

Organic matter and biofunctioning in tropical sandy soils and implications for their management

BLANCHART, E.¹; ALBRECHT, A.¹; BERNOUX, M.¹; BRAUMAN, A.²; CHOTTE, JL.¹; FELLER, C.¹; GANRY, F.³; HIEN, E.³; MANLAY, R.^{1,4}; MASSE, D.²; SALL, S.²; VILLENAVE, C.¹

¹ IRD, UR 179, 911 Avenue Agropolis, BP 64501, 34394 Montpellier cedex 5, France

² IRD, UR 179, Route des Hydrocarbures, BP 1386, Dakar, Senegal

³ CIRAD, avenue Agropolis, TA 40/01, 34398 Montpellier cedex 5, France

⁴ ENGREF, BP 44494, 34093 Montpellier Cedex 5, France

Abstract

Tropical sandy soils (or upper sandy horizons of tropical soils) have diverse physical and chemical constraints: poor structural stability (making soils sensitive to crusting, and compaction), poor nutrient holding capacity and low cation exchange capacity. In these soils, in which the clay content is low (3 to 15% by mass), organic matter is the main determinant of fertility, nutrient storage, aggregate stability, microbial and enzymatic activities. However, cultural practices or land uses aimed at increasing organic matter stocks have a minor impact if compared with the potential storage of organic matter in clayey soils. Nevertheless, this stock increase is possible in sandy soils and is mainly linked with the increase of the “vegetal debris” functional pool. Like organic matter, the abundance, activity, and diversity of soil biota are largely dependent upon land management. In these soils, biotic interactions such as termites-microorganisms or nematodes-microorganisms modify nutrient fluxes, N mineralization being higher in soil-feeding termite mounds or in the presence of bacterial feeding nematodes. Moreover, the management of organic residues represents a means to control the activity of soil microorganisms and the structure of nematode and other fauna populations.

An adequate management of organic matter (through fallows, improved fallows, pastures, exogenous organic inputs) through its consequences on soil biofunctioning, largely determines the agronomic (plant production) and environmental (carbon sequestration) potentials of sandy soils. In the present paper, we provide information on the biofunctioning in sandy soils, i.e., interactions existing between organic matter, biological activities (termites, earthworms, nematodes, microorganisms) and physical soil properties, in natural and cropped ecosystems. Data mainly originate from experiments and measurements from West (Senegal, Burkina Faso, Ivory Coast) and East (Kenya) Africa.

Introduction

Sandy soils are widely distributed in the tropics where they occupy most of arid and semi-arid areas. For instance, the total estimated extent of Arenosols is 900 million hectares, mainly in Western Australia, South America, South Africa, Sahel, and Arabia (WRB and FAO/Unesco soil map of the World). It is well known that these “problem soils” are characterized by a low soil organic carbon (SOC), a low cation exchange capacity (CEC), a high risk of nutrient leaching, a low structural stability, and a high sensitivity to erosion and to crusting. Both chemical fertility and physical stability are weak in these soils (Pieri, 1992; Sanchez & Logan,

1992). These characteristics are due to their sandy texture, the low reactivity of their clays, and to climatic conditions that often accompany tropical sandy soils. Due to their dominant mineralogy (generally: quartz, kaolinite, iron and aluminium oxides) and their sandy texture, the role of organic matter on the properties of these soils, on their potential of productivity and on the sustainability of agricultural systems is thus fundamental (Pieri, 1992; Feller et al., 1995b). The control of soil organic matter (SOM) on chemical (CEC, pH, some cations such as calcium and magnesium), and physical (porosity, structural stability) properties has often been demonstrated (Asadu et al., 1997). In sandy soils, it thus appears fundamental to manage all components that affect soil fertility: SOM, and soil biota. Biological processes are crucial to sustain the fertility of sandy soils as they control C and N fluxes (Menaut et al., 1985; Perry et al., 1989; Chotte et al., 1995; Lavelle, 1997). Like in other pedoclimatic zones, the assessment of C, N and P in agrosystems on tropical sandy soils is a useful tool to define sustainable intensification plans necessary to respond to population increases and global change issues (Manlay et al., 2002a, b, c).

In this paper, we will successively analyse (i) the specificity of sandy soils with regard to their organic status, (ii) the agronomic determinants of their organic status, (iii) the agronomic determinants of their biological activities and, (iv) the relationships between SOM and biota with regard to agroecosystem management. The three latter parts are based on case studies essentially from West Africa.

1. Organic status of tropical sandy soils

1.1. Relationships between soil organic matter and soil properties

SOM controls many chemical, physical and biological properties that affect the capacity of a soil to produce food, fibres and fuel. It is the main source of ecosystem energy, and also the main source and a temporary sink of nutrients for plants in the agrosystems. SOM plays a major role in soil fertility through different functions (Feller, 1995a):

- The storage of nutrients (“mineral supply” function). Some minerals like P, Ca, K, Mg are associated in a non-exchangeable form to SOM. They are released during OM decomposition and their dynamics is thus dependent on that of OM. In soils like sandy soils naturally poor in these elements, OM constitutes a interesting reserve for them.
- The increase in CEC (“exchange and sorption” function). This function is linked to the surface properties of soil organic and organo-mineral components: cation and anion exchange capacity, physical and chemical adsorption and desorption properties. These properties define the availability of some nutrients, cation equilibrium and the efficiency of fertilizers and xenobiotic molecules.
- The improvement of soil structural stability (“aggregation” function). Structural stability determines many soil physical and biological properties.
- The stimulation of faunal, microbial and enzymatic activities (“mineralization and immobilization” = “biological” function) that determines carbon C, nitrogen N and phosphorus P and sulphur S cycles. These elements follow successions of mineralization and microbial immobilization. This controls the fluxes of these elements in the soil-plant system (storage or losses) or between different soil compartments.

1.2. Relationships between soil organic carbon stocks and texture

Many works in West Africa showed that SOM content in soil surface horizons is dependent on soil texture (Jones, 1973; Boissezon, 1973; Feller et al., 1991). Feller (1995a) and Feller & Beare (1997) proposed to link linearly SOC content with fine soil particles 0-20 μm , i.e., clay + fine silt (C+FS) (Figure 1).

The relationship clearly indicates that the lower the clay + fine silt content, the lower the soil carbon content. Since this study, the same relationship has been observed in other tropical regions: in Senegal (Manlay et al., 2002b,c), in Martinique (West Indies) (Venkatapen et al., 2004). Tropical sandy soils are thus soils naturally poor in soil organic carbon.

Feller et al. (1991) showed that temperature was not a major determinant of SOC stocks differentiation in considered situations of West Africa (the effect of temperature is only expressed in altitude tropics with mean temperature below 18-20°C). Feller et al. (1991) observed also only a weak effect of rainfall on SOC stocks with a slight increase in C stock in the most humid areas. Taking into account the effect of fine particles (C+FS) and rainfall R, the relationships between SOC content and these factors was:

$$\text{SOC (gC.kg}^{-1}\text{ soil)} = 0.47 (\text{C+FS}) + 0.002 (\text{R}) - 1.74$$

Thus, tropical sandy soils are naturally poor in SOC. When analysing the contribution of Arenosols (main sandy soils) to the total SOC stocks in all World soils, it can be calculated that although Arenosols represent 4.4% (ca. 6 millions km^2) of total World soil area, these sandy soils contribute only to 0.6% (4.3 Pg C) of total SOC stock in the upper 30 cm (723 Pg C)¹.

1.3. Potential of carbon storage and sequestration in sandy soils

The potential of C storage can be assessed as the difference (ΔC) between SOC in native or perennial vegetation and SOC in annual crops. Feller et al. (1991, 2002) observed that ΔSOC are more important for clayey soils than for sandy soils (Figure 2). Similar observations were made for other part of the tropics (Manlay et al., 2002c; Venkatapen et al., 2004). In sandy soils, SOC content in native or perennial vegetation, or in improved systems characterized by high organic inputs are not much higher than SOC content in annual crops. In West Africa, decreases in C content following the installation of crops represents 30 to 40% of non-cropped soils (Hien, 2004). Moreover, these variations appear more rapid for sandy soils (less than 5 years) than for clayey soils (5 to 10 years). As a consequence, sandy soils have a very low potential of carbon storage, compared to clayey soils. The role of tropical sandy soils in the mitigation of atmosphere greenhouse gaz (GHG) is thus very weak. Manlay et al. (2002c) hypothesized that the contribution of these soils to the global mitigation of GHG release does not necessarily require a local carbon sequestration. Settling people may be a means to limit deforestation and carbon release from more humid areas or more clayey soils. This can be achieved by a cropping intensification.

1.4. Organic compartments in tropical sandy soils

The morphologic observations at different scales (optical, electronic microscopy) of SOM associated with different particle size fractions in ferruginous and ferrallitic soils allowed Feller (1979) to gather SOM into 3 compartments:

¹ The C stored in soil for different depth resulted from the combination of a soil map with estimates of C content by soil type. The spatial component is the vectorized format of the 1:5,000,000 Digital Soil Map of the World (DSMW - version 3.5, FAO, 1995). The C content by soil type are derived from information of 4,353 individual soil profiles contained in the World Inventory of Soil Emission Potentials (WISE) and published by Batjes (1996).

- The fraction 20-2000 μm is composed of plant debris at various stages of decomposition, associated with sand and coarse silt;
- The fraction 2-20 μm is made up of fungal and plant debris associated with fine silt and very stable organo-mineral aggregates;
- The fraction 0-2 μm consists of amorphous, colloidal OM, debris of plant and fungal walls associated with organo-mineral microaggregates.

Feller et al. (1991) and Feller (1995a) observed that these compartments vary with soil texture. In sandy to sandy-clayey soils of West Africa, the fractions 20-2000 μm and 0-2 μm represent 30 and 36% of total soil carbon, respectively, while in clayey soils, they represent 17 and 58% of total soil carbon, respectively. Feller (1995a) studied the effect of soil texture on the variations in total SOC content and in organic compartment C content in soils: (i) in a succession deforestation-cropping, and (ii) in a succession cropping-fallowing.

In the former succession, the installation of crops after deforestation leads to decreases in SOC contents by 40%, 44%, and 55% in sandy, sandy-clayey, and clayey soils, respectively. Decreases in total C content are thus more important for clayey soils than for sandy soils. In the sandy soil, most of C is lost in the coarse organic fraction (20-2000 μm) while in both other type of soils, total C loss is mainly due to losses in fine and medium-size fractions (0-2 and 2-20 μm) (Figure 3). For sandy soils, decrease in SOM is very rapid (3 years) for all fractions, even if the rate of decrease is lower for fine fractions than for coarse fractions.

Conversely, the installation of fallows after many years of cultivation leads to increase in SOC contents by 92%, 44%, and 36% in sandy, sandy-clayey, and clayey soils, respectively (Figure 4). In the sandy soil, most of C variation is linked to an increase in C of the coarse organic compartment (20-2000 μm); in the sandy-clayey soil, the C content of the three organic compartments increase while in the clayey soil, total C increase was linked to increase both in coarse and fine fractions. Low soil C content due to 10 years of cropping is rebuilt more rapidly (after 8 years of fallow) for 20-2000 μm fraction than for the other fractions (15 years of fallow).

As a consequence, the renewing rate of C in organic compartments decreases from coarse to fine fractions. Mean residence time of the coarse fraction and in the medium + fine fractions in sandy soils has been estimated to as 12 and 30 years, respectively. When analysing the sandy soils only, the half time life was estimated to 8, 18 and 22 years for $> 50 \mu\text{m}$, 2-50 μm and 0-2 μm fractions, respectively (Feller & Beare, 1997). This means that the coarse fraction (plant debris) in sandy soils plays a major role, in short- and medium-term SOM dynamics, on soil properties, and on soil-plant relationship.

In terms of agrosystem management, these results indicate that the restoration of SOM stock in sandy soils, which is linked to the dynamics of the coarse fraction, is possible in a medium-term (10 years). Conversely, SOM restoration in clayey soils is much longer and mostly concerns both fractions (Figure 5).

1.5. Functions of organic compartments

The three organic pools discussed above fill different functions in soils. As a whole, SOM is responsible for four main functions in soil: “mineral supply” function, “exchange and sorption” function, “aggregation” function, and “biological” function. The notion of functional compartment for SOM was discussed and quantified by Feller and co-authors (Feller 1995a; Feller et al., 2001). These authors demonstrated that in sandy tropical soils, the coarse organic compartment carries the biological function of the OM. This fraction plays an important energetic role as it represents more than 80% of easily decomposable C in sandy soils, but only 30% in clayey soils. On the other hand, medium (2-20 μm) and fine (0-2 μm) fractions are characterized in all soils by low C mineralization coefficients. Net N

mineralization coefficients of coarse fractions are generally low especially when C/N ratio of the fraction is high. This coefficient increases from coarse to fine fractions; thus, in clayey soils, more than 85% of N mineralized comes from the fine fraction (0-2 μm) whereas in sandy soils, more than 50% of N mineralized comes from fractions larger than 20 μm . Studies in West Africa also showed that CEC increases with the decrease of organic fraction size. In these soils, C content, especially that of the fine fraction (0-2 μm) controls soil CEC (Guibert, 1999).

As a consequence, the way SOM improves soil properties depend on the compartments in which it is found (Feller et al., 2001). SOM in fine and medium fractions influences the capacity of a soil to store and exchange nutrients. In this respect, the application of a manure along with a N fertilizer is favourable for preferential storage of C in the fine fractions, thus showing the advantage of this practice in the stabilization of SOM (Hien, 2004). Conversely, SOM in coarse fraction has a rapid turnover and carries biological functions (mineralization of C, N, P in a short term). This fraction is specifically functional in soils with less than 10% clay (Feller, 1995a). Its function is biological: short-term mineralization of C, N and P, and storage ability for N or non-exchangeable calcium. The role of plant debris in the biogeochemical functioning of sandy soils appears fundamental. This is especially true for N, as in sandy soils, N initial reserve and storage potential are low and SOM turnover is rapid (Blondel, 1971a, b, c, d, e; Pieri, 1992; Ruiz et al., 1995). From an agronomic point of view, there is a need to favour agricultural practices that allow an important and constant restitution of plant or animal debris: composts, manures, successions of crops with strong root systems, short fallows, agroforestry, etc. (Ganry, 1991; Pieri, 1992; Feller, 1995a; Ganry et al., 2001; Manlay et al., 2002b, c).

2. Residue management, organic matter and organic compartments in sandy soils: case studies

It has often been demonstrated, for sandy soils of West Africa, that cropping systems that do not imply high levels of organic restitutions to the soil, either on a root form (fallows, pastures) or on organic amendments, lead to the decrease of plant productivity and/or to soil degradation (acidification, decrease in structural stability). This decrease is often linked to a decrease in SOC stocks (Feller et al., 1987; Pieri, 1992). The agricultural development of tropical sandy soils is often hindered by the fact that the decay of SOM is much more rapid than in clayey soils. This acceleration results not only from the low level of clay but also from the pattern of hydrometry throughout the year, both emphasizing the oxidation of SOM. The phenomenon is made all the more intense by the low soil protective colloids content. The main question is: what is the relation between SOM and land productivity? Until the 1990s, the literature did not report a critical SOM content, assuming that the relation between SOM and productivity was more or less linear. Pieri (1992) studying Sudan-Sahel farming situations subjected to strong agro-environmental constraints showed that the strong relationship between the productivity of land and its organic richness were not rigorously linked. In Burkina Faso, Hien (2004) found a critical value of C in the soil, between 6 and 7 gC.g^{-1} soil. The yields of sorghum decreased below 6 gC.g^{-1} soil and stabilized above this value. Feller (1995a) established that the SOC threshold for the sustainability of agrosystems of Western Africa was 6.8 gC.g^{-1} soil, this result being close to that of Hien (2004).

Here, we analyse the effect of different land uses on total SOM and distribution of C within the different organic fractions. Most of studies presented here come from West Africa

(Senegal, Burkina Faso). Soils are sandy or sandy-clayey soils with sandy upper horizon; clay contents are always less than 15%.

2.1. Effect of annual crops and organic amendments

When natural vegetation is replaced with crops, one can observe a decrease in SOC stocks, and especially of C in the coarse fraction ($> 20 \mu\text{m}$) (Feller et al., 1991). Manlay et al. (2002c) noticed that in crops (millet, maize, rice) in South Senegal (region of Sare Yorobana, soil with less than 10% clay), 90% of total C, 90% of total P and 95% of total N were found in the soil. As millet and maize received higher organic inputs and nutrients (manure, crop residues) than groundnut, their C and N contents were higher. In this region, the improvement of soil organic status under continuous crop can only be achieved in fields close to compounds where organic inputs are available.

Feller et al. (1987) and Feller (1995a) measured the effect of organic amendments on total C contents and SOC distribution in organic compartments, in a succession groundnut-millet in sandy soils of Senegal. In the first study (soil with 4% clay), C content was 2.0 gC.kg^{-1} soil in the control and 2.4 gC.kg^{-1} soil in the treatment with buried compost. All added carbon was found in the $> 50 \mu\text{m}$ fraction (Figure 6). In a second experiment (soil with 4% clay), C content in the control was 1.8 g.kg^{-1} soil and it was 2.2 g.kg^{-1} soil in the treatment with a straw mulch. In this case, all added C was found in the $< 50 \mu\text{m}$ fraction. In the third experiment (soil with 8% clay), the presence of a straw mulch leads to an increase of C content (4.3 g.kg^{-1} soil) as compared to the control (3.1 g.kg^{-1} soil). C increase was mainly in $< 50 \mu\text{m}$ fraction and also in $> 50 \mu\text{m}$ fraction.

Organic transfers improve chemical properties in three ways: they are a net source of C and nutrients; they contribute to a gain in CEC and stimulate biological activity (Feller, 1995b; Asadu et al., 1997). Manlay et al. (2002c) observed also that organic practices in continuous crops had a more important effect on soil chemical status (P, Ca, K, CEC, S, pH) than following.

2.2. Effect of cover crops

In Benin, the introduction of a cover crop (*Mucuna pruriens* var. *utilis*, Fabaceae) in maize crops, on a sandy soil (10% clay) lead to an increase in SOC content, and especially in C of the $> 50 \mu\text{m}$ organic fraction (Figure 7) (Azontonde et al., 1998; Bayer et al., 2001; Barthès et al., 2004). On the opposite, increase in SOC content is mostly linked to C increase in the $< 50 \mu\text{m}$ fraction in clayey soils.

2.3. Effect of fallows and agroforestry

If the important decrease in SOC contents after deforestation in the tropics is well established (Maass, 1995), the potential of fallows to increase C contents has also been demonstrated (Manlay et al., 2002b). But the effect depends on soil texture, tree species, management, etc. (Szott et al., 1999). In sandy soils of Senegal, Manlay et al. (2000) measured an increase of SOC content with the age of fallows (4.7 gC.kg^{-1} soil in a 2-year old fallow, 9.0 gC.kg^{-1} soil in a 26-year old fallow). In the same time, calcium, magnesium and CEC increased with the age of fallows. With ageing fallows, coarse root biomass increases while herbaceous biomass decreases. Thus, in sandy soils, SOC increase with the age of the fallows is linked to an increase in tree root biomass and to more important litter inputs (Asadu et al., 1997; Floret, 1998). In most of agrosystems, especially those that are frequently burnt, as in West African Savannas, roots represent the main SOC source (Menaut et al., 1985; Manlay et al., 2000). In

South Senegal, the effect of fallowing on soil organic status was only noticeable in the upper 20 cm of soils, but there was no effect on soil physical properties (Manlay et al., 2002a). The installation of fallows rapidly led to increases in soil C content (by 30% in one year); this was due to a rapid development of trees. Then, SOC content increase was not so rapid (Figure 8), maybe because of a poor protection of SOM against oxidation by biological activities in sandy soils; thus the protection of SOM against mineralization, erosion and leaching is not very efficient (Feller & Beare, 1997). In fact, mesh-bag experiment showed that 40 to 60% of woody roots disappeared after 6 months of incubation (Manlay et al., 2004). Fallowing mostly affected the $> 50\mu\text{m}$ organic fraction whose contribution to total C doubled after crop abandonment. It also allowed a rapid restoration of N and available P contents (Friesen et al., 1997; Manlay et al., 2004).

In different sites of West Africa and West Indies, Feller (1995a) and Feller et al. (2001) obtained the same results as those obtained from South Senegal. Moreover, these authors demonstrated that in sandy soils, soil C increase observed in fallows (after crops) on sandy soils was mainly due to C increase in the $> 50 \mu\text{m}$ fraction, while in clayey soils, C increase in $< 50 \mu\text{m}$ fraction was mainly responsible for total soil C increase (Figure 9).

In Acacia plantations in Cameroon (soil with 5% clay), Harmand et al. (2000) measured after 4 years a SOC content increase as compared with continuous crops; this was mainly linked to an C increase in the $> 50 \mu\text{m}$ fraction. Agroforestry systems are often linked to a strong increase in the total SOC content of sandy soils (Figure 5).

As emphasized by Manlay et al. (2002c) C dynamics in fallows is a determining factor for following crops. A mineral fertilization without organic amendments leads to the mineralization of SOM and to a decrease in soil structure, pH and affects productivity (Pieri, 1992; Manlay et al., 2002c).

3. The biotic components in tropical sandy soils

As said above, SOM is the energetic source of soil biota and soil biota controls the dynamics of SOM, which is fundamental for the fertility and the properties of soils, and especially of sandy soils. Here we analyse some recent studies dealing with the relationships between land use, soil biota abundance and activity, SOM dynamics and plant productivity in sandy soils (West Africa).

3.1. Soil fauna

Soil fauna is known to influence soil chemical, physical and biological properties (Lavelle & Spain, 2001). Zoological groups more often studied with regard to plant productivity and soil properties are ecosystem engineers and nematodes. The former group gathers macroinvertebrates that modify soil physical organization through the production of biogenic structures, and modify the nature and availability of nutrients for other soil organisms (Jones et al., 1994; Lavelle, 1997). Main ecosystem engineers present in tropical sandy soils are termites and earthworms. Nematodes as they belong to different trophic categories affect soil microorganism communities (fungi and bacteria) and plants.

In sandy soils of the arid and semi-arid tropical areas, termites are generally the dominant group of soil macrofauna while earthworms are limited by low rainfall: below 800 mm of rainfall amount, earthworms become rare (Lavelle, 1983).

When present, the effect of earthworms on soil properties can be important. In the soil of the sub-humid savannas of Lamto, Ivory Coast (7% clay in the upper 20 cm of soil), communities are important (ca. $500 \text{ kg}\cdot\text{ha}^{-1}$) and earthworms annually ingest up to $1200 \text{ Mg soil}\cdot\text{ha}^{-1}$ (Lavelle, 1978). As a consequence, the upper cm of soil are made up of earthworm casts that

control physical and biological properties of soils (Blanchart, 1992; Martin & Marinissen, 1993; Blanchart et al., 1997). As showed in different field or laboratory experiments, earthworm activity tends to decrease C content of the coarse ($> 50 \mu\text{m}$) organic fraction and to increase C content of the fine organic fraction in casts, as compared to non-ingested soil (Figure 10, adapted from Villenave et al., 1999). In these water-stable biogenic structures, SOM is physically protected against mineralization (Martin, 1991; Blanchart et al., 1993; Lavelle et al., 1998). The mutualistic interactions between earthworms and microorganisms, which start in earthworm gut and end in casts lead to a strong increase in microbial activities and a subsequent release of nutrients (N, P). The effect of earthworms on SOM dynamics is different according to the duration we consider: in the short term, earthworms stimulate microbial activity, decompose OM and release nutrients available for plants while in the long term, earthworms protect SOM against mineralization. Nevertheless, the presence of earthworms in cropped soil (with sandy upper horizons) does not seem to affect SOC stocks in a medium-term (Villenave et al., 1999).

Many studies have recently been dedicated to termite communities and activities in West Africa: effect on erosion and infiltration (Mando et al., 1996; Léonard et al., 2004; Valentin et al., 2004), on organic resource disappearance and nutrient release (Brown & Whitford, 2003; Rouland et al., 2003; Zaady et al., 2003; Ouédraogo et al., 2004), on soil microbial communities (Brauman, 2000; Fall et al., 2001, 2004; Ndiaye et al., 2003, 2004a; Jouquet et al., 2005), on nest properties (Fall et al., 2001; Mora et al., 2005). In a mesh-bag experiment in South Senegal, Manlay et al. (2004) measured a more rapid and important root disappearance in presence of fauna (mass loss 70% of initial root biomass after 12 months) than in absence of soil fauna (mass loss less than 50%). Termites and ants allowed the reallocation of OM and increased its availability for mineralization (in the presence of fauna, only a few fraction of C was stabilized in soil). In sandy soils, the important consumption of organic inputs by heterotrophic organisms is fundamental for the fertility of agrosystems. Fallows (or agroforestry) allow the restoration of the biological control of ecosystem fertility (Manlay et al., 2002c). After crop abandonment, many studies show an increase of soil macrofauna (density, biomass, activity) (Fall, 1998; Manlay et al., 2000; Derouard, unpub. data). For instance, in South Senegal, the density of macrofauna was 3 times higher in a 10-year old fallow than in continuous crops (Fall, 1998). Some authors emphasize the importance of fallows in favouring ecosystem resilience and stability to climatic uncertainties, to poor nutrient status, and to poor physical stability thanks to the increase in soil diversity and density macrofauna and to root development (Menaut et al., 1985; Ewel, 1999; Manlay et al., 2002c).

The effect of termites on nematodes was studied in Senegal on a sandy soil and results showed that nematofauna structure in termite covers was comparable whatever the termite species, but it is different from that of the soil (0-10 cm). Many works show that plant parasitic nematode communities can be manipulated by managing vegetation, these nematodes being linked roots. Moreover, the pathogeny of nematodes depends on the structure of their community (Cadet & Spaul, 1998). For instance, it was demonstrated in Senegal that the presence of the species *Helicotylenchus dihystera* was associated with a reduction of the pathogeny of the whole nematode community because of the stimulation of root development (Villenave & Cadet, 2000). This species disappear with the establishment of crops after fallows; this may be due to the disappearance of woody roots. It thus seems necessary to preserve trees in agrosystems, and agroforestry could be a means to increase populations of *D. dihystera* and to reduce the impact of parasitic nematodes (Buresh & Tian, 1997).

3.2. Microorganisms

Microbial communities in soils are the actors of the decomposition of the organic matter. The complete decomposition of complex organic substrates such as organic residues relies on the succession of diverse microbial species characterized by different enzyme abilities (Swift et al., 1979; Zvyagintsev, 1994). In tropical sandy soils, very few investigations pointed out the importance of microbial community on decomposition processes.

3.2.a. Microbial status in fallows on tropical sandy soils

Organic and microbial status of soils (0-10 cm) under natural and improved fallows were studied in a Lixisol in two different field sites in Senegal (Sonkorong et Saré Yorobana) (Ndour et al., 1999; Ndour et al., 2001). At Sonkorong, soil organic matter and total microbial biomass were significantly higher in natural protected fallows than in non-protected ones and cultivated soils. No significant differences were recorded for non-protected situation, and cultivated soils. For managed situations, the duration of the fallow did not modify organic and microbial content of soils. Enzymes activities (β -glucosidase, amylase, chitinase, xylanase) were investigated in these situations. Principal component analyses revealed a relationship between enzyme activities and the age (4, 11, and 21 year-old) and the management of fallows (fenced versus grazed), the vegetation (natural, *Acacia holocерicea*, *Andropogon gayanus*). β -glucosidase and amylase were significantly higher in the oldest natural fallows. The highest xylanase activity was recorded for the *Andropogon gayanus* improved fallows. This fallow showed also the highest chitinase, similar to that of the 21 year-old natural fenced fallow. Amongst the different management of the fallows, the introduction of *Acacia holocерicea* depleted all the tested activities. In contrast comparisons between young and old fallows and crop plots at Saré Yorobana, did not show any significant differences. Coarser soil texture and higher frequency of land fires might explain these results.

Recent investigations on the impact fallow management on the diversity of the microbial community and the consequences of these modifications on soil organic decomposition function were carried out in a Lixisol (Senegal) (Sall et al., in press). Soil samples (0-10cm) taken from a 21 year fallow and a plot that had been cultivated for 4 years after lying fallow for 17 years were incubated with or without the addition of *Faidherbia albida* litter under laboratory conditions (28°C, 100 % WHC) for 240 hours. Microbial diversity was assessed by molecular techniques (Denaturing Gel Gradient Electrophoresis) and in situ catabolic potential (ISCP) (Degens et al., 2000). In the non-amended soil, the activity of microorganisms was greater in the fallow soil, which had a greater microbial diversity than that in the cultivated soil. However, other soil properties (carbon and organic nitrogen content, total microbial biomass) may also explain this result. For the amended soil, only the first 8 hours of incubation showed a difference between the fallow and cultivated soil. During this period, the CO₂ respiration in the fallow soil was higher than that recorded in the cultivated soil. This difference should be compared with the catabolic microbial diversity, which was higher in the fallow soil than in the cultivated soil. After this initial phase, the microbial community in the cultivated soil seemed to acquire similar functions to those in the fallow soil. These results show that the changes made to the microbial community by cultivation of a fallow over 4 years are not irreversible. The microbial community of this sandy soil very quickly recovers the same catabolic functions as those of the community in the fallow soil.

3.2.b. Effects of nematodes on microbial communities in tropical sandy soils

Nematodes can strongly affect microbial communities. In a microcosm experiment on a sandy soil (9,1%) from Senegal, the presence of bacterial feeding nematodes (*Zeldia punctata* or *Acrobeloides nanus* or *Cephalobus pseudoparvus*) led to a mean increase (+12 %) in maize biomass compared to control soils and reduced concentrations of soil ammonium by the end of the experiment (50 days). Moreover bacterial feeding nematode activity led to a significant decrease in microbial biomass (-28 %) and density of cultivable bacteria (-55 %), however, nematodes stimulated bacterial activity (+18 %) (Djigal et al., 2004).

3.3. Spatial distribution of biotic components

The distribution of organisms throughout the soil is controlled by the concentration in their substrates (Gray and Williams, 1971), soil water regime (Griffin, 1981), and soil structure (Elliott and Coleman, 1988; Hattori, 1988). Therefore any factors that modify these properties are likely to change the abundance and the activity of soil organisms.

3.3.a. Impact of termite biogenic structures on microbial abundance and diversity

In sub-sahelian sandy soils, termites are the only macrofauna actors during the dry season which last more than 7 months per year. Their activity translates mainly into the production of biogenic structures of various nature, size and constitution: mounds, soil sheeting², galleries and nest chambers. These soil translations are ecologically significant: in Senegal, 675 to 950 kg.ha⁻¹ of soil are moved on the surface in the form of sheetings and galleries (Lepage, 1974). In Kenya, soil translation exceeds 1000 kg.ha⁻¹ (Kooyman & Onk, 1987). In the desert ecosystem of Chihuahua, about 2600 kg.ha⁻¹ are transformed annually into sheetings (Mackay & Whitford, 1988). These foraging structures, aside from their quantitative importance, present physicochemical, enzymatic and microbiological characteristics, which do not only differ from the control soil but also reflect the diversity of the organisms that produced them (Seugé et al., 1999; Fall et al., 2001; Sall et al., 2002; Mora et al., 2003). Thus, in this ecological context characterized by a relative stability of edaphic factors (temperature, humidity, soil structure), termites represent one of the main factor governing the activity and diversity of the microbial community.

An experiment realized in Senegal (soil with 10-13% clay) demonstrated that the impact of termites on soil properties depends on their biotic affiliation (soil-feeding vs fungus growing) (Fall et al., 2001; Sall et al., 2002) and the type of structure, i.e., soil sheeting or nest, produced (Ndiaye et al., 2004a, b). Soil sheeting produced by the two main fungus growing termite species in Senegal (*Macrotermes subhyalonus* and *Odontotermes nilensis*) are characterized by an increased in organic C and mineral N, resulting in an increased in soil respiration whereas the microbial biomass was unchanged (Ndiaye et al., 2004a) and the enzymatic activities were weaker than in soil (Brauman, 2002). Interestingly, these soil structures harbour a very different population of nematodes (Villeneuve and 2005, submitted) and fungi (Diouf et al., 2005), which demonstrates the role of termite as soil engineers. These properties did not depend on the quality of the organic substrate recover by the termite sheeting. Interestingly, these biogenic structures could be considered as a phenotypic characteristic of the species, as a multivariate analysis of the physico-chemical, biochemical

² Sheetings are foraging structures which are built on the soil surface to protect termites from dessication and predators

and microbiological of biogenic structures allows the separation of structures produced by different species of termites and earthworms (Seuge, PhD Thesis).

As underlined before, the termite nest of the soil-feeding termite has very different characteristics. Nests of *Cubitermes niokoloensis* with 5 times more C, 7 to 15 more N and 4 times more carbohydrates (Sall et al., 2002) could be seen as hot spots of organic matter and nutrients compared to the poor surrounding savannah soil. Moreover, the microbial community of these nests seems less diverse and heavily dominated by actinomycetes (Fall et al., 2004, Fall et al. submitted). Regarding N dynamics, the nests of soil-feeding termites present a decrease in potential denitrification and an inhibition of potential nitrification with the surrounding soil (Ndiaye et al., 2004). We could underline that the low or absence of the nitrification process seems a general feature of termite structures (sheeting and nest), showing a deep impact of termite on the global nitrogen cycle. Such modifications lead to important increases in NH_4 and NO_3 contents in biogenic structures (100 times more mineral N in nests of *C. niokoloensis* than in the soil). The absence of nitrification in termite nests despite high nitrate contents remains not completely understood. Brauman et al. (2002, 2003) hypothesised a termite or actinomycete origin (production of bactericide) or an inhibition by phenolic compounds presents in the nest.

In conclusion, termite mounds like earthworm constitute, in the context of the sandy tropical soil characterized by an intense mineralization rate, site of SOM preservations. The results reinforce the view of biogenic structures as earthworms cast and termite's nest as true soil functional compartments like the rhizosphere.

3.3.b. Impact of soil structure

Soil is composed of an assemblage of solid particles and voids and represents the most complex habitat for organisms. Many authors have examined the effects of soil structure on the distribution and activities of the soil biota, including work on the distribution of soil microorganisms in particle-size fractions (Elliott, 1986; Gupta and Germida, 1988; Hattori, 1988; Kabir et al., 1994) and soil porosity (Killham et al., 1993).). Much of the difficulty in studying the relationships between soil structure and soil microbial distribution and activity is based on our lack of knowledge of microorganisms in undisturbed soil habitats. Therefore a gentle physical soil fractionation method based on a slaking procedure was developed and adapted for sandy soils (Chotte et al., 1993, 2002). This method has been used to describe the distribution of nematodes and microorganisms as part of a broader programme³ dealing with the impact of fallow shortening on soil fertility and biofunctioning.

* Distribution of the nematode community within pores versus aggregates

Very few studies deal with the location in soil and activity of free living and plant parasitic nematodes. In the soil (14% clay) of Thyssé-Kaymor (Senegal), the repartition of nematodes in different soil fractions (aggregates > 200 μm), inter-aggregates pores, fresh organic matter) vary according to their trophic behaviour (Figure 11) (Villenave, unpublished data).

Bacterial-feeding nematodes were essentially localized in inter-aggregate pores (> 50 %) and an important proportion of these nematodes was localized in fresh organic matter (24 %). A relatively similar distribution was observed for fungal-feeding nematodes. The other trophic groups presented slightly different distributions: plant-feeders had more than 50% of their total number in aggregates > 200 μm . Predators were essentially localized in inter-aggregate pores. The density of bacterial-feeding nematodes was 17 times higher in the outer part of

³ “Reduction of the Fallow Length, Biodiversity and Sustainable Development in Central and West Africa” (TS3-CT93-0220, DG12 HSMU) (Floret, 1998)

soil aggregates (e.g. in inter-aggregate pores and in fresh organic matter per g dry soil) than in the inner part.

In a sandy soil (17% clay) nematode activity (at a density of about 10 bacterivorous Cephalobidae per gram of dry soil during 21 days) led to modifications of the structure of the microbial community of the outer part of the soil (macroporosity) whereas changes were not significant at the scale of the total soil. Nematodes mainly and directly affected bacteria present in their influence area. In a clayey soil, the proportion of bacteria physically protected from nematodes is higher than in a sandy soil; so the influence of these organisms on the whole microbial community might be lower than in sandy soil.

* Distribution of microbial community within soil aggregates

The distribution of the microbial community within soil aggregates has been investigated in different fallow situations in order to test the impact i) of soil structure on microbial abundance and diversity, and ii) of fallow management. These studies have been carried out in a Lixisol (Senegal) (Chotte & Jocteur-Monrozier, 1999; Chotte et al., 2002). These investigations indicated that long-term fallow (19 y) under *Pennisetum* was found to stimulate aggregation, while all clay particles were easily dispersed from the 3 y fallow soil. Hot spots of potential N₂ fixation (Acetylene Reduction Activity, ARA) were observed in coarse soil fractions (> 50 µm), suggesting that these microhabitats were favourable to active N₂ fixers. In contrast, more than 70 % of the N₂ fixing microorganisms and 90 % of the recovered *Azospirillum* were isolated from the dispersible clay fraction (0-2 µm). The reduction of the fallow period was responsible for the decrease of the amount of nitrogen potentially fixed by free-living bacteria. This was not due to the diminution of their abundance but to fact that environmental conditions favourable to their activity are not at their best in young fallow soil (lack of macro aggregates > 2000 µm). Diversity of *Azospirillum* species was assessed by hybridization with specific genetic probes on colonies within each fraction. This approach revealed the abundance of *A. irakense* in the 3y fallow soil fractions only and a selective effect of fallow on *A. brasilense* / *A. amazonense* genomic species in the 19y fallow soil. Similar works compared the distribution of cellulolytic bacteria. These bacteria, mostly represented by non-filamentous cells, were mainly located within the organic residues (24 % of the total number) and the silt-size aggregates (2-50 µm) (58 %).

These studies clearly reveal that the changes of microbial communities as a result of modifications of land uses would have remain hidden if the investigation had been restricted to the non-fractionated soil. Current studies indicate that land management could have a deep impact of the functional diversity (denitrifier community) depending on the location in the different aggregate size fractions (Assigbetsé, personal com.). Further studies are needed to measure the consequence of the modifications in term of N₂O fluxes, and the processes responsible for them.

3.4. Nitrogen mineralization in tropical sandy soils

In sandy soils, the evolution of mineral N during wet season can be divided into two main phases. The first phase is characterised by a significant net mineralization called nitrogen flush (on average 58 kg.ha⁻¹ on 1 m in Centre of Senegal); during this period (about 20 days) the net nitrification is also significant and it favours N losses by leaching originally largely of the acidification⁴. The second phase is characterised by a net mineralization and a very low to non-existent nitrifying activity (Blondel, 1971a, b, c). During this phase, the plant modifies the equilibrium by increasing mineralization when the mineral N contents of soil are low and

⁴ Acidification results from nutrients exportation (Ca and Mg uptake by crops) and leaching (Ca and Mg leached and le "pilot" anions are nitrate and to a lesser degree chloride) (Pieri, 1992)

promoting immobilization when these contents are high (Blondel, 1971d; Reydellet et al., 1997). The microbial biomass (BM-C) expressed as a percent of total soil organic C was higher than in temperate soil. The BM-C increased during rainy season. This might be a key factor in nitrogen flush at onset of rainy season in dry tropical areas, which is essential for installation of crop (Niane-Badiane et al., 1999).

Like for temperate agro-systems, plant N nutrition relies on soil organic stock, since most of N taken up by plants derives from N organic stock, even in fertilized plots (Niane-Badiane et al., 1999). Therefore, several studies have been targeted toward the manipulation of inorganic N fluxes through the management of organic resources at the field scale. The dynamics and the extent to which organic components decompose depend on soil characteristics and substrate quality. Quality of organic residues can be assessed by C to N ratio (Giller & Cadisch 1997), N content (Vigil & Kissel 1991), soluble-C content (Reinersten et al. 1984), lignin content (Berg 1986), lignin-to-N (Vigil & Kissel 1991), polyphenol-to-N (Palm and Sanchez 1991), and (polyphenol plus lignin)-to-N (Constantinides & Fownes 1994) ratios. Several studies have been carried out in semi arid zones of West Africa (Senegal, Burkina Faso) to determine the impact of various litters on mineralization processes. Soil nitrogen mineralization patterns were investigated under field conditions in the presence of five leaf litters of different qualities, *Faidherbia albida* A. Chev., *Azadirachta indica* A. Juss., *Andropogon gayanus* Kunth., *Casuarina equisetifolia* forsk., and *Eragrostis tremula* Steud (Diallo et al., 2005). Any relationship could be drawn between litter quality (N content, cellulose, hemicellulose, lignin) and N mineralization during a mid-term field experimentation (12 months). In the presence of these litters, the concentration of inorganic N was higher than that in the control plot (without litter amendment). When comparing the inorganic N pattern in *C. equisetifolia* and *F. albida* amended soils, a higher inorganic N was measured in soil amended with *C. equisetifolia* despite the fact that *F. albida* had the lowest C to N ratio (21.4). The processes were then investigated during a 60 days laboratory incubation to compare the effect of *Andropogon gayanus*, *Casuarina equisetifolia*, *Faidherbia albida* on C and N dynamics in the presence or not of a source of inorganic N (Sall et al., 2003). The results indicated that during the first stage of incubation, CO₂-C evolved was significantly correlated with the soluble C content of the litter. The pattern of soil inorganic N varied according to the litter quality. However, a similar immobilisation was obtained in soil amended with *Andropogon gayanus* and *Casuarina equisetifolia*, despite the fact that these materials have very different C:N ratios (51, and 35, respectively). The abundance of polyphenols in the *Casuarina equisetifolia* litter may explain this result. In fact, several studies have mentioned the negative effect of polyphenols on N mineralization processes (Palm and Sanchez 1991). The addition of inorganic N modified the patterns of CO₂-C respiration and net N immobilization. The magnitude of these modifications varied according to the litter quality.

These studies indicated that the management of organic resources could be view as a means to modify N fluxes (and CO₂) in sandy soils. However the definition of an accurate indicator to predict the decomposition of organic residues can not be based on a single parameter. It should take into account several litter characteristics (e.g. ratio of soluble C to phenol content, etc). Moreover, the impact of the characteristics of the organic constituents on the gross CO₂-C and inorganic N fluxes and on the diversity and function of soil microorganisms must be addressed.

Conclusion

Productivity of ecosystems characterized by sandy soils is generally low because of erratic rainfall pattern and soil texture; this results in a poor nutrient availability and unstable structure (Pieri, 1992). Studies on soil fertility, SOM dynamics and soil biofunctioning in sandy soils of West Africa, as presented above, emphasized the importance of coarse plant debris and soil biota in controlling most of physical, chemical and biological soil properties. The essential of the beneficial effect of organic management of soil fertility by fallows and manures is based on mineralization processes rather than on humification ones; this means that SOM content is a questionable indicator of the fertility of sandy soils and of the sustainability of agrosystems (Feller, 1995b). The response of biota to sandy soil constraints is a control of soil stability and porosity (perennial rooting systems, fauna, microorganisms), a conservative management of inputs protected either in root biomass or in stable organic compounds (Menaut et al., 1985; Izac & Swift, 1994; Chotte et al., 1995; Giller et al., 1997). In sandy soils, biological mechanisms play a crucial role on processes driving plant nutrition. This has three implications:

- A particular attention should be given to SOM and biological processes. Studies confirm that in sandy soils, the coarse organic fraction ($> 50 \mu\text{m}$) is the main relevant one (Feller et al., 2001).
- Soil biological components should be characterized and root component should be included in SOM total.
- Sandy soils should be seen as living and dynamic milieux.

As a consequence, SOC losses linked to biological activities (fauna and microorganisms) is the price to pay to maintain suitable soil organization and functioning (Perry et al., 1989; Manlay et al., 2002c).

As a consequence, cropping alternatives should take into account the traditional functions of fallows, i.e., biomass production and increase in biological diversity and activity (Feller et al., 1990; Pate, 1997; Manlay et al., 2000).

From a C sequestration point of view, although sandy soils have a poor potential of C storage, it seems possible to double C stocks in cropping systems through the integration of a tree component in culture and to use mineral fertilizers in order to stabilize SOM (Woomer et al., 1998). It seems also necessary to provide more important incomes to populations through intensified agrosystems; this would limit the need for other soils whose C storage potential is more important (more clayey Soils, more humid zones). In West African savannas, as long term fallows are hard to achieve and as crop residues are often exported (fuel, building materials, cattle food), solutions could be rotations of crops with strong rooting systems, improved short-term fallows or agroforestry systems. Other practices such as hay-making, cover crops, slash-and-mulch, compost, no-till or integration of livestock could also be successful to increase or maintain C stocks and to make systems sustainable (Vierich & Stoop, 1990; Manlay et al., 2002c). Also, to increase SOC stocks, one can either increase C inputs or decrease SOM biodegradation processes. The first method consists in providing prehumified OM (composted manures), or to manage the quantity and quality of residues. The second method is to protect the soil with cover plants. The quality of SOM is an essential determinant of C storage (Feller & Ganry, 1982).

To limit fertility deterioration by acidification and allelopathy, appropriate cultural practices must be applied: varieties and agricultural profile (dense and deeply penetrating root system must be improved), crop rotation (monoculture is a poor practice; it neither improves the SOM balance nor sustains crop yield) and sowing date (early sowing date in semi-arid zone), and organic material applied (manure or compost, root residues possess the desirable quality).

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Figure caption

Figure 1: Relationships between soil organic content and clay + fine silt content in tropical 1:1 (low activity clay LAC) and 2:1 (high activity clay HAC) soils (adapted from Feller & Beare, 1997).

Figure 2: Effect of land use and soil texture on SOC content in different tropical soils (Feller, unpub. data)

Figure 3: Effect of installation of crops after deforestation on SOC contents in soil and in three organic compartments. Variation in C content (ΔC) between native vegetation and crops (adapted from Feller, 1995a).

Figure 4: Effect of installation of fallows after cultivation on SOC contents in soil and in three organic compartments. Variation in C content (ΔC) between crops and fallows (adapted from Feller, 1995a).

Figure 5: Variation in C content (ΔC) in two soil organic (fine and coarse) fractions as a function of soil texture in improved systems as compared with traditional systems (unpublished, adapted from Feller et al., 2002).

Figure 6: Variations in C content in two soil organic fractions between control and treatments with organic amendments in three experiments (see text for details) (unpublished, adapted from Feller et al., 2002).

Figure 7: Variation in C content (ΔC) in two organic fractions in systems with cover crops, as compared with traditional systems without cover crops. Effect of *Mucuna pruriens* in sandy soils in Benin, and effect of no-tillage with cover crops in clayey soils in Brazil (two situations PD1 and PD2) (Azontonde et al., 1999; Bayer et al., 2001).

Figure 8: Effect of the age of fallows on C, Ca and Mg contents in South Senegal (Manlay et al., 2000).

Figure 9: Variation in C content (ΔC) in two soil organic fractions in fallows, as compared with continuous crops, in soils with different clay contents (Feller, 1995a).

Figure 10: Variation in C content (ΔC) in two organic fractions in soils (clay content from 8 to 22%) with inoculated earthworms as compared with soils without earthworms. Data come from different laboratory (incubation) and field (cultivation) experiments. Duration of the experiments is indicated (adapted by Feller, 2002, from Villenave et al., 1999).

Figure 11: Distribution of the different feeding groups of soil nematodes between soil fractions (in % of the total nematode number in the soil sample)

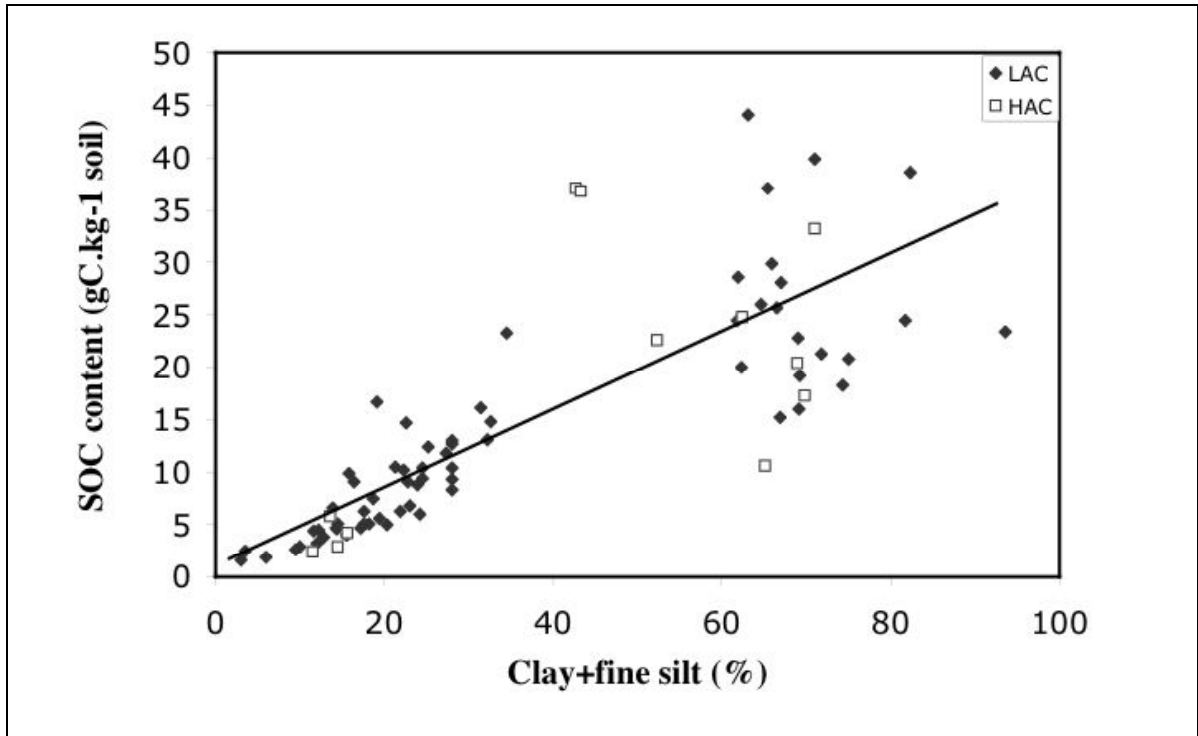


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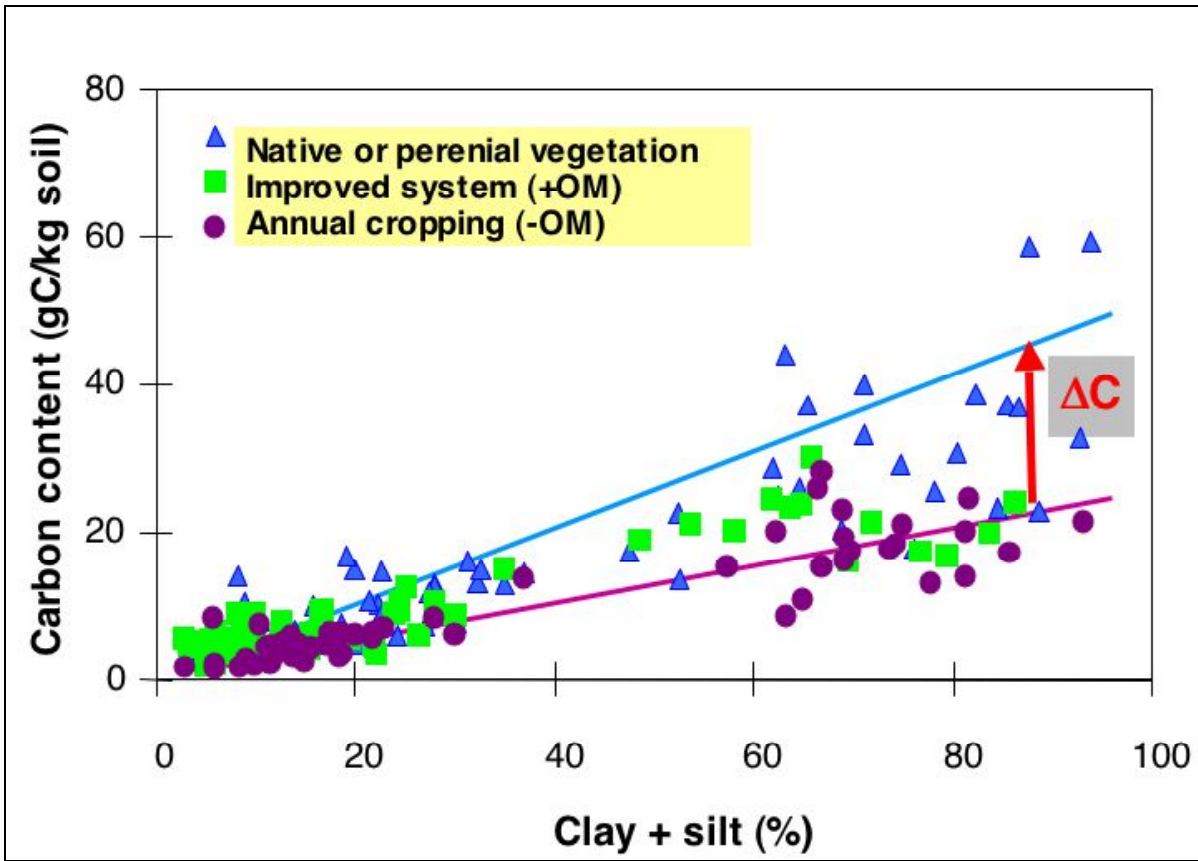


Figure 2: Effect of land use and soil texture on SOC content in different tropical soils (Feller, unpub. data).

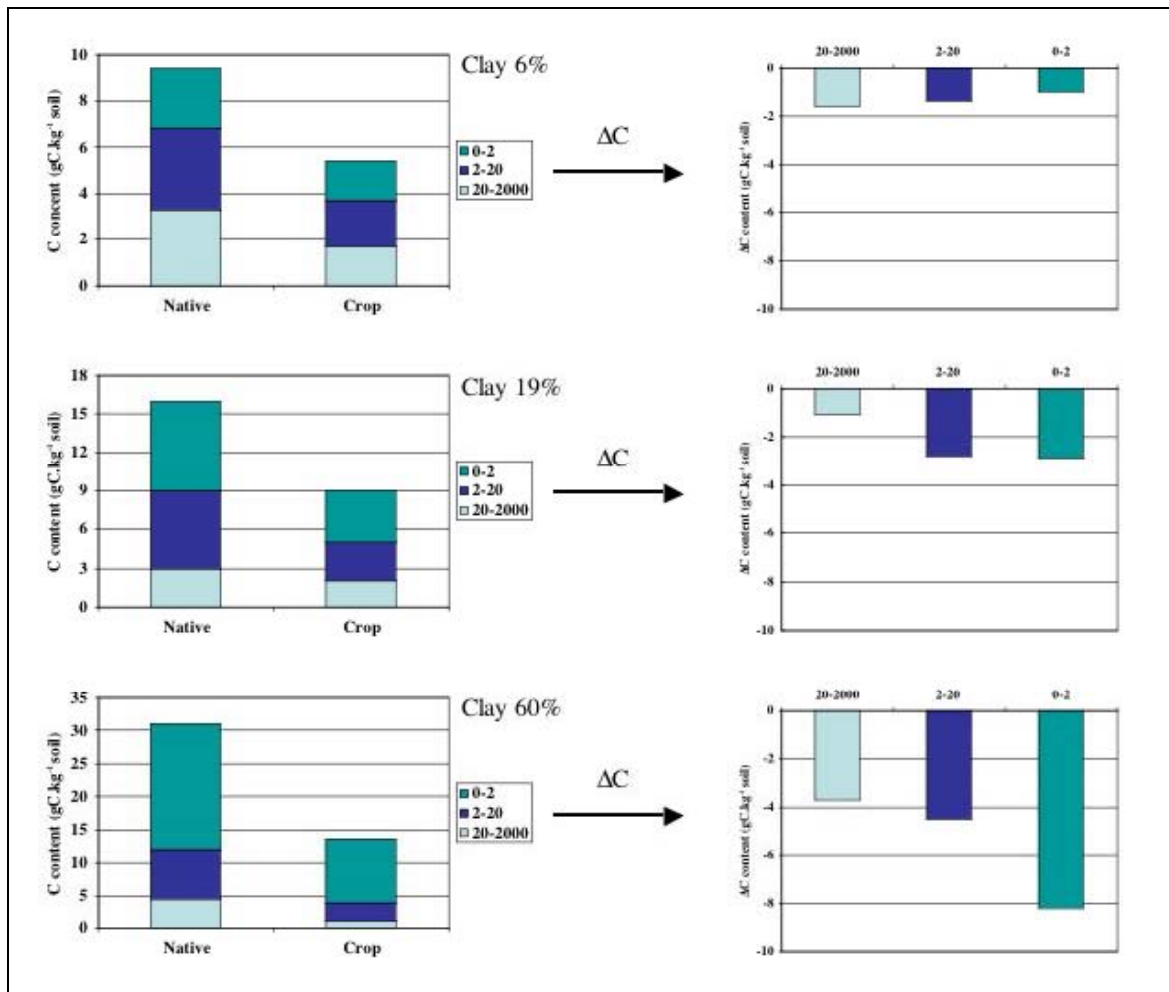


Figure 3: Effect of installation of crops after deforestation on SOC contents in soil and in three organic compartments. Variation in C content (ΔC) between native vegetation and crops (adapted from Feller, 1995a).

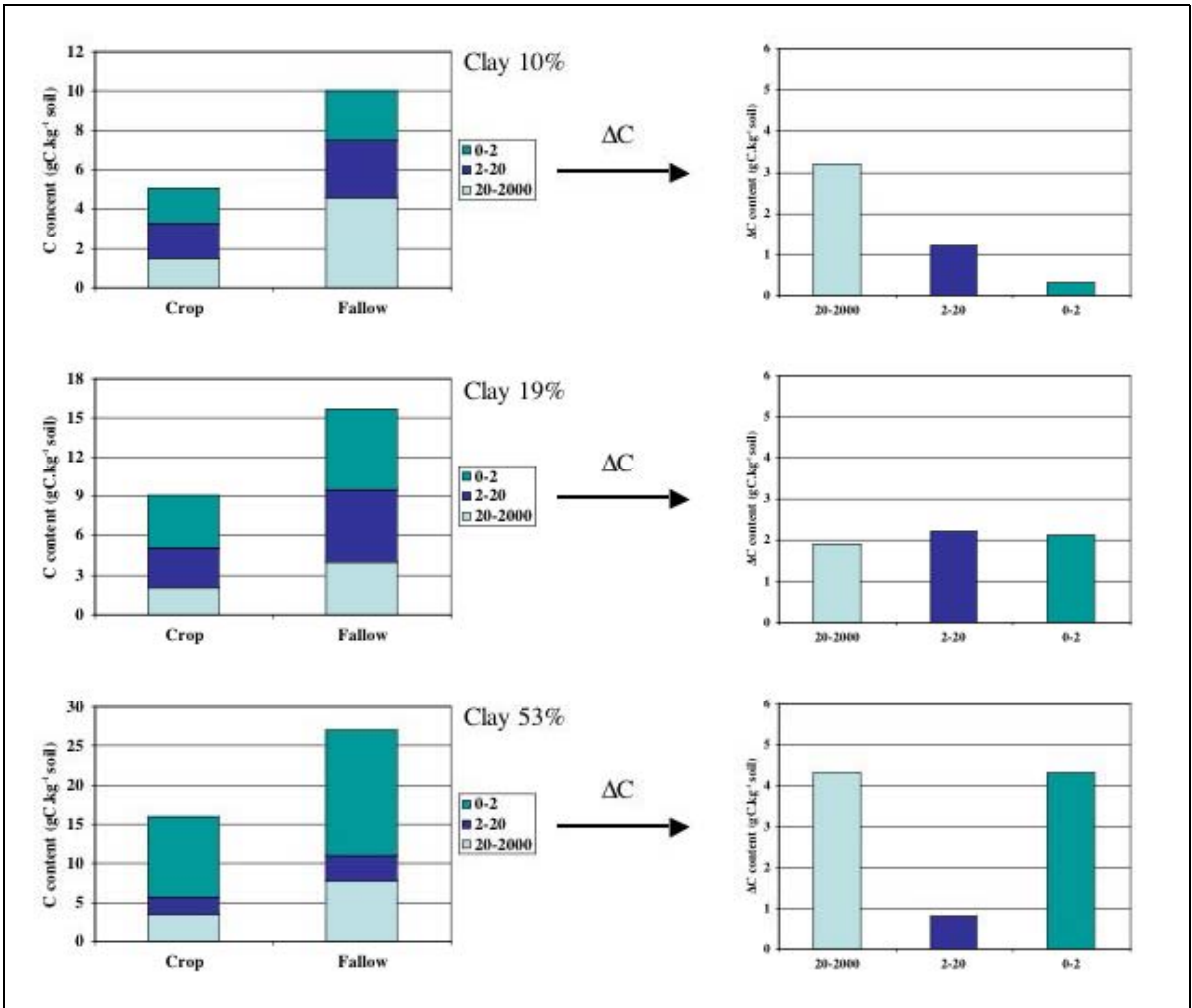


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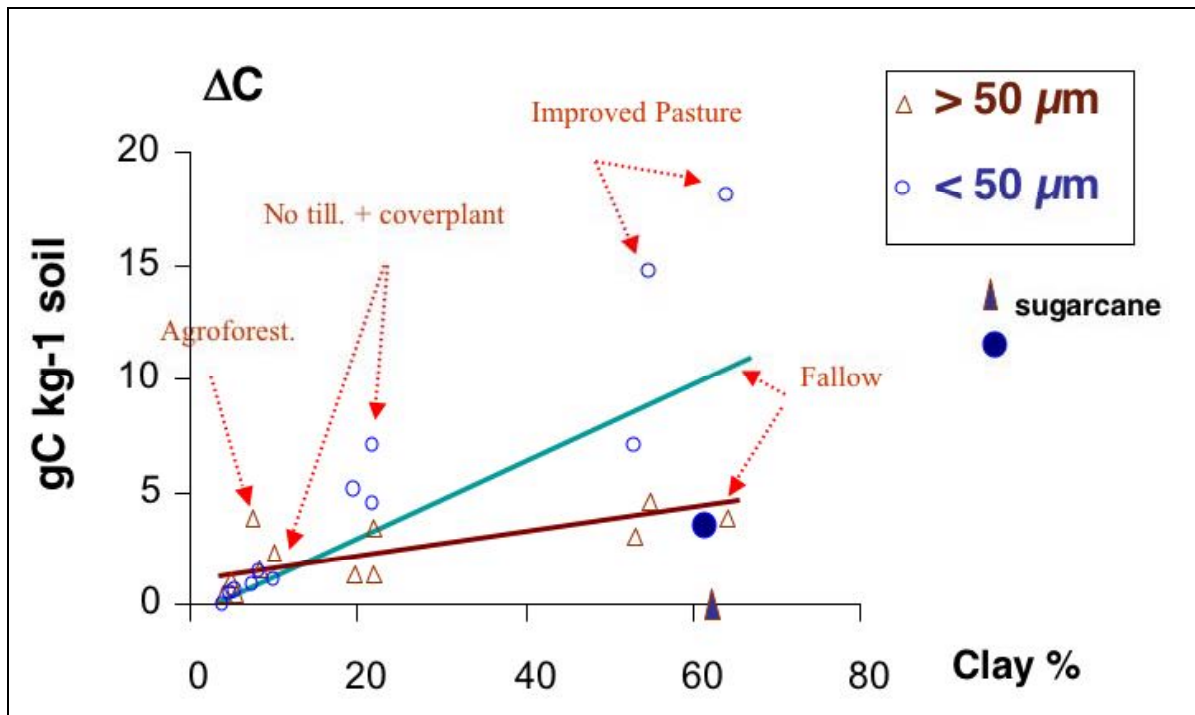


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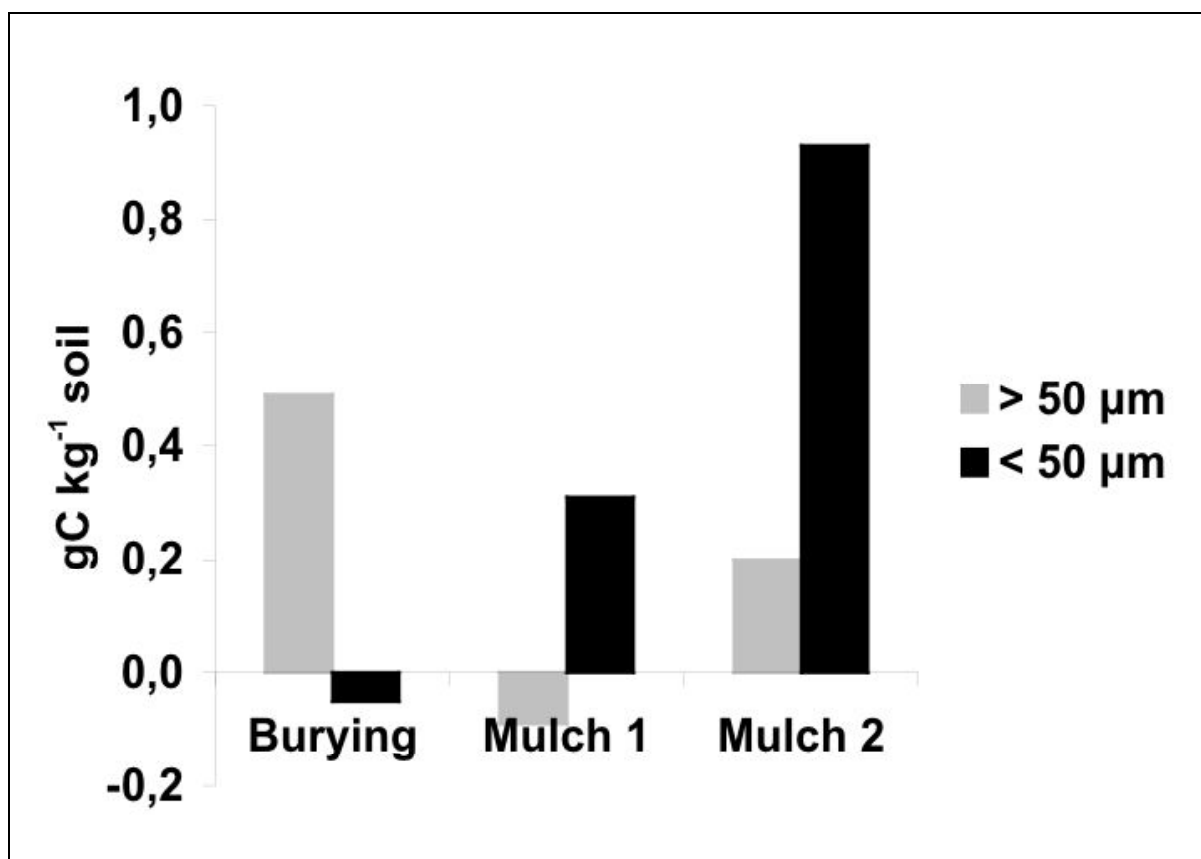


Figure 6: Variations in C content in two soil organic fractions between control and treatments with organic amendments in three experiments (see text for details) (unpublished, adapted from Feller et al., 2002).

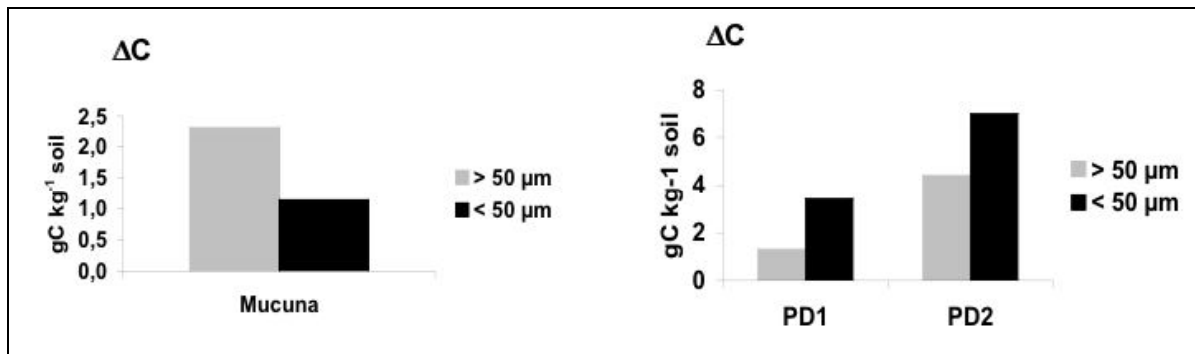


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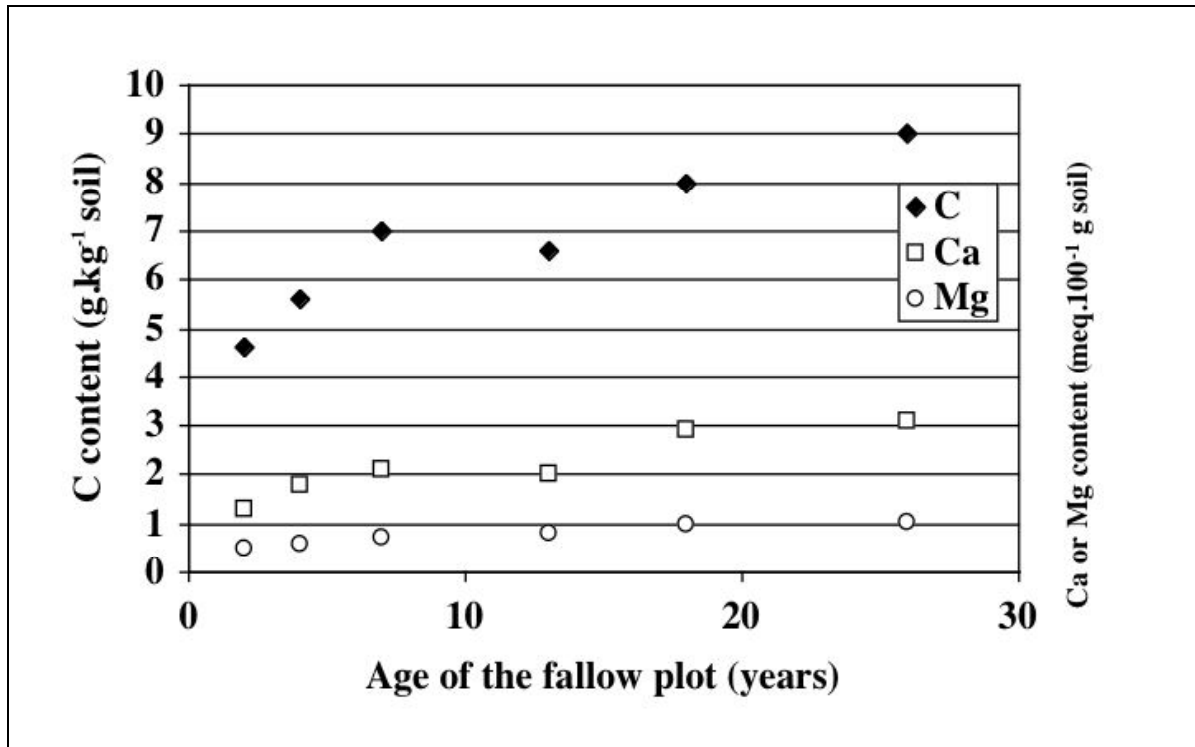


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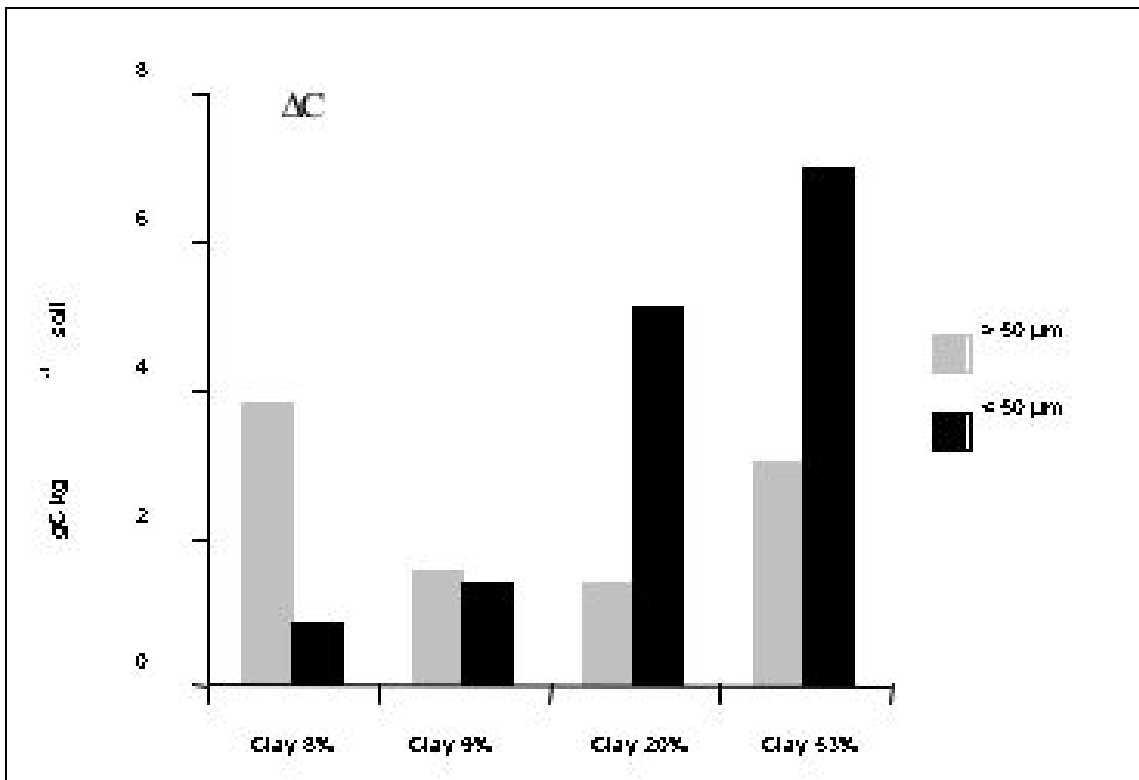


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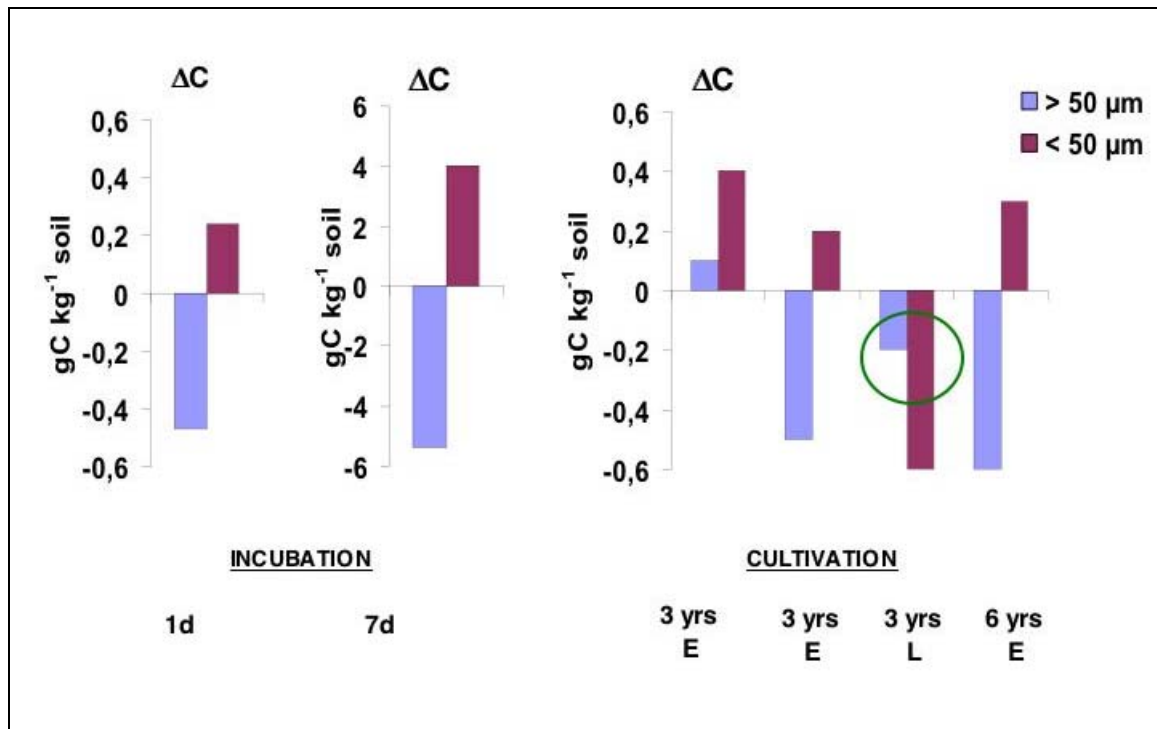


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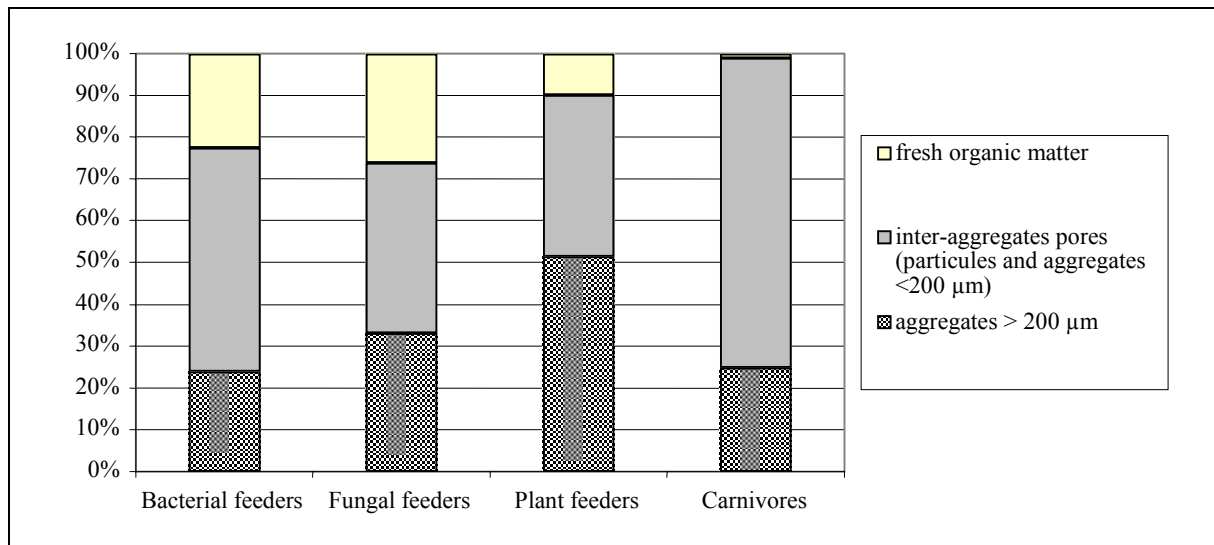


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