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ORIGINAL PAPER

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Natural nitrogen-15 abundance and carbohydrate content and composition of organic matter particle-size fractions from a sandy soil

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Abstract Sandy soil samples collected from under a woody/grass savanna in the Lamto experimental area (6° 13N, 5°20W; Côte d'Ivoire, West Africa), were fractionated according to particle size with the aim of measuring the natural abundance of ^{15}N and determining the contents and composition of hydrolysable carbohydrates of soil organo-mineral particles for a better understanding of the contribution of each individual fraction to the soil function. The contributions of the fractions <20 μm to the total pool of organic matter were 77% for C and 84% for N. Larger amounts of carbohydrates were found in the clay and silt fractions (3,784–6,043 μg g^{-1} soil). The carbohydrate composition indicated that microbe-derived carbohydrates [e.g. galactose (Gal) and mannose (Man)] accumulated preferentially in the fine fractions while plant-derived sugars [e.g. arabinose (Ara) and xylose (Xyl)] were dominant in coarse fractions. A negative relationship was observed between C:N ratio and ^{15}N natural abundance on the one hand, and on the other hand between C:N and (Gal+Man):(Ara+Xyl), Man:(Ara+Xyl) and Man:Xyl ratios, clearly indicating that the chemistry of the organic materials of the particle-size fractions reflects a change from soil chemistry dominated by plant materials to that dominated by microbial biomass and metabolites. The contribution of a given fraction to soil microbial activity is controlled by the quality or quantity of associated soil organic matter, its microbial biomass and also by the accumulation of microbial-derived carbohydrates which can be resynthesized or recycled.

Keywords Tropical soils · Natural abundance of nitrogen-15 · Soil physical fractionation · Soil carbohydrates · Soil organic matter

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Introduction

A conceptual view of the biochemical transformation of organic matter in soil concerns the amount of organic matter going through different stages of degradation, from coarse dead plant materials to evolved humified organic matter tens or hundreds of years old. The newly incorporated plant residues are generally associated to coarse particles, while the old organic matter is associated to fine particles (Oades and Ladd 1977; Feller et al. 1991a). Soil organic matter (SOM) can thus be considered as a continuum of compounds more or less accessible to microorganisms, more or less abundant, each contributing to nutrient production. From a theoretical point of view, it should be possible to predict the potential of microbial activity in a soil from a good knowledge of the chemical composition of the organic matter. The chemical quality of SOM can be assessed by the measurement of the C mineralisation ratio (Dommergues 1960), the measurement of the natural abundance of ^{15}N in soil as an indicator of the stage of SOM humification (Mariotti et al. 1980), the identification and measurement of molecules that are known to influence the rate of microbial activity, such as polysaccharides (Martin 1946; Cheshire 1979; Shen and Bartha 1997).

The fractionation of soil into size classes of organo-mineral particles is a useful tool with which to study SOM

dynamics at the microorganism scale because it integrates both chemical and spatial determinants of microbial distribution and activity (Christensen 1992; Ladd et al. 1996). The distributions of organic matter according to particle size and the contribution of each particle size to soil microbial activities of C and N mineralisation have been studied in the Lamto savanna ecosystem (Nacro et al. 1996). These authors showed that 68% of the potential microbial respiration was located on the organo-mineral particles <20 µm, with the C mineralisation rate >3 times lower than that of coarse particles. The current work was carried out on the same samples analysed by Nacro et al. (1996) with the aim of measuring the natural abundance of ^{15}N and determining the contents and composition of hydrolysable carbohydrates of soil organo-mineral particles for a better understanding of the real contribution of each individual fraction to the soil function. This may help to highlight the mechanisms which control the accumulation and mineralisation of SOM in the Lamto savanna ecosystem.

Materials and methods

Site

Soil samples were collected from under a woody/grass savanna in the Lamto experimental area (6°13N, 5°20W; Côte d'Ivoire, West Africa). The mean annual temperature is 27°C and rainfall averages 1,200 mm year^{-1}, with a dry season from December to February and a wet season from March to July. The most common parent material is granite and granite-derived sands, which have produced Acrisol (FAO-UNESCO 1989) with a superficial gravelly horizon. Soils are sandy or very sandy and organic C does not exceed 1.2%. P, K, and Ca contents are low; pH ranges from 5 to 7 (Nacro et al. 1996). The clay content is low (8%), with kaolinite as the prominent clay mineral, and the total amount of exchangeable bases is below 4 cmol kg^{-1}. In the most common savanna environment where the study took place, the grass layer is dominated by *Hyparrhenia diplandra* and *H. smithiana* and the tree layer by *Borassus aethiopum*, *Piliostigma thonningii*, *Bridelia ferruginea*, *Cussonia barteri* and *Crossopteryx febrifuga*. The total primary production (grasses+trees) amounts to 26–36 Mg ha^{-1} year^{-1} and occurs mainly in the roots of perennial grasses (Menaut and César 1979). Bush fires occur yearly in the dry season and burn ca. 80% of the standing grass biomass.

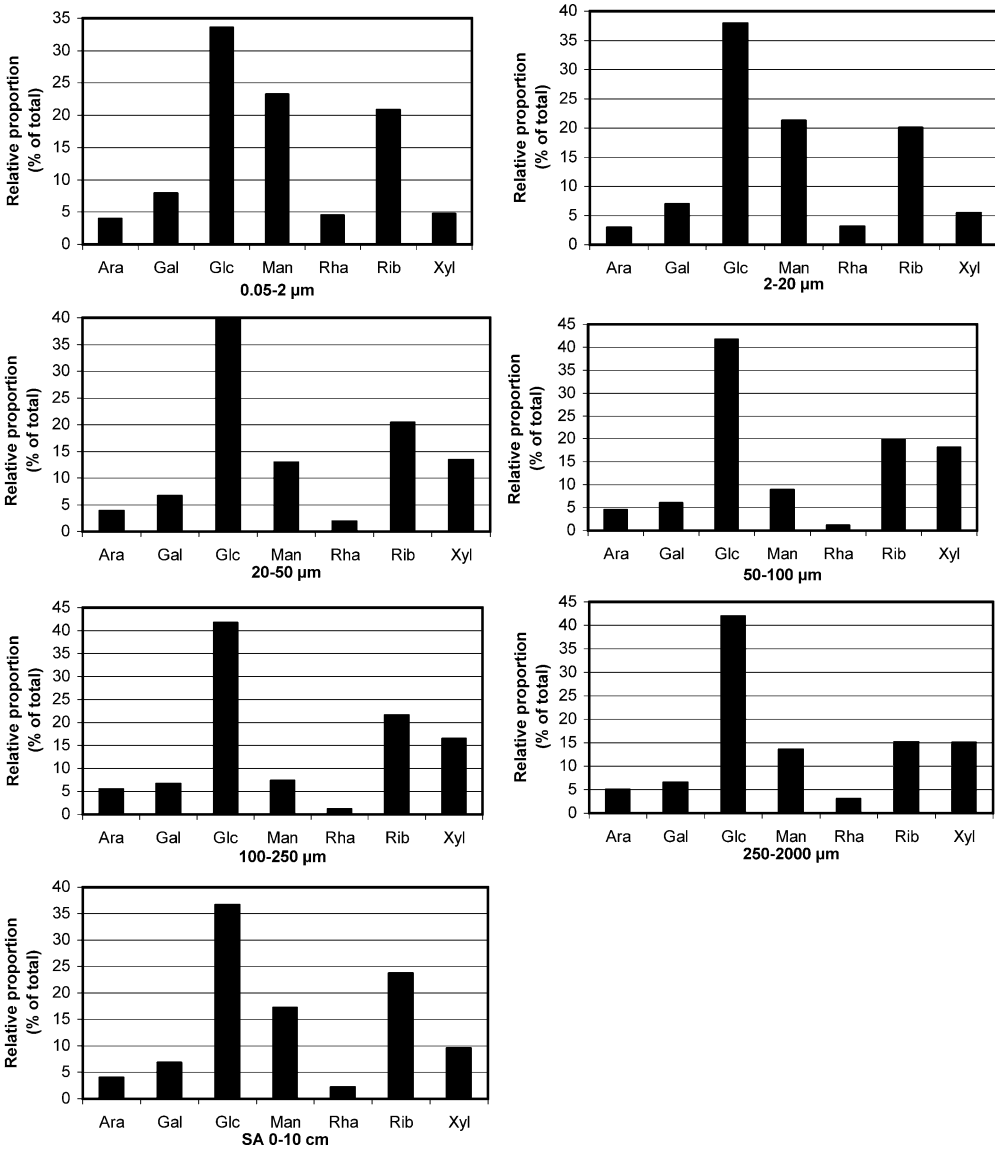

Fig. 1 Monosaccharide distribution of the shrubby savanna soil and its particle-size fractions. *Ara* Arabinose, *Gal* galactose, *Glc* glucose, *Man* mannose, *Rha* rhamnose, *Rib* ribose, *Xyl* xylose

Table 1 Apparent texture (physical fractionation) of the whole soil, organic C and N contents of fractions, C:N ratios of shrubby savanna and natural abundance of ^{15}N of fractions and whole soil, and distribution of C and N pools among fractions. SEs *in parentheses*. *SS* Whole soil from shrubby savanna

	Physical fractionation (g 100 g^{-1} soil, n=3)	C (μg g^{-1} fraction)	N (μg g^{-1} fraction)	$\delta^{15}N$ (‰)	C:N	C (μg g^{-1} soil)	N (μg g^{-1} soil)
0.05–2 μm	8.49 (0.86)	34,850 (212)	3,430 (14)	8.9 (0.4)	10	2,297 (14)	226 (1)
2–20 μm	6.37 (1.13)	39,550 (353)	2,460 (42)	6.9 (0.2)	16	3,729 (33)	232 (4)
20–50 μm	4.09 (0.14)	11,750 (212)	635 (21)	6.0 (0.2)	18	503 (9)	27 (1)
50–100 μm	9.14 (1.12)	3,800 (0)	220 (14)	5.5 (0.3)	17	326 (0)	19 (1)
100–250 μm	22.54 (2.11)	1,550 (71)	60 (0)	4.1 (0.2)	26	373 (17)	14 (0)
250–2,000 μm	49.27 (2.70)	1,150 (71)	55 (7)	2.1 (0.1)	21	555 (34)	26 (3)
Yield	99.90	–	–	–	–	7,783	544
SS 0–10 cm	100	–		6.1 (0.1)	16	8,400	530

Soil sampling and texture measurement

Soil cores (8 cm diameter) were randomly collected between 0 and 10 cm depth in triplicate, between tussocks to avoid contamination by root litter organic matter. The samples were air dried and gently passed through a 2-mm-mesh sieve in order to disrupt macro-aggregates. The fraction >2,000 μm was discarded. Texture was measured according to Balesdent et al. (1991); after organic matter was destroyed by adding 200 ml of H_2O_2 to 20 g soil, the soil mixture was maintained at 20°C for 6 h and then 60°C for 16 h. Distilled water (300 ml) and 25 ml hexametaphosphate (40 g l^{-1}) were then added and the samples shaken for 16 h at 175 r.p.m. The aqueous suspension was sieved through 250-, 100- and 50-μm meshes. The 0–50 μm fraction was sonicated at 25 J ml^{-1} (Branson Sonifier 450) and passed through a 20-μm sieve in water. The 0–20 μm fraction was centrifuged (Sorvall RC 3B Plus, Du Pont De Nemours) to isolate a 2–20 μm fraction and a 0.05–2 μm fraction. Centrifugation speed and time were calculated according to Tanner and Jackson (1948) and Jackson (1956). The resulting six fractions were dried at 40°C; these fractions were: 250–2,000 μm (coarse sand), 100–250 μm (fine sand), 100–50 μm (very fine sand), 20–50 μm (coarse silt), 2–20 μm (fine silt), and 0.05–2 μm (clay).

Isolation of size fractions

The organo-mineral particles of the soil were separated into six size classes as above, but without using H_2O_2 and hexametaphosphate. Soils were dispersed by shaking with four 1-cm-diameter balls for 2 h, then for 14 h without balls (Feller et al. 1991b), and sonicated at low energy (25 J ml^{-1}). Only particles <50 μm were also sonicated to minimize the disruption of large organic particles (Balesdent et al. 1991). Most of the water used during fractionation and the 0–0.05 μm fraction were discarded. The fractions were dried at 40°C. The samples (soils and fractions) were kept separate, crushed with a mortar to a very fine powder for chemical analysis.

Chemical analysis

On each soil sample, organic C was determined by potassium dichromate oxidation and titration of excess dichromate with ammonium iron (II) sulphate (Anne 1945). Total N was measured by the Kjeldahl method with a Kjeltec Auto Analyser 1030 (Tecator) (Bonneau and Souchier 1979). The ^{15}N isotopic ratios of SOM were measured on an elemental analyser (CHN NA 1500, Carlo Erba) coupled (He flux) to a Fisons Optima isotope ratio mass spectrometer (Mariotti 1983). Results were expressed in relative $\delta^{15}N$ units: $\delta^{15}N‰=[(R_{sample}-R_{standard})/R_{standard}]\times1000$, where R was the isotopic ratio $^{15}N/^{14}N$. Atmospheric N_2 was used as the standard (Mariotti 1983). Repeated measurement of organic matter (internal reference) yielded a precision of 0.2‰.

Carbohydrate monomers released by acid hydrolysis were analysed by capillary gas chromatography (Larré-Larrouy and Feller 1997). Aliqots (2 g) were hydrolysed with cold 12 M H_2SO_4 for 16 h, and refluxed at 100°C with 0.5 M H_2SO_4 for 5 h. Hydrolysates were neutralised by $SrCO_3$, filtered, evaporated to dryness on a rotary evaporator and then dried under vacuum over P_2O_5. Gas chromatography was performed on a Delsi-Nermag DI 200 gas chromatograph equipped with a flame ionization detector and a capillary injection column, SP-2330 (15 m×0.25 mm internal diameter.×0.2 μm film) with He as carrier gas at 0.7 bar. Temperature was programmed from 170 to 230°C at a rate of 4°C min^{-1}. Chromatograms were performed with a Delsi Nermag Enica 31 integration system.

Results

Soil texture, quality of fractionation, C and N concentrations

The soil sampled was sandy with 49% coarse sand, 22% fine sand, 9% very fine sand, 4% coarse silt, 6% fine silt and only 8% clay in the 0–10 cm layer. Texture of the organo-mineral particles obtained without treatment with H_2O_2 was similar to that of particles obtained with H_2O_2 (P>0.05). The mean recovery of soil solids was 99% dry soil (Table 1). The C and N contents were, respectively, 8,400 and 530 μg g^{-1} dry soil. The mean recovery of organic C and total N in the six particle size fractions was, respectively, 93 and 103%. These are probably related to the experimental and analytical conditions, particularly the loss of soluble compounds for C (Christensen 1992) and susceptibility of organic compounds to Kjeldahl mineralisation for N, particularly in separate organo-mineral fractions (Tan and Troth 1981). Both C and N concentrations in fractions varied in the following order: clay>fine silt>coarse silt>very fine sand>fine sand>coarse sand (Table 1). The C:N ratios were lower in fine than in coarse fractions.

Table 2 Pentoses, hexoses and deoxyhexoses and total sugar concentrations (μg g^{-1} fraction or μg g^{-1} soil), relative contribution of sugar-C to organic C in each fraction, and contribution of sugar-C to whole soil organic C in each fraction

	Pentoses	Hexoses	Deoxyhexoses	Total	C (% fraction C)	C (% soil C)
SS (0–10 cm)[a]	699	1,137	41	1,877	–	7.5
0.05–2 μm	1,113	2,445	168	3,784	4.4	0.7
2–20 μm	1,710	3,988	188	6,043	6.1	0.6
20–50 μm	1,571	2,476	77	4,173	14.3	3.3
50–100 μm	794	1,056	20	1,870	19.8	2.3
100–250 μm	480	615	12	1,107	29.8	1.2
250–2,000 μm	139	245	12	396	14.4	0.3

[a]SS (μg g^{-1} fraction or μg g^{-1} soil)

^{15}N natural abundance in soil and size separates

The natural abundance of ^{15}N in the whole soil was 6.1‰ and in the fractions, it increased with decreasing particle size. The lowest ^{15}N natural abundance was measured in coarse (2.1‰) sand and the highest in clay (8.9‰) (Table 1).

Monosaccharide concentration in the particle-size fractions

All the fractions as whole soil were characterized by greater amounts of hexoses (55–66%) than pentoses (28–43%). Deoxyhexoses (1–4%) were always found in small quantities (Table 2). The largest concentration of carbohydrates was found in the fine (6,043 μg g^{-1} fraction) and coarse silt fractions (4,173 μg g^{-1} fraction), followed by clay fraction (3,784 μg g^{-1} fraction). The lowest concentration was found in the coarse sand-size particle (396 μg g^{-1} fractions). Carbohydrate-C, as a percentage of total fraction C, was lower in the clay and silt fractions (4–14%) than in sands (14–30%). The carbohydrate-C, as a percentage of total soil C, was higher in the coarse fractions (0.3–3.3%) than in the fine ones (0.6–0.7%) (Table 2). Glucose was the most abundant monosaccharide in all the fractions and represented between 34 and 49% of total monosaccharides ((Fig. 1, Table 3). The following most abundant sugars were mannose (Man) and ribose in the fine fractions (21–23% and 20–21%, respectively), and ribose (15–21%) or xylose (Xyl; 13–18%) in the coarse ones. Acid and basic sugars were found in minor quantities, only in silts. Fructose and fucose were under the detection limit in all the samples. The main pools of sugars were located in the silt (570 μg) and fine sand (266 μg) fractions and the lowest in the coarse silt (179 μg) and very fine sand (160 μg) fractions (Table 4).

Discussion

Total C and N distribution in size separates

The contribution of the fractions >20 μm to the total pool of organic matter was only 23% for C and 16% for N (Table 1), i.e. substantially less than generally observed in savanna sandy soils (30% for C and 25% for N; Feller et al. 1991c). This could be due to: (1) sample treatment, (2) local climatic conditions, or (3) a soil texture effect. It has been shown that substantial transfers of organic matter from coarse to fine fractions does not occur during the fractionation process if sonication is applied on particles finer than 50 μm (Balesdent et al. 1991). More likely, rate of decomposition of root litter and plant debris was high due to the long wet season with high temperatures and soil water leading to a low relative contribution of the >20 μm fractions to total SOM. This hypothesis is confirmed by the results of Martin et al. (1990) on the natural abundance of ^{13}C in whole soil and fractions in Lamto, showing a high turnover of coarse particle C compared with that of clay C. Lastly, Christensen (1992) showed that the C enrichment factor between whole soil and the clay fraction, i.e. the ratio % of C in clay fraction to %C in whole soil, decreases following a power function with increasing clay content. As clay content in our soil is particularly low (ca. 8%), a high enrichment factor was expected: it was 4 in our soil, i.e. much higher than the values quoted by Christensen (1992).

Table 3 Monosaccharide composition of the SS and particle-size fractions (μg g^{-1} fraction or μg g^{-1} soil). *Gal-N* Galactosamine, *Glc-N* glucosamine, *Gal-ac* galacturonic acid, *Glc-ac* glucuronic acid; for other abbreviations, see Fig. 1 and Table 1

	Xyl	Rib	Ara	Rha	Man	Gal	Glc	Gal-N	Glc-N	Gal-ac	Glc-ac
SS (0–10 cm)[a]	179	445	75	41	322	128	687	0	0	0	0
0.05–2 μm	177	788	148	168	876	299	1,270	57	0	0	0
2–20 μm	327	1,208	176	188	1,282	418	2,288	0	69	61	26
20–50 μm	558	852	161	77	538	275	1,663	0	21	16	12
50–100 μm	338	371	84	20	166	111	779	0	0	0	0
100–250 μm	181	239	60	12	81	73	461	0	0	0	0
250–2,000 μm	59	60	19	12	54	26	166	0	0	0	0

[a]SS (μg g^{-1} fraction or μg g^{-1} soil)

Table 4 Distribution and nature of sugars in the soil and its particle size fractions (μg g^{-1} soil)

	0.05–2 μm	2–20 μm	20–50 μm	50–100 μm	100–250 μm	250–2,000 μm	Yield	SS (0–10 cm)
All sugars	249	570	179	160	266	191	1,616	1,877
Microbial sugars	197	437	87	54	86	88	950	–
Plant sugars	52	133	92	106	180	103	666	–

The C:N ratios of clay (10), fine silt (16) and coarse particles (21) were close to those (10, 16 and 19, respectively) reported for a large range of West African soils (Feller et al. 1991a). They decreased with particle size, indicating an increasing degree of humification from coarse to fine particles (Catroux and Schnitzer 1987; Feller et al. 1991b). The C:N ratio of clay particles was lower than that of whole soil while C:N ratios of silt and sand particles were higher as shown by Christensen (1992) for a wide range of soils. The difference between clay particles and whole soil C:N ratios generally does not exceed 1 or 2 units, especially in temperate soil. In Lamto, it reaches 5 units, likely due to intense microbial activities in the soil and then, rapid decomposition of SOM favoured by pedo-climatic conditions at the study site, leading to a low accumulation of organic compounds in clay fraction. On the contrary, the C:N ratio of particles >20 μm are much higher than that of whole soil (up to 10 units), suggesting that these fractions include significant amounts of macro-organic matter newly incorporated into the soil system (Christensen 1992). In other words, SOM consists of diverse fractions ranging from young and biologically active to old and less active pools. The coarse particles being less humified, may have a strong quantitative impact on mineral nutrient production in spite of their small contribution to the whole SOM pool (23%).

Natural ^{15}N abundance in size separates

During transformation of organic compounds, the bonds formed with a light isotope are more swiftly broken down than those formed with heavy isotopes. In this way, N transformations result in the enrichment of heavy isotopes in the remaining material (Mariotti et al. 1980), the highest natural abundance in ^{15}N being expected in the most transformed organic matter pool. The enrichment of ^{15}N as decomposition takes place is also due to preferential losses of the lighter isotope as a gas. In our soil, the natural abundance of ^{15}N regularly increased from the coarser to the finer fraction. With respect to their content in ^{15}N, the fractions can be arranged in the following increasing order: 250–2,000 μm<100–250 μm<50–100 μm<20–50 μm<2–20 μm<0.05–2 μm (Table 1). This arrangement results in a negative relationship between C:N ratio and ^{15}N natural abundance (Table 1): C:N ratios decreased with decreasing particle size while ^{15}N values increased. This confirms that the spatial arrangement of the particles results in the spatial segregation of the different stages of organic matter transformation. Indeed, the natural abundance of ^{15}N in the coarse sand fraction (2.1‰) was close to that of living grasses (−1.3‰; Abbadie et al. 1992), showing clearly that the organic matter associated with the coarse fractions is not very different from fresh plant material and has undergone only slight biochemical transformation, as previously suggested by their high C:N ratio. On the contrary, the difference between the natural abundance of ^{15}N in clay particles and living grasses exceeds 10 $\delta^{15}N$ units, indicating that SOM in clay has undergone many microbial transformations.

Monosaccharide distribution in size separates

The smallest concentration of carbohydrates was measured in the sands and the highest in the fine and coarse silt fractions. These results agree with most previously reported data (Cheshire et al. 1990; Solomon et al. 2002; Kiem and Kögel-Knabner 2003). Exceptions are reports by Puget et al. (1999) on two silty soils in France, and by Amelung et al. (1999) on North American grassland soils in which the particulate organic matter was richer in monosaccharides than clay and silt fractions. Moreover, clay can be either richer or poorer in carbohydrates than silt (e.g. Amelung et al. 1999). The monosaccharide concentration of the organo-mineral fractions is therefore very variable among soils and no general rule can be found. This variability can be related to local climatic conditions or to technical accuracy. For example, Amelung et al. (1999) suggested that the concentration of acidic sugars decreases in silt and fine sand as mean annual temperature decreases, but increases in all fractions <250 μm as mean annual precipitation increases. Rodionov et al. (1999) showed variations of the concentration of polysaccharides related to the ratio of mean annual precipitation to potential evaporation. The efficiency of the dispersion can also alter the results, especially when dispersion is incomplete. In our study, the low energy of the ultrasonic treatment (25 J ml^{-1}) could have induced an incomplete dispersion of sand resulting in the presence of clay-sized fractions in silt-sized aggregates, increasing the apparent concentration in sugars of the silt fraction at the expense of clay fraction. If we calculate the distribution of the carbohydrates over the six particle-size fractions by multiplying the carbohydrate concentration in each particle-size fraction (Table 2) by the relative weight of this fraction (Table 1), we can also see that the sum of carbohydrates in the size separates is 14% lower than the amount determined directly on the whole soil (Table 4). This difference could be due to the loss of hydrosoluble polysaccharides through the water eliminated during the fractionation procedure. It has to be noted that this loss of

Table 5 (Gal+Man):(Ara+Xyl), Man:Xyl and Man:(Ara+Xyl) ratios of shrubby savanna whole soil and particle-size fractions. For abbreviations, see Fig. 1

	SS (0–10 cm)	0.05–2 (μm)	2–20 (μm)	20–50 (μm)	50–100 (μm)	100–250 (μm)	250–2,000 (μm)
Gal + ManAra + Xyl	1.8	3.6	3.4	1.1	0.7	0.6	1.0
ManXyl	1.8	4.9	3.9	1.0	0.5	0.4	0.9
Man(Ara + Xyl)	1.3	2.7	2.5	0.7	0.4	0.3	0.7

carbohydrates is higher than the loss of total organic C (5%), which could alter partly the sugar concentrations measured in the fractions.

The low content in carbohydrates of the sand-size particles (fractions >50 μm), confirms that observed on savanna soil in Senegal (Sall et al. 2002). This suggests rapid decomposition of the plant debris and rapid metabolism of the plant sugars, as the difference between clay and whole soil C:N ratios suggested. To distinguish between the plant- and microorganism-derived monosaccharides, several authors proposed the calculation of ratios between specific sugars. Indeed, some monosaccharides, such as galactose (Gal) and Man are mainly synthesized by microbial populations while others, such as arabinose (Ara) and Xyl, mainly come from plants. Turchenek and Oades (1979) and Oades (1984) proposed to use the ratio *R*1=(Gal+Man):(Ara+Xyl) to assess the relative contribution of plants and microorganisms to the accumulation of carbohydrates in soils; the higher the ratio, the greater the microbial contribution to the soil carbohydrate fraction. However, substantial quantities of Gal (Baldock et al. 1987) and Xyl (Murayama 1977) have often been observed in plant materials. Moreover, soil microorganisms are able to synthesize Ara (Murayama 1977). It was therefore suggested that the ratios *R*2=Man:(Ara+Xyl) and *R*3=Xyl:Man can be more accurate indicators of the origin of soil carbohydrates than the previous ratios (Baldock et al. 1987; Murayama 1977). The three ratios were used in this study, but to make the comparisons easier, the ratio *R*4=Man:Xyl ratio was preferred to Xyl:Man. All the ratios showed that the carbohydrate composition differed between size separates (Table 5); the general trend was the increase in the ratios with decreasing particle size, as observed for tropical (Feller and Beare 1997; Solomon et al. 2002) and temperate soils (Kiem and Kögel-Knabner 2003). In the coarse fractions (>20 μm), the ratios were close to or <1, indicating a dominance of plant-derived carbohydrates. In the fine fractions (<20 μm), where most of the soil carbohydrates are located, the ratios were >2, indicating that the sugars are exclusively made of microbially derived compounds as in many soils studied previously (Amelung et al. 1999; Sall et al. 2002; Kiem and Kögel-Knabner 2003). Indeed, microbial biomass and cell debris and products are most concentrated in the <50 μm-size components of the particle-size fractions (Ladd et al. 1996).

Conclusions

A negative relationship was observed between the C:N ratio and ^{15}N natural abundance on the one hand, and on the other hand between C:N and (Gal+Man):(Ara+Xyl), Man:(Ara+Xyl) and Man:Xyl ratios. These results indicate that the chemistry of the organic materials of the particle-size fractions reflects a change from a soil chemistry dominated by plant materials to one dominated by microbial biomass and metabolites (Ladd et al. 1996). They also clearly supported evidence that fine particle organic matter has undergone many microbial transformations. Thus, the contribution of these fractions to soil microbial activity should be less than that of the coarse fractions. Nevertheless, Nacro et al. (1996) showed that 68% of the potential microbial respiration was located on the organo-mineral particles <20 μm. How can most of the soil microbial activities occur in the fine organo-mineral fractions known as old and less active pools? This probably results from: (1) the location of heterotrophic soil microorganisms on fine fractions probably because of their size and the protection offered from predation (Ladd et al. 1996), (2) the accumulation of microbially derived carbohydrates which can be resynthesized or recycled by soil microorganisms, and/or (3) the mineralization of soluble organic substrates carried by the soil solution (Killham et al. 1993). Therefore, the contribution of a given fraction to the soil microbial activity is not only controlled by the distribution and quality of SOM, but also by the location of microorganisms. The C:N ratio and the ^{15}N value are not sufficient to predict the potential biological activity of a given organo-mineral fraction. The use of labelled substrates will provide a better understanding and identification of the real contribution of each fraction.

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References

Abbadie L, Mariotti A, Menaut JC (1992) Independence of savanna grasses from soil organic matter for their nitrogen supply. Ecology 73:608–613

Amelung W, Flach KW, Zech W (1999) Neutral and acidic sugars in particle-size fractions as influenced by climate. Soil Sci Soc Am J 63:865–873

Anne P (1945) Sur le dosage rapide du carbone organique des sols. Ann Agron 2:162–172

Baldock JA, Kay BD, Schnitzer M (1987) Influence of cropping treatment on the monosaccharide content of the hydrolysates of a soil and its aggregate fractions. Can J Soil Sci 67:489–499

Balesdent J, Pétraud J-P, Feller C (1991) Effets des ultrasons sur la distribution granulométrique des matières organiques des sols. Sci Sol 29:95–106

Bonneau M, Souchier B (1979) Pédologie. 2. Propriétés et constituants du sol. Masson, Paris

Catroux G, Schnitzer M (1987) Chemical, spectroscopic, and biological characteristics of the organic matter in particle size fractions separated from an Aquoll. Soil Sci Soc Am J 51:1200–1207

Cheshire MV (1979) Nature and origin of carbohydrates in soil. Academic Press, London

Cheshire WV, Christensen BT, Sorensen LH (1990) Labelled and native sugars in particle-size fractions from soil incubated with ^{14}C straw for 6 to 18 years. J Soil Sci 44:29–39

Christensen BT (1992) Physical fractionation of soil and organic matter in primary particle size and density separates. Adv Soil Sci 20:1–90

Dommergues Y (1960) La notion de coefficient de minéralisation du carbone dans les sols. Agron Trop 15:54–60

FAO-UNESCO (1989) Carte mondiale des sols, légende revisée. FAO-UNESCO

Feller C, Beare MH (1997) Physical control of soil organic matter dynamics in the tropics. Geoderma 79:69–116

Feller C, François C, Villemin G, Portal JM, Toutain F Morel JL (1991a) Nature des matières organiques associées aux fractions argileuses d'un sol ferrallitique. C R Acad Sci Paris 312:1491–1497

Feller C, Burtin C, Gerard B, Balesdent J (1991b) Utilisation des résines sodiques et des ultrasons dans le fractionnement granulométrique de la matière organique des sols. Intérêts et limites. Sci Sol 29:77–93

Feller C, Fritsch E, Poss R, Valentin C (1991c) Effet de la texture sur le stockage et la dynamique des matières organiques dans quelques sols ferrugineux et ferrallitiques (Afrique de l'Ouest, en particulier). Cah ORSTOM Ser Pedol 26:25–36

Jackson ML (1956) Soil chemical analysis advanced course. Department of Soil Science, University of Madison, Wis.

Kiem R, Kögel-Knabner I (2003) Contribution of lignin and polysaccharides to the refractory carbon pool in C-depleted arable soils. Soil Biol Biochem 35:101–118

Killham K, Amato M, Ladd JN (1993) Effect of substrate location in soil and soil pore-water regime on carbon turnover. Soil Biol Biochem 25:57–62

Ladd JN, Foster RC, Nannipieri P, Oades JM (1996) Soil structure and biological activity. In: Stotzky G, Bollag JM (eds) Soil Biochem 9:23–78

Larré-Larrouy MC, Feller C (1997) Determination of carbohydrates in two ferralitic soils and their particle-size fractions: analysis by capillary gaz chromatography after derivation by silylation. Soil Biol Biochem 29:1585–1589

Mariotti A (1983) Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. Nature 303:685–687

Mariotti A, Pierre D, Vedy JC, Bruckert S (1980) The abundance of natural nitrogen 15 in the organic matter of soils along an altictudinal gradient. Catena 7:293–300

Martin JP (1946) Microorganisms and soil aggregation. II. Influence of bacterial polysaccharides on soil structure. Soil Sci 61:151–166

Martin A, Mariotti A, Balesdent J, Lavelle P, Vuattoux R (1990) Estimate of organic matter turnover rate in a savanna soil by ^{13}C natural abundance measurements. Soil Biol Biochem 22:517–523

Menaut JC, César J (1979) Structure and primary productivity of Lamto savannas, Ivory Coast. Ecology 60:1197–1210

Murayama S (1977) Saccharides in some Japanese paddy soils. J Soil Sci Plant Nutr 23:479–489

Nacro HB, Benest D, Abbadie L (1996) Distribution of microbial activities and organic matter according to particle size in a humid savanna soil (Lamto, Côte d'Ivoire). Soil Biol Biochem 28:1687–1697

Oades JM (1984) Soil organic matter and structural stability: mechanisms and implications for management. Plant Soil 76:319–337

Oades JM, Ladd JN (1977) Biochemical properties. In: Russel JS, Greacen FL (eds) Soil factors in crop production in a semi-arid environment. University of Queensland, Queensland, pp 126–160

Puget P, Angers DA, Chenu C (1999) Nature of carbohydrates associated with water-stable aggregates of two cultivated soils. Soil Biol Biochem 31:55–63

Rodionov A, Amelung W, Urusevskaja I, Zech W (1999) Climatic effect on lignin and polysaccharides in particle-size fractions of zonal steppe soils, Russia. J Soil Sci Plant Nutr 162:231–238

Sall S, Brauman A, Fall S, Rouland C, Mimabi E, Chotte J-L (2002) Variation in the distribution of monosaccharides in soils fractions in the mounds of termites with different feeding habits (Senegal). Biol Fertil Soils 36:232–239

Shen JK, Bartha R (1997) Priming effect of glucose polymers in soil-based biodegradation tests. Soil Biol Biochem 29:1195–1198

Solomon D, Fritzsche F, Tekalign M, Lehmann J, Zech W (2002) Soil organic matter composition in the subhumid Ethiopian highlands as influenced by deforestation and agricultural management. Soil Sci Soc Am J 66:68–82

Tan KH, Troth PS (1981) Increasing sensitivity of organic matter and nitrogen analysis using soil separates. Soil Sci Soc Am J 45:574–577

Tanner CB, Jackson ML (1948) Nomographs of sedimentation times for soil particles under gravity or centrifugal acceleration. Soil Sci Soc Am Proc 12:60–65

Turchenek LW, Oades JM (1979) Fractionation of organo-mineral complexes by sedimentation and density techniques. Geoderma 21:311–344