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Modelling the continuous exchange of nitrogen between microbial decomposers, the organs and symbionts of plants, soil reserves and the atmosphere

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ABSTRACT

Most of the C and N models published over past decades are based on parameters not always linked to the environment and underestimate the role of microorganisms. They are often over-parameterized, which can give multiple solutions for flow calculations between state variables. This work proposes a modelling method centred on the functioning of living organisms in order to calculate flow parameters using data on N stocks in decomposers, plant organs, symbiotic microorganisms, and the soil compartments. The model was settled via a complex N fixing and intercropping system of durum wheat/faba bean compared to the cropping of pure durum wheat and pure faba bean, all in the context of organic farming invaded by weeds and weeded by hand just before flowering. To avoid perturbation of natural exchanges of C and N, no fertilizer was added from 1997 to 2011.

The equation system defined for the association of any number of plants, as well as parameters previously published for C-flow calculations were used, and only a few parameters specific to N flows were added, and are discussed. The results showed the strong link between N and C in the environment. The calculations converge toward an unique set of solutions that is consistent with literature data when available. The labile organic N of microbial origin was modelled as the main potentially available stock. Living microorganisms stored about 1% of total N, which was close to the N stock in faba bean and four times more than stock in durum wheat. Inorganic N was immobilized before flowering in competition with N requirement of durum wheat roots. Net N mineralization, mainly from decomposition of faba bean roots, started too late to improve wheat production. During the cropping period, weeds accounted for losses of 20 kg N ha^{-1}, while the atmospheric N_2 fixation of 90 kg N ha^{-1} was close to the total microbial immobilization. The model associating microbial and plant flows of C and N in complex plant covers, appears as a robust tool to quantify the exchanges of the earth organisms with the soil and atmosphere. It enables to propose essential recommendations to improve as well agro-ecology as predictions of global changes of C and N stocks.

1. Introduction

Although named *Azote* by Lavoisier, which means lifeless because inert in gaseous form compared to oxygen, this atmospheric element is probably better named nitrogen (N) in its multiple ionic and organic forms essential to life. It undergoes many transformations of very variable kinetics, inside and outside the soil in the nitrogen cycle (Jetten, 2008), current models of crop production like Ceres (Ritchie and Otter, 1984), Epic (Williams et al., 1989) or Stics (Brisson et al., 1998) integrate management of N conjointly with that of carbon (C) and water. Living plants store a weak part of the global N stock mainly by absorption of mineral N by roots, especially nitrates (Inselsbacher et al., 2013), and fixation of atmospheric N_2 by bacterial biosynthesis of ammonium (Unkovich and Baldock, 2008). Nevertheless, there is much

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less inorganic N available for plant growth than the organic N linked to C forms produced by plants and microbial decomposers (Lin et al., 2000; Pansu and Gautheyrou, 2006). This underlines the complexity of the N cycle and the need of models describing precisely the N mineralization and immobilization processes linked to evolutions of the microbial biomass and organic substrates. Indeed, the numerous N models reviewed by Manzoni and Porporato (2009) are not always linked to C, sometimes poorly mechanistic and not really centred on the functional ecology of the plant-microbe systems. For Pansu et al. (2009) the published models were over parameterized, two third of them needed parameters not linked to environmental variables, one third did not use explicitly a microbial compartment and none of them considered really the functional role of microorganisms. A new generation was often awaited to connect more deeply the C and N cycles (Gärdenäs et al., 2011), to really express the direct microbial control over decomposition and N exchanges (Blagodatsky et al., 2010; Todd-Brown et al., 2012) possibly at the cellular scale (Gras et al., 2011), if necessary to bridge the gap between linear models and laws of microbial growth (Neill and Gignoux, 2006) and generally to consider more deeply the role of microorganisms in a new green revolution.

Using isotopic data collected from various ecosystems, Pansu et al. (2014) proposed to link the N and C cycles to the functional ecology of soil microbial biomass defined by the MOMOS model (Pansu et al., 2010) parameterized only by 7 kinetic constant all linked to climate, and some of them to soil physical properties and quality of organic inputs. They compared two assumptions (i) microbial homeostasis (constant C:N ratio of soil microorganisms) to reduce the model complexity and the risks of over-parameterization, and (ii) variable microbial C:N ratio to take account of a succession of decomposer communities (Wu et al., 2012) and their diversity (Philippot et al., 2013). The results showed that homeostasis was not always an acceptable hypothesis but could be considered as a valid approximation, especially in hot, well-drained plain areas (Pansu et al., 2014) where prokaryotes are particularly active, confirming the MOMOS expectation to predict the functional ecology of these soil microbial communities (Sikorski, 2015).

Microorganisms representing the largest part of the earth life need plant substrates as C sources with large research questions about the competition or the synergy with plants for the N nutrients (van der Heijden et al., 2008). Corre-Hellou et al. (2009) have modelled crop growth and N accumulation in pea-barley intercrops. Jensen et al. (2010) reported substantial savings of N fertilizer by symbiotic fixation of faba bean cropping systems and the need to increase associated knowledges about the N exchanges between roots and microorganisms. Ibrahim et al. (2016) have used the Momos model, coupled with a soil water model and a plant production module, to simulate the continuous exchanges of C in intercropping of durum wheat and faba bean. This has allowed for example to estimate separately root tissue respirations and microbial respiration as attempted by Morell et al. (2012) with the Motor model (Verberne et al., 1990). This paper aims to extend the study of Ibrahim et al. (2016) to the continuous N exchanges between the same living organisms, the soil and the atmosphere. The objective was to test the equation system as a new tool to simulate the N exchange flows using measurements of state variables available in the field experiment of Ibrahim et al. (2016). For a model not over parameterized, the values of the flow parameters must converge to a unique set of solutions independently of the set of initial values. The inputs of N to microorganisms can be calculated from MOMOS-C simulation of the death of each organ and symbiont of each plant (Ibrahim et al., 2016) divided by its corresponding C-to-N ratio (which can be available in data bases). The modelling method should enable to estimate threshold values of microbial C-to-N ratio regulating immobilization or mineralization of inorganic N from decomposer microorganisms. And simultaneously to estimate essential parameters of N exchanges for plant growth: time functions of absorption of inorganic N by roots, N fixation by symbiosis, N transfers to roots, shoots, grains, and N losses in environment. Such estimations complementary to that of Ibrahim et al. (2016) must help to clarify essential points of ecosystem functioning such as: (i) how do decomposer organisms affect N accessibility or depletion for plant roots, is microbial homeostasis a valid assumption to control N exchanges in the legume-cereal system? (ii) how do the N exchanges between living organisms affect flows of photosynthesised C and crop yields? How can the N use by cereal roots be improved by atmospheric fixation of legume symbionts?

More generally, this paper aims to propose two finalities: (i) a methodology to understand and improve the C and N exchanges and the resulting yields whatever are the crops and the number of plants in interaction, (ii) a tool to model the exchanges of C and N at larger scales, highlighting the data bases which have to be collected from literature, approximations, or experiments analogous to that of this paper.

2. Materials and methods

2.1. Field experiment and data collection

The field experiment and soil were described in detail by Ibrahim et al. (2016). The soil was a loamy chromic Cambisol with an alkaline pH of 8.2 which greatly differentiate it from the tropical soils of model calibration and validation. This experiment was carried out at the *Institut National de la Recherche Agronomique* (INRA) Mediterranean station of Mauguio (43°37′12.60″N/3°59′07.12″E),[1] France. Plots of 6 m × 10 m were cultivated with three crop systems (four field replicates) using organic farming methods applied since 1997 without any fertilizer addition (1) durum wheat (*Triticum durum* Desf. *c.v.* LA1823) monocrop at a density of 100 ± 23 plants m^{-2} (2) faba bean (*Vicia faba L. c.v.* "Castel") monocrop at a density of 17 ± 7 plants m^{-2}, and (3) durum wheat LA1823 - faba bean Castel intercrop at a density of 72 ± 28 durum wheat m^{-2} and 16 ± 6 faba bean plants m^{-2}. The low fertility allowed only these low plant densities but gave optimal conditions to quantify natural exchanges of N between living organisms not masked by external inputs of N. Four whole plants (roots and shoots) of durum wheat and four of faba bean were collected from each plot during growth (1st sampling period) and at maturity (3rd sampling period), 10 plants of each species were taken during flowering (2nd sampling period). A particular attention was necessary to recover the main part of the plant roots using garden forks, several diggings around the selected plants were sometimes necessary and the sampling was not possible on too dry soils. At the same times, two replicate soil samples were collected in 500 mL stainless steel cylinders from the 0–5 cm and 25–30 cm layers from each plot to determine the soil moisture and bulk density.

The soil near the roots was collected from the field, by careful separation by hand from roots, and preserved in iceboxes (4 plots × 3 crop systems × 4 replicates) then gently crushed by hand, without drying, through a 4 × 4 mm grid sieve. The coarse and fine fractions were weighed, recognisable root fragments were separated and joined to their corresponding plant sample, and the fine fraction was kept without drying at 4 °C for analysis of microbial N on one part, analysis of total N after drying at 60 °C and grinding at 0.2 µm on the other part. The roots were separated from shoots and washed in deionized water. The root nodules were separated manually and the grains were separated from the shoots. All organs were dried at 60 °C for 2 days and weighed. For subsequent N analysis, samples of each plant organ and soil were grouped and ground to 0.2 mm in a steel planetary ball mill.

The microbial N was determined within two days after sampling by fumigation-extraction (Brookes et al., 1985; Vance et al., 1987)

[1] There was a mistake in coordinates of Ibrahim et al. (2016) which are not in degrees minutes seconds as indicated but in degrees decimal minutes which corresponds to degrees minutes seconds of this paper.