-0.145**	0.067	0.057*	0.450**	-0.237**	0.126**	1.000					
pH	-0.024	-0.047	0.070	-0.106**	0.031	0.083*	0.369**	0.348**	1.000				
OM	0.109**	0.111**	-0.035	0.138**	-0.107**	-0.102*	-0.168**	-0.530**	-0.239**	1.000			
OC	0.094*	0.094*	-0.062	0.120**	-0.104*	-0.076	-0.162**	-0.552**	-0.228**	0.863**	1.000		
TN	0.764**	0.057	0.011	0.123**	-0.013	-0.068	-0.088*	-0.290**	-0.148**	0.312**	0.284**	1.000	
OC/TN	-0.318**	0.063	-0.037	0.040	-0.093*	0.001	-0.046	-0.128**	-0.061	0.122**	0.083*	-0.315**	1.000

** Correlation is significant at the 0.01 level.
* Correlation is significant at the 0.05 level.

2.3 MODELING TN STOCKS BY SEM

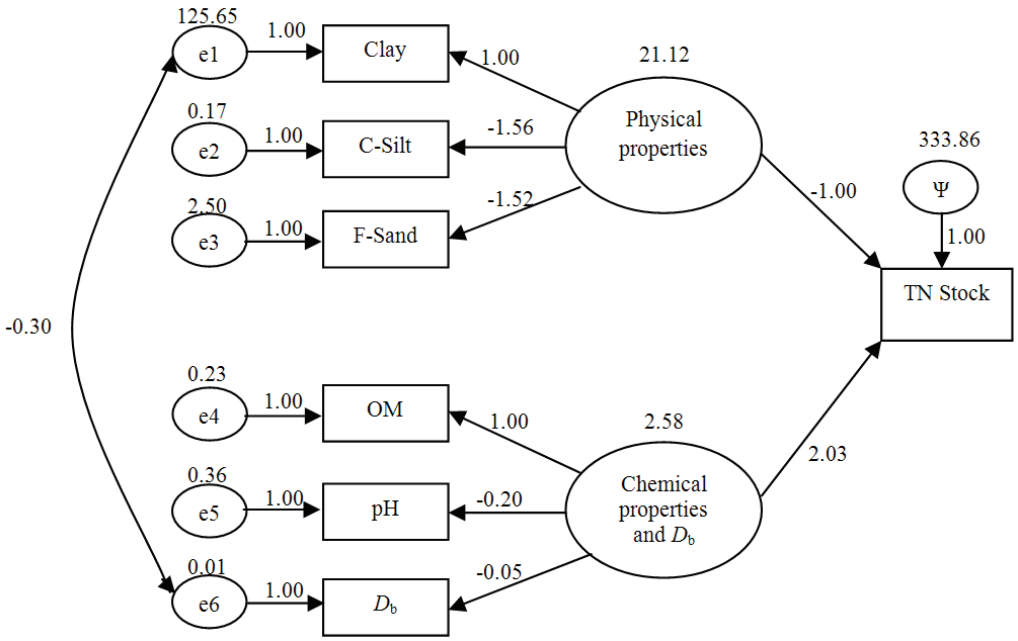
2.3.1 SEM FOR CLAYEY SOILS

Statistical modeling is an accepted scientific practice. In this study, we use the structural equation modeling (SEM), this methodology is characterized by: (i) translation of the soil rather complicated phenomena and to express it in terms of environmental conceptual factors and (ii) consolidation, after exploratory factor analysis (EFA, exploratory factor analysis: EFA), factors measured in question with the observed variables assuming explicitly that alone can not explain the latent variable.

We followed the following methodology: (i) firstly, through an exploratory factor analysis (or PCA), we created a conceptual model explaining the organic carbon content in this stage, we use the statistical software SPSS 16.0, (ii) then, after determining the latent structure, we conducted a confirmatory factor analysis (CFA), at this level, we test statistically the relationships between variables using the software Amos 4.0. Using this method, our model provided more accurate estimates due to estimation error term. The steps in the structural equation modeling are well

detailed by Brahim *et al.,* (2011b).

After carrying out the different steps, we built the model of nitrogen stocks in the clayey soils of Tunisia. The model is focused on figure 3. We found that the TN stock is determined by two variables. The first latent variable "*Physical properties*" with three indicator variables, Clay, C-Silt and F-Sand. The second latent variable "*Chemical properties and* D_b" is measured by three observed variables, OM, pH and D_b. The principle of the selection of these indicators is based on the results of principal component analysis (PCA). Figure 2 shows the covariance between measurement errors for the observable indicators of latent exogenous variables (δ1 and δ6), bulk density (D_b) is generally associated with clay (Jones, 1983; Bernoux *et al.,* 1998; Benites *et al.,* 2007). The model has a value of χ^2 = 2 46 742 (Degree of Freedom DF = 12), and the value χ^2/DF = 3.89 (<5) is satisfactory according to James *et al.,* (1982).



Note: χ^2 (Chi-square) = 46.742; DF (Degrees of Freedom) = 12; GFI (Goodness of Fit Index) = 0.972; AGFI (Adjusted Goodness of Fit Index)= 0.936; RMR (Root Mean Square Residual) = 3.217; NFI (Normed Fit Index) = 0.974; PGFI (Parsimony Goodness of Fit Index) = 0.417; RFI (Relative Fit Index) = 0.954; IFI (Incremental Fit Index) = 0.980; TLI (Bentler-Bonett non-normed fit index or NNFI) = 0.966; CFI (Comparative Fit Index) = 0.980; RMSEA (Root Mean Square Error of Approximation) = 0.080.

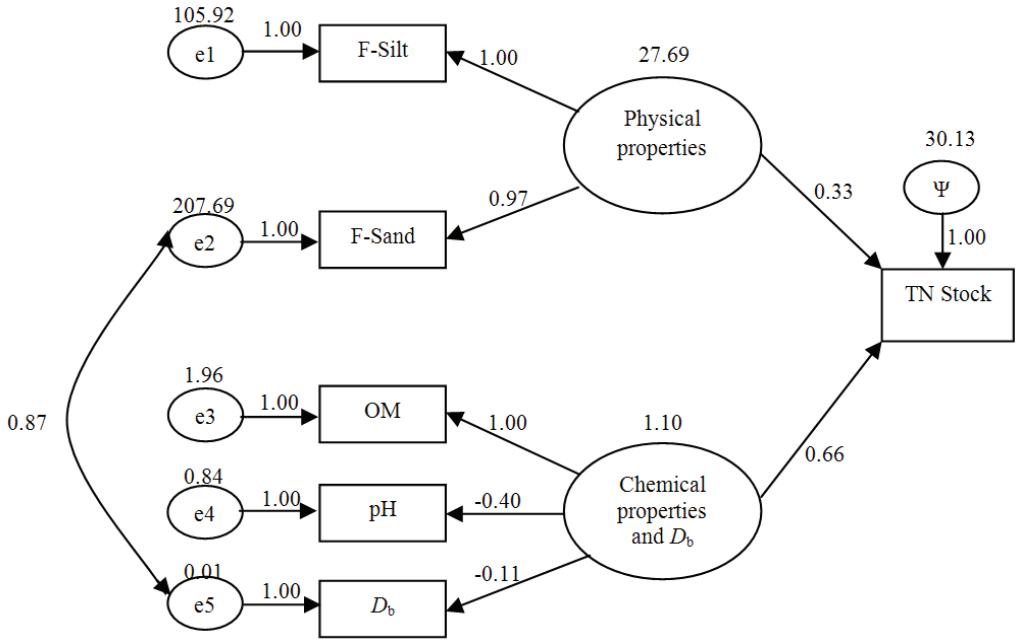
Fig. 3 The estimated parameters of the model predicting TN stock in Tunisian clayey soils

From the RMR value of 0.032, we can conclude that this model is acceptable. According to the GFI and AGFI whose values 0.972 and 0.936 respectively, we can conclude that our model is also satisfactory. In the case of this model value is 0.417 PGFI this index takes into account the complexity of the model (Mulaik *et al.*, 1989). Generally, the index of parsimony is accepted for a lower threshold than that of adjustment index. In our case the PGFI is also acceptable because of this low value. With regard to the index CFI it provides a comprehensive measure of covariance in the data, and the value 0.980 for a model was considered representative (Bentler, 1989) suggesting that the model represents an appropriate form of data. Finally, the RMSEA takes into account the error of approximation. It is independent of the sample size of the database and the complexity of the model (Browne and Cudeck, 1989, 1993). Values less than 0.080 indicate a good model fit.

2.3.2 SEM FOR SANDY SOILS

We performed the same way for modeling TN stock in sandy soils than TN stock modeling in clay soils. The resulting model is focused on figure 4. Latent variables in sandy soils are "*chemical properties and* D_b" and "*physical properties*". These two latent variables are related to the observed variables. We have assumed that the first latent variable "physical properties" as an indicator variables measured, the F-Silt and F-Sand. The second latent variable is measured by two variables observable pH, OM and D_b.

The principle of selection of these indicators is based on the findings of the analysis by PCA. Because naturally the bulk density (D_b) is associated with the mineral fraction of the soil (Jones, 1983; Jones and Morugán 2007; Bernoux *et al.*, 1998; Benites *et al.*, 2007), we show the covariance between measures errors for the observed indicators of exogenous latent variables (δ2 and δ5).



Note: χ^2 = 14.727; DF = 7; GFI = 0.992; AGFI = 0.976; RMR = 1.207; NFI = 0.970; PGFI = 0.331; RFI = 0.935; IFI = 0.984; TLI = 0.965; CFI = 0.984; RMSEA = 0.043.

Fig. 4 The estimated parameters of the model predicting TN stock in Tunisian sandy soils

The model has a value of χ^2 = 14.724 (degree of freedom df = 7), and the value χ^2/df = 2.10 (<5) is satisfactory according to James *et al.*, (1982). From RMR of 1.207; we can conclude that this model is acceptable. From the values of GFI= 0.992 and AGFI = 0.976, we can conclude that the model is also satisfactory. PGFI value of 0.331 is significant according to Mulaik *et al.*, (1989). Relative Fit Index and Incremental Fit Index (0.935 and 0.984) are representative values and the model is acceptable. The CFI and TLI values which are 0.984 and 0.965 respectively suggest that the model represent an appropriate form of data.

The RMSEA takes into account the error of approximation. It is independent of the sample size and the complexity of the model. According to Browne and Cudeck (1989, 1993) values below 0.08 indicate a good fit of the model, in this model RMSEA = 0.043.

2.4 COMPARISON OF THE TWO TYPES OF MODELS (PTFS AND SEM)

After modeling the stock of total nitrogen in clayey and sandy soils of Tunisia by two methods, with pedotransfer functions (PTFs) and with the structural equations, we conclude that the PTFs do not take into account all the variables of the soil, and in both soil types we obtained models with "physical properties" that are coarse and fine silt for clayey soils, and coarse silt for sandy soils. Although the models are significant ($p < 0.05$) they have low R values. However, they show that silt is a fraction in the intercalation of essential stock of total nitrogen in different Tunisian soils.

For structural equations modeling (SEM), we tested the interaction of different physicochemical variables at the same time, we understand that, in addition to the silt fraction, which is essential in the storage already determined by PTFs, other variables can control the stock. Using SEM, we have built and tested two models, which provides an adequate explanation for the change in the stock of total nitrogen in two types of soil: clayey and sandy.

The results show that in clayey soils, the *chemical & bulk density properties* play the most important role in the control of the stock of total nitrogen. In fact, pH, OM and D_b are the main variables responsible for the storage of total nitrogen with γ (coefficients of exogenous latent variables) = 2.03 against γ = -1.00 for *physical properties* (clay, coarse silt and fine sand). The same result is obtained with sandy soils, where the results show that the *chemical & bulk density properties* (pH, OM and D_b) with γ = 0.66 are the best indicators of the stock of total nitrogen as factors physical with γ = 0.33.

The soils of arid and semi-arid Mediterranean area are threatened by erosion and desertification, and the recovery of these degraded lands requires sequestration of organic matter and total nitrogen among other inhibits both phenomena and improves fertility soil. Both models illustrate the main factors affecting the organic stock in the clayey and sandy soils.

With both types of models (PTF's and SEM) are founded at the level of the Tunisian aridisols, TN is related to the fine particles of the soil, primarily to the silt.

These results are in corroboration with its several soil studies in temperate and tropical zones. The stabilization of OC and TN by association with silt and clay particles has been investigated in many studies. Several studies reported a relationship between clay or silt plus clay content and the preservation of OC and TN (Feller and Beare, 1997; Hassink, 1997). It has also been reported that not only the clay content but also the clay type influences the preservation of OC and TN (Ladd *et al.*, 1992; Torn *et al.*, 1997; Sorensen, 1971). Feller *et al.,* (1996) linked critical values of soil organic matter for both soil fertility and erodibility in tropical soils. A critical threshold of soil organic matter, based on a linear equation utilizing soil silt and clay content, was useful in predicting the sustained fertility and productivity of a collection of tropical soils (Feller and Beare, 1997). Six *et al.,* (2001) regressed the amount of OC associated with silt and clay content (%) for tropical and temperate soils and both regression lines were significant, indicating a positive influence of clay and silt particles on OC stabilization. However, the coefficient of determination was lower in temperate than in tropical soils. Results also indicate a lower stabilization of OC per unit of silt and clay particles and, hence, a lower OC protective capacity of the silt and clay particles in tropical versus temperate soils.

3. CONCLUSION

The current study shows that changes in the stock of total nitrogen with soil texture are positively correlated with the chemical and physical properties of the soil.

After performing a principal components analysis (PCA), and pedotransfer equations (PTFs) it was found that the physical properties of soils can explain better storage than chemical properties. And this result is validated in two soil types (clayey and sandy).

With the structural equation modeling (SEM), two models were constructed. These models have provided a satisfactory explanation of the variance of the stock of total nitrogen in two different soil types (clayey and sandy).

The results show that the physical and chemical properties have independent effects on the stock. Indeed, the results show that in clay soils, chemical properties

and bulk density are the most important role in controlling the stock of nitrogen. Organic matter, pH, and D_b are the main variables responsible for the storage of OC linked to? Physical properties which are clay, coarse silt and fine sand. Similarly, in sandy soils results show that chemical factors (i.e. OM, pH and D_b) are the best indicators of the TN stock that the physical properties (fine silt and fine sand).

We can build relationships with simple PTFs to explain the stock of nitrogen in two soils when we have a small number of variables, although the SEM is the best in the explanation because of complexity with all variables. Results also suggest that SEM models explain better the total nitrogen stock than PTFs models.

Soils at semi-arid Mediterranean climate are specially threaten by erosion and desertification phenomena and the restoration of these soils needs a carbon and nitrogen sequestration which inhibit these two phenomena and enhance soils fertility.

Both models illustrate the key factors influencing the nitrogen storage in clay and sandy soils. Finally, the two models could be generalized in all arid and semi-arid Mediterranean area.

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CHAPITRE III

MODELISATION DU ROLE FONCTIONNEL DES MICRO-ORGANISMES DANS LES ECHANGES JOURNALIERS DU CARBONE ENTRE L'ATMOSPHERE, LES PLANTES ET LE SOL

Ce chapitre correspond à l'article publié dans la revue internationale «*Procedia Environmental Sciences*» (19 (2013) 96-105, doi: 10.1016/j.proenv.2013.06.011) et qui s'intitule: **"Modelling the functional role of microorganisms in the daily exchanges of carbon between atmosphere, plants and soil".**

Dans le but de quantifier le transfert significatif de carbone organique (CO) entre les sols et l'atmosphère, ce chapitre vise à répondre à deux questions:
(i) le modèle MOMOS pourrait-il prédire l'évolution journalière à court terme de CO alimentées par l'exsudation de matières organiques dans les systèmes complexes ;
(ii) pourrait-on coupler les équations de décomposition du CO avec des modules différentes de production de CO et de proposer une nouvelle théorie pour l'agro-écologie (sol et agriculture) et le changement climatique.

Résumé

Plusieurs recherches sur les stocks de carbone organique (CO) au niveau de la couche superficielle du sol ont mis l'accent sur les prévisions semi-mécanistes des stocks à long terme et non pas sur les processus microbiens agissant sur les transformations du CO. La littérature montre l'absence d'études concernant la modélisation des échanges à courte durée entre l'atmosphère, les plantes, les rhizobiums et les autres micro-organismes du sol. Nous pensons que c'est à cause du rôle mécaniste peu considéré des micro-organismes dans la plupart des modèles existants. La théorie la plus utilisée pour modéliser le système complexe des différentes formes de CO est celle des compartiments, avec des propositions linéaires ou non-linéaires. La plupart des modèles ne considèrent pas explicitement un compartiment microbien actif et sont souvent surparamétrés. En revanche, la proposition du modèle MOMOS définit linéairement le rôle fonctionnel des micro-organismes avec seulement un terme non-linéaire lié à la respiration microbienne. Il utilise seulement 7 paramètres cinétiques ayant une définition écologique claire et des liaisons sont proposées avec le climat (tous les paramètres), la texture du sol ou le pH (taux de respiration microbienne), et les propriétés biologiques des entrées de débris (taux de dégradation enzymatique de débris végétaux et de la mortalité microbienne). Les 3 autres paramètres (taux de stabilisation d'humus et l'assimilation enzymatique de l'humus labile et stable) ont été trouvé uniquement liés au climat, suggérant une qualité des matériaux humifiés plus constante que les formes de CO provenant des plantes. En couplage avec l'eau du sol et les modules de production, le modèle apparaît comme une nouvelle base théorique pour décrire le cycle de la vie et de ses applications à l'agro-écologie et au changement global.

Mots clés: Modélisation; carbone; sol; plante; matière organique.

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 a quality of humified materials 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.

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

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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 the C exchanges, 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. MODELLING THE KEY ROLE OF MICROORGANISMS

MOMOS (Modelling Organic transformations by Micro-Organisms of Soil, (Fig.1) 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 [2], and soil texture [3]. It has been proposed to predict the evolution of ^{14}C tracer in two ecosystems [4]. Then it was validated in six other contrasted ecosystems of the tropical area [5]. It has been successfully used to quantify the turnover of OC in Andean fallow ecosystems [6] and to regulate the daily exchanges of C between plant organs, nodule rhizobia, microorganisms and atmosphere in cereal legume intercropping in Mediterranean conditions [7].

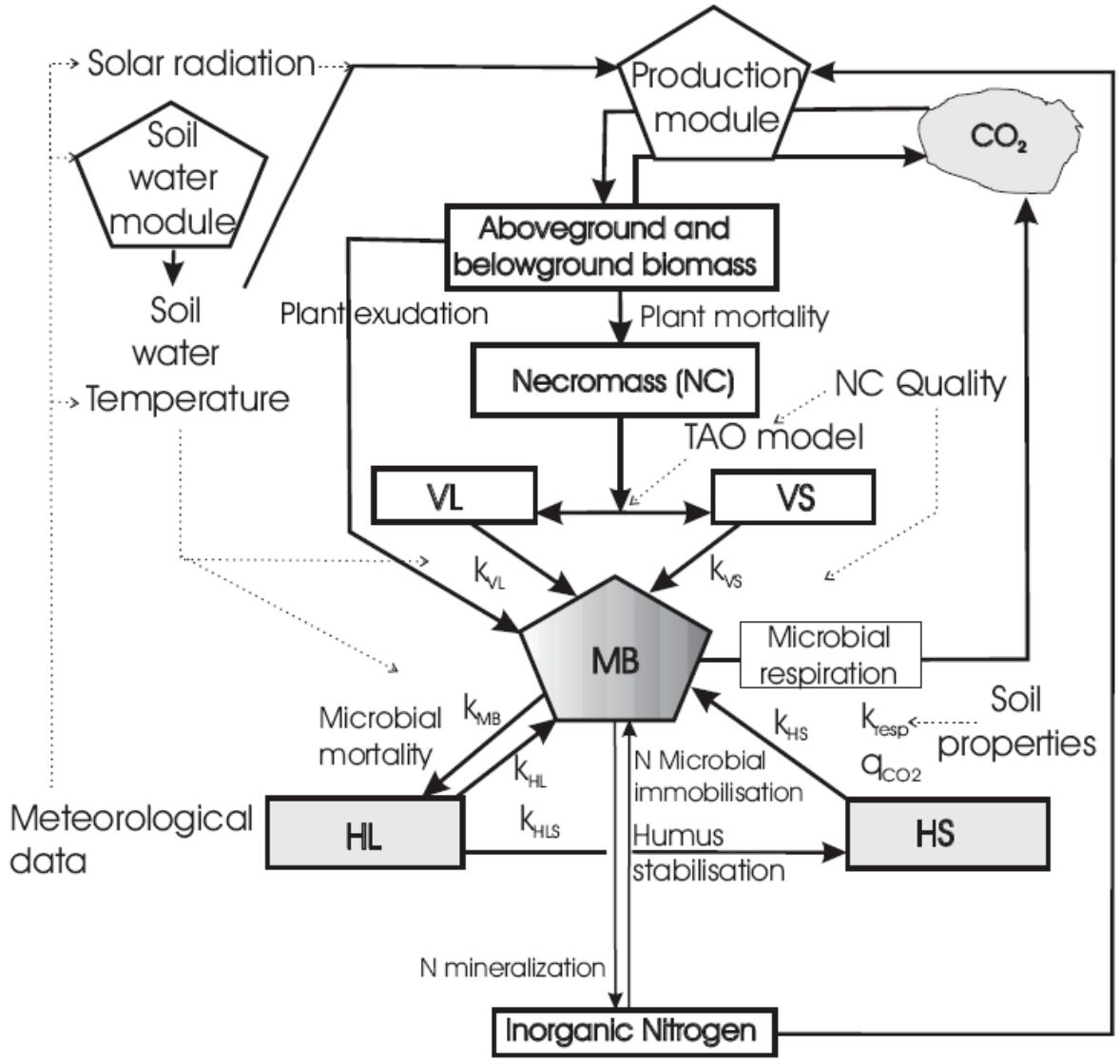

Fig. 1 The MOMOS model, coupled with soil water and production modules: MB is microbial biomass, VL and VS are the labile and stable debris of vegetal origin entering the soil, HL and HS are the labile and stable humus fractions, k_{VL}, k_{VS}, k_{HL}, and k_{HS} are the daily rates of enzymatic breakdown 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. 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:

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

where **x** is the vector of the state variables (C content of compartments), $\dot{\mathbf{x}}$ is the vector of the derivatives of **x** (day^{-1}), **A** is the matrix of the model parameters, **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 [5, 8], 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 [5]. $f(\theta)$ is the function of the soil water content normalised to the water holding capacity (WHC) of the soil[5]:

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

The soil water content (θ) was predicted using the SAHEL [9] 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 **A** and vector **x** for the model are:

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

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

The kinetics of total C decrease by microbial respiration $\dot{\mathbf{C}}$ for the five compartments is:

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

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

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

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[5]:

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

Alternately another transfer function linking k_{resp} to soil pH can be used [5]. 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) [2]. 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}.

2.3. FORMULATION FOR ISOTOPIC TRACERS

Previous studies using isotopic tracers enabled to define the term values of the matrix **A** in equation 1 as the initial values of the vector **x** were known (from the ^{14}C content and quality of ^{14}C labelled materials that were added) and all values of vector **B** = 0 (no inputs of labelled C from plants). Equations 1 and 4 became:

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

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

2.4. 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, 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:

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

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 [10] used in calibration experiment[4,11],

- roots, shoots and symbiotic nodules in the Mauguio intercropped system [7]:

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[10] was used; for wheat-fababean intercropping, another production module was defined[7];
- qualitative estimate of necromass to divide each input into labile and stable fractions in the MOMOS decomposition processes.

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 [8, 12-14]. The model has since been validated on tropical materials[15], 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[12]:

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

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 τ_{NC}, the C:N ratio of input necromass NC from each plant organ. An increase of τ_{NC} was modelled as decreasing the assimilation rates of labile (k_{VL}) and stable (k_{VS}) NC compartments [2]:

$$k_{VL} = MAX(0.65 - 0.0019\ \tau_{NC}, 0.1) \quad (13)$$

$$k_{VS} = MAX(0.0037 - 0.000026\ \tau_{NC}, 0.00005) \quad (13')$$

An increase of τ_{NC} was also found to increase the rate of microbial mortality[11]:

$$k_{MB} = MIN(0.42 + 0.0012\ \tau_{NC}, 0.8) \quad (14)$$

Equations 13 and 13' were applied separately to each of the five NC inputs, while τ_{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

^{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.

2.7. 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 [16]. 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 [17]. 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[18].

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 [7].

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 [19,20]. 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 [10] has been used to predict carbon evolution [11] 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.

3.3. SHORT TERM MICROBIAL EXCHANGE IN COMPLEX AGRO-SYSTEMS

Another C production module was written [7] in place of Faprom [10] 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.

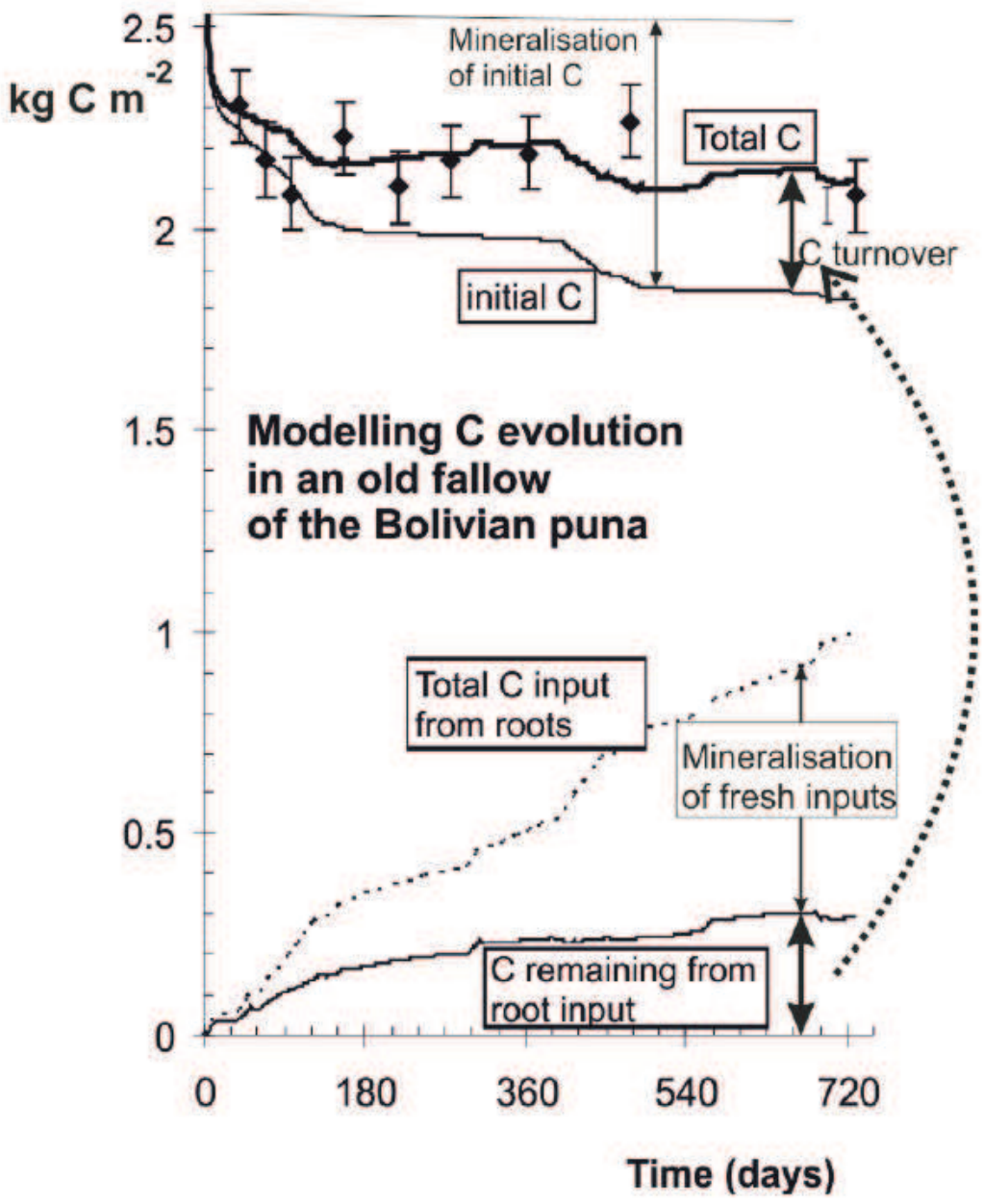

Fig. 2 Modelling of the turnover of carbon in a fallow plot of the Bolivian puna [10]

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 of 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 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.

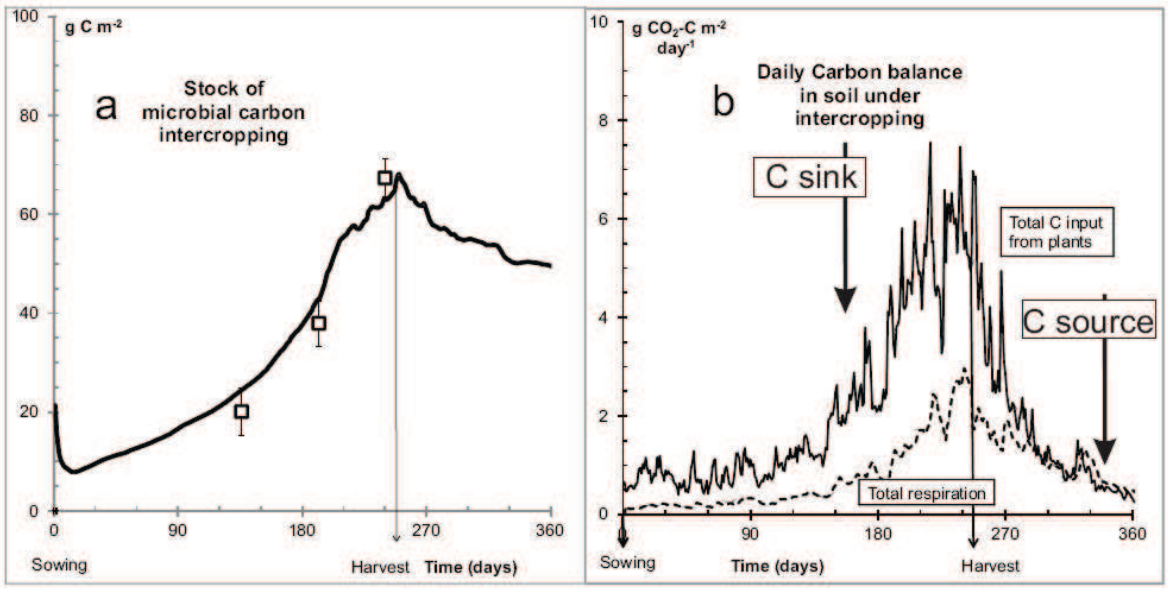

Fig. 3 a) Measured and modelled daily evolution of the microbial C stocks during the growth of durum wheat and faba bean in intercropped plots; b) modelled evolution of total C inputs and outputs in soil during intercropping [7].

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CHAPITRE IV

L'ECHANGE JOURNALIER DU CARBONE DANS LE SYSTEME : ORGANISMES VIVANTS-SOL-ATMOSPHERE

Ce chapitre correspond à l'article soumis pour la revue internationale «*European Journal of Agronomy*» et qui s'intitule:"**The daily exchange of carbon between living organisms, the soil and the atmosphere".**

Résumé

La couche supérieure du sol stocke la plus grande réserve de carbone organique (CO) dans le système sol-plante-atmosphère et joue un rôle fondamental dans la nutrition et l'équilibre de la Terre (Smith et al. 2008). De nombreuses études récentes ont modélisé les variations des stocks OC causées par des changements dans la gestion des terres et l'utilisation à moyen terme (plusieurs années) à plus terme (plusieurs décennies) où des données étaient disponibles, p.e. 10 ans (Jenkinson et al. 1999) et 30 ans (Kintché et al. 2010) dans un système de culture de rotation, 5 ans (Romanyaa et al. 2000) et 18 ans (Palosuo et al. 2012) dans les systèmes forestiers (Farage et al 2007;.... Nieto et al. 2010), 4 ans en cultures bioénergétiques (Garten et al. 2010), 12 ans après le feu et la sécheresse dans les prairies et les zones arbustives (Martí-Roura et al. 2011), 13 ans de dans le labour et changements de fertilisation azoté (Alvaro Fuentes-et al. 2012) et 24 ans d'amendements organiques (Heitkamp et al. 2012). Quelques études ont utilisé des prévisions plus mécanistes sur des périodes plus courtes, par exemple flux journalier d'eau et des émissions de gaz dans le sol (Parton et al 2010;. 2005 Del Grosso et al.), la simulation et le développement d'espèces de légumineuses (Robertson et al, 2002.), simulation de croissance des cultures et fixation de l'azote dans les cultures intercalaires céréales-légumineuses (Corre-Hellou et al 2009), la quantification de la fixation biologique d'azote (Liu et al 2011.) et les relations entre la respiration du sol, la production végétale et de la température (Yuste et al. 2004; Dornbush et al. 2006). Toutefois, les références publiées manquent de prédictions mécanistes des transferts journaliers de C entre sol-plante-atmosphère en compte dans les modèles utilisés. Bien que certaines propositions récentes prennent mieux en compte l'activité microbienne (Allison et al, 2010; Schimel et al., 2003), pour Todd-Brown et al. (2012) les modèles actuels ne représentent pas un contrôle microbien direct sur la décomposition", une nouvelle génération de modèles est nécessaire «pour capturer les mécanismes microbiens sans complexité mathématique excessive » (Todd-Brown et al. 2012) et quantifier "le rôle crucial des micro-organismes dans la régulation de la dynamique du carbone du sol" (Jizhong Zhou et al. 2011).
Notre étude concernait le suivi et la modélisation de l'échange continu de carbone organique entre les organes végétaux, les micro-organismes décomposeurs et fixateurs d'un système complexe intercalaire « céréales-légumineuse ». Les fonctions correctives du modèle liées aux données météorologiques ont mis en évidence une limitation conjointe des croissances végétales et des transformations microbiennes par la température en hiver et la disponibilité de l'eau en été. Dans un sol non fertile, 62% de la production de blé dur et 77% de la production de fèveroles ont été alloués aux racines et ensuite perdus principalement par la respiration des racines pour le blé, et par la mortalité racinaires pour les fèveroles qui ont fourni 50% de CO journalier des racines pour la croissance microbienne. Le système est modélisé comme un puits de carbone durant l'année de culture intercalaire avec un stockage

à court terme dans la réserve des métabolites microbiens labiles. La modélisation a aussi mis en évidence que l'effet de l'activité des nodules sur la croissance des parties aériennes serait, comme la respiration microbienne, un processus non linéaire. Depuis ce travail une nouvelle base théorique est maintenant disponible pour l'agro-écologie et le changement global.

Mots clés: Carbone organique; dioxyde de carbone; modèle; biomasse microbienne; simulation.

The daily exchange of carbon between living organisms, the soil and the atmosphere

(Submitted August 2013)

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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**.** The continuous exchange of OC between plant organs, micro-organisms, soil compartments and the atmosphere were modelled on one year data of a complex intercropped system. The model weather functions showed that the plant growths and the microbial transformations were limited by temperature in winter and water's availability in summer. In a low fertility soil, 62% of the production of durum wheat and 77% of the production of faba beans was allocated to roots and then lost mainly by root respiration for wheat, and by root mortality for faba beans which supplied 50% of the daily root OC for microbial growth. The stored OC increased over the year in the soil's reserve of labile microbial metabolites, and the effect of root-nodule activity on shoot growth was modelled as a non-linear process. A new theoretical basis is available for agro-ecology and climate previsions.

Keywords: Soil organic carbon, carbon dioxide, Model, Microbial biomass, Simulation

1. INTRODUCTION

The soil upper layer has the largest reserve of organic carbon (OC) in the soil-plant-atmosphere system and plays a fundamental role in nutrition and equilibrium of the earth (Smith et al. 2008). Many recent studies have modelled the changes in OC stocks caused by changes in land management and use over the medium term (several years) to long term (several decades) periods where OC data is available, such as 10 years (Jenkinson et al. 1999) and 30 years (Kintché et al. 2010) in a crop rotation system, 5 years (Romanyaa et al. 2000) and 18 years (Palosuo el al. 2012) in forest systems (Farage et al. 2007; Nieto et al. 2010), 50 years in farming and soil management systems, 4 years in bioenergy cropping (Garten et al. 2010), 12 years after fire and drought in grasslands and shrublands (Martí-Roura et al. 2011), 13 years under tillage and N fertilization changes (Alvaro-Fuentes et al. 2012) and 24 years of organic amendments (Heitkamp et al. 2012).

Some other studies have used more mechanistic predictions over shorter periods e.g. daily fluxes of water and greenhouse gases in soil (Parton et al. 2010; Del Grosso et al. 2005), simulation and development of legume species (Robertson et al. 2002), simulation of crop growth and nitrogen fixation in legume-cereal intercropping (Corre-Hellou et al. 2009), quantification of biological N fixation (Liu et al. 2011) and relationships between soil respiration, plant production and temperature (Yuste et al. 2004; Dornbush et al. 2006). However, published references lack mechanistic predictions of the daily or sub-daily transfers of C between plants, soil compartments and the atmosphere. We believe that it is because the functional role of micro-organisms was neglected in many models which focused mainly on changes of total C stocks, rather than on changes within the various OC pools with varying stabilities. Although some models are appearing that take account of microbial activity (Allison et al. 2010; Pansu et al. 2010; Schimel et al. 2003), in general "current global models do not represent direct microbial control over decomposition" (Todd-Brown et al. 2012), a new generation of models is required "to capture fundamental microbial mechanisms without excessive mathematical complexity" (Todd-Brown et al. 2012) and quantify "the crucial roles of microorganisms in regulating soil carbon dynamics" (Jizhong Zhou et al. 2011).

This study set out to model the daily transfers of C between plant organs, micro-organisms, the soil compartments and the atmosphere during one year of intercropping wheat and faba beans. The model used was MOMOS (Modelling Organic transformations by Micro-Organisms of Soils) which is focused on the activity of the microbial biomass (MB, figure 1). MOMOS was developed using isotopic data for OC fluxes at two sites (Pansu et al. 2004) and validated at six different sites over a wide range of altitudes and climates, which proved also its sensitivity to weather conditions (Pansu et al. 2010). The challenge of this study was to extend the applicability of MOMOS as a new theoretical basis for agro-ecology (i) by testing the equation system on a Mediterranean calcareous environment using the parameters and functions for climate, inputs and soil textures that had been calibrated and validated in acidic tropical conditions (Bottner et al. 2006; Pansu et al.

2007; Pansu et al. 2010), (ii) by modelling a complex agro-ecosystem (cereal-legume intercropping) by coupling the decomposition equations to a water module and new predictive modules for the quantitative and qualitative daily production and mortality of plant materials entering the soil.

2. MATERIALS AND METHODS

2.1 FIELD EXPERIMENT

The field experiment was carried out in a station of the *Institut National de la Recherche Agronomique* (INRA), located at Mauguio (43°37'32''N/3°59'20''E), south-east of Montpellier, France. The climate is Mediterranean with large seasonal and night/day fluctuations. For 2011, total rainfall was 631 mm with minima at 4 mm in August and December, and maxima at 268 mm in November, mean annual temperature was 16.4°C with mean minimal values at 2.4°C in January and mean maximal values at 28.5°C in August. Data was collected in a part of the station managed using organic methods. The experimental plots were located on a gentle slope (~ 0.5 %) with a soil with a partly decarbonatated brown-reddish upper horizon (~ 60 cm thick) on Pliocene calcareous molasse, classified as chromic Cambisol in international soil classifications (FAO 1988) and Fersialsol in the French soil reference system (Baize et al. 2008). The texture was loamy (USDA triangle) with 21.9±3.6% (mean±SD) 0-2 µm clay, 25.2±2.4% 2-20 µm fine-silt and 21.5±1.1% 20-50 µm coarse-silt. The Cation Exchange Capacity (CEC) was 21.8 ± 1.2 cmol kg^{-1}. The carbonate content was 1.7±1.2% of $CaCO_3$ and the pH was alkaline (8.2±0.1). 6×10 m plots were used with three crops cultivated using organic farming methods (1) durum wheat (*Triticum durum*) cultivar LA1823 monocrop (2) faba beans (*Vicia faba)* cultivar "Castel" monocrop and (3) durum wheat LA1823 - faba bean Castel intercrop. There were four field replicates per crop. The means±SDs of the plant densities for the four replicates were 100±23 durum wheat plants m^{-2} for (1), 17±7 faba bean plants m^{-2} for (2) and 72±28 durum wheat m^{-2} and 16±6 faba bean plants m^{-2} for (3). Seed was sown in drills at 11 cm spacing.

2.2 DATA COLLECTION

Four whole plants (roots and shoots) of durum wheat and four of faba bean were collected from each plot during growth (1st sampling period), 10 plants of each species were taken during flowering (2nd sampling period) and four of each species were taken at maturity (3rd sampling period). 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 (Pansu et al. 2001).

For microbial biomass (MB) determination, at each sampling occasion the near-root soil was collected from the field and preserved in iceboxes (4 plots×4 modalities × 4 replicates), as preliminary tests (not published) had shown a significantly greater microbial biomass in the near-root soil than in the soil far from plants. These samples were then homogenised and crushed without drying and passed through a 4×4 mm grid sieve in the laboratory (Pansu et al. 2001). 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, since preliminary tests (unpublished) had shown a significant increase in the MB in one week of storage at 4°C.

The soil MB carbon was determined by fumigation-extraction. 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 (Joergensen et al. 1996).

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 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. For a plot of bulk density *bd*, ponderal soil moisture *Wp*, and coarse gravel fraction *Cf*, total OC stock in g C m^{-2} of the 0-30 cm soil layer = $300 \times bd \times (cC - CO_3\text{-}C)(1\text{-}Wp)(1\text{-}Cf)$. For a mass of subsample m_S and a microbial extract of 30 mL, the microbial C stock in g m^{-2} was $MB\text{-}C = 9 \times bd \times MB\text{-}cC \times (1\text{-}Wp)(1\text{-}Cf)/m_S$. For a total mass m_P in g of each part of *n* sampled plants with a concentration m_P-cC in g g^{-1} and a density of *d* plants m^{-2}, the C stock in each part in g m^{-2} was $m_P\text{-}cC \times d \times m_P/n$.

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}. In hot summer periods (2nd and 3rd sampling periods) the soil surface temperature varied from 36 to 51°C and the CO_2-C flux decreased on the days when the soil temperature was well above the optimum temperature for microbial functioning (equation 2). A corrective function was then derived by regression of the flux *vs* temperature and applied to estimate an unbiased average daily flux: for the 2nd sampling period, the corrected flux was the measured flux + 0.043(T°C-36). For the third sampling period the corrected flux was the measured flux + 0.042(T°C-22). No correction was necessary for the 1st sampling period.

2.3 MODELLING MICROBIAL TRANSFORMATIONS

MOMOS (Modelling Organic transformations by Micro-Organisms of Soil, figure 1 was designed as a five compartment model and validated using isotopic tracer experiments (Pansu et al. 2004; 2010). It is based on the functional ecology of soil microbial biomass (MB) which increases by 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 (Pansu et al. 2004; 2007; Bottner et al. 2006). 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 MOMOS equation:

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

where **x** is the vector of the state variables (C content of compartments), $\dot{\mathbf{x}}$ is the vector of the derivatives of **x** (day^{-1}), **A** is the matrix of the model parameters, **B** is a vector determining the external C input from plants previously used to quantify rhizodeposed C (Pansu et al. 2009). *f*(*T*) is an exponential function of temperature:

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

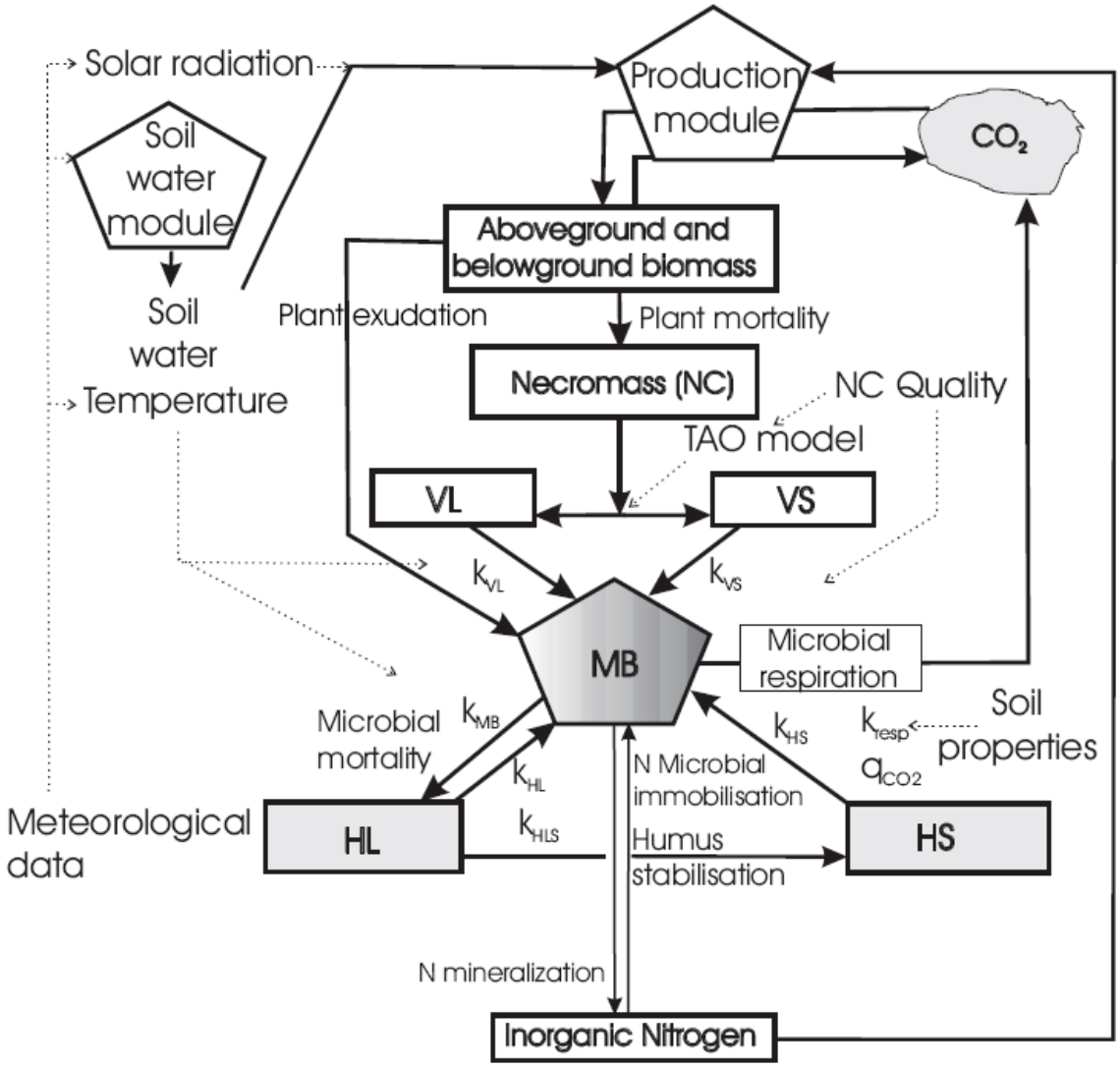

Fig.1 The MOMOS model, coupled with the soil water model and the cereal / legume C production module (Figure 2): MB is microbial biomass, VL and VS are the labile and stable debris of vegetal origin entering the soil, HL and HS are the labile and stable humus fractions, k_{VL}, k_{VS}, k_{HL}, and k_{HS} 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

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 (Pansu et al. 2010; Thuriès et al. 2001), 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 (Pansu et al. 2010). $f(\theta)$ is the function of the soil water content normalised to the water holding capacity (WHC) of the soil (Pansu et al. 2010):

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

The soil water content (θ) was predicted using the SAHEL model (Penning de Vries et al. 1989), based on meteorological data collected at the Montpellier Fréjorgues airport weather station, 4 km from the study site, and possibly corrected by rainfall meters near the experimental plots. The data included air temperature, rainfall, 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:

$$\mathbf{A} = \begin{pmatrix} -k_{VL} & 0 & 0 & 0 & 0 \\ 0 & -k_{VS} & 0 & 0 & 0 \\ k_{VL} & k_{VS} & -(q_{CO_2} + k_{MB}) & k_{HL} & k_{HS} \\ 0 & 0 & k_{MB} & -(k_{HL} + k_{HS}) & 0 \\ 0 & 0 & 0 & k_{HLS} & -k_{HS} \end{pmatrix}$$

$$and \ \mathbf{x} = \begin{pmatrix} x_{VL} \\ x_{VS} \\ x_{MB} \\ x_{HL} \\ x_{HS} \end{pmatrix} \tag{4}$$

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

$$\dot{c} = \sum_{i=1}^{5} \dot{x_i} = -f(T)\, f(\theta)\, q_{CO_2}\, x_{MB} \tag{5}$$

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

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

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_{0-20}) by the transfer function using the two sites used for calibrating the model plus the six sites used for validating the model (Pansu et al. 2010):

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

The rates of enzymatic digestion of labile (k_{VL}) and stable (k_{VS}) plant materials (equations 17 and 17'), and the microbial mortality rate (k_{MB}) are linked to the type of organic inputs (equation 18) (Bottner et al. 2006). 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 (Pansu et al. 2004;2007;2010):

- 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}.

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). For this study, the previously defined matrix **A** was used 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 plant shoots, roots and nodules. Equation 1 became:

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

where j ϵ[cereal shoot NC, cereal root NC, legume shoot NC, legume root NC, nodule NC]

The elements of **B***j* were estimated in two stages:

- Quantitative estimate of necromass input from each plant part (see below),
- Qualitative estimate of necromass to divide each input into labile and stable fractions in the MOMOS decomposition processes (see below).

2.4 MODELLING PLANT AND RHIZOBIUM PRODUCTIONS

To produce these estimates a simplified predictive module of the production of shoot C and root C for cereals and legumes (figure 2) was set up and coupled with MOMOS (figure 1). This production module is driven primarily for each plant by a standard growth law with (i) an optimum relative growth rate τ_{GC} for cereals and τ_{GL} for legumes, and (ii) a maximum C biomass max_{BC} for cereals and max_{BL} for legumes. Unlike applications for forest systems, the growth parameters can be calculated to fit measured data throughout the whole cropping period. The module assumes that plant growth is also controlled by $f(T)f(\theta)$, the climate correction factor used for microbial functioning (equation 1), and by aerial biomass C, CAB for cereals and LAB for legumes, based on the foliar surface of each plant species. The daily production of carbon CDP for cereals and LDP for legumes is:

$$\mathrm{CDP} = \tau_{GC}\, f(T)f(\theta)\,\mathrm{CAB}\left(1 - \frac{\mathrm{CAB}}{\mathrm{max}_{BC}}\right) \qquad (9)$$

$$\mathrm{LDP} = \tau_{GL}\, f(T)f(\theta)\,\mathrm{LAB}\,(1 - \mathrm{LAB}/\mathrm{max}_{BL}) \qquad (9')$$

for time t between the sowing time t_S and the harvest time t_H, and CDP = LDP = 0 for $t>t_H$.

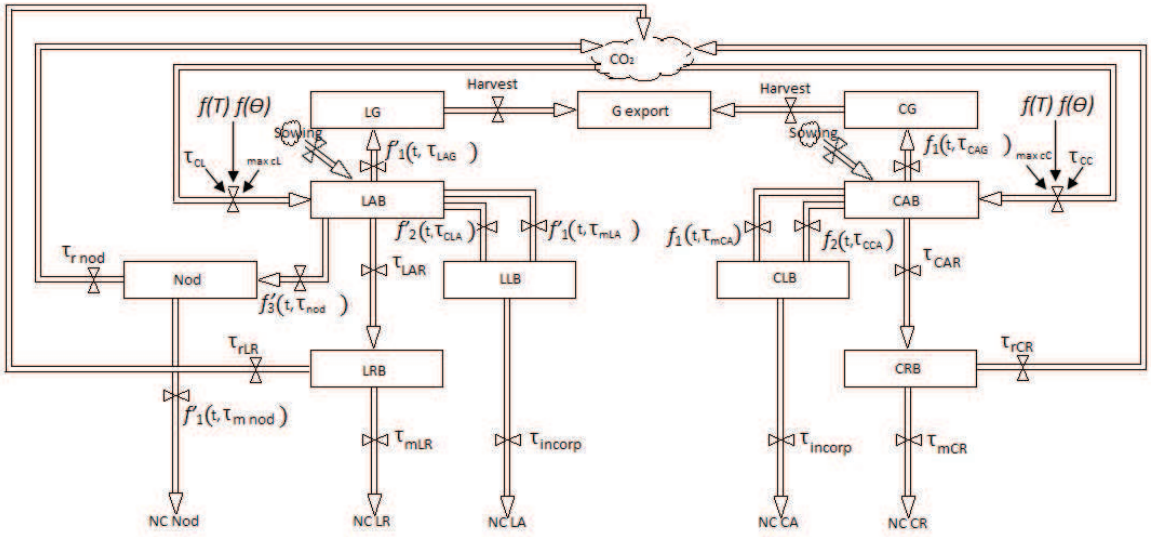

Fig.2 The C production module for the cereal / legume intercropping: CAB and LAB are the aerial biomasses of cereals and legumes, CG and LG are the grains of cereals and legumes, CRB and LRB are the cereal and legume root biomasses, CLB and LLB are the cereal and legume litter necromasses, NC CA, NC CR, NC LA , NC LR and NC Nod are the daily inputs of necromass (NC) from the cereal aerial litter (CA), cereal roots (CR), legume aerial litter (LA), legume roots (LR) and nodules (Nod) in the decomposition process (B*j* vector, equation 8)

The daily carbon production was partly allocated to roots using allocation rates τ_{CAR} for cereals and τ_{LAR} for legumes. The model used a constant fraction of C production allocated to roots throughout the growth process. Another part of the C production was transferred to grain (G) depending on the time functions f_1 and f'_1 (see below) and the transfer rates τ_{CAG} for cereals and τ_{LAG} for legumes. Part of the aerial biomass was transferred to litter by natural mortality assuming daily aerial mortality rates τ_{mCA} and $\tau_{mLA,}$ and time functions f_1 and f'_1 for cereals and legumes, respectively. The model assumed that a significant amount of dead aerial matter begins to fall on the litter at the start of grain formation. Part of the C production was transferred to litter during harvest, using the same cutting rate τ_c and time function f_2 for both cereals and legumes. For legumes, part of daily C production was transferred to nodule production at a rate τ_{nod} associated with a time function f'_3. The shoot biomasses, CAB for cereals and LAB for legumes, were then modelled:

$$LAB = \int_{t=t_s}^{t_H} (CDP(1 - \tau_{CAR} - f_1(t, \tau_{CAG})) - CAB(f_1(t, \tau_{mCA}) + f_2(t, \tau_c)))dt \quad (10)$$

$$LAB = \int_{t=t_s}^{t_H} (LDP(1 - \tau_{LAR} - f'_1(t, \tau_{LAG}) - f'_3(t, \tau_{nod})) - LAB(f'_1(t, \tau_{mLA}) + f_2(t, \tau_c)))dt \quad (10')$$

Carbon grain production, CG for cereal and LG for legume, was modelled:

$$CG = \int_{t=t_s}^{t_H} CDP\, f_1(t, \tau_{CAG})dt - Harvest \quad (11)$$

$$LG = \int_{t=t_s}^{t_H} LDP\, f'_1(t, \tau_{LAG})dt - Harvest \quad (11')$$

where Harvest was C exported by grain production at harvest time t_H, and was 0 for $t \neq t_H$.

The model considers that cereal and legume litter falls onto the soil by natural mortality during the harvest. A part of each litter is modelled as being incorporated into the 0-30 cm by soil fauna at a constant daily rate of incorporation τ_{incorp}, assuming that incorporation does not depend on litter quality. The litter biomass C CLB for cereals and LLB for legumes were integrated daily:

$$CLB = \int_{t=t_s}^{t_H} (CAB\,(f_1(t,\tau_{mCA}) + f_2(t,\tau_c)) - CLB\tau_{incorp})dt \qquad (12)$$

$$LLB = \int_{t=t_s}^{t_H} (LAB\,(f'_1(t,\tau_{mLA}) + f'_2(t,\tau_c)) - LLB\tau_{incorp})dt \qquad (12')$$

The model considers that root compartments are driven by daily allocation at rates τ_{CAR} and τ_{LAR} of net C production and by daily outputs by root respiration (τ_r) and mortality (τ_m). The root C biomass CRB for cereals and LRB for legumes were then modelled by:

$$CRB = \int_{t=t_s}^{t_H} (CDP\,\tau_{CAR} - CRB\,(\tau_{mCR} + \tau_{rCR}))dt \qquad (13)$$

$$LRB = \int_{t=t_s}^{t_H} (LDP\,\tau_{LAR} - LRB\,(\tau_{mLR} + \tau_{rLR}))dt \qquad (13')$$

The model assumes that legume nodular C production for N symbiotic fixation (Nod) is driven by daily input of the part $f'_3(t,\tau_{nod})$ of plant C production, by daily

outputs of nodule respiration at rate $\tau_{r\ nod}$ and by nodule mortality function $f_1(t,\tau_{m\ nod})$. From field observations, the same time function was used for legume grain production and nodular mortality (when grain production is completed, plant production decreases and nodules are not then required); the resulting equation of nodule C compartment was:

$$Nod = \int_{t=t_s}^{t_H} (LDP\, f'_3(t,\tau_{nod}) - Nod(f'_1(t,\tau_{m\ nod}) + \tau_{r\ nod}))dt \qquad (14)$$

The model assumed that time functions f_1, f'_1, were Gaussian functions (derivatives of the Verhulst logistic curve) with the parameters for the optimum time (C_{opt} / L_{opt} table 1) and deviation time (C_{tD} / L_{tD} table 1) of C transfer to grains and C transfers to litter by shoot mortality, with a similar function f'_3, controlling C transfer for nodule growth. The time function $f_2(t)$ was set to 0 for all t except at harvest time where $f_2(t) = 1$. All values found for growth, transfer and mortality parameters are given in table 1. The outputs of the production module (NC-CR, NC-CA, NC-LR, NC-LA, and NC-Nod, figure 2 are the inputs in the $\mathbf{B}_j$ vectors (equation 8) for decomposition. It was then necessary to split all these inputs into labile and stable materials using qualitative estimation of these five types of necromass.

2.5 MODELING OF 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 (Thuriès et al. 2001; 2002; Pansu et al. 2003a; 2003b). The model has since been validated on tropical materials (Kaboré et al. 2011), 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 (Thuriès et al. 2002):

$$C_o = 7.18\ C_{OM} + 0.14\ Lig/N_{OM} - 3.84 \quad (15)$$

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.

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

$$If C_o > 0:\ P'_L = 0.099\ flab + 0.14\ Hem, and\ P_S = 1.61\ Lig + 0.62\ Ash_{OM} \quad (16)$$

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 (figure 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 τ_{NC}, the C:N ratio of input necromass NC from each plant organ. An increase of τ_{NC} was modelled as decreasing the assimilation rates of labile (k_{VL}) and stable (k_{VS}) NC compartments (Martí-Roura et al. 2011):

$$k_{VL} = MAX(0.65 - 0.0019\,\eta_{NC}, 0.1) \quad (17)$$

$$k_{VS} = MAX(0.0037 - 0.000026\,\eta_{NC}, 0.00005) \quad (17')$$

An increase of τ_{NC} was also found to increase the rate of microbial mortality (Bottner et al. 2006):

$$k_{MB} = MIN(0.42 + 0.0012\,\eta_{NC}, 0.8) \qquad (18)$$

In this work, equations 17 and 17' were applied separately to each of the five NC inputs, while τ_{NC} in equation 18 was calculated each day by the model from the sums of C and N of the five inputs materials entering MB.

2.6 CALCULATION TOOLS

C-CO_2 fluxes were calculated from field respiration measurements by LI-COR (http://www.licor.com). Other data calculations on C in liquid and solid phases were calculated using the software built in to the Shimadzu TOC-V_{CSH} and Fisons Instruments NA2000 analysers. All results were transferred to standard spreadsheets to obtain the density of all carbon forms in g m^{-2}.

ANOVA, F tests of residue comparisons, mean and confidence interval calculations and other statistical operations were performed using Statgraphics (www.sigmaplus.fr).

VENSIM (http://www.vensim.com/) was used for moisture calculations using the SAHEL model (Penning de Vries et al. 1989) and all C cycle calculations coupling TAO, MOMOS and the C production module for the cereal / legume intercropping described above. Euler's method was used for numerical integration of the differential equations and parameters were fitted using Powell's conjugate gradient descent method. Knowing the **A** matrix (Equation 4) and its associated relationships with climate (Equations 1, 2, 3), soil texture (Equation 7), and quality of inputs (Equations 15, 16, 17, 17', 18) this work aimed to demonstrate that initial values of **x** vector (Equation 1) and all the eco-physiological parameters τ and time functions *f* (Equations 9 to 14), which are difficult to estimate by other methods, could be optimized by the calculation system, to adjust simultaneously all the collected data. The scientific question was to propose a calculation theory, actually missing, for agro-ecology.

3. RESULTS AND DISCUSSION

3.1 THE EFFECT OF THE WEATHER ON LIFE PROCESSES

The first function examined was that of the weather which was defined to act simultaneously on all microbial and chemical transformations and plant growth (Equations1, 2, 3 and 8). The measured values of water content in the upper and lower layers of soil in this study (4 plot replicates×2 depth×2 sampling replicates×3 sampling occasions) were significantly predicted by the SAHEL model (Figure 3a). The minor differences may originate from differences between the soil layers used for sampling and predictions. SAHEL predicted the water content of the two layers 0-15 cm (continuous line on figure 3a) and 15-30 cm (dashed line). Samples were taken from the 0-5 cm soil layer (filled squares) and the 25-30 cm soil layer (open squares). Measurements at 0-5cm were significantly closer to the predictions for the 0-15 cm layer and measurements at 25-30 cm were closer to the predictions for the 15-30 cm layer. The C cycle calculations for the 0-30 cm layer used the mean of the daily predicted water content in the 0-15 and 15-30 cm layers.

The figure 3b shows the functions of water content (mm mm^{-1}), temperature (°C) and their product applied to plant growth and to microbial transformations of OC. The water content function varied from 1 in winter and after rainfall to less than 0.3 in dry summer periods. The temperature function varied from 0.1-0.3 in winter to 0.6-0.9 in hot periods in summer and at the beginning of autumn. The product was close to the temperature function in winter, suggesting that temperature is the primary factor controlling the functioning of living organisms in these periods. However, the water content function dominated over the temperature function in summer, indicating that the life processes are controlled primarily by water content in hot periods of this Mediterranean zone.

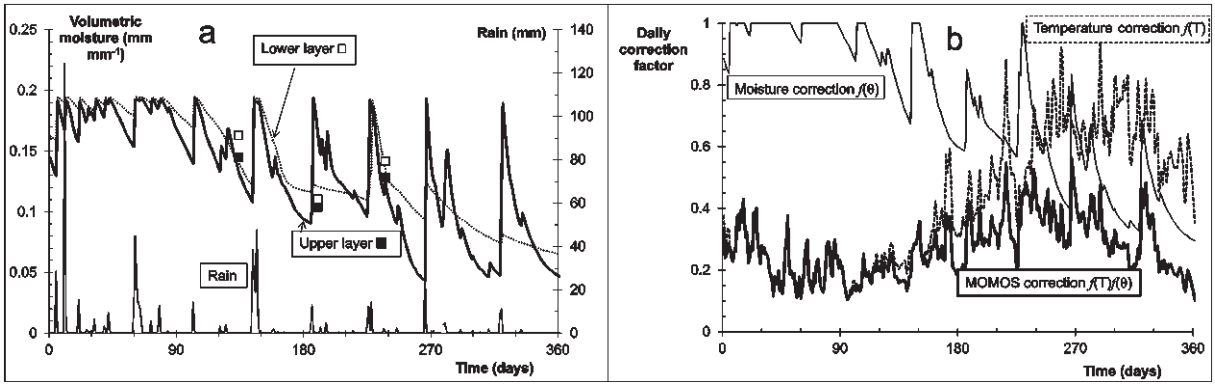

Fig.3 a- Water content measured at cylinder sampling and modelled in the 0-15 cm and the 15-30 cm layers of the soil; b- daily function of temperature, water content and the product of the temperature and water content functions applied to plant growth and microbial processes in the 0-30 cm soil layer of the intercrop

3.2 C TRANSFER FROM ATMOSPHERE TO PLANTS

Table 1 shows the fitted values for each growth parameter involved in plant production and C transfer to the plants, (equations 9 to 14). It also includes (i) Biomax, the measured maximum biomass of each plant (max_{BC} in equation 9 and max_{BL} in 9'), (ii) time function parameters which regulate periods of grain and nodule formation (equations 11, 11' and 14) during cropping, (iii) initial values of MOMOS compartments (**x** vector in equations 1, 4 and 8), (iv) values of C_0^{MB} (microbial biomass at steady state, equation 6), and τ_{incorp} (rate of incorporation of litter to soil by macro fauna, equations 12 and 12'). All other values previously found for MOMOS parameters were retained for this study. *F* tests showed that the measured data shown in figure 4 corresponded with the model predictions at 1% significance for aerial and grain C biomasses of wheat and faba beans, at 5% significance for faba bean root C and was not significant at 5% for wheat root C. All predicted values were included in confidence intervals of the measured data (not shown on figure 4 for clarity).

Table 1 Eco-physiological parameters and initial values of soil C compartments calculated in the cropping systems

Function	*Parameter*			*Crop*		
	Symbol	Description	Units	Wheat1	Faba beans[1]	Interc[2]
Cereal growth parameters	τ_{GC}	Relative growth rate	day^{-1}	0.201		0.172
	τ_{CAR}	Allocation rate to roots	-	0.552		0.625
	τ_{CAG}	Transfer rate to grain	-	0.414		0.367
	Biomax	Prod. max. (all parts)	$g\ m^{-2}$	156.16		80.77
Cereal mortality	τ_{mCR}	Root mortality rate	d^{-1}	0.001		0.051
	τ_{mCA}	Aerial mortality rate	d^{-1}	0.537		10-5
Legume growth parameters	τ_{GL}	Relative growth rate	d-1		0.390	0.417
	τ_{LAR}	Allocation rate to roots	-		0.700	0.792
	τ_{LAG}	Transfer rate to grain	-		0.015	0.310
	τ_{nod}	Allocation rate to nodules	-		0.00034	0.00013
	Biomax	Prod. max (all parts)	$g\ m^{-2}$		182.63	154.36
Legume mortality	τ_{mLR}	Root mortality rate	d^{-1}		0.365	0.515
	τ_{mLA}	Aerial mortality rate	d^{-1}		0.00064	0.052
	τ_{mnod}	Nodule mortality rate	d^{-1}		10-6	10-6
Root and nodule respiration	τ_{rCR}	Root resp. rate, cereal	d^{-1}	0.011		0.197
	τ_{rLR}	Root resp rate, legume	d^{-1}		0.027	0.0058
	τ_{rnod}	Nodule resp rate	d^{-1}		0.031	0.0149
Litter incorporation	τ_{incorp}	Litter to soil incorporation rate	d^{-1}	0.0014	0.0868	0.0333
Time function $f_1(t)$ Cereal	C_{opt}	Opt time grain growth	day	191.9 d		182.4
	C_{tD}	Dev. time grain growth	d	0.107		0.113
Time function $f'_1(t)$ legume	L_{opt}	Opt time grain growth	d		220	190.9
	L_{tD}	Dev time grain growth	d		0.037	0.156
Time function $f'_3(t)$ nodules	nod_{opt}	Opt time nodule growth	d			0.001
	nod_{tD}	Dev time nodule growth	d			0.01
MB	C_0^{MB}	MB-C at steady state	$g\ m^{-2}$	30	29.9	21.4
x initial values humus	HL	Labile humus	$g\ m^{-2}$	351	0.3	0.1
	HS	Stable humus	$g\ m^{-2}$	1788	1643.6	2409
x initial values plant debris	VS1	of legume roots	$g\ m^{-2}$	197	200	87.6
	VS2	of cereal roots	$g\ m^{-2}$	200	200	193.8
	VS3	of legume litter	$g\ m^{-2}$	199	200	150.7
	VS4	of cereal litter	$g\ m^{-2}$	200	200	192.9

[1] pure cropping, [2] intercropping

Simulated total biomass C production did not increase in the intercropped plots in this experiment. At harvest, the simulated total C biomass production (stem, leaves, roots, and grains) was 192 g C m^{-2} for faba bean plots, 276 g C m^{-2} for wheat plots and 230 g C m^{-2} for intercropped wheat faba bean plots. The corresponding total grain production was 51, 84, and 75 g C m^{-2} for wheat, faba bean and wheat-faba bean intercropping, respectively (figure 4c). Over the year, 75 g grain-C m^{-2} was exported from the wheat-faba bean intercropped plots: 50 g m^{-2} in faba bean grains and 25 g m^{-2} in wheat grains.

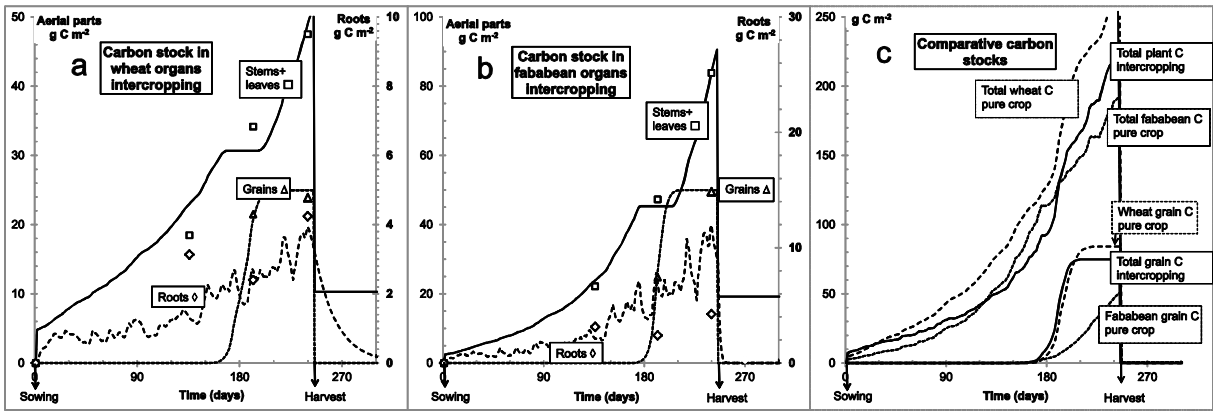

Fig.4 The measured and modelled C in the plant parts of the intercropped cereal-legume: a- wheat shoots, roots and grains; b- faba bean shoots, roots and grains; c- total production of the intercrop compared to monoculture

3.3 TRANSFER OF C FROM PLANTS TO MICRO-ORGANISMS AND THE ATMOSPHERE

Figure 5a shows the measured and predicted values of the stock of microbial C in the intercropped plots. The modelled decrease at sowing should originate from soil tillage; the modelled increase at harvest should originate from additional debris input. The *F*-test showed that the measured values corresponded with the model predictions at 1% significance. For the 1st and 2nd sampling periods, the predicted values were within the 95% confidence intervals of the measured values. The slight underestimation in the 3rd sampling period could originate from an underestimation of litter fall and root mortality before the harvest since the faba bean plants were black and dried at the 3rd sampling period (maturity).

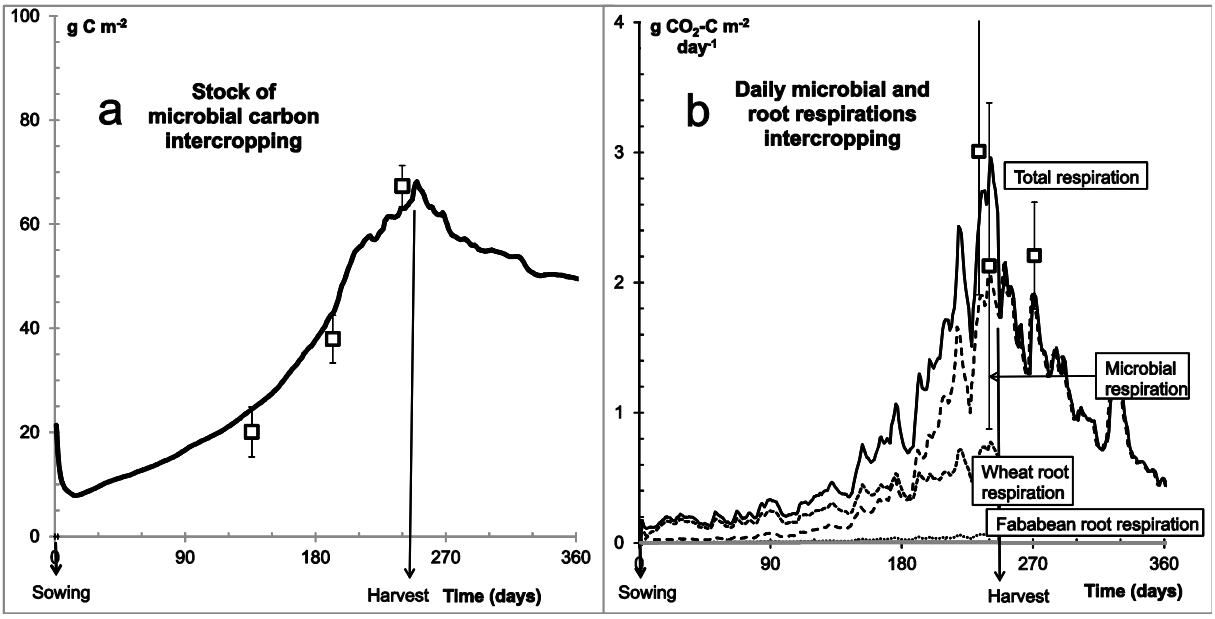

Fig.5 a- The measured values with 95% confidence intervals, and the modelled values of microbial C for intercropping, b- the measured total respiration at soil surface with 95% confidence intervals, and modelled values of root, micro-organism and total respiration

Figure 5b shows the mean CO_2 flux for the intercropping (4 modalities × 4 plot replicates × 6 replicates by plots) and the modelled respiration of micro-organisms and plant roots. The 1st sampling period was for active plants during grain formation, the 2nd sampling period was at the end of grain formation and the 3rd sampling period was after harvest. The confidence intervals of measurements in the 2nd and 3rd periods included the predicted values for microbial and root+microbial respiration (with the modelled root respiration stopped after the harvest). The modelled microbial respiration was lower than the measurement in the 1st period, although root+microbial respiration agreed significantly with the measurements. The C production module predicted that the wheat root respiration was much greater than the faba bean root respiration. However, the faba bean root mortality was predicted to be much greater than the wheat root mortality.

3.4 TRANSFER OF C IN SOIL AND BALANCE OF SOIL-ATMOSPHERE EXCHANGES

Figure 6a shows the total C over the year for the intercrop. The predicted values increased up to harvest and then decreased by microbial respiration when input from photosynthesis was stopped. The predicted values were all within the 95% confidence intervals of the measured values and the *F* test showed that the measured and modelled increase of total C values was not significant at 5%. This illustrates that total C measurement is not suitable for quantifying short term C sequestration, as attempted in many medium and long term measurements (see introduction).

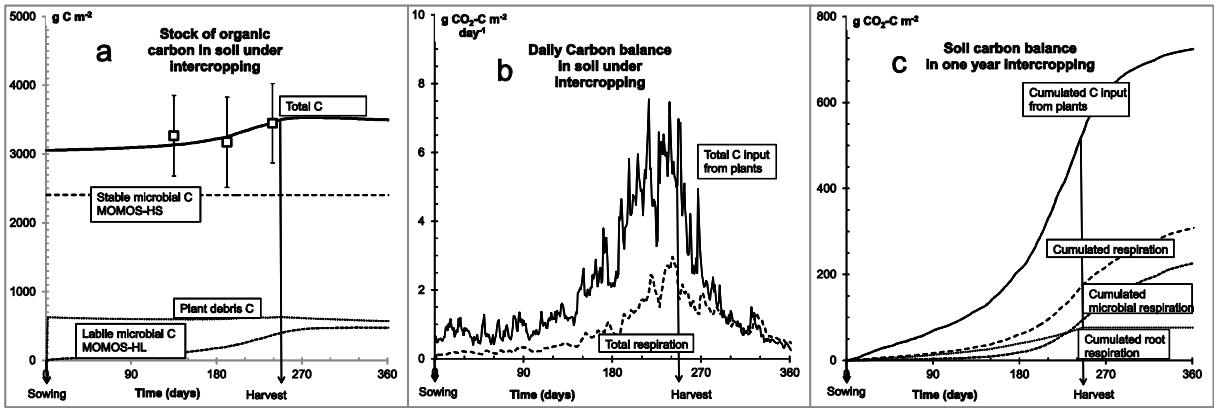

Fig.6 a- The measured values of soil total C with 95% confidence intervals, and modelled values of total C and C in the plant debris and labile and stable compartments of microbial origin, b- the daily balance of C inputs in soil from photosynthesised material and C losses by respiration, c- the cumulated values of C input and output over one year of intercropping

Figure 6b 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 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 (table 1). The C inputs remained greater than the C output by respiration until 45 days after harvest and then the predicted respiration was greater than the C inputs, although both inputs and outputs were lowered by the weather conditions during this period (figure 3). Integration of all C inputs and

outputs showed a net transfer of C from atmosphere to soil over the year for the intercrop (figure 6c). At 360 d after sowing, the cumulated inputs to soil were modelled as 724 g C m^{-2} and the cumulated outputs by respiration were 307 g C m^{-2}, giving storage of 417 g C m^{-2} from crop residues over the year.

3.5 C TRANSFER IN THE RHIZOBIAL SYMBIOSIS

Figure 7a shows the faba bean root nodule biomass for symbiotic fixation of atmospheric N (SNF). The measured nodule-C values (open squares in figure 7a) had very wide confidence intervals, which show the difficulty of estimating nodule-C by field sampling. The predicted faba bean nodule biomass was lower in the intercrop (continuous line figure 7a) than in monoculture. Even when corrected by the plant biomass at the maximum nodulation, nodule-C values were 2.6% of total-C in faba bean monoculture and only 1.6% of total-C in intercropped faba beans. The cumulated nodule respiration over the year was modelled at 0.70 g CO_2-C m^{-2} for intercropping and 3.73 g CO_2-C m^{-2} for monoculture, indicating a nodule respiration of 2.3 g CO_2-C g^{-1} nodule-C in intercropped plots and 4.7 g CO_2-C g^{-1} nodule-C in monoculture plots. Overall in this experiment, both nodular production and nodular respiration in intercrops were about half of the production and respiration in faba bean monocultures.

The figure 7b shows the predicted slopes of the stem+leaf C against the nodule C. Similar relationships were observed between the total faba bean C against the nodule C (not shown).

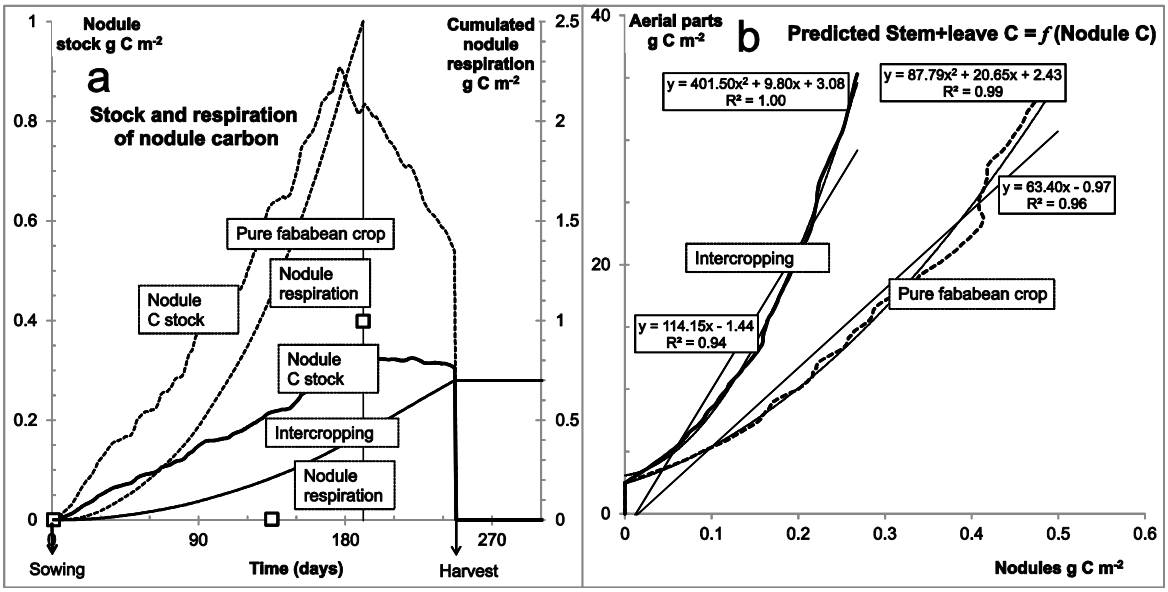

Fig.7 a- the measured values (open squares with 95% confidence intervals) and the predicted C stock in nodules for symbiotic N fixation (left axis, continuous line for intercropping, dashed lines for pure faba bean cropping) and the predicted nodular respiration (right axis, continuous line for intercropping, dashed line for pure cropping), b- the predicted relationships between shoot C and nodule C of faba bean in intercropping (continuous line) and in monoculture (dashed line)

This shows that the slope for intercropping is twice that of faba bean monoculture, suggesting a nodular efficiency for nitrogen fixation higher in intercropping than in faba bean monoculture. The predicted shoot C was 121.6 times the nodule C less 1.9 g C m^{-2} over the whole year of intercropping. This agrees with experimental measurements of faba bean plants sampled at flowering: shoot biomass = 129.5 times the nodule biomass + 7.7 g m^{-2} (not published). The shoot-C:nod-C ratios measured and modelled in this experiment were greater than those found in hydro/aeroponic growth of legumes, from 3 for bean genotypes with low N fixation efficiency to 50 for bean genotypes with higher N fixation efficiency (Rodiño et al. 2009), and in the range 4 to 13 for cowpea genotypes (Alkama et al. 2009). But nodule biomass is always much higher in hydro/aeroponic media than in soil, with nodules being less efficient at fixing N than nodules in soil. The best fits to the measurements shown in figure 7b were not linear but second order, i.e. the aerial biomass C was not linearly proportional to the nodule biomass C but the second order coefficients were significant.

4. CONCLUSION

This study has demonstrated that it is possible to predict the daily C exchanges between plants, soil and the atmosphere by modelling "a direct microbial control over decomposition" (Pansu et al. 2010). This new application of the MOMOS model used only the data for the local (i) climate, (ii) soil properties, (iii) plant C production and (iv) microbial, inorganic and total C. The rest of the parameters and functions for the MOMOS model, that had previously been determined for other climate, inputs and soil properties, were retained in this work. This shows that the MOMOS model is becoming more generic. The model was initially calibrated for two different ecosystems at high altitude (Schimel and Weintraub 2003) and then validated for 6 other sites with contrasted climatic and edaphic characteristics from 65 to 3940 m (Dornbush et al. 2006), all with acid tropical conditions. Though our aim was not another validation, this study proves again the model applicability on the collected data of on intercropping at 3 m in Mediterranean calcareous conditions and it would seem that the equation system is probably usable in most terrestrial environments. A net OC sequestration of 417 g C m^{-2} was predicted in intercropping but was this storage a long term sequestration? MOMOS simulates two compartments of stable C: HS, formed by stabilisation of humus which gave the most stable soil compounds with a modelled decomposition rate of 0.00005 d^{-1} (38 years half-life), and VS, stable plant debris with a modelled decomposition rate of 0.003 d^{-1} (0.6 year half-life). The HS and VS C stocks were modelled as almost constant over this one year experiment (figure 6a), with a slight decrease from 2407 to 2402 g C m^{-2} for HS and from 628 to 570 g C m^{-2} for VS. The modelled increase in C stocks resulted from a very small increase in labile plant material (VL compartment) from 0 to 0.9 g C m^{-2} but mostly from the increase in labile microbial metabolites (HL compartment) from 0.1 to 474 g C m^{-2}. The model predicted that HL was the main short term reserve for microbial activity and no long term C storage was predicted.

The calibration of the model provided the parameters given in table 1 and did not provide multiple sets of parameters for the initial values of the vector **x** (equations 1 and 8) and production parameters (vectors **B***j*). This suggests that the model is

parsimonious (Ockham's razor, *lex parsimoniae*), with a minimum number of well-defined parameters. It appears to be a powerful tool for evaluating eco-physiological parameters that are difficult to assess by other methods in agro-ecological systems. The equation system of this paper is proposed as a new calculation tool, actually missing in agro-ecology and global change studies.

The initial values of the **x** vector (equations 1 and 8) were calculated at the same time as the plant growth parameters. As for eco-physiological parameters these initial values are difficult to estimate accurately by the existing laboratory methods (Pansu and Gautheyrou 2006), so it appeared interesting to propose a calculation method. A possible extension of the research would be to measure these initial values by physical or chemical separation (Pansu and Gautheyrou 2006). In this study the sum of the initial values of the various types of plant debris (figure 4; table 1) was 627 g C m^{-2} which represented 20.5% of soil organic C, a plausible value for this soil which was relatively rich in coarse fractions and had low fertility. The initial values of other compartments amounted to less than 1% for MB and HL, and 79% for HS, which was also reasonable taking into account the half-lives of 1.5, 14, and 13863 days for MB, HL, and HS, respectively.

The calculated relative growth rate was close to 0.2 g g^{-1} day^{-1} for wheat in monoculture or intercropped (τ_{GC} in table 1 and equation 9). This appears consistent with the literature with τ_{GC} in the range 0.06-0.18 for the 2 months after sowing (Khan et al. 2005) or 0.11-0.26 g g^{-1} day^{-1} for the first 20 days (Rahnama et al. 2010). The calculated relative growth rates were about two times greater for faba beans at about 0.4 g g^{-1} day^{-1} (τ_{GL} in equation 9′ and table 1). This also appears to be consistent with published results of 0.40-0.50 at 2-3 months after sowing (Crawford et al. 2000).

The allocation rates of photosynthetic C to roots (τ_{CAR} for cereal and τ_{LAR} for legume) were calculated as 0.5-0.6 for wheat and 0.7-0.8 for faba beans, with the highest values for the intercropping, indicating that there may have been interspecific competition for nutrients. These values, higher than the 0.3-0.4 measured in controlled conditions for *Medicago truncatula* (El-Metwally and Abdelhamid 2008),

could be explained by the need for the roots to search for nutrients in these low fertility plots and consequently low aerial production and yields. There were net differences in the fate of this C allocated to roots between the two species. The mortality rates of the wheat roots (τ_{mCR} in equation 13 and Table1) were low, in the range 0.001-0.051 g g^{-1} d^{-1}, similarly to published values for other graminea (Fitter et al. 1998), and much lower than the growth rate reported for wheat roots before flowering (Steingrobe et al. 2001). The mortality rates were significantly higher for faba beans (τ_{mLR} in equation 13' and table 1), in the range 0.365-0.515 g g^{-1} d^{-1} with the highest values for intercropping. The mortality of the faba bean roots should provide a significant input of C and N for microbial assimilation and respiration. On the other hand, the simulated root respiration rates (τ_{rCR} and τ_{rLR} in table 1) in intercropping were higher for wheat than for faba beans. The wheat roots would have higher losses of C by respiration as a result of the growth energy required to explore higher volumes of soil for plant nutrition. All of these eco-physiological parameters need to be verified in other agricultural systems. Most other existing methods of determination are difficult to implement and the results are subject to large variations due to environmental conditions (Watson et al. 2000). In this study, the experimental plots were designed for several experiments and did not concentrate on just the carbon turnover which was modelled. Plant productivity was low (figure 4) as the soil management changed to organic agriculture in 1998 and had received no input of organic or inorganic fertiliser since 1998. Before the experiment, the previous crop was durum wheat, with the removal of grain and restitution of the straw residue. The crops were invaded by weeds, mainly vetches, poppies and wild oats, which were weeded by hand. The faba bean leaves were attacked by rust and the nodules were attacked by weevils, fortunately in the later stages of growth, when there was probably less demand for N fixation. All these additional life systems were ignored in this modelling study. Nevertheless, the model was able to predict the main C cycle in these complex transfer conditions. The calculated parameter values were in accordance with logical deduction and the literature. As legume-cereal associations are complex agricultural systems, the production module of the model

described in this paper (figure 2, equations 9-14) can be easily simplified or adapted to other systems.

These results predicted that the nodule biomasses and respiration would be lower in the intercrop than in the mono culture (figure 7a) but with the shoot-C : nod-C ratio higher in the intercrop (figure 7b). The model predicted a higher growth rate and higher mortality of faba bean roots in the intercrop than in monoculture (table 1) and a lower nodule production and activity in the intercrop. Further research is needed on the mechanisms of root-nodule interaction with plant growth. The mechanism should be active after the beginning of nodule depletion, since from this study, the shoot-C was modelled as a second order function of nod-C with a positive coefficient for the second order term. As the MOMOS model required a non-linear equation to predict the microbial respiration, the effect of root-nodule activity on plant growth could also be non-linear.

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CHAPITRE V
L'ECHANGE JOURNALIER DE L'AZOTE DANS LE SYSTEME : ORGANISMES VIVANTS-SOL-ATMOSPHERE

Ce chapitre correspond à l'article soumis pour la revue internationale « *Agronomy for Sustainable Development* » et qui s'intitule: "**The daily exchange of nitrogen between living organisms, the soil and the atmosphere".**

Résumé

Ce travail est la suite du chapitre 4 qui a pour but la prédiction de l'échange journalier du carbone dans le système : organismes vivants-sol-atmosphère dans un agro-système céréale-légumineuse

Le modèle utilisé précédemment, est calibré et validé par des expériences de traceurs dans différents écosystèmes, il est centré sur l'écologie fonctionnelle des microorganismes. Les compartiments organiques d'origine microbienne ont été modélisés comme le principal stock d'azote (N) dans la culture intercalaire, l'humus stable est constant, alors que N stocké dans l'humus labile constitue la réserve principale pour durabilité de la production microbienne et végétale future.

Le stock microbien représente moins de 1% de N stocké dans les compartiments humifiés par les microorganismes, mais s'avère 4 fois plus grand que N stocké dans les parties aériennes de céréales et équivalent à N stocké dans les parties aériennes de la légumineuse.

La partie majeure de l'azote inorganique du sol a été modélisée comme immobilisée journalièrement par les micro-organismes en liaison avec le climat pendant les six premiers mois après le semis, et minéralisé après 6 mois suite à la mortalité et la décomposition des racines des légumineuses, les organismes décomposeurs peuvent être considérés comme homéostatiques dans ce système.

L'autre partie de l'N inorganique du sol été absorbée par les racines des céréales principalement après cinq mois, et l'azote atmosphérique N2 était principalement fixés par les bactéries symbiotiques des racines des légumineuses avec un maximum de fixation journalière entre 2 et 6 mois après le semis; au total la fixation pendant la saison des cultures intercalaires ont été estimées par 90 kg N ha^{-1} soit légèrement plus que l'immobilisation nette de 50 kg N ha^{-1}.

Les pertes d'azote inorganique ont été modélisées comme le stock de 20 kg N ha^{-1} dans les mauvaises herbes. Cette modélisation d'N explique pourquoi les rendements C ont été trouvés plus bas dans les cultures intercalaires que dans les cultures pures de céréales: la céréale utilisée à besoin d'azote inorganique avant sa fourniture par minéralisation microbienne des débris de légumineuses. Deux propositions sont suggérées par l'étude pour améliorer les systèmes céréales-légumineuses : rotation à la place de cultures intercalaires, ou des cultures intercalaires améliorées par la sélection des céréales à floraison tardive et/ou de légumineuses à floraison précoce.

Mots clés: Modélisation, azote; échange journalier ; sol.

THE DAILY EXCHANGE OF NITROGEN BETWEEN THE SOIL, THE ATMOSPHERE, MICROORGANISMS AND PLANTS

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ABSTRACT

This work complete a previous modelling study which predicted the daily exchange of carbon (C) between living organisms, the soil, and the atmosphere in an intercropping legume-cereal. The used model, previously calibrated and validated with tracer experiments in various ecosystems, is centred on functional ecology of microorganisms. The organic compartments of microbial origin were modelled as the main storage of nitrogen (N) in the intercropping; the stable humus remained constant, when labile humus was stored as the main reserve for sustainability of the microbial and plant production. The microbial storage represented less than 1% of transformed N in organic forms, but was 4 times greater than maximal N in the cereal shoots and equivalent to N stored in the legume shoots. The main part of inorganic N was modelled as immobilized by microorganisms during the first 6 months after sowing, and mineralized after 6 months mainly from mortality and decomposition of legume roots; decomposer organisms can be considered as homeostatic. Inorganic N was adsorbed by cereal roots mainly after 5 months and atmospheric N_2 was mainly fixed by bacteria symbiotic of legume roots between 2 and 6 months after sowing; fixation during the intercropping season was estimated at 90 kg N ha^{-1} slightly higher than net immobilization of 50 kg N ha^{-1}. Losses of inorganic N were modelled as the storage of 20 kg N ha^{-1} in weeds. This N modelling explains why C yields were found lower in

intercropping than in pure cropping of cereal: the used cereal requires inorganic N earlier than the microbial mineralization of legume debris. Two research orientations are suggested: rotations cereal-legumes in place of intercropping or improving intercropping by selection of late-flowering cereals and/or early-flowering legumes.

Keywords: Modelling, soil, agronomy, nitrogen, daily exchange

1. INTRODUCTION

After atmospheric carbon (C) and elemental constituents of water, Nitrogen (N) of the soil is the most important element for plant development. N is a very dynamic element, and undergoes many transformations inside and outside the soil, defined as the nitrogen cycle (Galloway et al. 2004; Bothe et al. 2007; Jetten 2008). The living plants store about 5% of the global N stock mainly by root adsorption of mineral N, especially in nitrate form (Inselsbacher et al. 2013), and fixation of atmospheric N_2 for biosynthesis of ammonium by bacteria in symbiosis with legume roots (Newton, 1987; Unkovich and Baldock, 2008). But mineral N produced both by mineralization and N_2 fixation represents the weakest part of soil N compared to organic forms generated by plants and microbial decomposers (Lin et al. 2000; Pansu and Gautheyrou 2006), underlining the complexity of the N cycle. Mechanistic models, linking C and N cycles (Gärdenäs et al. 2011), are expected to give an accurate prediction of the transfers of N between organic and inorganic compartments of various stabilities. Nevertheless, the published models of N cycle are not always linked to C and sometimes poorly mechanistic (Manzoni and Porporato 2009). Most of them propose a compartmental definition depending on a particular application, (e.g Molina et al. 1983; Parton et al. 1987;; Hansen et al. 1991 ; Carter et al. 1993 ; Dou and Fox 1995; Quemada and Cabrera 1995; Richter and Benbi 1996; Aber et al. 1997 ; Brisson et al. 1998; Mueller et al. 1998; Garnier et al. 2001 ; Nicolardot et al. 2001; Pansu and Thuriès 2003 Pansu et al. 2004; Neill and Gignoux 2006 ; Jégo et al. 2012; Tipping et al. 2012, and Oulehle et al. 2012) but for Todd-Brown et al. (2012) "current global models do not represent direct microbial control over decomposition" and a new generation is required. It was proposed to "bridge the gap between first order

decay of substrates and Monod kinetics of microbial growth" (Neill and Gignoux 2006), and to model the microbial biomass as the driving force of decomposition sometimes at cellular scale (Gras et al. 2011). From tracer experiments in various ecosystems, Pansu et al. (2013) have linked the C and N cycles around the functional ecology of microbial biomass in the MOMOS model. They compared the two hypothesis of homeostasie, or variable quality of microorganisms which could better integrates the succession of microbial communities (Wu 2012), and the microbial diversity (Philippot et al. 2013), but increases the model complexity and risks of over-parameterization. The results of Pansu et al. (2013) demonstrated an evolution of microbial quality along the experiment especially in cold and wet areas, but the microbial homeostasie could be considered globally as a valuable hypothesis, especially in hot and well-drained plain areas. Another aspect concerns the interactions of competition or synergy between plants and microorganisms (van der Heijden et al. 2013). Ibrahim et al. (2013) used MOMOS, in coupling with a soil water module and a C production module, to quantify the daily exchanges of C between plants and microorganisms, the soil and the atmosphere in a legume-cereal intercropping. The aim of this work is to extend this study to the daily exchanges of N between the same living organisms, the soil and the atmosphere, which could help to clarify few essential questions:

- can the microorganisms be considered as homeostatic in this intercropping system?
- can the model bring new insights about interaction between plants and microorganisms?
- can the modelled N transfers explain the variations in C transfers and crop yields?
- can we define ways to improve intercropping and compare intercropping to rotations of pure crops of cereals and legumes?

2. MATERIALS AND METHODS

2.1 FIELD EXPERIMENT

The field experiment was described in Ibrahim et al. (2013). Briefly, it was carried out in a station of the *Institut National de la Recherche Agronomique* (INRA), located at Mauguio (43°37′32′′N / 3°59′20′′E), France in a Mediterranean. The experimental plots were located on a gentle slope (~ 0.5 %) with a soil with a partly decarbonatated brown-reddish upper horizon (~ 60 cm thick) on Pliocene calcareous molasse, classified as chromic Cambisol in international soil classifications.

6×10 m plots were used with three crops cultivated (four field replicates) using organic farming methods (1) durum wheat (*Triticum durum*) cultivar LA1823 monocrop at density 100±23 plants m^{-2} (2) faba beans (*Vicia faba)* cultivar "Castel" monocrop at 17±7 plants m^{-2}, and (3) durum wheat LA1823 - faba bean Castel intercrop at 72±28 durum wheat m^{-2} and 16±6 faba bean plants m^{-2}.

2.2 DATA COLLECTION

Four whole plants (roots and shoots) of durum wheat and four of faba bean were collected from each plot during growth (1st sampling period), 10 plants of each species were taken during flowering (2nd sampling period) and four of each species were taken at maturity (3rd sampling period). 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 to determine the soil moisture and bulk density.

The near-root soil was collected from the field and preserved in iceboxes (4 plots×4 modalities×4 replicates), as preliminary tests (not published) had shown a significantly greater microbial biomass in the near-root soil than in the soil far from plants. These samples were homogenized and gently crushed by hand without drying through a 4×4 mm grid sieve. The coarse and fine fractions were weighed and the fine fraction was kept without drying at 4°C before MB determination within two days after sampling.

The microbial C and N were determined by fumigation-extraction. 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 287 min and sterilized by filtration on a 0.2 µm membrane syringe. The liquid filtrates were stored in sterile plastic tubes at 4°C before C and N analysis in aqueous phase (Shimadzu TOC-VCSH analyser). The soil microbial concentration (MB-cC and MB-cN) 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 C factor k_C = 0.45 and a N factor k_N = 0.54 (Joergensen 1996). N results in no fumigated samples represented Inorganic-cN.

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 and N analysis, samples of each part were grouped and ground to 0.2 mm in a steel planetary ball mill.

A dry combustion elemental analyzer (NA2000, Fisons Instruments) was used for C and N analysis of the soil and plant parts. All C and N concentrations (for N, total-cN in mg g^{-1}, MB-cN, and inorganic-cN in µg mL^{-1}) were converted to stocks (g N m^{-2}) on the 0-30 cm layer. For a plot of bulk density *bd*, ponderal soil moisture *Wp*, and coarse gravel fraction *Cf*, total ON stock in g N m^{-2} of the 0-30 cm soil layer = 300 × *bd* ×(cN)(1-*Wp*)(1-*Cf*).

For a mass of subsample m_S and a microbial extract of 30 mL, the microbial N stock in g m^{-2} was MB-N = 9×*bd*×MB-cN×(1-*Wp*)(1-*Cf*)/m_S, the inorganic N stock was inorganicN = 9×*bd*×Inorganic-cN×(1-*Wp*)(1-*Cf*)/m_S. For a total mass m_P in g of each part of *n* sampled plants with a concentration m_P-cN in g g^{-1} and a density of *d* plants m^{-2}, the N stock in each part in g m^{-2} was m_P-cN×*d*×m_P/*n*. See Ibrahim et al. (2013) for measurements of CO_2-C respiration.

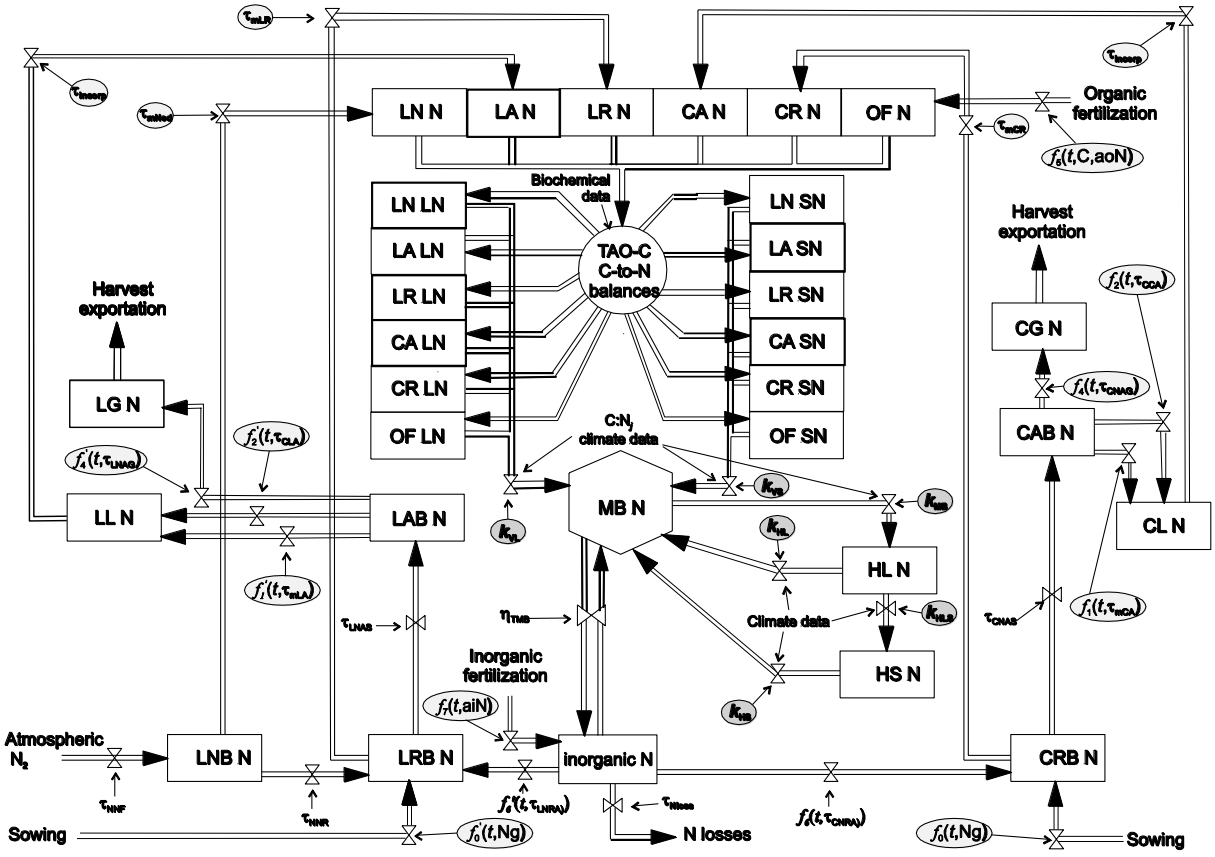

Fig. 1 Flow diagram of N exchanges between plant organs and microorganisms in the MOMOS model. Parameters in dark grey ellipses are those previously defined in MOMOS calibration and validation with isotopic tracers (see equations in 2.3) and preserved in this work; parameters in light grey ellipses are those previously defined to model the C cycle (Ibrahim et al. 2013; Table 1) and preserved in this N cycle study of the same intercropping; other parameters are those specifically defined for the N cycle (Table 2); N, LN, and SN are nitrogen, labile, and stables N fractions of necromasses, respectively; LN, LA, LR are legume nodule, aerial, and root debris, respectively; CA, CR are cereal aerial and root debris, respectively; MB and inorgN are microbial biomass and inorganic N, respectively; HL is labile humus, HS is stable humus; CRB and LRB are cereal and legume root biomasses, respectively; CAB and LAB are cereal and legume aerial biomasses, respectively; CL and LL are cereal and legume litters, respectively; CG and LG are cereal and grain biomasses, respectively; OF and aiN are organic and inorganic fertilizers, respectively (set to 0 at all times in this study).

2.3 THE DECOMPOSITION MODEL MOMOS

As carbon and nitrogen are closely associated in living organisms, it was assumed by Pansu et al. (2013) that the nitrogen cycle could be modelled in MOMOS-N in the same way as the carbon cycle in MOMOS-C (Pansu et al. 2004; 2010), using the subscript e (either C or N) to differentiate each element in the model.

MOMOS (Fig. 1) was defined as a five compartment model centred on the activity of soil microbial biomass (MBe) that grows by assimilation of labile (VLe) and stable (VSe) fractions of plant necromass (NC) as well as labile (HLe) and stable (HSe) fractions of humus.

The microbial mortality regulates humus formation. The only process which is considered more a chemical process than a biological process is humus stabilization from HLe to HSe. The only difference between the C and N models is in the outputs from MBe to inorganic forms of C (CO_2-C) and N (NH_4-N) or possibly inputs from inorganic N into MB_N. MOMOS has only seven first order kinetic parameters (dimension day^{-1}) and does not need the partitioning coefficients used in other decomposition models. All the C and N parameters are conditioned by functions of the soil temperature and water content ranging from 0 to 1, as in the general MOMOS equation:

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

where $\mathbf{x_e}$ is the vector of the state variables (C or N content of the compartments), $\dot{\mathbf{x}}_\mathbf{e}$ is the vector of the derivatives of $\mathbf{x_e}$, $\mathbf{A_e}$ is the model parameter matrix for each organic element, $\mathbf{B_e}$ is a vector determining the external C and N inputs (see Pansu et al. 2009 for C inputs from living roots) and $f(T)$ is an exponential function of temperature (Pansu et al. 2010):

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

where T is the actual daily temperature of soil (0-30 cm layer) set equal to the air temperature; T_{opt} is the optimum decomposition temperature set to 28°C, a

temperature often used to perform laboratory experiments under optimum conditions (Thuriès et al. 2002); Q_{10} is the factor by which the rate increases with a 10°C increase in temperature, set to 2.2 as in Pansu et al. (2010);

$f(\theta)$ of equation 1 is the response function to soil moisture expressed as a fraction of the WHC (Table 1, see discussion in Pansu et al. 2010):

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

The soil water content θ was predicted using the SAHEL model (Penning de Vries and van Laar, 1982). This model calculates the daily water content for each soil layer using meteorological data (daily minimum and maximum temperature, precipitation and latitude), WHC (Table 1) and plant cover as inputs. Meteorological data for the period over which the experiment was carried out was collected from the Montpellier airport weather station near the experimental site Pansu et al. (2010)

The model matrices $\mathbf{A_C}$ and $\mathbf{A_N}$ are:

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

$$\mathbf{A_N} = \begin{vmatrix} -k_{\mathrm{VL}} & 0 & 0 & 0 & 0 \\ 0 & -k_{\mathrm{VS}} & 0 & 0 & 0 \\ k_{\mathrm{VL}} & k_{\mathrm{VS}} & -\left(f\left(x_{\mathrm{C,MB}} x_{\mathrm{N,MB}}\right) / f(T) f(\theta) x_{\mathrm{N,MB}} + k_{\mathrm{MB}}\right) & k_{\mathrm{HL}} & k_{\mathrm{HS}} \\ 0 & 0 & k_{\mathrm{MB}} & -\left(k_{\mathrm{HL}} + k_{\mathrm{HLS}}\right) & 0 \\ 0 & 0 & 0 & k_{\mathrm{HLS}} & -k_{\mathrm{HS}} \end{vmatrix} \tag{4}$$

The vectors $\mathbf{x_C}$ and $\mathbf{x_N}$ of the C and N concentrations in each compartment are:

Table 1 Eco-physiological parameters of the C cycle (Ibrahim et al. 2013) retained to model conjointly the N cycle in this study.

Function	*Parameter*			*Crop*		
	Symbol	Description	Units	Wheat[1]	Faba beans1	Interc[2]
Cereal growth parameters	τ_{GC}	Relative growth rate	day^{-1}	0.201		0.172
	τ_{CAR}	Allocation rate to roots	-	0.552		0.625
	τ_{CAG}	Transfer rate to grain	-	0.414		0.367
	Biomax	Prod. max. (all parts)	$g\ m^{-2}$	156.16		80.77
Cereal mortality	τ_{mCR}	Root mortality rate	d^{-1}	0.001		0.051
	τmCA	Aerial mortality rate	d^{-1}	0.537		10^{-5}
Legume growth parameters	τ_{GL}	Relative growth rate	d^{-1}		0.390	0.417
	τ_{LAR}	Allocation rate to roots	-		0.700	0.792
	τ_{LAG}	Transfer rate to grain	-		0.015	0.310
	τ_{nod}	Allocation rate to nodules	-		0.00034	0.00013
	Biomax	Prod. max (all parts)	$g\ m^{-2}$		182.63	154.36
Legume mortality	τ_{mLR}	Root mortality rate	d^{-1}		0.365	0.515
	τ_{mLA}	Aerial mortality rate	d^{-1}		0.00064	0.052
	τ_{mnod}	Nodule mortality rate	d^{-1}		10-6	10^{-6}
Root and nodule respiration	τ_{rCR}	Root resp. rate, cereal	d^{-1}	0.011		0.197
	τ_{rLR}	Root resp rate, legume	d^{-1}		0.027	0.0058
	τ_{rnod}	Nodule resp rate	d^{-1}		0.031	0.0149
Litter incorporation	τincorp	Litter to soil incorporation rate	d^{-1}	0.0014	0.0868	0.0333
Time function $f_1(t)$ Cereal	C_{opt}	Opt time grain growth	day	191.9 d		182.4
	C_{tD}	Dev. time grain growth	d	0.107		0.113
Time function $f'_1(t)$ legume	L_{opt}	Opt time grain growth	d		220	190.9
	L_{tD}	Dev time grain growth	d		0.037	0.156
Time function $f_3(t)$ nodules	n_{odopt}	Opt time nodule growth	d			0.001
	n_{odtD}	Dev time nodule growth	d			0.01
MB	$C0^{MB}$	MB-C at steady state	$g\ m^{-2}$	30	29.9	21.4
x initial values humus	HL	Labile humus	$g\ m^{-2}$	351	0.3	0.1
	HS	Stable humus	$g\ m^{-2}$	1788	1643.6	2409
x initial values plant debris	VS1	of legume roots	$g\ m^{-2}$	197	200	87.6
	VS2	of cereal roots	$g\ m^{-2}$	200	200	193.8
	VS3	of legume litter	$g\ m^{-2}$	199	200	150.7
	VS4	of cereal litter	$g\ m^{-2}$	200	200	192.9

[1] pure cropping, [2] intercropping

$$\mathbf{x}_C = \begin{bmatrix} x_{\mathrm{C,VL}} \\ x_{\mathrm{C,VS}} \\ x_{\mathrm{C,MB}} \\ x_{\mathrm{C,HL}} \\ x_{\mathrm{C,HS}} \end{bmatrix} \quad \mathbf{x}_N = \begin{bmatrix} x_{\mathrm{N,VL}} \\ x_{\mathrm{N,VS}} \\ x_{\mathrm{N,MB}} \\ x_{\mathrm{N,HL}} \\ x_{\mathrm{N,HS}} \end{bmatrix} \tag{4'}$$

and the C:N ratios of each compartment are: $C:N_i = \frac{x_{C,i}}{x_{N,i}}$

For each incubation period, the derivative of total C evolution is:

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

The eq. 5 previously given for MOMOS-C (Pansu et al. 2010) had an optimum $\dot{c}$ which must be multiplied by $f(T)f(\theta)$ to give a $\dot{c}$ adjusted for weather conditions. qCO_2 on the right-hand scale of Fig. 3c-8c of Pansu *et al.* (2010) must be changed to $f(T)f(\theta)\,qCO_2$

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

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

where C^0_{MB} is an estimate of the biomass at steady state, k_{resp} is the respiration coefficient (day^{-1}) adjusted from the equation proposed by Pansu et al. (2010) to the 0-20 µm fine texture fraction ($F_{0\text{-}20}$) of soil:

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

The rates of enzymatic digestion of labile (k_{VL}) and stable (k_{VS}) plant materials (equations 21 and 21'), and the microbial mortality rate (k_{MB}) are linked to the type

of organic inputs (equation 22) (Bottner et al. 2006). 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 (Pansu et al. 2004; 2007; 2010):

- 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}.

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). For this study, the previously defined matrix **A** was used 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 plant shoots, roots and nodules. Equation 1 became:

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

where $j \in$ [cereal shoot NC, cereal root NC, legume shoot NC, legume root NC, nodule NC] (only restitution of dead materials without other organic amendment, OF N (Fig.1) = 0 for all t)

If C_i is the amount of C added from a given plant material j at time t and f_{Sj} is its stable fraction, the $\mathbf{B}_C$ vector of C inputs was daily adjusted by the balance equation:

$$B^j_{C,VL}(t) = (1-f_{Sj})\,C_j,\ B^j_{C,VS}(t) = f_{Sj}\,C_j,\ B^j_{C,MB}(t) = B^j_{C,HL}(t) = B^j_{C,HS}(t) = 0 \qquad (9)$$

The stable fraction f_{Sj} was estimated as that of the stable compartment of the TAO (Transformation of Added Organic materials) model (eq.20; Thuriès et al. 2002)

from biochemical composition of each type of necromass NC_j, which gave fs_j = 0.175 for faba bean roots, 0.186 for durum wheat roots, 0.229 for faba bean litter, 0.114 for durum wheat litter, and 0.01 for symbiotic nodules.

For each incubation period, the derivative of the total organic N is the negative of the derivative of mineralized N and is expressed by:

$$\dot{N} = \sum_{i=1}^{5} \dot{x}_{i,N} = -f(x_{C,MB}, x_{N,MB}) \quad (10)$$

where positive values of the function $f(x_{C,MB}, x_{N,MB})$ correspond to N mineralization of microbial N and negative values correspond to microbial immobilization of inorganic N. If η_{NCj} is the C:N ratio of a given NC_j, and η_{VSj} the C:N ratio of its stable fraction, the $\mathbf{B}_N$ vector of N inputs was daily adjusted by the balance equation:

$$B^j_{N,VL}(t) = \left(\frac{1}{\eta_{NCj}} - \frac{fs_j}{\eta_{VSj}}\right) C_j,\ B^j_{N,VS}(t) = \frac{fs_j}{\eta_{VSj}} C_j,$$

$$B^j_{N,MB}(t) = B^j_{N,HL}(t) = B^j_{N,HS}(t) = 0 \quad (11)$$

The function $f(x_{C,MB}, x_{N,MB})$ of equation 7 was defined in terms of η^{lim}_{MB}, the target value for the C:N ratio of the MB (η_{MB}), assuming a constant η^{lim}_{MB} ratio throughout incubation:

$$f(x_{C,MB}, x_{N,MB}) = x_{N,MB} - \frac{x_{C,MB}}{\eta^{lim}_{MB}} \quad (12)$$

For decomposition, the only one parameter fitted for each site was η^{lim}_{MB}, all the other parameters and functions linking them to environmental conditions (eq. 1, 7, 21, 21′, 22) being those fitted by previous ^{14}C simulations (Pansu et al., 2004; 2010), see discussion in 4.1 below, and used in the agro-ecological simulations of this paper.

The elements of $\mathbf{B}^j$ were estimated in two stages:

Quantitative estimate of necromass input from each plant part (see 2.4. below),

Qualitative estimate of necromass to divide each input into labile and stable fractions in the MOMOS decomposition processes (see 2.5. below).

For decomposition, the organic flows from plant debris to MB run in the same way for C and N, then they could be modelled by the same equations and parameters. But for living plants the C flow is directed from atmosphere, to leaves, roots and microorganisms when the N flow is directed from soil or atmosphere to roots and roots symbiotic nodules, then to aerial parts of the plants, Complementary equations were necessary to adjust N transfers (see 2.6 below) conjointly with other equations for C and N cycle.

2.4 MODELLING PLANT AND RHIZOBIUM C PRODUCTIONS

To produce these estimates a simplified predictive module of the production of shoot C and root C for cereals and legumes was set up and coupled with MOMOS (Ibrahim et al., 2013). It was driven primarily for each plant by a standard growth law with (i) an optimum relative growth rate τ_{GC} for cereals and τ_{GL} for legumes, and (ii) a maximum C biomass max_{BC} for cereals and max_{BL} for legumes. The module assumed that plant growth is also controlled by $f(T)f(\theta)$, the climate correction factor used for microbial functioning (equation 1), and by aerial biomass C, CAB for cereals and LAB for legumes, linked to the foliar surface of each plant species. The daily production of carbon CDP for cereals and LDP for legumes was:

$$CDP = \tau_{GC} f(T)f(\theta)\, CAB\, (1-CAB/max_{BC}) \quad (13)$$

$$LDP = \tau_{GL} f(T)f(\theta)\, LAB\, (1-LAB/max_{BL}) \quad (13')$$

for time t between the sowing time t_S and the harvest time t_H, and CDP = LDP = 0 for $t>t_H$.

The daily carbon production was partly allocated to roots using allocation rates τ_{CAR} for cereals and τ_{LAR} for legumes and another part was transferred to grain (G) depending on the time functions f_1 and f'_1 (see below) and the transfer rates τ_{CAG} for cereals and τ_{LAG} for legumes. Part of the aerial biomass was transferred to litter by natural mortality assuming daily aerial mortality rates τ_{mCA} and $\tau_{mLA,}$ and time functions f_1 and f'_1 for cereals and legumes, respectively. Part of the C production was transferred to litter during harvest, using the same cutting rate τ_c and time function f_2 for both cereals and legumes. For legumes, part of daily C production was transferred to nodule production at a rate τ_{nod} associated with a time function f'_3. The shoot biomasses, CAB for cereals and LAB for legumes, were then modelled:

$$\mathrm{CAB} = \int_{t=t_S}^{t_H} \left(\mathrm{CDP}\left(1-\tau_{\mathrm{CAR}} - f_1\left(t,\tau_{\mathrm{CAG}}\right)\right) - \mathrm{CAB}\left(f_1\left(t,\tau_{\mathrm{mCA}}\right) + f_2\left(t,\tau_c\right)\right)\right)dt \tag{14}$$

$$\mathrm{LAB} = \int_{t=t_S}^{t_H} \left(\mathrm{LDP}\left(1-\tau_{\mathrm{LAR}} - f'_1\left(t,\tau_{\mathrm{LAG}}\right) - f'_3\left(t,\tau_{\mathrm{nod}}\right)\right) - \mathrm{LAB}\left(f'_1\left(t,\tau_{\mathrm{mLA}}\right) + f_2\left(t,\tau_c\right)\right)\right)dt \tag{14'}$$

Carbon grain stock, CG for cereal and LG for legume, was modelled by:

$$\mathrm{CG} = \int_{t=t_s}^{t_H} \mathrm{CDP}\, f_1\left(t,\tau_{\mathrm{CAG}}\right)dt \;-\; \mathrm{Harvest_C} \tag{15}$$

$$\mathrm{LG} = \int_{t=t_s}^{t_H} \mathrm{LDP}\, f_1'\left(t,\tau_{\mathrm{CAG}}\right)dt \;-\; \mathrm{Harvest_L} \tag{15'}$$

where $\mathrm{Harvest_C}$ for cereal and $\mathrm{Harvest_l}$ for legume were C exported in grain at harvest time t_H, and was 0 for all $t \neq t_H$.

The model considers that cereal and legume litters fall onto the soil by natural mortality and during the harvest. A part of each litter is modelled as being incorporated into the 0-30 cm soil layer by fauna at a constant daily rate of

incorporation τ_{incorp}, assuming that incorporation does not depend on litter quality. The litter C, CLB for cereals and LLB for legumes, were:

$$CLB = \int_{t=t_S}^{t_H} \left(CAB \left(f_1(t, \tau_{mCA}) + f_2(t, \tau_c) \right) - CLB\, \tau_{incorp} \right) dt \tag{16}$$

$$LLB = \int_{t=t_S}^{t_H} \left(LAB \left(f'_1(t, \tau_{mLA}) + f'_2(t, \tau_c) \right) - LLB\, \tau_{incorp} \right) dt \tag{16'}$$

The model considers that root compartments are driven by daily allocation at rates τ_{CAR} and τ_{LAR} of net C production and by daily outputs by root respiration (τ_r) and mortality (τ_m). The root C biomass CRB for cereals and LRB for legumes were then modelled by:

$$CRB = \int_{t=t_S}^{t_H} \left(CDP\, \tau_{CAR} - CRB \left(\tau_{mCR} + \tau_{rCR} \right) \right) dt \tag{17}$$

$$LRB = \int_{t=t_S}^{t_H} \left(LDP\, \tau_{LAR} - LRB \left(\tau_{mLR} + \tau_{rLR} \right) \right) dt \tag{17'}$$

The C production of legume nodules for N symbiotic fixation (Nod) was modelled by daily input of the part $f'_3(t,\tau_{nod})$ of plant C production minus outputs by nodule respiration at rate $\tau_{r\,nod}$ and by nodule mortality function $f_1(t,\tau_{m\,nod})$. From field observations, the same time function was used for legume grain production and nodular mortality (when grain production is completed, plant production decreases and nodules are not then required); the resulting equation of nodule C compartment was:

$$Nod = \int_{t=t_S}^{t_H} \left(CDP\, f'_3(t, \tau_{nod}) - Nod \left(f'_1(t, \tau_{m\,nod}) + \tau_{r\,nod} \right) \right) dt \tag{18}$$

The model assumed that time functions f_1, f'_1, were Gaussian functions (derivatives of the Verhulst logistic curve) with the parameters for the optimum

time (C_{opt} / L_{opt} table 1) and deviation time (C_{tD} / L_{tD} table 1) of C transfer to grains and C transfers to litter by shoot mortality, with a similar function f'_3, controlling C transfer for nodule growth. The time function $f_2(t)$ was set to 0 for all t except at harvest time where $f_2(t) = 1$. All values given in table 1 for growth, transfer and mortality parameters are preserved in N cycle modelling. The outputs of the production module (NC-CR, NC-CA, NC-LR, NC-LA, and NC-Nod are the inputs in the decomposition part. No fertilizer was used, OF N (Fig.1) was set to 0 for all t. It was then necessary to split all these inputs into labile and stable materials (Fig.1) using qualitative estimation of the five types of debris which gave the B_C^j vectors (equation 9) for decomposition (see 2.5 below).

2.5 MODELING OF QUALITY OF NECROMASS ENTERING THE SOIL

The TAO (Transformation of Added Organic materials) model was designed to describe the transformation of C and N from organic amendments and fertilizers in soils from temperate areas in controlled laboratory conditions (Thuriès et al. 2001; 2002; Pansu et al. 2003a; 2003b). The model has since been validated on tropical materials (Kaboré et al. 2011), and the TAO-C version describing carbon transformations, enables 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 mineralization.

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 (Thuriès et al. 2002):

$$C_o = 7.18\ C_{OM} + 0.14\ Lig/N_{OM} - 3.84 \qquad (19)$$

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 fertilizers 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 $P_S = 1.61\ Lig + 0.62\ Ash_{OM}$ (20)

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 (Fig.1).

Another factor which determines decomposition in MOMOS is τ_{NC}, the C:N ratio of input necromass NC from each plant organ. An increase of τ_{NC} was modelled as decreasing the assimilation rates of labile (k_{VL}) and stable (k_{VS}) NC compartments (Martí-Roura et al. 2011):

$$k_{VL} = MAX(0.65 - 0.0019\ \tau_{NC}, 0.1) \quad (21)$$

$$k_{VS} = MAX(0.0037 - 0.000026\ \tau_{NC}, 0.00005) \quad (21')$$

An increase of τ_{NC} was also found to increase the rate of microbial mortality (Bottner et al. 2006):

$$k_{MB} = MIN(0.42 + 0.0012\ \tau_{NC}, 0.8) \quad (22)$$

In this work, equations 17 and 17' were applied separately to each of the five NC inputs, while τ_{NC} in equation 18 was calculated each day by the model from the sums of C and N of the five inputs materials entering MB.

2.6 MODELLING N TRANSFERS THROUGH PLANT ORGANS AND SYMBIOSIS

The flow diagrams (Fig. 1) and above equation system show transfers of N closely associated with most of C transfers during plant production and microbial decomposition:

- the values of MOMOS parameters and their relationships with climate (eq.1), edaphic properties (eq.7) and quality of organic inputs (eq. 20-22) previously found in tracer studies (Pansu et al. 2004; 2007; 2010; Bottner et al. 2006) and further preserved in the C cycle of this cereal legume intercropping (Ibrahim et al. 2013), were also used in this study of N transfers (dark grey ellipses in Fig.1);
- the time functions regulating litter production, nodule production (Ibrahim et al. 2013; not shown in Fig.1), and grain growths in the C cycle (Ibrahim et al. 2013) were also preserved in the N cycle (light gray ellipses in Fig.1); only the optimal and deviation times of N transfers to grains were found slightly different from that of C transfers; another time functions $f_6(t,\tau_{CNRA})$ for cereal and $f_6'(t,\tau_{LNRA})$ for legumes were defined to regulate inorganic N transfers to roots;
- the values of rates of daily production (above eq.13 and 13') and other transfer rates (above eq.14-18) were also preserved in the N cycle.

The only parameters calculated specifically to model for N cycle were those of Table 2, the most important being:

- η_{TMB}, the threshold value of the microbial C:N ratio regulating the exchanges between microorganisms and inorganic N,
- τ_{CNRA} and τ_{LNRA} regulating root adsorption of inorganic N, τ_{CNAS} and τ_{LNAS} regulating N transfers from plant roots to plant shoots,
- τ_{CNAG} and τ_{LNAG} regulating N transfers from plant shoots to plaint grains.

Two parameters specific of N fixation were added:

- τ_{NNF}, the rate of symbiotic fixation of atmospheric N_2 from the nodular biomass (*Nod* eq.18)

Table 2 Additional parameters used to model the N cycle conjointly with the C cycle (parameters of Table 1)

Function	*Parameter*		*Crop*			
	Symbol	Description	Unit	Wheat[1]	Faba bean[1]	Intercrop[2]
Cereal N parameters	τ_{CNAS}	N allocation rate to shoots	day^{-1}	0.331		1
	τ_{CNAG}	N transfer rate to grains	d^{-1}	0.0106		0.0118
	τ_{CNRA}	Rate of root N adsorption	g^{-1} root C d^{-1}	0.0121		0.0044
Legume and nodule N parameters	τ_{LNAS}	N allocation rate to shoots	d^{-1}		0.243	0.2135
	τ_{LNAG}	N transfer rate to grains	d^{-1}		0.728	1
	τ_{LNRA}	Rate of root N adsorption	g^{-1} root C d^{-1}		0.0212	0.0185
	τ_{NNF}	Rate of nodule N fixation	g^{-1} nod C d^{-1}		0.0078	0.0108
	τ_{NNR}	Rate of N transfer from nodules to root	d^{-1}		1	1
N losses	τ_{Nloss}	Rate of losses of inorganic N	d^{-1}	0.0024	0.0012	0.0024
C:N ratios	η_{TMB}	MB C:N threshold ratio for mineralization/immobilization	-	9.87	11.24	9.87
	η_{HS}	C:N ratio of stable humus	-	8.38	8.14	9.11
Time functions	C_{NRAt}	Optimal time of cereal N root adsorption	d	174.8		174.8
	C_{NRAtD}	Deviation time of cereal N root adsorption	d	0.068		0.068
	L_{NRAt}	Optimal time of legume N root adsorption	d		225.1	225.1
	L_{NRAtD}	Deviation time of legume N root adsorption	d		0.042	0.042

[1] pure cropping, [2] intercropping

- τ_{NNR}, the rate of transfer of fixed N from nodules to roots.

Another parameter τ_{Nloss} was added to regulate loss of inorganic N from the soil and the intercropping system (see discussion in 4.2 below). Using these parameters, the nitrogen contents in plant roots CRB N for cereals and LRB N for legumes were then modelled by:

$$\text{CRB N} = \int_{t=t_s}^{t_H} \left(f_0(t, \text{Ng}) + f_6(t, \tau_{\text{CNRA}}) \text{CRB - CRB N}(\tau_{\text{CNAS}} + \tau_{\text{mCR}}) \right) dt \qquad (23)$$

$$\text{LRB N} = \int_{t=t_s}^{t_H} \left(f_0'(t, \text{Ng}) + f_6'(t, \tau_{\text{LNRA}}) \text{LRB} + \tau_{\text{NNR}} \text{LNB N - LRB N}(\tau_{\text{LNAS}} + \tau_{\text{mLR}}) \right) dt \qquad (23')$$

where

- $f_0(t, \text{Ng})$ for cereal and $f_0'(t, \text{Ng})$ for legume = grain N (Ng) when $t = t_s$ and $f_0(t, \text{Ng}) = f_0'(t, \text{Ng}) = 0$ when $t \neq t_s$;

- $f_6(t, \tau_{\text{CNRA}})$ for cereal and $f_6'(t, \text{LNRA})$ for legumes regulates inorganic N adsorption by roots, which is proportional to the legume root biomass expressed in C stock unit;

- $\tau_{\text{NNR}} \text{LNB N}$ regulates N transfer from symbiotic nodules to roots;

- other terms regulate losses of N from roots by transfer to shoots and root mortality.

The resulting daily evolution of inorganic N compartment (inorgN in Fig.1) was the sum of daily mineralization or immobilization (eq.10 and 12) and eventual inorganic fertilization minus root adsorptions by cereal and legume and losses out of the system:

$$\dot{\text{inorgN}} = f(x_{\text{C,MB}}, x_{\text{N,MB}}) + f_7(t, \text{aiNa}) - f_6(t, \tau_{\text{CNRA}}) \text{CRB} - f_6'(t, \tau_{\text{LNRA}}) \text{LRB} - \tau_{\text{Nloss}} \text{inorgN} \qquad (24)$$

The N content in legume symbiotic nodules was:

$$\text{LNB N} = \int_{t=t_S}^{t_H} \left(\tau_{\text{NNF}}\ Nod - \tau_{\text{NNR}} \text{LNB N}\right) dt \tag{25}$$

The N contents CSB N of cereal aerial shoots and LSB N of legume shoots were:

$$\text{CAB N} = \int_{t=t_s}^{t_H} \left(\text{CRB N}\ \tau_{\text{CNAS}} - \text{CAB N}\left(f_1\ (t, \tau_{\text{mCA}}) + f_2\ (t, \tau_{\text{CCA}}\right) + f_4(t, \tau_{\text{CAG}})\right) dt \tag{26}$$

$$\text{LAB N} = \int_{t=t_s}^{t_H} \left(\text{LRB N}\ \tau_{\text{CNAS}} - \text{LAB N}\left(f_1^{'}(t, \tau_{\text{mCA}}) + f_2^{'}(t, \tau_{\text{CCA}}\right) + f_4^{'}(t, \tau_{\text{CAG}})\right) dt \tag{26'}$$

The grain growth of cereal CG N and legume LG N mobilize N from shoots:

$$\text{CG N} = \int_{t=t_s}^{t_H} \text{CAB N}\ f_4(t, \tau_{\text{CAG}})\, dt \ \text{- Harvest N}_{\text{C}} \tag{27}$$

$$\text{LG N} = \int_{t=t_s}^{t_H} \text{LAB N}\ f_4^{'}(t, \tau_{\text{LAG}})\, dt \ \text{- Harvest N}_{\text{L}} \tag{27'}$$

where Harvest N_C for cereal and Harvest N_L for legume were N exported in grains at harvest time t_H, and was 0 for $t \neq t_H$.

As for C, litter N is modelled as the balance of accumulation by shoot mortality and cutting minus incorporation in surface soil by fauna:

$$\text{CL N} = \int_{t=t_S}^{t_H} \left(\text{CAB N}\left(f_1\ (t, \tau_{\text{mCA}}) + f_2\ (t, \tau_{\text{CCA}})\right) - \text{CL N}\, \tau_{\text{incorp}}\right) dt \tag{28}$$

$$\text{LL N} = \int_{t=t_S}^{t_H} \left(\text{LAB N}\left(f_1^{'}(t, \tau_{\text{mLA}}) + f_2^{'}(t, \tau_{\text{CLA}})\right) - \text{LL N}\, \tau_{\text{incorp}}\right) dt \tag{28'}$$

The necromasses entering each day in the soil decomposition process were (Fig.1):

$$\text{CR N} = \tau_{\text{mCR}}\ \text{CRB N};\ \text{LR N} = \tau_{\text{mLR}}\ \text{LRB N};\ \text{CA N} = \tau_{\text{incorp}}\ \text{CL N};\ \text{LA N} = \tau_{\text{incorp}}\ \text{LL N};$$

$$\text{LN N} = \tau_{\text{mNod}}\ \text{LNB N} \tag{29}$$

There was no fertilization in this essay so OF N = 0 for all t.

2.7 CALCULATION TOOLS

Calculations on C and N in liquid and solid phases used the software of the Shimadzu TOC-V_{CSH} and Fisons Instruments NA2000 analysers. C-CO_2 fluxes were calculated from field respiration measurements by LI-COR (http://www.licor.com). All results were transferred to standard spreadsheets to obtain the density of all C and N forms in g m^{-2}.

ANOVA, F tests of residue comparisons, mean and confidence interval calculations and other statistical operations were performed using Statgraphics (www.sigmaplus.fr).

VENSIM (http://www.vensim.com/) was used for moisture calculations using the SAHEL model (Penning de Vries and van Laar 1982) and all C and N cycle calculations coupling TAO, MOMOS and the C production and N transfer modules for the cereal / legume intercropping described above. Euler's method was used for numerical integration of the differential equations and parameters were fitted using Powell's conjugate gradient descent method. Knowing the **A** matrix (Equation 4) and its associated relationships with climate (Equations 1, 2, 3), soil texture (Equation 7), and quality of inputs (Equations 15, 16, 17, 17', 18) this work aimed to demonstrate that the eco-physiological parameters τ and time functions *f* (Equations 9 to 14), which are difficult to estimate by other methods, could be optimized by the calculation system, to adjust simultaneously all the collected data

3. RESULTS

3.1. MICROBIAL CONTROL OF ORGANIC N

Stocks and exchanges of N between organic compartments are summarized on Fig.2. The modelled increase of 44 g m^{-2} of total N was not significantly greater than the confidence interval of the mean of measured data (F test). It corresponded approximately to the increase of the labile humus of microbial origin (HL, Fig.1) whereas N of stable HS compartment was modelled as stable with a weak decrease from 264.4 to 263.9 g N m^{-2} (Fig.3a). The amount of total plant debris remaining in top soil from four origins (roots and litters of durum wheat and faba bean) was modelled as an approximately constant value of 0.6-0.7 g N m^{-2} during the entire cycle except an increase which began near 150 d after sowing to reach a plateau in range 0.9-1.1 g N m^{-2} at 200-250 d after sowing, and a maximal value of 1.4 g N m^{-2} at harvest (Fig.2a).

This N stock of plant debris was modelled as the integration of the daily input from mortality of plant organs minus the daily microbial assimilation of debris, which was about 0.1 g N m^{-2} d^{-1} from sowing to 150 d after sowing (Fig.2b). After 150 d, the microbial assimilation increased to a plateau of 0.3-0.5 g N m^{-2} d^{-1} and reached a maximal value of 0.7 g N m^{-2} d^{-1} immediately after harvest then it decreased quasi exponentially to a value less than 0.01 g N m^{-2} d^{-1} at one year after sowing (Fig.2b). The rate of microbial assimilation of N from plant debris was modelled as close to the rate of microbial assimilation of N from labile humus at the 1st step of plant growth, from sowing to 210 d after sowing. Then, the rate of N assimilation of labile humus became increasingly greater than the N assimilation of plant debris until 2 months after harvest. Labile humus was modelled as almost the unique source of N for microorganisms after 2 months following the harvest (Fig.2b).

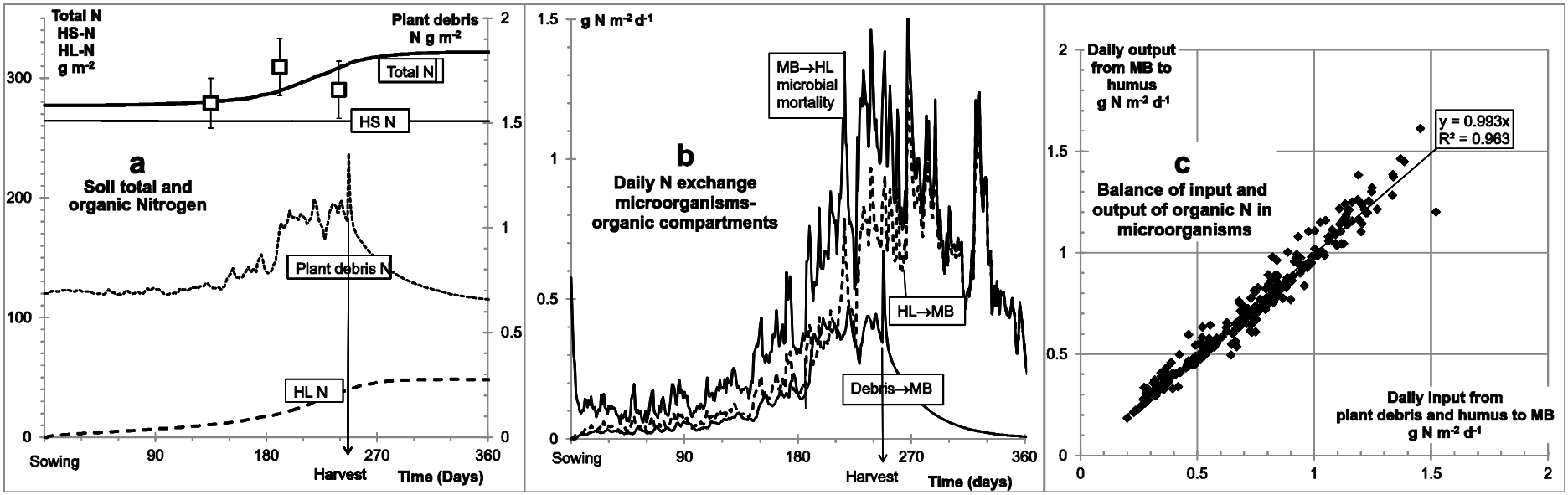

Fig. 2 Flows of organic N directed by microorganisms: a) predicted and measured values with 95% confidence intervals of soil total N, and predicted N in plant debris and labile and stable humified compartments, b) daily exchange of N between microorganisms, plant debris and labile humus, c) daily balance of input and output of organic N in microorganisms.

During the entire intercropping cycle, the daily output of N from microorganisms to humus by microbial mortality (Fig.2b) was modelled approximately as the sum of daily inputs by enzymatic assimilation of plant debris and humus, with variations linked to climate conditions. Microbial inputs (MI) have been significantly adjusted to microbial outputs (MO) by the equation MI = 0.993 MO, that means that organic N daily taken for microbial growth was about 7‰ of the organic N exchanged by microorganisms (Fig.2c). The other part of N necessary to microbial growth was immobilized by microorganisms from inorganic N of soil (see section 3.2 below).

3.2. MICROBIAL CONTROL OF INORGANIC N

The Fig. 3 summarizes the stocks and consecutive flows of inorganic N in exchange with soil microorganisms and symbiotic microorganisms. These stocks and exchanges concerned weak N amounts compared to the stocks and exchanges of organic forms of N (see 3.2 above and Fig.2): microbial N was 0.7-2.3% of total organic N and 4-14% of N transferred to labile humus (HL compartment), inorganic N ranged from 0.02-3.3% of total organic N and 0.1-20% of N stored in HL. Fig.3a shows an increase of microbial N which follows the increase of plant restitutions during intercropping from 1-2 g N m^{-2} at sowing to 6-7 g N m^{-2} at harvest, and a decrease after harvest when C supply from plant photosynthesis was stopped. The corresponding increase observed and modelled for microbial C varied from 10-20 g C m^{-2} at sowing to 60-70 g C m^{-2} at harvest (Ibrahim et al., 2013). As for MB-C, the MB-N data were significantly predicted at 1% risk (F test) by MOMOS and all predictions were inside the confidence intervals of mean observed values.

The flow of inorganic N was modelled as immobilized by microorganisms during the early times of intercropping until 150 d after sowing where first periods of net mineralization occurred, then were followed by changes between mineralization-immobilization depending on climate conditions, then by dominance of mineralization after harvest (Fig.3b). The cumulated immobilization was predicted as maximal at near 9 g N m^{-2} in the period 150-270 days after sowing, then slowed

down by mineralization giving a balance of 5 g immobilized N m^{-2} at 360 d (Fig.3b). The stock of inorganic N was modelled with a strong decrease under the effect of the microbial and plant uptake from 10 g N m^{-2} at sowing to 0.06 g N m^{-2} at 166 d after sowing. Then it kept this weak value until harvest where it increased again following the decrease of microbial biomass (Fig.3a). Though the prediction of measured values was not significant (*F* test), the predicted values were inside the confidence interval of the 1st measurement and were only weakly underpredicted for the others data (Fig.3a).

The daily fixation of atmospheric N was modelled as having a quasi linear increase from 10 to 90 d after sowing reaching its maximal value of 0.05 g N m^{-2} d^{-1} during the interval 90-180 d and then decreased again quasi linearly until about 0.01 g N m^{-2} d^{-1} at harvest where symbiotic fixation was stopped (Fig.3c). Overall, the total N fixation by symbiotic nodular rhizobia was estimated at 9 g N m^{-2} during the intercropping (Fig.3c), a value similar to the total immobilisation of inorganic N by the other microorganisms (Fig.3b).

3.3. PLANT UPTAKE AND RESTITUTION OF N

The measured and predicted values of N stored in organs of the intercropping plants are shown on Fig.4a for durum wheat and on Fig.4b for faba bean. N stored in plants was very weak compared to organic N of soil compartments and was weaker than N stored in living microorganisms. The main part of the vegetal N was stored in shoots: the N stored in shoots of durum wheat corresponded to 4-24% of N of living microorganisms, the N stored in shoots of faba bean corresponded to 2-100% of N of soil microorganisms. The model predicted significantly, at 1% risk, the grain production of durum wheat and faba bean. The prediction of N of other plant organs was not significant, but confidence intervals of mean measured values were high (4 plot replicates × 4 sampling replicates, not shown on Fig.4 for readability) and all predicted values were inside these confidence intervals.

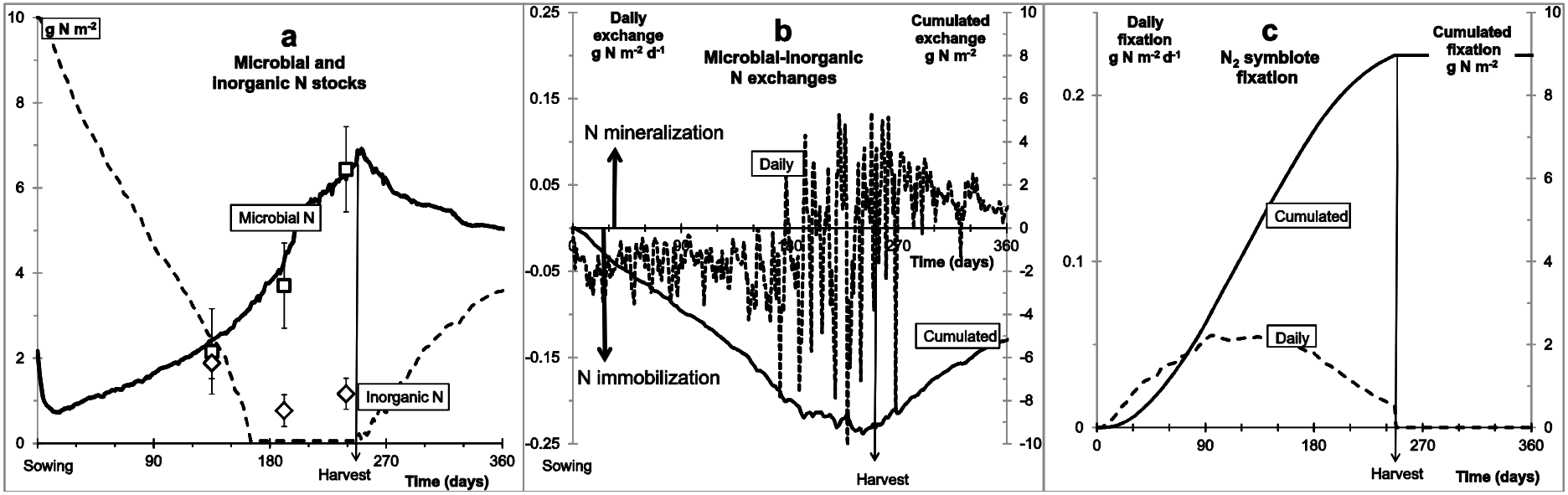

Fig. 3 Flows of inorganic nitrogen in exchange with microorganisms: a) The mean measured values with 95% confidence intervals, and the predicted values of inorganic- and microbial-N in intercropped plots, b) prediction of daily and cumulated microbial exchanges of inorganic N during the cereal-legume intercropping, c) prediction of daily and cumulated fixation of atmospheric N2 during intercropping.

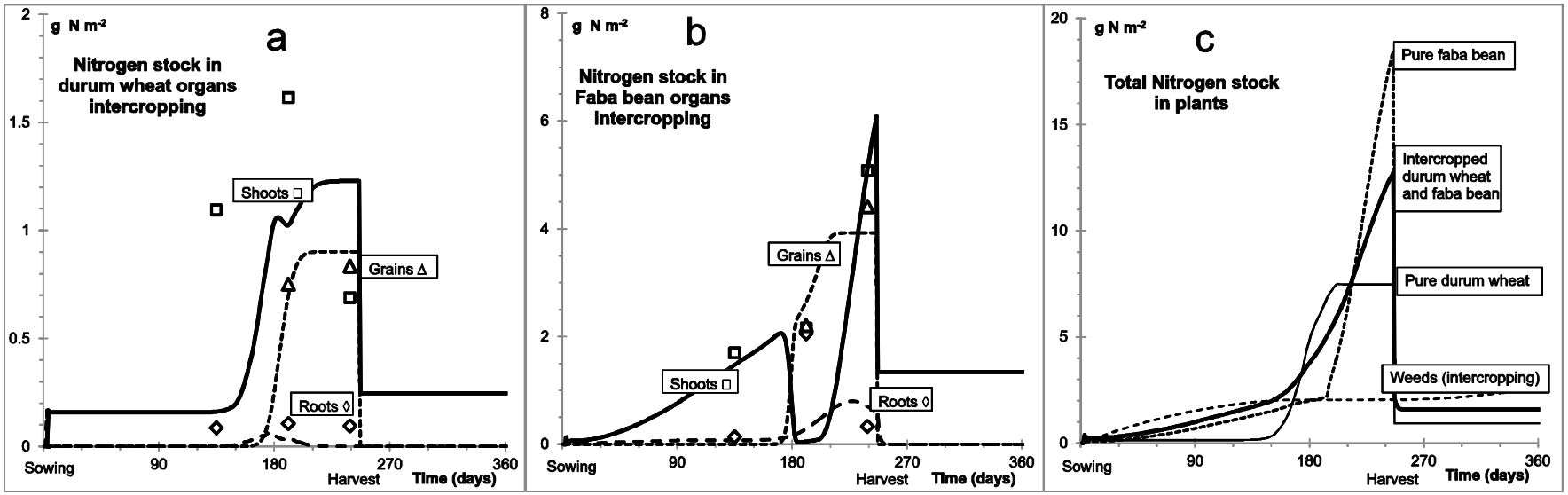

Fig. 4 The measured and modelled N in the plant parts of the intercropped cereal-legume a) wheat shoots, roots and grains, b) faba bean shoots, roots and grains; c) total N stock of the intercrop compared to monocultures.

For both plants, N remaining in roots was about 10% of N stored in shoots (Figs.4a and 4b). At grain formation the stock of N was modelled as transferred to grains, this gave a temporary decrease of N in other aerial parts, especially for faba bean (Fig.4b).

The productivities of these plots had been compared by Ibrahim et al. (2013) for the faba bean-durum wheat intercropping, pure faba bean, and pure durum wheat. For total C (shoot+root+grain of the two plants), maximal production was observed for pure cropping of durum wheat, medium production for intercropping, and minimal production for pure cropping of faba bean. This order is inversed for N storage in crops; Fig.4c shows storage of N in plants of about 19 g N m^{-2} for pure faba bean, 13 g N m^{-2} for intercropping, and 7 g N m^{-2} for pure durum wheat. Ibrahim et al. (2013) have mentioned the low plant productivities of the plot managed in organic agriculture with no fertilizer input since 1998. The crops were invaded by weeds, mainly vetches, poppies and wild oats, which were weeded by hand. The N stock in weeds was estimated at 2.0 g N m^{-2} in intercropping which was significant in terms of N loss for crops and correctly predicted by the model (Fig.4c); one of the modelling results is that the whole of N losses (Fig.1) of this experiment can be assimilated to N storage by weeds.

4. DISCUSSION

4.1. ROBUSTNESS AND PARSIMONY OF THE MICROBIAL MODEL

All parameter values and relationships with the climate conditions, the edaphic properties, the quality of the organic inputs, previously obtained with ^{14}C isotopic tracers for calibration (Pansu et al. 2004) and validation of the C model (Pansu et al. 2010) have been preserved in this study. The ecophysiological parameters additionally defined for prediction of C transfer between plant organs, microorganisms, the soil and the atmosphere, in this intercropping have been also preserved for this work on N predictions (Table 1, Ibrahim et al. 2013). Additionally, this work confirms the result of Pansu et al. (2013) based in

simultaneous ^{14}C and ^{15}N transfers: the N cycle can be predicted in strong association with the C cycle, by programming in addition the exchanges by mineralization or immobilization between inorganic N and microorganisms. So, this work illustrates the robustness of the MOMOS model, which can run in various conditions and climate areas, from acidic tropical conditions in MOMOS calibration and validation, to calcareous Mediterranean conditions in this work, with the same set of equations and parameters linking the model to climate conditions, the edaphic properties, and the quality of the organic inputs. The equations system presented above in 2.3 and 2.5, links the environmental conditions with the microbial ecological functions describing:

(1) enzymatic assimilation of C and N from labile and stable plant debris linked to climate and quality of debris,
(2) enzymatic assimilation linked to climate of labile and stable C and N forms of humus,
(3) microbial respiration linked to soil texture and to climate conditions, describing the output of C from soil to atmosphere proportional both to the growth and the activity of microorganisms,
(4) microbial mortality linked to climate and quality of microorganisms and inputs of plant debris, giving the C and N forms of labile humus,
(5) chemical stabilization linked to climate of a weak part of the C and N forms of humus,
(6) microbial exchange of N between MB and inorganic N linked to the quality of the microorganisms and their substrate.

Except for N exchange (6) between MB and inorganic N, MOMOS does not include parameters not related to temperature and moisture, like the efficiency factors often used in other models. Thus, this model could be the most sensitive to climate change, and the most parsimonious (Ockham's razor, *lex parsimoniae*), in terms of definition of its equations and parameters.

4.2. PARAMETERS SPECIFIC OF THE MAIN FLOWS OF N IN LIVING ORGANISMS

Only the values of ecophysiological parameters of Table 2 have been optimized specifically for the N cycle. They included:

(1) two functions of time to regulate adsorption of inorganic N by roots,

(2) two rates of adsorption of inorganic N by unit of root-C of cereal and legume,

(3) four parameters regulating for both plants (i) transfer of N from roots to shoots, (ii) transfer to grains,

(4) two rhizobium parameters regulating (i) rate of N fixation by unit of nodule-C, (ii) rate of transfer of N from nodule to legume roots.

(5) two optimal values of C:N ratios of microorganisms (parameter 6 in above section 4.1) and stable humus (the C:N ratios of plant materials, were measured, the C:N ratio of labile humus was calculated each day by a balance equation),

(6) a rate of N losses out of the intercropping system,

Concerning the two functions of time (1), the maximal adsorption of inorganic N was at 175 days after sowing for cereal roots and 225 days after sowing for legume roots (Table 2). These values were near the optimal times found for the growth of grains of 182 d for durum wheat and 191 d for faba bean (Table 1). But this study should clarify a difference between the physiological functioning of cereal and legume. The stock of N of cereal was lower than in legume and N seems more quickly transferred from roots to shoots (Fig.4a and 4b). This could explain that cereal needs to adsorb inorganic N from soil before the early days of grain formation. Conversely, aerial parts of legume contain larger amounts of N than cereal, due probably at the transfer from rhizobium and roots. In the early days of grain formation, the source of N for grains was shoot-N, the rate of N adsorption by roots was maximal only in a second stage of grain formation (Fig.4b). This mechanism explains why yields were lower in intercropping than in pure culture of wheat in the studied system. The development of the cereal grains occurred too earlier than maximal N release by mineralization of dead nodules and roots of the

legume (Fig.4b). In these conditions most of the mineralized N was stored again in legume organs (Fig.4c), and was not a benefit for cereal production.

The rate of N adsorption by roots (2) was found greater for legume than for cereal (Table 2). But these rates must be multiplied by root biomass, here assimilated to root C to give total daily adsorption. It could be better to dispose of the root specific surface instead of root-C since the roots of cereal are much longer and thin than legume roots. Though for Shi et al. (2013), the root N uptake of wheat should be better correlated to the root mass than to root length, the cereal root system in field conditions is able to explore a much larger soil domain than the legume roots (Ibrahim et al. 2013). The rate of root N adsorption has been found greater in pure cropping than in intercropping, traducing probably the limitation of inorganic N available in intercropping in period of high N requirement by plants and microorganisms (Fig.3a). The sum of root adsorption rates of cereal and legume in intercropping was found equal to the root adsorption rate of legume in pure cropping.

The rate of N allocation to shoots (3) was found greater for the cereal than for the legume (Table 2) though N accumulation in shoots was greater for legume (Fig.4b) than for cereal (Fig.4a), probably as a consequence of N fixation and greater rate of root adsorption in legume than in cereal. Conversely, the rate of N transfer to grains was found greater for legume than for cereal (Table 2), traducing again probably a difference between the physiological properties of the cereal and the legume. In the 1st phase of grain formation, the transfer of N from shoots to grain was higher for legume (Fig.4b) than for cereal (Fig.4a); the maximal N requirement for grain growth of cereal corresponded to the maximal value of the predicted N in root (Fig.4a), N adsorbed by roots was modelled as transferred more quickly for grain growth in cereal than in legume with temporary storage in shoots lower for cereal than for legume.

The rate τ_{NNF} of fixation of atmospheric N_2 (4) was near 1 g N for 100 g nod C by day with a value slightly higher in intercropping than in pure legume crop

(Table 2), and corresponded to a total fixation of 9 g N m^{-2} for the entire cycle (Fig.3c). This value was not measured but introduced as a plausible value before τ_{NNF} optimisation. In absence of that value, the optimized τ_{NNF} overestimated the N fixation (near 40 g N m^{-2}) compared to literature data well developed in the last decennia since the 1st estimations by total nitrogen accumulation of the crop (Larue and Patterson, 1981); N fixation in Canadian soils has been estimated in range 5-30 g N m^{-2} (50-300 kg N ha^{-1}) depending on the legume specie (Yang et al. 2010) not quoting faba bean; López-Bellido et al. (2006) estimated the N fixed by faba bean in rotation with cereals in range 3.9-14.4 g N m^{-2}; for Jensen et al. (2010) Faba bean has the highest average reliance on N_2 fixation and could save up to 10-20 g N m^{-2} in the amount of N fertilizer required to maximize the yield of crops grown after faba bean; some other experiments will be necessary to check if our mechanistic modelling could be a new field method of quantification of N fixation; the other methods using generally ^{15}N measurement (Chalk and Ladha 1999) are often not very accurate and possibly heavy to implement. From this experiment, the τ_{NNR} parameter regulating transfer rate of N from nodule to root can be eliminated of the model because its value was optimized at 1 in both intercropping and pure legume cropping. Each day, the fixed N_2 was entirely transferred to legume root then for a part transferred to legume shoots, and for the other part transferred to soil microorganisms by root mortality, which was found ten times higher for legume than for cereal (Table1).

The threshold η_{TMB} of C:N ratio of microorganisms (5) is the parameter of prime importance to regulate mineralization or immobilization of N (Fig.2b). In this work MB is assumed to be homeostatic, which is a more plausible hypothesis for well drained systems of plains than for wet systems of cold or mountain areas (Pansu et al. 2013). The immobilization of inorganic N from soil was requested when the current C:N ratio of MB was greater than the threshold value optimized at 9.87 in intercropping (Table 2), otherwise the N mineralization occurred when C:N ratio of MB was lower than 9.87. The threshold value found slightly higher in pure cropping than in intercropping corresponded to higher N mineralization in

pure cropping. The C:N ratio of stable humus η_{HS} was optimized at 9.11 in intercropping (Table 2), which indicates a high reserve of stable organic N in this soil, it should be interesting to measure η_{HS} but the measurement is not standardized, it can be time-consuming and subject to errors between physical or chemical approaches (Pansu et al. 2006).

The rate τ_{Nloss} of N losses out of the intercropping system (6) was estimated at 0.24% of inorganic nitrogen by day (Table 2) which enabled to estimate total losses of 2 g N m^{-2} near the amount of N measured in weeds after hand weeding of the plots 150 d after sowing. So in this system, the N loss during intercropping was assimilated to N stored in weeds, N losses in the atmosphere and groundwater can be neglected.

5. CONCLUSION

This work and that of Pansu et al. (2013) demonstrate the strong link between the cycles of C and N in ecosystems. The main difference concerned the flows of C and N between organic and inorganic molecules. Carbon has been modelled as removed from organic phase by microbial respiration and reincorporated by plant photosynthesis. Nitrogen has been modelled as removed from organic phase by microbial mineralization, and reincorporated by the microbial assimilation, root assimilation, and the symbiotic fixation. Despite the link between the two elements, their stream is inversed in living organisms. The flow of C has been modelled from atmosphere toward plants and soil microorganisms, when the flow of N has been modelled from microorganisms (both microbial mineralization and symbiotic fixation) toward roots and shoots of plants. The key to optimize crop production by using ecological mechanisms will be to adjust the demand of N for plants linked to C photosynthesis, and microbial production of inorganic N linked to the C availability for microorganisms. In the intercropping example of this study:

(1) the amounts of C and N in organic compartments of microbial origin represent the principal reserves in soil; the stable humus HS is the highest reserve which can sustain a latent functioning of the living organisms for very long periods, with a very weak daily assimilation, not sufficient to sustain a high crop production; the second high reserve is modelled in labile humified compartment HL, which is the main short term stock for the microbial functioning and the plant growth;

(2) the living organisms store much less of C and N than humus but can be modelled as the actors of all the transformations, with a reserve higher in microorganisms than in plants; in this intercropping, the decomposer microorganisms immobilize the largest part of inorganic N of soil in the early 6 months after sowing, then mineralize N when substrate plant debris increased; the fixing by symbiotic microorganisms from atmospheric N was modelled as its maximal from 90 to 180 days after sowing; total fixed N was equivalent to total N immobilization during the intercropping;

(3) the flows of photosynthetic C are different for the cereal and the legume (Ibrahim et al. 2013): the cereal mobilized C for the root growth to find nutriments with a relatively weak root mortality but a high loss of C by root respiration, probably the growth energy source (Amthor 2000); the root respiration was found high for barley when no N fertilizer was used (Morell et al. 2012) like in our system; in contrast for the legume, loss of C by root respiration was much weaker than for cereal, but the transfer of C and N to soil microorganisms by root mortality was the highest;

(4) this intercropping did not increased the total C production by legume and cereal which was lower than the production of pure cropping of the cereal (Ibrahim et al. 2013); the simultaneous modelling of the N cycle enables to explain this observation: the durum wheat (*Triticum durum*) cultivar LA1823 needs a maximum of inorganic nitrogen just before grain formation at 150-180 d after sowing; the developed root system of durum wheat must find the inorganic N by soil exploration; at this time the available N was mainly stored in the legume shoots, then transferred to the grains and stored again in shoots then transferred

to decomposer microorganisms which gave inorganic N after the plant requirements.

Consequently, the research to improve the intercropping of legumes and cereals will select associations between species of late-flowering cereals and/or early-flowering legume to improve the efficiency of utilization by the cereal root of mineral N resulting from the microbial decomposition of the N rich legume debris. From this mechanistic modelling, the microorganisms appear of prime importance to bind the growth of the plants in intercropping. Only the whole of microbial decomposers and rhizobia have to be considered for prediction of our entire data set, the arbuscular mycorrhiza (Chalk et al. 2006) have not been considered specifically. In compatible conditions for N transfers, the cereal species could be improved to increase grain yields by reduced losses of C for root development.

Alternately, for the selected plants of this experiment, the annual rotations of durum wheat and faba bean, well recognized for its large ecological services (Köpke and Nemecek 2010), will be preferred to intercropping. This practise is the most in use actually (Jensen et al. 2010), but it should be optimized by another complementary research of mechanistic modelling to enhance N use efficiency (Fageria and Baligar 2005) by avoiding possible losses of potentially available N (inorganic N plus N of living organisms plus N of labile humus HL) between the legume cropping and that of cereal.

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CONCLUSION GÉNÉRALE

Conclusion générale

L'objectif principal de cette thèse consistait en l'estimation journalière des flux de carbone et d'azote entre les composantes sol-plante-atmosphère dans les systèmes complexes.

Après un bref rappel dans le **chapitre 1** sur les deux éléments chimiques carbone (C) et azote (N), leurs rôles fondamentaux au cœur de la vie et leurs enjeux agronomiques et environnementaux, le reste des résultats obtenus dans cette thèse peuvent êtres ainsi résumés :

Chapitre 2 : les facteurs qui influent le stock d'azote total dans les sols de Tunisie

Après avoir rassemblé les sols de Tunisie en deux bases de données, une pour les sols argileux (170 profils) et l'autre pour les sols sableux (285 profils), (i) nous avons effectué dans une première étape d'analyse statistique, l'analyse en composantes principales (ACP) suivie par l'élaboration des équations de pédotransfert (PTF). Nous avons constaté que les propriétés physiques des sols expliquent mieux le stockage d'azote que les propriétés chimiques. Ce résultat, est valide dans les deux types de sol, c'est-à-dire au niveau des sols, argileux sableux. (ii) Nous avons procédé dans une deuxième étape à la modélisation par les équations structurelles (MES), et deux modèles ont été construits. Ces modèles ont fourni une explication satisfaisante de la variation du stock d'azote total dans les deux différents types de sols (argileux et sableux).

Les résultats montrent que les propriétés physiques et chimiques ont des effets indépendants sur le stock. En effet, dans les sols argileux, les *propriétés chimiques* et la densité apparente (D_b) ont le rôle le plus important dans le contrôle du stock d'azote. La matière organique, le pH et D_b sont les principales variables responsables pour le stockage de l'NT liées aux *propriétés physiques* qui sont l'argile, le limon grossier et le sable fin. De même pour les sols sableux, les

résultats montrent que les facteurs chimiques (MO et pH) et la D_b sont les meilleurs indicateurs de l'NT que les propriétés physiques (limon et sable fin).
Nous pouvons établir des relations avec les PTF simples pour expliquer le stock d'azote dans deux sols lorsque nous avons un petit nombre de variables, mais la modélisation par les équations structurelles (MES) est la meilleure, en raison de son explication statistiques même en cas de complexité entre toutes les variables. Les résultats suggèrent également que les modèles SEM expliquent mieux le stock d'azote total que les modèles PTF.
Les sols sous climat méditerranéen semi-aride sont spécialement menacés par les phénomènes d'érosion hydrique et éolienne, ainsi que par la désertification. Ils montrent dans certaines zones mêmes des états avancés de dégradation. La restauration de ces sols nécessite la séquestration du carbone et d'azote qui inhibent ces deux phénomènes et améliore leurs fertilités. A partir de nos deux modèles, nous avons illustré les facteurs clés qui influent sur le stockage de l'azote dans les sols argileux et dans les sols sableux. Ces deux modèles pourraient être généralisés dans toutes les zones arides et semi-arides au niveau de la rive sud méditerranéenne.

Chapitres 3 & 4 : Les échanges journaliers du carbone entre atmosphère-plante-sol (Expérimentation faite sur des sols méditerranéens du site expérimental de l'INRA à Mauguio-Montpellier).

Nous avons montré que la prédiction des échanges journaliers de C entre les plantes, le sol et l'atmosphère est possible en modélisant "le contrôle direct de la décomposition microbienne". Cette nouvelle application du modèle MOMOS utilise uniquement (i) les données du climat local, (ii) les propriétés des sols, (iii) la production du C végétale et (iv) le carbone microbien, inorganiques et total. Le reste des paramètres et les fonctions du modèle MOMOS, qui sont établis pour les autres climats, les entrées et les propriétés du sol, sont retenus dans ce travail.

Cela montre que le modèle MOMOS est de plus en plus générique. Le modèle est initialement calibré pour deux écosystèmes différents à haute altitude, puis validé pour 6 autres sites présentant des caractéristiques climatiques et édaphiques contrastées 65-3940 m, le tout avec des conditions tropicales acides. Bien que notre objectif n'était pas autre validation, cette étude prouve encore une fois l'applicabilité du modèle avec des données recueillies sur des intercalaires à 3 m d'altitude dans les sols calcaires méditerranéens et il semblerait que le système d'équations est probablement utile dans la plupart des environnements terrestres.

Une séquestration nette du carbone organique de 417 gCm^{-2} est prédite dans les cultures associées. MOMOS simule deux compartiments de C stable: HS, formé par la stabilisation de l'humus qui a donné la composition du sol les plus stables avec un taux de décomposition modélisé de 0,00005 j^{-1} (une demi-vie = 38 années) et VS, débris végétaux stable avec un taux de décomposition modélisé de 0,003 j^{-1} (demi-vie = 0,6 ans). Les stocks de C HS et VS sont modélisés comme des quasi constantes au cours de cette année expérimentale, avec une légère baisse de 2407 à 2402 gCm^{-2} pour HS et 628 à 570 gCm^{-2} pour VS.

L'augmentation dans les stocks de carbone résulte d'une très faible augmentation de la matière végétale labile (compartiment VL) de 0 à 0,9 gCm^{-2} mais surtout de l'augmentation des métabolites microbiens labiles (compartiment HL) de 0,1 à 474 gCm^{-2}. Le modèle prédit que l'HL la principale réserve à court terme pour l'activité microbienne et pas le stock de C à long terme.

Le calibrage du modèle suggère que le modèle est parcimonieux, avec un minimum de paramètres bien définis. Il semble être un outil puissant pour évaluer les paramètres éco-physiologiques qui sont difficiles à évaluer par d'autres méthodes dans les systèmes agro-écologiques. Le système d'équations de ce travail est proposé comme un nouvel outil de calcul, dans les changements globaux.

La somme des valeurs initiales des différents types de débris végétaux était 627 gCm^{-2} qui représentent 20,5% du C organique des sols, une valeur plausible pour ce sol qui était relativement riche en fractions grossières et avec une faible fertilité.

Les valeurs initiales des autres compartiments s'élèvent à moins de 1% pour BM et HL, et 79% pour HS, qui était également raisonnable en tenant compte des demi-vies de 1.5, 14 et 13863 jours pour BM, HL et HS respectivement.

Le taux de croissance relative calculé est proche de 0,2 gg^{-1} $jour^{-1}$ pour le blé en monoculture ou en association (τGC). Cela semble cohérent avec la littérature avec τGC dans la gamme de 0,06 à 0,18 pour les 2 mois après le semis ou de 0,11 à 0,26 gg^{-1} $jour^{-1}$ pour les 20 premiers jours. Les taux de croissance relatifs calculés sont environ deux fois plus élevés pour les fèveroles avec 0,4 gg^{-1} $jour^{-1}$ (τGL). Cela semble également être cohérent avec la littérature de 0,40-0,50 à 2-3 mois après le semis.

Les taux d'allocations du C par la photosynthèse aux racines (τCAR de céréales et τLAR pour les légumineuses) sont calculés 0,5-0,6 pour le blé et 0,7-0,8 pour les fèveroles, avec des valeurs élevées dans les associations, ce qui indique qu'il peut y avoir eu une concurrence interspécifique pour nutriments. Il y avait des différences nettes dans le devenir du C alloué aux racines entre les deux espèces. Les taux de mortalité des racines de blé (τmCR) ne sont pas élevés, dans la gamme 0,001 à 0,051 gg^{-1} j^{-1}, identique avec des valeurs publiées pour les autres graminées, et très inférieure au taux de croissance rapporté aux racines de blé avant la floraison. Les taux de mortalité sont significativement plus élevés pour les fèveroles (τmLR), dans la gamme de 0,365 à 0,515 gg^{-1} j^{-1} avec les valeurs les plus élevées pour les cultures en associations. La mortalité des racines des féveroles doit apporter une contribution significative dans l'entrée de C et N pour l'assimilation et la respiration microbiennes. D'autre part, les taux de respiration des racines (τrCR et τrLR) dans les cultures associées sont plus élevés pour le blé que pour la féverole. Les racines de blé ont des pertes plus élevées de C par la respiration à la suite de l'énergie de croissance nécessaire pour explorer le maximum des volumes de sol pour la nutrition des plantes.

Nos résultats ont prédit que les biomasses des nodules et la respiration seraient inférieurs à la culture associée de la monoculture, mais avec le rapport shoot-

C:nod-C plus élevée dans la culture associées. Le modèle a prédit un taux de croissance plus élevé et une mortalité plus élevée des racines de féveroles dans la culture associée et une faible production des nodules dans la culture intercalaire.

Notre modèle a permis de prédire le cycle de C dans des conditions de transfert complexes. Les valeurs des paramètres calculés sont en accord avec la logique et la littérature. Comme les associations légumineuses-céréales sont des systèmes agricoles complexes, le module de production du modèle décrit dans ce travail peut être facilement simplifiées ou adaptées à d'autres systèmes sur d'autres sols.

Chapitre 5 Les échanges journaliers d'azote entre atmosphère-plante-sol (Expérimentation faite sur des sols méditerranéens du site expérimental de l'INRA à Mauguio-Montpellier).

Ce travail montre le lien étroit entre les cycles de C et N dans les écosystèmes. La principale différence concerne les flux de C et d'N entre les molécules organiques et inorganiques. Le carbone a été modélisé comme retiré de la phase organique par la respiration microbienne et réintégrée par la photosynthèse des plantes. L'azote a été modélisé comme retiré de la phase organique par minéralisation microbienne, et réintégrée par l'assimilation microbienne, l'assimilation de la racine, et la fixation symbiotique.

Malgré le lien entre les deux éléments, leur flux est inversé dans les organismes vivants. Le flux de C a été modélisé à partir de l'atmosphère vers les plantes et les microorganismes du sol, alors que le débit de N a été modélisé des micro-organismes (à la fois la minéralisation microbienne et fixation symbiotique) vers les racines et les parties aériennes des végétaux. La méthodologie pour optimiser la production végétale en utilisant des mécanismes écologiques sera d'ajuster la demande d'azote par les plantes liées au C de la photosynthèse et la production microbienne de l'azote inorganique lié à la disponibilité de C par les microorganismes. Dans l'exemple intercalaire de cette étude nous avons obtenu:

1) les quantités de C et N dans les compartiments organiques d'origine microbien représentent les principales réserves dans le sol , l'humus stable HS est le réserve le plus élevé qui peut maintenir un fonctionnement latent des organismes vivants pour des périodes très longues, la seconde réserve est modélisée en humus labile HL , qui est le principal réserve à court terme pour le fonctionnement microbien et la croissance des plantes.

2) les organismes vivants stockent beaucoup moins de C et N que l'humus, mais peuvent être modélisés comme des acteurs de toutes les transformations, avec une réserve plus élevée chez les microorganismes que dans les plantes, dans cette culture associée, les microorganismes décomposeurs immobilisent la plus grande partie de N inorganique du sol dans les 6 premiers mois après le semis, puis minéralisent N lorsque le substrat les débris végétaux augmente, la fixation par les microorganismes symbiotiques de l'azote atmosphérique a été modélisée comme sa maximale de 90 à 180 jours après le semis; la fixation de N total est équivalent à l'immobilisation de N total au cours des associations céréales-légumineuses.

3) les flux de C sont différents pour les céréales et les légumineuses. En effet, les céréales mobilisent le C pour la croissance des racines pour trouver les nutriments avec une mortalité des racines relativement faible mais une forte perte de C par la respiration des racines, peut-être c'est la source d'énergie de croissance. La respiration racinaire a été trouvé élevé pour l'orge quand aucun engrais azoté n'a été utilisé, en revanche pour la légumineuse, la perte de C par la respiration racinaire était beaucoup plus faible par rapport a celle des céréales, mais le transfert de C et N pour les microorganismes du sol par la mortalité des racines est plus élevé.

4) Ces associations n'ont pas augmenté la production totale de C par les légumineuses et les céréales, la production des monocultures blé est plus élevée. La modélisation simultanée du cycle d'N permet d'expliquer cette observation, le blé dur 1823 (Triticum durum) a besoin d'un maximum d'azote inorganique juste avant la formation du grain à 150-180 jours après le semis, le système racinaire développé de blé dur doit trouver l'N inorganique par l'exploration du sol. A ce stade l'N disponible est principalement stocké dans les parties aériennes des

légumineuses, puis transféré aux grains et stocké à nouveau dans les parties aériennes puis transféré à des micro-organismes décomposeurs qui vont donner l'N inorganique après les besoins des plantes.

Par conséquence, pour améliorer les cultures associées des légumineuses et des céréales, deux propositions possibles , des céréales à floraison tardive et/ou de légumineuses à floraison précoce pour améliorer l'efficacité de l'utilisation par les racines des céréales de l'azote minéral provenant de la décomposition microbienne débris des légumineuses riches en N.

A partir de cette modélisation mécaniste, les micro-organismes apparaissent d'une importance primordiale pour lier la croissance des plantes en culture intercalaire. Seul l'ensemble des décomposeurs microbiens et rhizobium doivent être considérés pour la prédiction de notre jeu de données complet, les mycorhizes à arbuscules n'ont pas été spécifiquement examinés. Dans des conditions compatibles pour les transferts d'N, les espèces de céréales pourraient être améliorées pour accroître le rendement par la réduction des pertes de C pour le développement des racines.