Modeling the functional role of the microorganisms in the daily exchanges of carbon and nitrogen in intercropping system under Mediterranean conditions

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Abstract. Carbon (C) and nitrogen (N) sequestration in plants and soil micro-organisms is considered as a major phenomenon against global warming. The modeling of this phenomenon aims at highlighting the role that the legumes-cereals mixed crop can play in the reduction of greenhouse gases. It is based on field experiments in maize (*Zea mays L*.)-common bean (*Phaseolus vulgaris L*.) intercropped system of the cereal agroecosystem in Setif region of Algeria. For this purpose, the MOMOS model was selected and validated in a calcareous soil and low phosphorus (P) conditions. It revealed some mechanisms that control the C and N sequestration in the compartments of the complex soil-plant-atmosphere-microorganism system. CN modeling results show that the daily growth of intercropped maize with common beans is positively correlated with the microbial CN transformation during the cropping cycle, under limited P and N conditions. Thus, this approach revealed the functional role of rhizobial symbiosis in maintaining the balance between the different C and N exchanges from soil to atmosphere and from atmosphere to soil.

Key words: modeling, carbon, nitrogen, sequestration, intercropping.

INTRODUCTION

The superficial layers of the terrestrial globe contain the largest reserves of organic carbon (C) and nitrogen (N) potentially available for plant growth (Ladd et al., 1992). These two elements are also essential constituents of organic matter (OM), which plays a crucial role in maintaining and improving soil fertility by its beneficial effects on physical, chemical and biological properties and more particularly on sequestration of soil C (Ladd et al., 1992). Also, microbial biomass (MB) constitutes a transformation matrix for organic matter in the soil and acts as a labile reservoir of nutrients available to plants, especially for C and N (Srivastava et al., 1989).

The importance of soil organic matter (SOM) pools depends on the input of crop residues and losses of C. These losses are caused either by heterotrophic respiration during the decomposition of SOM by MB or by autotrophic respiration of symbiotic bacteria (Ibrahim et al., 2013).

Several studies focus on crop production and the N cycle including the symbiotic fixation of atmospheric nitrogen (N_2) during crop cycles (Corre-Hellou et al., 2009, Liu et al., 2011). Other studies attempt to link soil respiration to crop production based on pedoclimatic variability (Yuste et al., 2004, Dornbush et al., 2006). However, the data from the literature lack accuracy on the simulation of the daily dynamics of C and N transferred between the plant, soil and atmosphere.

Commonly used cultural practices such as fertilization, pesticide treatments and monoculture, contribute significantly to the degradation of environmental fertility by reducing biological diversity and by increasing the emissions of CO₂ sequestered in the atmosphere (Horrigan et al., 2002). Therefore, the ecosystem approach remains the surest way to avoid the harmful consequences of these practices in conventional agrosystems. This includes, in particular, the ecological services of atmospheric nitrogen fixation and the processes of complementarity and facilitation of legumes by promoting their interactions with soil micro-organisms (Latati et al., 2016, 2017). Indeed, a positive effect on cereals when intercropped with legumes has been demonstrated with biomass accumulation and yield increase (Betencourt et al., 2012, Latati et al., 2013, 2014). This positive effect was confirmed for cowpea-maize (Latati et al., 2014), chickpea-durum wheat (Betencourt et al., 2012) and bean-maize intercropping (Dahmardeh et al., 2010, Latati et al., 2013, 2016 and 2017). However, the increase in cereal yield in intercropping is not due only to the increase in N resources via symbiotic N2 fixation but also to other mechanisms patterns, i.e. enzyme activity, may show at least similar increases of soil fertility, e.i. C, N and P mobilization abilities (Bargaz et al., 2017, 2018).

To better understand the dynamics of N and C in Mediterranean soils, mechanistic models can answer several pertinent questions. They make it possible, for example, to distinguish the compartments of plant origin, generally located in coarse fractions of the soil, from those of microbial origin located in the finer fractions (Pansu et al., 2009).

In Algerian soils, a first quantification of N, following that of C in an agroecosystem cereal production of Setif, revealed a fragility of the reserves and the need to change agricultural practices with a soil preservation management (Latati et al., 2016, 2017). Under different environmental conditions, several modeling studies of stock variations of C and N in several production systems (Pansu et al., 2004, 2009 and 2010) are available and allow a better understanding and adapting the models.

In contrast with other published propositions which need long term comparisons to quantify the C exchanges, our work studies, in the short term, the cycles of C and N by the validation of the MOMOS model (Micro-Organismes et Matière Organique du Sol, i.e. soil microorganism and organic matter model) on the basis of the CN data collected in the cereal agro-ecosystem of Setif region in the northeast of Algeria. It presents the genesis of the MOMOS model which is centred on microbial functioning and appears very sensitive to meteorological, edaphic and biological conditions. It is therefore important to answer two questions: (i) could MOMOS predict the daily evolution at short term of living and dead forms of organic carbon in complex systems, (ii) Could the equations be used to simulate the C and N flows into microbial symbiotic nodules of

intercropped legume roots by checking the simulation against field measurements data of root nodule biomasses?

MATERIALS AND METHODS

Experimental site

The experiment was carried out in the commune of El Kharba ($35^{\circ}58'11"$ N and $5^{\circ}14'90"$ E), Algeria (North Africa), north of Setif region. This site has already been studied in previous researches (Latati et al., 2016; 2017). The choice of this site is justified by the results of Latati et al., (2016 and 2017) which report a high efficiency use of rhizobial symbiosis and the presence of P-deficient and calcareous soils. The climate of Setif is Mediterranean characterized by a harsh winter and a hot and dry summer. The average temperature during the four months of the growing cycle varies between 20.7 °C and 28.1 °C. The maximum temperature (37.1 °C) is recorded during the month of August, while the minimum temperature (13.7 °C) is recorded during the month of September. The maximum rainfall is recorded in September with 28.2 mm. Climatic data are collected from the Meteorological Station of Setif. All the physicochemical characteristics of the soil as well as the experimental device were done as previously reported (Latati et al., 2016).

Sampling and data collection

The data were collected at the first stage of growth at 20 days after sowing (DAS), early flowering (50 DAS), full flowering (75–80 DAS) and at harvest stage (112 DAS). A physicochemical characterization of the initial soil is carried out before sowing. Samples are taken at random. The whole plant is torn off and for each crop modality the rhizospheric soil of the harvested plants is taken. For the fallow, 4 to 5 soil samples on 30 cm deep layer are taken randomly using the same sampling technique used for the other crop modalities.

The complementary data were used for the calibration (field experiment during 2018 growing season at the farmer's plots in the commune of El Kharba) of some parameters such as; the initial values of soil compartments, plant debris and ecophysiological parameters of both intercropped maize and common bean.

Determination of the stable fraction and the labile fraction of humus by NIRS analysis

In order to determine the different labile and stable fractions of the OM, in both root and shoot part of the maize and the common bean, a near-infrared spectroscopy (NIRS) was carried out in the laboratory of INRA Sup-Agro of Montpellier (France) using a NIRS System 6500 reflection spectrometer. NIRS analysis is a non-destructive method of physical analysis based on the selective absorption of electromagnetic radiations with a wavelength near-infrared range (1,100–2,500 nm) by OM components. The absorbance of infrared radiation by a material is characterized by the superposition of the atomic bonds which determines the chemical constitution of the studied material (Barthès et al., 2008). In practice, crushed samples (plant powder) are placed in the spectrophotometer (NIR System 6500) where they are illuminated by monochromatic radiation whose wavelength varies from 400 to 2,500 nm. The amount of light radiation

reflected by the surface of the sample is measured and all these measurements allow obtaining an absorbance spectrum.

Determination of soil microbial biomass

Funigation-extraction is a reliable technique for measuring the overall size of soil microbial biomass. This method was developed by Vance et al. (1987) and adapted by Wu et al., (1990). It consists in treating the soil with chloroform vapor, which lyses the microorganisms' cells. The cells' compounds obtained were extracted with a solution of K_2SO_4 at 0.05M for C and 0.5M for N. The soil samples (10 mg) were placed in glass Petri dishes and then placed in a desiccator. A Becher containing 50 mL of chloroform (CHCl₃) and pumice is introduced into the desiccator until the boiling of CHCl₃ for 2 minutes. The desiccator was then placed in the shade at 20–25 °C for 24 h. The microbial biomasses according to N (MBN) and C (MBC) were extracted from the funigated samples while the extraction of the non-funigated samples was carried out immediately after weighing the soil samples.

The microbial stock was calculated from the difference between fumigated and non-fumigated soil samples:

$$MBN = [TN(fumigated) - TN(not fumigated)]/kn$$
(1)

Total nitrogen (TN) determined by the KJELDAHL method, with a correction factor Kn = 0.54

$$MBC = [OrgC(fum) - OrgC(not fum)]/kn$$
(2)

The organic carbon (Org-C) in the solution is determined by the SHUMADZU method, with a correction factor Kc = 0.45 (Joergensen, 1996).

MOMOS Model

The MOMOS model (soil microorganism and organic matter model) is a mechanistic model of OM decomposition defining the functional ecology of MB. It was developed in such a way as to limit the parameters of the system studied to the transfer rates between the compartments which could be adjusted by incubation experiments with isotopic tracing (Pansu et al., 2010, Ibrahim et al., 2013). No application on open complex systems with regular flows has yet been published except for Ibrahim *et al.* (2013). The proposed MOMOS model was coupled with the SAHEL model (soils' water) and the FARPROM model (fallow and plant production) (Pansu et al., 2009).

Mathematical Formulation of MOMOS

All parameters of the MOMOS model are related to soil moisture and temperature (T). This is probably one of the most climate-sensitive models with the general equation:

$$\dot{\mathbf{C}} = \mathbf{f}(\mathbf{T})\mathbf{f}(\theta)\mathbf{A}\mathbf{x} + \mathbf{B}$$
(3)

 \dot{C} is the vector of the variable that represents the concentration of C and N in the five compartments of the model (Aerial and root biomass, Microbial biomass, Necromass, Stable humus and labile humus), Ax is the matrix of model parameters, B is the vector representing the C and N inputs, f (T) is the function of the temperature given by equation (Pansu et al., 2004, 2010, Ibrahim et al., 2013).

Data processing and calculation tools

All concentrations of C and N and those of MB in soil (total-C mg g^{-1} and MBC $\mu g mL^{-1}$) are converted to C and N stock in the 0 to 30 cm depth layer by applying the following equation:

Total C or N g C m
$$- 2 = 300 \times ds \times (CN)(1 - Wp)(1 - Cf)$$
 (4)

$$BC g CBM m - 2 = 9 \times ds \times MBCN \times (1 - Wp)(1 - Cf)/ms$$
(5)

where ds – density of the soil; wp – soil moisture; cf – proportion of coarse fraction of soil; CN – total C and N concentration (mg g^{-1}); ms – weight of the soil sample used in the extraction solution (10 g).

The simulation of the daily soil moisture is carried out by the SAHEL model. This model of soil water management is based on two computational versions of potential evapotranspiration according to available climate data collected at the Setif meteorological station. In this context, two versions of the SAHEL model are used:

There is a simplified version using daily maximum and minimum temperature data and another more elaborate version taking into account wind speed and water vapor pressure (Pansu et al., 2007). In addition, the simulation of daily soil moisture is carried out by the SAHEL model (Penning et al., 1989). Moreover, the daily prediction of the C and N cycles evolution during the vegetative cycle on the MOMOS model coupled with that of TAO is established on the VENSIM 5.9 modeling platform (http://www.vensim.com) under the license 8082006 CIRAD.

RESULTS AND DISCUSSION

Fig. 1 shows a good adjustment of simulated soil volumetric moisture values to those measured in the upper and lower soil layers during all the phenological stages of the cropping cycle. Small differences between the measured and predicted data may exist due to the different soil layers taken into account during sampling. The daily soil moisture data measured on a 0-5 cm layer of depth in our experiment are relatively close to the data predicted by the SAHEL model on a 0-15 cm depth layer. The same simulation results are observed on the deeper layer (15–30 cm) and are well adjusted with the moisture data measured on the 25 to 30 cm layer. All simulations of C and N in the different compartments of the soil were carried out at a depth of 0 to 30 cm using the average values of the simulated volumetric humidity on the two layers of depth 0-15 cm and 15-30 cm.

In the case of C and N transfer into the different organs of the plant and microorganism, Figs 2, 3 and 4 shows a significant adjustment (at 5% significance) based on the F-test between the simulated values of C and N transferred to the different parts of the plant (roots, aerial part and nodules) and those measured in maize-bean intercropping. However, the high significant level between the predicted and the measured data is observed for CN transferred to shoot and nodular biomass, particularly for intercropped common bean (Fig. 2a, 3a and 4), while some simulated values are relatively distant compared with the data measured for the roots (Fig. 2b, Fig. 3b).

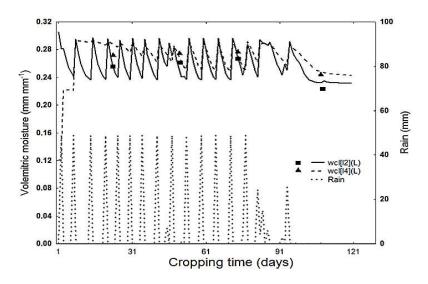


Figure 1. Modelled and measured daily moisture in the surface layer of the soil (wcl2: 0–15 cm) and deeper (wcl4: 15–30) during the growing cycle of the maize-bean intercropping.

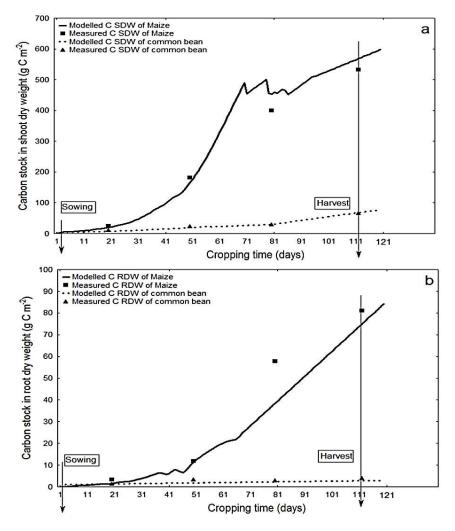


Figure 2. Measured with 95% confidence intervals and modelled values of carbon shoot (a) and root (b) stock in intercropping.

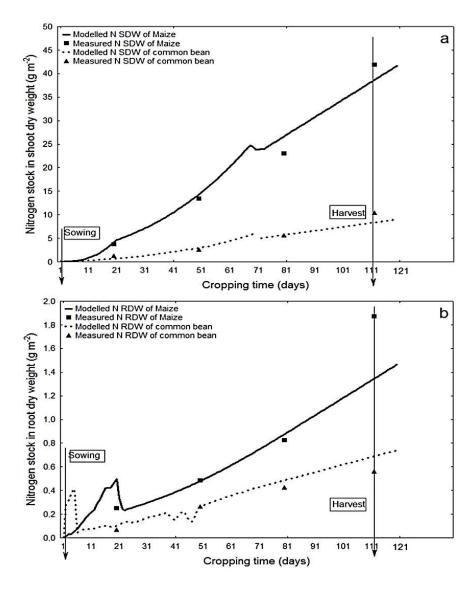


Figure 3. Measured with 95% confidence intervals and modelled values of nitrogen shoot (a) and root (b) stock in intercropping.

However, the transfer of C and N in the shoot and root portion increases from sowing until the end of the crop cycle (harvest). The highest rate is observed during the period from the beginning of flowering (51 DAS) to the full flowering stage (71 DAS). Moreover, the CN transferred to the nodules biomass (NB) reached its optimum (N-NB = 0.88 g m^{-2} and C-NB = 0.06 g m^{-2}) during the flowering stage and then decreased regularly until the end of cropping time (120 days) (Fig. 4).

Indeed, Fig. 5 shows that CN values in soil as well as microbial biomass values are perfectly (at 5% significance) adjusted with field-measured CN data and is fully included in the 95% confidence interval. Moreover, the dynamics of the C and N stock in the soil pass through two phases of evolution (Fig. 5, a). The first phase is characterized by a slight increase in C and N stocks in the soil during the period from sowing to the end of flowering; while the second phase shows a slight decrease in stocks from full flowering to harvest stage.

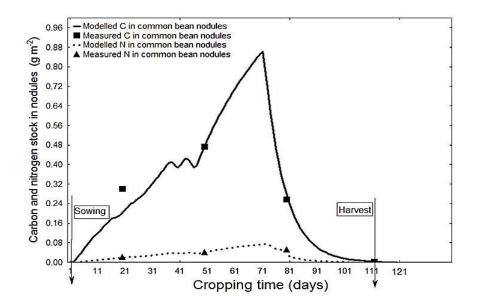


Figure 4. Measured with 95% confidence intervals and modelled values of carbon stock in nodules of intercropped common bean.

The decrease in C and N soil stocks in maize-common beans intercropping is justified by the transfer of these latter elements to shoot and root biomass of intercropped species, particularly during the seeds formation and development. Compared to the relatively stable evolution of CN stocks in soil, CN stocks of MB shows a rapid evolution, particularly at the flowering stage, which recorded the maximum value of MBC (40 g m⁻²) and MBN (3.5 g m^{-2}) (Fig. 5, b and c). However, MBC and MBN underwent a remarkable decrease, particularly from full flowering to early seed formation (83 DAS) and accompanied by a decrease in CN stocks in nodules during the same period, probably due to the decomposition of the nodules biomass after their senescence (Fig. 5, b).

This study demonstrated the possibility of predicting the daily interactions of CN between the different organs of the plant, soil and atmosphere, by modeling the functional role of microorganisms, in particular N₂-fixing rhizobial bacteria. The MOMOS model defines microbial growth by assimilation of the labile and stable compartments of plant residues and humus as well as root exudates with a simulation of C and N fluxes in the different pools of the soil-plant-microorganism system (Pansu et al., 2009).

The MOMOS model becomes increasingly a generic model since its first application in tropical ecosystems (Pansu et al., 2004, 2010), and its validation under Mediterranean soil conditions in the durum-faba intercropping system at French agrosystems (Ibrahim et al., 2013). F tests showed that the measured data were matched the model predictions at 1 to 5% significance for all studied parameters, the MOMOS model appears to be an effective tool for collecting and analyzing eco-physiological parameters, which are difficult to obtain by experimental methods in different agro-ecological systems.

Despite an increase in C and N stocks in the shoot and root biomass of intercropped maize and common bean, the total C and N stock in the soil remains relatively stable after 21 days of sowing and up to the flowering stage (Fig. 5, a). This dynamics of the

CN fluxes in soil and biomass compartments is identical to the dynamics reported in other experiments describing the assimilated C and N distribution in the plant and soil (Butler et al., 2004, Ibrahim et al., 2013).

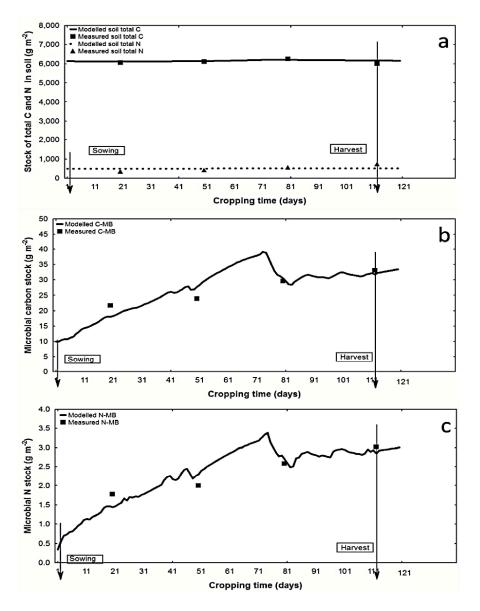


Figure 5. Measured with 95% confidence intervals and modelled values of total carbon and nitrogen in the soil(a), microbial carbon (b) and microbial nitrogen (c) in intercropping.

The increase in the daily CN flow in the plant biomass (Figs 2 and 3) is accompanied by a strong accumulation of these elements in the biomass of the nodules and that of the soil microorganisms particularly during the flowering stage (Fig. 5, b and c). The daily modeling of the CN exchanges between the plant and the soil clearly revealed the role of soil microorganisms in stimulating CN transfers in the maize and common beans grown under intercropping. Moreover, the total C and N inputs did not directly change CN stocks during the cropping cycle. Microbial biomass provides information on the biological functioning of the soil and is rapidly affected by changes in agricultural practices (Marchand, 2003).

C and N constitute an energy source for micro-organisms, which stimulates their growth and activity. Moreover, microorganisms stimulate rhizodeposition and in this case, C is the most rapidly available to be transferred to the rhizosphere where it would be assimilated by microorganisms (Bazot et al., 2005). The results of simulation of the daily flows of N during the flowering period seem to confirm the high concentration of N observed in both shoot and root biomasses and in the rhizospheric soil of the two intercropped species (Latati et al., 2013 and 2017). These authors reported a strong stimulation of common bean growth when intercropped with maize through the symbiotic N₂ fixation of rhizobial bacteria. Microbial biomass is characterized by rapid turnover compared to other constituents of organic matter especially total C and N (Pansu et al., 2010). It is a sensitive indicator of the evolution of cropping systems according to sustainable cropping practices, particularly in the maize-common bean intercropping system (Sparling et al., 1998).

Furthermore, Fig. 6 shows the CO_2 flux data measured in the maize-common bean intercropping. All respirations (respiration of nodules, roots and microbial respiration) are simulated from the total respiration of the soil. The measured values of the total respiration are strongly adjusted with the daily data simulated during the cropping cycle. A slight difference in simulation, observed in total respiration, is due to an overestimation of the data measured during the first sampling period (21 days after sowing) (Fig. 4). This difference may be explained by the presence of weeds on the experimental field during the growth stage. In addition, autotrophic respiration (root and nodular respiration) and heterotrophic (microbial respiration) increase markedly between sowing and late flowering, reaching the maximum values of this activity. Moreover, a decrease in soil respiration was observed during the same period (83 DAS), indicating a decrease in microbial CN stocks (Fig. 6).

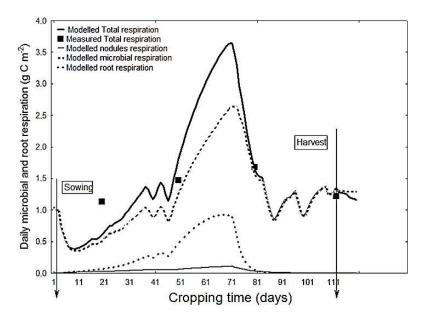


Figure 6. Measured total respiration at soil surface with 95% confidence intervals, and modelled values of root, microbial, nodules and total respirations.

The decrease in both total soil respiration and soil C stocks are accompanied by a strong sequestration of C in the shoot and root of both intercropped maize and common bean especially during seed formation and development (Fig. 6). Plants respire for growth. The results obtained in Fig. 4 show a fast increase in total soil respiration under maize-common bean intercropping during the period from 21 to 70 DAS. Respiration increases due to an increase in biomass production (Schapendonk et al., 1997, Bargaz et al., 2012). Moreover, the decrease in the different components of soil respiration during the harvest stage can be explained by the mortality of the root system which represents the majority respiration of total respiration (Bazot et al., 2005).

Our results are in agreement with those published by Thornton et al. (2004), on the cultivation of ray grass in hydroaeropia. Ibrahim et al. (2013) reported an increase in soil respiration throughout the crop cycle under legumes (faba bean) -cereal (durum wheat) intercropping system. This contradicts our results especially during the last stage of crop development (Fig. 6).

Our results show that the evolution of microbial respiration as well as that of nodules is proportional to that of microbial biomass throughout the flowering period. The same rate of evolution observed between biomass and microbial respiration can be justified by the increasing evolution of the different communities of microorganisms including rhizobia. These results confirm those reported by Pansu et al., (2007, 2009) during the validation of the MOMOS model.

In order to determine the nature and degree of divergence between the different pools of C that may affect N_2 fixation in the common bean-maize intercropping, the relationship between C in the nodular pool and that in the shoot was studied. Moreover, the relationship between the nodular sequestered C and the CN exchanges with the atmosphere via symbiotic N_2 fixation and nodular respiration is studied since nodules formation (21 DAS) to the end of flowering stage (81 DAS).

Fig. 7, a and b show a significant and positive correlation between the C sequestered in the nodules and that stored in the shoot biomass of intercropped common bean ($R^2 = 0.53^*$) and maize ($R^2 = 0.51^*$). These positive correlations confirm the efficiency of rhizobial symbiosis by intercropped common bean and the contribution of nodules in facilitating C sequestration processes in the shoot biomass of both intercropped common bean and maize (Fig. 7, a and b). The C sequestered in the nodular biomass presents a highly significant and positive correlation ($R^2 = 0.99^{***}$) with the flow of C released by nodular respiration (Fig. 7c). Similarly, the fixed nitrogen is positively correlated ($R^2 = 0.69^{**}$) with the sequestered C in the nodules (Fig. 7, d). This correlation confirms the high efficiency of common beans-rhizobia symbiosis when it was grown intercropped with maize and consequently the increase in N transfers in the different compartments (microbial biomass, stem and nodules) particularly during the flowering stage (Figs 2, 3 and 4).

The simulation results show a positive relationship between the predicted values of the C nodular biomass and the C stock in either common bean or maize shoot in intercropping (Fig. 5). However, the estimation of the use efficiency of rhizobian symbiosis (UERS), defined by the ratio between the simulated C of the nodule and shoot biomass, showed a relatively low value (low coefficient of determination, $R^2 = 0.53$) compared with that measured (Bargaz et al., 2012, Latati et al., 2014, 2016) and in hydroaeropia by Alkama et al., (2009). These authors reported correlations between the shoot and nodule biomass with $R^2 > 0.7$. Recent research has demonstrated the positive

effect of N_2 fixation by legumes intercropped with cereals. It results in biomass accumulation and yield increase through N-resource facilitation especially for intercropped cereals (Zhang et al., 2004, Betencourt et al., 2012, Latati et al., 2016). Several studies have focused on the interaction between nodular permeability to oxygen (nodular respiration) and nodular biomass. These studies have shown in a hydroaeropiccontrolled environment that the oxygen nodular permeability is increased under P deficiency (Saber et al., 2008, Alkama et al., 2009).

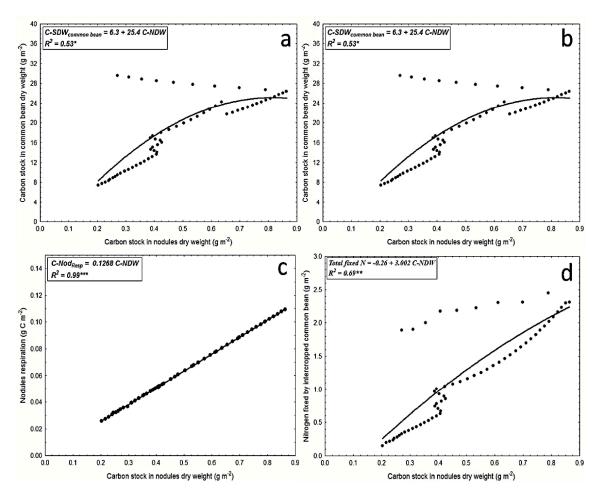


Figure 7. Correlation of modelled values of nodular carbon stock with common bean (a) and maize (b) shoot carbon stock, nodules respiration (c) and the modeled values of fixed nitrogen by intercropped common bean (d).

The application of the MOMOS model allows the simulation of the nodular respiration as well as the quantity of N fixed during the critical phase of symbiotic fixation of N₂. The simulation results show a strong correlation ($R^2 = 0.69$) of N fixed with the C stored in the nodular biomass and, on the other hand, a very strong correlation ($R^2 = 0.99$) of the nodular respiration with the C nodular biomass. It has been shown that the increase in nodular respiration depends on the symbiotic fixation of nitrogen. Alkama et al. (2009) reported that nodular respiration in common beans is positively correlated with the symbiotic fixation of atmospheric nitrogen. The same authors found that the

common bean root nodules excrete in their rhizosphere an amount of H^+ which is correlated with the nodular permeability (nodular respiration).

In this present research the validation of the MOMOS model on the CN data of the maize-bean intercropping system in P-deficient soil revealed two mechanisms, namely the C (nodular respiration) and N (symbiotic N_2 fixation) exchange processes. These mechanisms may explain the physiological behavior of maize and common bean in intercropping with the stimulation of EURS (Latati et al., 2013, 2016) and rhizosphere acidification (Latati et al., 2014), which are relatively related to the nodular respiration of intercropped common bean.

CONCLUSION

The validation of the MOMOS model with the collected CN data in intercropping system makes it possible to demonstrate the functional role of the microorganisms including that of the rhizobial symbiosis via the stimulation of the nodular respiration during the biological N_2 fixation. Indeed, the results obtained make it possible to define relationships between the microbial biomass and its feeding (by the shoot and roots necromasses compartments), the nodulation controlling the N_2 (from the atmosphere to the soil) and CO_2 (from the soil to the atmosphere) exchanges. Also, these results highlighted the crucial role of intercropped common bean symbiosis in maintaining the balance between the different CN exchanges, particularly with the soil and the atmosphere under low P soil conditions. It is now proved that the accuracy of the MOMOS model is perfectly adapted to the study of the CN dynamics in Mediterranean soils, especially Algerian soils which are relatively poor in OM. MOMOS predicted the restoration of soil fertility in C and N using the maize-bean intercropping systems.

In the face of climate change, the choice of cropping system is of considerable importance in developing sustainable agriculture. For this, the legumes-cereals intercropping is a promising alternative to meet this expectation by sustainably supplying nitrogen and phosphorus, which are essential elements for plant production.

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