Review

Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils

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Abstract

The relationship between soil structure and the ability of soil to stabilize soil organic matter (SOM) is a key element in soil C dynamics that has either been overlooked or treated in a cursory fashion when developing SOM models. The purpose of this paper is to review current knowledge of SOM dynamics within the framework of a newly proposed soil C saturation concept. Initially, we distinguish SOM that is protected against decomposition by various mechanisms from that which is not protected from decomposition. Methods of quantification and characteristics of three SOM pools defined as protected are discussed. Soil organic matter can be: (1) physically stabilized, or protected from decomposition, through microaggregation, or (2) intimate association with silt and clay particles, and (3) can be biochemically stabilized through the formation of recalcitrant SOM compounds. In addition to behavior of each SOM pool, we discuss implications of changes in land management on processes by which SOM compounds undergo protection and release. The characteristics and responses to changes in land use or land management are described for the light fraction (LF) and particulate organic matter (POM). We defined the LF and POM not occluded within microaggregates (53–250 μm sized aggregates as unprotected. Our conclusions are illustrated in a new conceptual SOM model that differs from most SOM models in that the model state variables are measurable SOM pools. We suggest that physicochemical characteristics inherent to soils define the maximum protective capacity of these pools, which limits increases in SOM (i.e. C sequestration) with increased organic residue inputs.

Introduction

Most current models of SOM dynamics assume first-order kinetics for the decomposition of various conceptual pools of organic matter (McGill, 1996; Paustian, 1994), which means that equilibrium C stocks are linearly proportional to C inputs (Paustian et al., 1997). These models predict that soil C stocks can, in theory, be increased without limit, provided that C inputs increase without limit, i.e. there are no assumptions of soil C saturation. While these models have been largely successful in representing SOM dynamics under current conditions and management practices (e.g. Parton et al., 1987, 1994; Paustian et

al., 1992; Powlson et al., 1996), usually for soils with low to moderate C levels (e.g. <5%), there is some question of their validity for projecting longer term SOM dynamics under scenarios of ever increasing C inputs (e.g. Donigian et al., 1997). Such scenarios are particularly relevant with the development of new technology designed to promote soil C sequestration through increasing plant C inputs.

Native soil C levels reflect the balance of C inputs and C losses under native conditions (i.e. productivity, moisture and temperature regimes), but do not necessarily represent an upper limit in soil C stocks. Empirical evidence demonstrates that C levels in intensively managed agricultural and pastoral ecosystems can exceed those under native conditions. Phosphorous fertilization of Australian pasture soils can increase soil C by 150% or more relative to the native condition

(Barrow, 1969; Ridley et al., 1990; Russell 1960). Soil C levels under long-term grassland ('near native') vegetation have also been exceeded in high productivity mid-western no-tillage (NT) systems (Ismail et al., 1994) as well as in sod plots with altered vegetation (Follett et al., 1997). Hence, native soil C levels may not be an appropriate measure of the ultimate C sink capacity of soils.

There are several lines of evidence that suggest the existence of a C saturation level based on physiochemical processes that stabilize or protect organic compounds in soils. While many long-term field experiments exhibit a proportional relationship between C inputs and soil C content across treatments (Larson et al., 1972; Paustian et al., 1997), some experiments in high C soils show little or no increase in soil C content with two to three fold increases in C inputs (Campbell et al., 1991; Paustian et al., 1997; Solberg et al., 1997). Various physical properties (e.g. silt plus clay content and microaggregation) of soil are thought to be involved in the protection of organic materials from decomposer organism. However, these properties and their exerted protection seem to be limited by their characteristics (e.g. surface area), which is consistent with a saturation phenomenon (Hassink, 1997; Kemper and Koch, 1966).

A number of soil organic matter models have been developed in the last 30 years. Most of these models represent the heterogeneity of SOM by defining several pools, typically three to five, which vary in their intrinsic decay rates and in the factors which control decomposition rates (see reviews by McGill, 1996; Parton, et al., 1994; Paustian, 1994). Alternative formulations, whereby specific decomposition rate varies as a function of a continuous SOM quality spectrum (i.e. instead of discrete pools), have also been developed (e.g. Bosatta and Agren, 1996). However, in either case, the representation of the model pools (or quality spectrum) is primarily conceptual in nature. While such models can be successfully validated using measurements of total organic carbon and isotopic ratios of total C (e.g. Jenkinson and Rayner, 1977), the individual pools are generally only loosely associated with measurable quantities obtained with existing analytical methods. Consequently, it is not straightforward to falsify or test the internal dynamics of C transfers between pools and changes in pool sizes of the current SOM models with conceptual pool definitions because a direct comparison to measured pool changes is not possible.

A closer linkage between theoretical and measurable pools of SOM can be made by explicitly defining model pools to coincide with measurable quantities or by devising more functional laboratory fractionation procedures or both. The phrases 'modeling the measurable' and 'measuring the modelable' have been coined as representing the two approaches towards a closer reconciliation between theoretical and experimental work on SOM (Christensen, 1996; Elliott et al., 1996).

Various attempts have been made to correlate analytical laboratory fractions with conceptual model pools, with limited success. Motavalli et al. (1994) compared laboratory measurements of C mineralization with simulations by the Century model (Parton et al., 1994) for several tropical soils. When the active and slow pools in the model were initialized using laboratory determinations of microbial + soluble C for the active pool and light fraction for the slow pool, C mineralization was consistently underestimated, although all fractions were highly significantly correlated to C mineralization in a regression analysis. Magid et al. (1996) unsuccessfully attempted to trace ^{14}C labeled plant materials using three size-density fractionation methods to define an 'active' pool. Metherell (1992) found that the slow pool in Century was much larger than the particulate organic matter (POM) fraction isolated from a Haplustoll by Cambardella and Elliott (1992). However, Balesdent (1996) found that POM isolated after mild disruption corresponds to the plant structural compartment (RPM) of the Rothamsted carbon model (Jenkinson and Rayner, 1997). Acid hydrolysis has been used to estimate Century's passive C pool (Paul et al., 1997a; Trumbore, 1993), but it seems to slightly overestimate the size (Paul et al., 1997a; Trumbore, 1993), though not the C turnover rate, of the passive pool (Trumbore, 1993). Nevertheless, Paul et al. (1999) used extended laboratory incubations in combination with acid hydrolysis to define an active, slow and passive pool of C and were successful in modeling the evolution of CO_2 in the field based on these pools. These studies suggest that attempting to measure the modelable has had minimal success to date.

There have been a few recent attempts to more closely integrate models and measurements of physicochemically defined pools by 'modeling the measurable', although Elliott et al. (1996) and Christensen (1996) have presented conceptual models for this approach. Arah (2000) proposed an approach based on analytically defined pools and measurements of ^{13}C
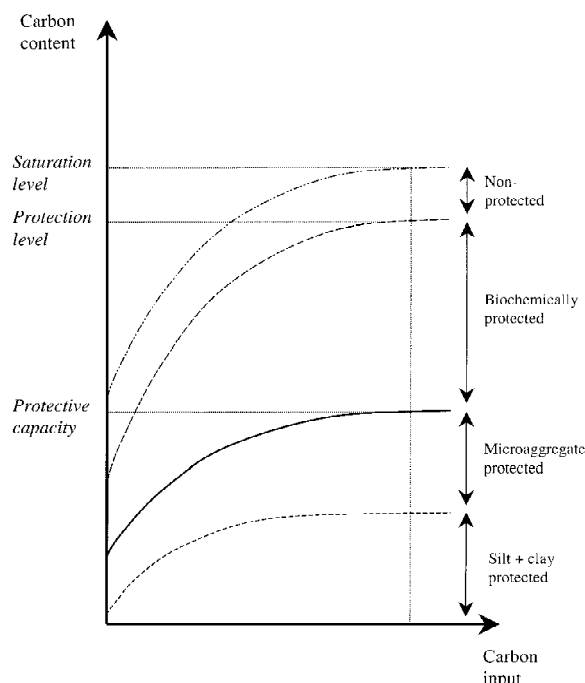
Figure 1. The protective capacity of soil (which governs the silt- and clay protected C and microaggregate protected C pools), the biochemically stabilized C pool and the unprotected C pool define a maximum C content for soils. The pool size of each fraction is determined by their unique stabilizing mechanisms.

and ^{15}N stable isotope tracers to derive parameters for a model with measurable pools. The approach considers all possible transformations between measured C and N pools and devises a system of equations using observed changes in total C and N and ^{13}C and ^{15}N for each fraction to solve all model unknowns. Necessary requirements of such an approach are that the analytical fractions are distinct and together account for the total carbon inventory.

The objective of this review paper is to summarize current knowledge on SOM dynamics and stabilization and to synthesize this information into a conceptual SOM model based on physicochemically defined SOM pools. This new model defines a soil C-saturation capacity, or a maximum soil C storage potential, determined by the physicochemical properties of the soil. We propose that the conceptual model developed from this knowledge may form the basis for a simulation model with physicochemically measurable SOM pools as state variables rather than with the biologically defined pools by Paul et al. (1999).

Protected SOM: Stabilization mechanisms, characteristics, and dynamics

Three main mechanisms of SOM stabilization have been proposed: (1) chemical stabilization, (2) physical protection and (3) biochemical stabilization (Christensen, 1996; Stevenson, 1994). Chemical stabilization of SOM is understood to be the result of the chemical or physicochemical binding between SOM and soil minerals (i.e. clay and silt particles). Indeed, many studies have reported a relationship between stabilization of organic C and N in soils and clay or silt plus clay content (Feller and Beare, 1997; Hassink, 1997; Ladd et al., 1985; Merckx et al., 1985; Sorensen, 1972). In addition to the clay content, clay type (i.e. 2:1 versus 1:1 versus allophanic clay minerals) influences the stabilization of organic C and N (Feller and Beare, 1997; Ladd et al. 1992; Sorensen, 1972; Torn et al., 1997). Physical protection by aggregates is indicated by the positive influence of aggregation on the accumulation of SOM (e.g. Edwards and Bremner, 1967; Elliott, 1986; Jastrow, 1996; Tisdall and Oades, 1982; Six et al., 2000a). Aggregates physically protect SOM by forming physical barriers between microbes and enzymes and their substrates and controlling food web interactions and consequently microbial turnover (Elliott and Coleman, 1988). Biochemical stabilization is understood as the stabilization of SOM due to its own chemical composition (e.g. recalcitrant compounds such as lignin and polyphenols) and through chemical complexing processes (e.g. condensation reactions) in soil. For our analyses, we divide the protected SOM pool into three pools according to the three stabilization mechanisms described (Figure 1). The three SOM pools are the silt- and clay-protected SOM (silt and clay defined as <53 μm organomineral complexes), microaggregate-protected SOM (microaggregates defined as 53–250 μm aggregates), and biochemically protected SOM.

Chemical stabilization: Silt- and clay-protected SOM

The protection of SOM by silt and clay particles is well established (Feller and Beare, 1997; Hassink, 1997; Ladd et al., 1985; Sorensen, 1972). Hassink (1997) examined the relationship between SOM fractions and soil texture and found a relationship between the silt- and clay-associated C and soil texture, though he did not find any correlation between texture and amount of C in the sand-sized fraction (i.e. POM C). Based on these findings, he defined the capacity

Table 1. Regression equations relating silt plus clay proportion to silt and clay associated C

Size class[a]	Ecosystem	Intercept	Slope	r^2
0–20 μm	Cultivated	4.38±0.68[b]	0.26±0.01	0.41
	Grassland	2.21±1.94	0.42±0.08	0.44
	Forest	−2.51±0.55	0.63±0.01	0.55
0–50 μm	Cultivated	7.18±3.04	0.2±0.04	0.54
	Grassland	16.33±4.69	0.32±0.07	0.35
	Forest	16.24±6.01	0.24±0.08	0.35

Size class	Clay type	Intercept	Slope	r^2
0–20 μm	1:1	1.22±0.37	0.30±0.01	0.74
	2:1	3.86±0.49	0.41±0.01	0.39
0–50 μm	1:1	5.5±5.93	0.26±0.13	0.38
	2:1	14.76±2.37	0.21±0.03	0.07

[a]Two size classes for silt and clay were reported in the literature.
[b]Value±95% confidence interval.

of soil to preserve C by its association with silt and clay particles. Studies investigating the retention of specific microbial products (i.e. amino sugars) corroborate the proposition of Hassink (1997) that C associated with primary organomineral complexes are chemically protected and the amount of protection increased with an increased silt plus clay proportion of the soil (Chantigny et al., 1997; Guggenberger et al., 1999; Puget et al., 1999; Sorensen, 1972). Puget et al. (1999) reported an enrichment of microbial derived carbohydrates in the silt plus clay fraction compared to the sand fraction of no-tilled and conventional tilled soils. However, the amount stabilized by silt and clay differs among microbial products. For example, Guggenberger et al. (1999) reported a higher increase of glucosamine than muramic acid under no-tillage at sites with a high silt plus clay content. A reexamination of the data presented by Chantigny et al. (1997) leads to the observation that the glucosamine/muramic acid ratio was only higher in perennial systems compared to annual systems in a silty clay loam soil and not in a clay loam soil. The silty clay loam soil had a higher silt plus clay content.

We expanded the analysis of Hassink (1997) of the physical protection capacity for C associated with primary organomineral complexes (Figure 2) across ecosystems (i.e. forest, grassland, and cultivated systems), clay types (i.e. 1:1 versus 2:1), and size ranges for clay and silt (0–20 μm and 0–50 μm; see Ap-
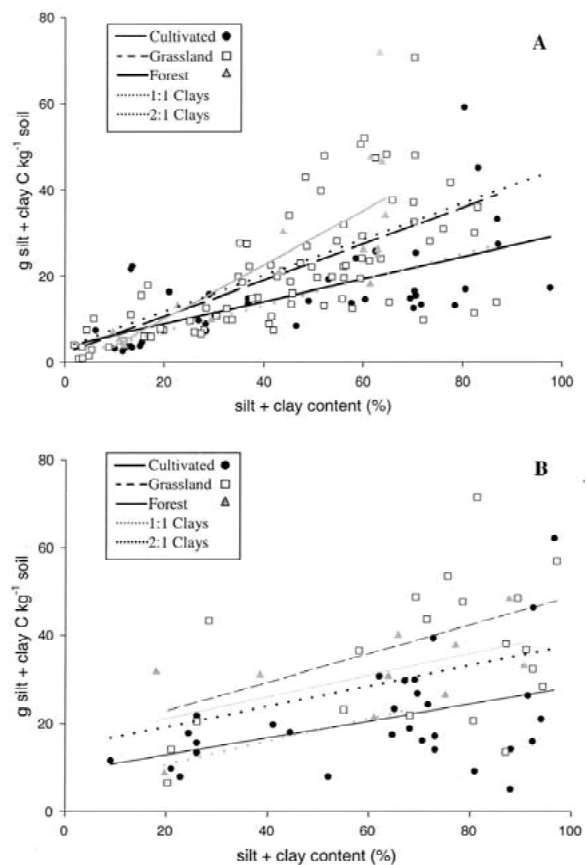

Figure 2. The relationship between silt+clay content (%) and silt+clay associated C (g silt+clay C kg^{-1} soil) for grassland, forest and cultivated ecosystems. A differentiation between 1:1 clay and 2:1 clay dominated soils is also made. The relationships indicate a maximum of C associated with silt and clay (i.e. C saturation level for the clay and silt particles), which differs between forest and grassland ecosystems and between clay types. Two size boundaries for silt+clay were used (A) 0–20 μm and (B) 0–50 μm.

pendices for details). Following the methodology of Hassink (1997) we performed regressions (Figure 2 and Table 1) between the C content associated with silt and clay particles (g C associated with silt and clay particles kg^{-1} soil; *Y* axis) and the proportion of silt and clay particles (g silt plus clay g^{-1} soil; *X* axis). All regressions were significant ($P<0.05$) and comparison of regression lines revealed that the influence of soil texture on mineral-associated C content differed depending on the size range used for clay and silt particles. Consequently, we did regressions for two different size classes of silt and clay particles (i.e. 0–20 μm and 0–50 μm; Figure 2 and Table 1). The intercept for the 0–50 μm silt and clay particles was significantly higher than for the 0–20 μm silt and clay particles (Table 1). This difference in intercept was

probably a result of the presence of larger sized (20–50 μm) silt-sized aggregates in the 0–50 μm than in the 0–20 μm silt and clay particles. These larger silt-sized aggregates have more C per unit material because additional C binds the primary organomineral complexes into silt-sized aggregates (Tisdall and Oades, 1982). However the difference in intercept might also be the result of POM particles of the size 20–50 μm associated with the 0–50 μm fraction (Turchenek and Oades, 1979). Intercepts for cultivated and forest ecosystems were significantly different for the 0–50 μm particles, but were only marginally significantly different ($P < 0.06$) for the 0–20 μm particles. Slopes for grassland soils (0–20 μm particles) were significantly different than those for forest and cultivated soils. The differences between grasslands and cultivated lands are likely due to differences in input and disturbance, which causes a release of SOM and consequently increased C availability for decomposition. An explanation for the significantly different slopes for grassland and forest soils (Table 1) is not immediately apparent. Especially that the slope is higher for forest than grassland slopes. This is in contrast to the suggestion that grassland-derived soils have a higher potential of C stabilization than forest-derived because of their higher base saturation (Collins et al., 2000; Kononova, 1966). Consequently, this difference in C stabilization by silt and clay particles between forest and grassland systems should be investigated further.

In contrast to Hassink (1997), we found significantly different relationships for 1:1 clays versus 2:1 clays regressions and for the cultivated versus grassland regressions (Figure 2 and Table 1) for the 0–20 μm particles. The effect of clay type was also significant for the 0–50 μm particles. This lower stabilization of C in 1:1 clay dominated soils is probably mostly related to the differences between the clay types (see below). However, the effect of climate can not be ignored in this comparison because most 1:1 clay dominated soils were located in (sub)tropical regions. The higher temperature and moisture regimes in (sub)tropical regions probably also induce a faster decomposition rate and therefore contributes to the lower stabilization of C by the 1:1 clays. Nevertheless we believe that the type of clay plays an important role because different types of clay (i.e. 1:1 and 2:1 clays) have substantial differences in CEC and specific surface (Greenland, 1965) and should, consequently, have different capacities to adsorb organic materials. In addition, Fe- and Al-oxides are most often found in soils dominated by 1:1 minerals and are strong flocculants. By

being strong flocculants, Fe- and Al-oxides can reduce even further the available surface for adsorption of SOM. We are not certain why soils examined by Hassink (1997) did not follow this reduced capacity to adsorb organic materials; few soils dominated by 1:1 clays, however, were included in the data set used by Hassink (1997) and most of them had a low carbon content. Nevertheless, the difference between the two studies might also be a result of the contrasting effect the associated Fe- and Al-oxides can have. The strong flocculating oxides can reduce available surface (see above) but they might also co-flocculate SOM and consequently stabilize it. Therefore, it appears that mechanisms with contrasting effects on SOM stabilization exist and the net effect still needs to be investigated. The different regression lines for grassland and cultivated systems are in accordance with Feller et al. (1997). They also found a significant lower slope for the regression line between the amount of 0–2 μm particles and the C contained in the 0–2 μm fraction of cultivated soils compared to non-cultivated soils. The lack of influence of cultivation on the silt and clay associated C observed by Hassink (1997) was probably a result of the low proportion of silt and clay and high SOM contents of the soils used. The silt- and clay-associated C formed a small fraction of the total C in his soils. Consequently, sand-associated C accounted for the majority of total soil C. Given this dominance of sand-associated C and its greater sensitivity to cultivation than silt- and clay-associated C (Cambardella and Elliott, 1992), in which C is transferred from the sand associated fraction to the silt- and clay-associated fractions during decomposition (Guggenberger et al., 1994), a loss of silt- and clay-associated C upon cultivation is likely to be minimal.

In summary, we found, as Hassink (1997) did, a direct relationship between silt plus clay content of soil and the amount of silt- and clay-protected soil C, indicating a saturation level for silt and clay associated C. This relationship was different between different types of land use, different clay types, and for different determinations of silt plus clay size class. Also, the silt- and clay-associated soil organic matter was reduced by cultivation.

Physical protection: Microaggregate-protected SOM

The physical protection exerted by macro- and/or microaggregates on POM C is attributed to: (1) the compartmentalization of substrate and microbial bio-

mass (Killham et al., 1993; van Veen and Kuikman, 1990), (2) the reduced diffusion of oxygen into macro- and especially microaggregates (Sexstone et al., 1985) which leads to a reduced activity within the aggregates (Sollins et al., 1996), and (3) the compartmentalization of microbial biomass and microbial grazers (Elliott et al., 1980). The compartmentalization between substrate and microbes by macro- and microaggregates is indicated by the highest abundance of microbes on the outer part of the aggregates (Hattori, 1988) and a substantial part of SOM being at the center of the aggregates (Elliott and Coleman, 1988; Golchin et al., 1994). In addition, Bartlett and Doner (1988) reported a higher loss of amino acids by respiration from the aggregate surfaces than from within aggregates. Priesack and Kisser-Priesack (1993) showed that the rate of glucose utilization decreased with distance into the aggregate. The inaccessibility of substrate for microbes within aggregates is due to pore size exclusion and related to the water-filled porosity (Killham et al., 1993).

Many studies have documented a positive influence of aggregation on the accumulation of SOM (Angers et al., 1997; Besnard et al., 1996; Cambardella and Elliott, 1993; Franzluebbers and Arshad, 1997; Gale et al., 2000; Golchin et al., 1994, 1995; Jastrow, 1996; Monreal and Kodama, 1997; Paustian et al., 2000; Puget et al., 1995, 1996; Six et al., 1998, 1999, 2000a). Cultivation causes a release of C by breaking up the aggregate structures, thereby increasing availability of C. More specifically, cultivation leads to a loss of C-rich macroaggregates and an increase of C-depleted microaggregates (Elliott, 1986; Six et al., 2000a). The inclusion of SOM in aggregates also leads to a qualitative change of SOM. For example, Golchin et al. (1994) reported significant differences in chemical structure between the free and occluded (i.e. within aggregates) light fraction. The occluded light fraction had higher C and N concentrations than the free light fraction and contained more alkyl C (i.e. long chains of C compounds such as fatty acids, lipids, cutin acids, proteins and peptides) and less O-alkyl C (e.g. carbohydrates and polysaccharides). These data suggest that during the transformation of free into intraaggregate light fraction there is a selective decomposition of easily decomposable carbohydrates (i.e. O-alkyl C) and preservation of recalcitrant long-chained C (i.e. alkyl C) (Golchin et al., 1994). Golchin et al. (1995) also found that cultivation decreased the O-alkyl content of the occluded SOM. They suggested that this difference is a result of the continuous

disruption of aggregates, which leads to a faster mineralization of SOM and a preferential loss of readily available O-alkyl C. Hence, the enhanced protection of SOM by aggregates in less disturbed soil results in an accumulation of more labile C than would be maintained in a disturbed soil.

Recent studies indicate that the macroaggregate (>250 μm) structure exerts a minimal amount of physical protection (Beare et al., 1994; Elliott, 1986; Pulleman and Marinissen, 2001), whereas SOM is protected from decomposition in free (i.e. not within macroaggregates) microaggregates (<250 μm) (Balesdent et al., 2000; Besnard et al., 1996; Skjemstad et al., 1996) and in microaggregates within macroaggregates (Denef et al., 2001; Six et al., 2000b). Beare et al. (1994) and Elliott (1986) found an increase in C mineralization when they crushed macroaggregates, but the increase in mineralization only accounted for 1–2% of the C content of the macroaggregates. In addition, no difference in C mineralization between crushed and uncrushed macroaggregates has been observed (Pulleman and Marinissen, 2001). In contrast, C mineralization of crushed free microaggregates was three to four times higher than crushed macroaggregates (Bossuyt et al., 2002). Gregorich et al. (1989) observed a substantial higher C mineralization when microaggregates within the soil were disrupted than when lower disruptive energies were used that did not break up microaggregates. Jastrow et al. (1996), using ^{13}C natural abundance technique, calculated that the average turnover time of C in free microaggregates was 412 yr, whereas the average turnover time for macroaggregate associated C was only 140 yr in the surface 10 cm. These studies clearly indicate that C stabilization is greater within free microaggregates than within macroaggregates. Further corroborating evidence for the crucial role microaggregates play in C sequestration were reported by Angers et al. (1997), Besnard et al. (1996), Gale et al. (2000) and Six et al. (2000b). Angers et al. (1997) found in a field incubation experiment with ^{13}C and ^{15}N labeled wheat straw that wheat-derived C was predominantly stored and stabilized in free microaggregates. Gale et al. (2000) reported similar C stabilization within free microaggregates in an incubation study with ^{14}C-labeled root material. Upon conversion of forest to maize cultivation, Besnard et al. (1996) found a preferential accumulation of maize- and forest-derived POM-C in microaggregates compared to other soil fractions. Six et al. (1999) observed a decrease in fine intra-macroaggregate-POM (i.e. 53–250 μm sized POM

(fine iPOM) predominantly stabilized in microaggregates within macroaggregates (Six et al., 2000b)) under plough tillage compared to no-till. However, there was no difference in coarse intra-macroaggregate POM (i.e. 250–2000 μm POM not stabilized by the microaggregates within macroaggregates) between tillage systems at three of the four sites studied. They concluded that the incorporation and stabilization of fine POM-C into microaggregates within macroaggregates and free microaggregates under no-tillage is a dominant factor for protection of the fine-sized fraction of POM. Nevertheless, the dynamics of macroaggregates are crucial for the sequestration of C because it influences the formation of microaggregates and the sequestration of C within these microaggregates (Six et al., 2000b). That is, rapid turnover of macroaggregates reduces the formation of microaggregates within macroaggregates and the resulting stabilization of C within these microaggregates (Six et al., 1998, 1999, 2000b).

Though the incorporation of POM into microaggregates (versus bonding to clay surfaces; i.e. chemical mechanism) seems to be the main process for protection of POM, the clay content and type of soil exert an indirect influence on the protection of POM-C by affecting aggregate dynamics. Franzluebbers and Arshad (1997) suggested that physical protection of POM within aggregates increases with clay content since mineralization of POM-C relative to whole-SOM-C after dispersion and aggregation both increased with increasing clay content (Franzluebbers and Arshad, 1996). Different clay types lead to different mechanisms involved in aggregation (Oades and Waters, 1991) and will therefore influence differently the protection of POM through microaggregation. Within the 2:1 clay minerals, clay minerals with a high CEC and larger specific surface, such as montmorillonite and vermiculite, have a higher binding potential than clay minerals with a lower CEC and smaller specific surface, such as illite (Greenland, 1965). In contrast to the 2:1 minerals, kaolinite and especially Fe- and Al-oxides have a high flocculation capacity due to electrostatic interactions through their positive charges (Dixon, 1989; Schofield and Samson, 1954). Even though, different mechanisms prevail in soils with different clay types, soils seem to have a maximum level of aggregate stability. Kemper and Koch (1966) observed that aggregate stability increased to a maximum level with clay content and free Fe-oxides content. Since the physical protection of POM seems to be mostly determined by microaggregation, we hypothes-

ize that the maximum physical protection capacity for SOM is determined by the maximum microaggregation, which is in turn determined by clay content, clay type.

Biochemical stabilization: Biochemically-protected SOM

In this review, a detailed description of the influence of biochemical stabilization on SOM dynamics will not be given, we refer to an excellent review on this subject by Cadisch and Giller (1997). Nevertheless, biochemical stabilization of SOM needs to be considered to define the soil C-saturation level within a certain ecosystem (Figure 1). Biochemical stabilization or protection of SOM occurs due to the complex chemical composition of the organic materials. This complex chemical composition can be an inherent property of the plant material (referred to as residue quality) or be attained during decomposition through the condensation and complexation of decomposition residues, rendering them more resistant to subsequent decomposition. Therefore the third pool in our model (Figure 1) is a SOM pool that is stabilized by its inherent or acquired biochemical resistance to decomposition. This pool is akin to that referred to as the 'passive' SOM pool (Parton et al., 1987) and its size has been equated to the non-hydrolyzable fraction (Leavitt et al., 1996; Paul et al., 1995; Trumbore 1993). Using ^{14}C dating, it has been found that, in the surface soil layer, the non-hydrolyzable C is approximately 1300 years older than total soil C (Paul et al., 1997a, 2001). Several studies have found that the non-hydrolyzable fraction in temperate soils includes very old C (Anderson and Paul, 1984; Paul et al., 1999; Trumbore, 1993; Trumbore et al., 1996) and acid hydrolysis removes proteins, nucleic acids, and polysaccharides (Schnitzer and Khan, 1972) which are believed to be more chemically labile than other C compounds, such as aromatic humified components and wax-derived long chain aliphatics (Paul et al., 1997a). The stabilization of this pool and consequent old age is probably predominantly the result of its biochemical composition. However, Balesdent (1996) did not find any great differences in dynamics between the non-hydrolyzable and hydrolyzable C fraction and therefore questioned the relationship between biodegradability and hydrolyzability. Nevertheless, we chose the hydrolysis technique to differentiate an older and passive C pool, because we think it is the simplest and best available technique to define

such pool and others (Paul et al., 1995, 1999, 2001; Trumbore, 1993) have shown it to be an appropriate technique for such applications. The size of this pool is also likely to be limited since the mean age of C in the passive pool is generally much younger than the pedogenic age of the soil.

Unprotected SOM: Characteristics and dynamics

Recently derived, partially decomposed plant residues that are not closely associated with soil minerals constitute the unprotected SOM pool. We suggest that this unprotected SOM pool is measurable as either the light fraction (LF) or POM fraction and therefore consider these two fractions as conceptually similar pools even though differences in characteristics do exist between them (see below). Many studies have found that the LF and POM, especially coarse POM (>250 μm), are relatively easily decomposable and are greatly depleted upon cultivation (e.g. Cambardella and Elliott, 1992; Six et al., 1999; Solomon et al., 2000), indicating their relatively unprotected (biochemical and physical) status. The POM and the LF are isolated by size and/or density separation. Many different size classes, densities, and degrees of soil dispersion before isolation are used, confounding comparisons among studies. The LF is isolated by flotation in a high-density liquid after a certain degree of disruption or even complete dispersion of the soil (Janzen et al., 1992; Meijboom et al., 1995; Sollins et al., 1984). The yield of LF depends strongly on the density used and the level of soil dispersion before the density flotation. In order to isolate unprotected LF, microaggregates should not be broken up before flotation (see above). Consequently, unprotected LF is only isolated after a minimal level of dispersion of the soil, i.e. the disruption level used, should break up only macroaggregates and not microaggregates. We define unprotected POM as the 53–2000 μm sized POM not contained within microaggregates and protected POM as 53–250 μm sized POM contained within microaggregates. Since the macroaggregate versus microaggregate boundary is size determined, a size separation methodology is more standardazible than a density separation methodology for the isolation of protected versus unprotected SOM as defined in this review. A specific method is described in the last section of this review. For this paper we review the available information for both the LF and POM independent of methodology used because: (1) characteristics of the two fractions are fairly similar (see Table 2), and (2) most studies did not differentiate between protected and unprotected LF and POM.

Plant Origin of unprotected SOM

Both the LF and POM are mainly comprised of plant residues, but also contain seeds and microbial debris, such as fungal hyphae and spores (Besnard et al., 1996; Dalal and Mayer, 1986a,b; Molloy and Speir, 1977; Oades et al., 1987). Several authors have also reported the presence of charcoal in LF and POM (Cambardella and Elliott, 1992; Greenland and Ford, 1964; Molloy and Speir, 1977; Skjemstad et al., 1990). The predominantly plant origin of LF and POM is easily verifiable under a microscope and is also confirmed by many biochemical characterization studies on these fractions. First, several studies have indicated a lower carbohydrate concentration in POM and LF compared to the smaller-sized or heavier fractions, respectively (Angers and Mehuys, 1990; Catroux and Schnitzer, 1987; Cheshire and Mundie, 1981; Greenland and Ford, 1964; Guggenberger et al., 1994; Murayama et al., 1979; Oades et al., 1987; Skjemstad et al., 1986; Solomon et al., 2000). However, a higher carbohydrate-C enrichment ratio in the POM fraction than in the clay-sized fraction has been reported (Dalal and Henry, 1988; Guggenberger et al., 1994). Despite these contradictory results on carbohydrate content among the above-mentioned studies, all studies observed a lower ((M)annose+(G)alactose)/((A)rabinose + (X)ylose) ratio for POM and LF compared to smaller-sized and heavier fractions, respectively. Second, the thermogram of POM obtained by pyrolysis-field ionization mass spectrometry had a sharp maximum at 370 °C, symmetrical peak shapes and a simultaneous evolution of phenols, lignin monomers, lignin dimers and alkylaromatics (Schulten et al., 1993). Third, POM was enriched in phenolic CuO oxidation products (vanillyl (V), syringyl (S), and cinnamyl (C), (VSC)) with a low acid-to-aldehyde ratio's of the vanillyl units [(ac/al)$_v$] and had high syringyl-to-vanillyl ratio (S/V), indicating a high lignin content which is only little altered by microbes (Amelung et al., 1999; Guggenberger et al., 1994; Six et al., 2001; Solomon et al., 2000).

Even though the above described characteristics indicate the predominantly plant origin of the LF and POM fraction, they also indicate a partial decomposition stage and microbial contribution to these fractions. The intermediate stage between plant mater-

Table 2. General characteristics of the light fraction (LF) and particulate organic matter (POM)

| Characteristics |
| --- |
| 1. Consists of plant residues in various stages of decomposition. |
| 2. Presence of charcoal |
| 3. Mannose+Galactose/Arabinose+Xylose ratio is low |
| 4. High O-alkyl content |
| 5. High C/N ratio |
| 6. Low net N mineralization potential |
| 7. Labile SOM pool |
| 8. High lignin content (Vanillyl, Syringyl, Cinnamyl content high; Phenylpropenoic acid/benzoic acid ratio high) |
| 9. Microbial biomass and microbial debris are associated with LF |
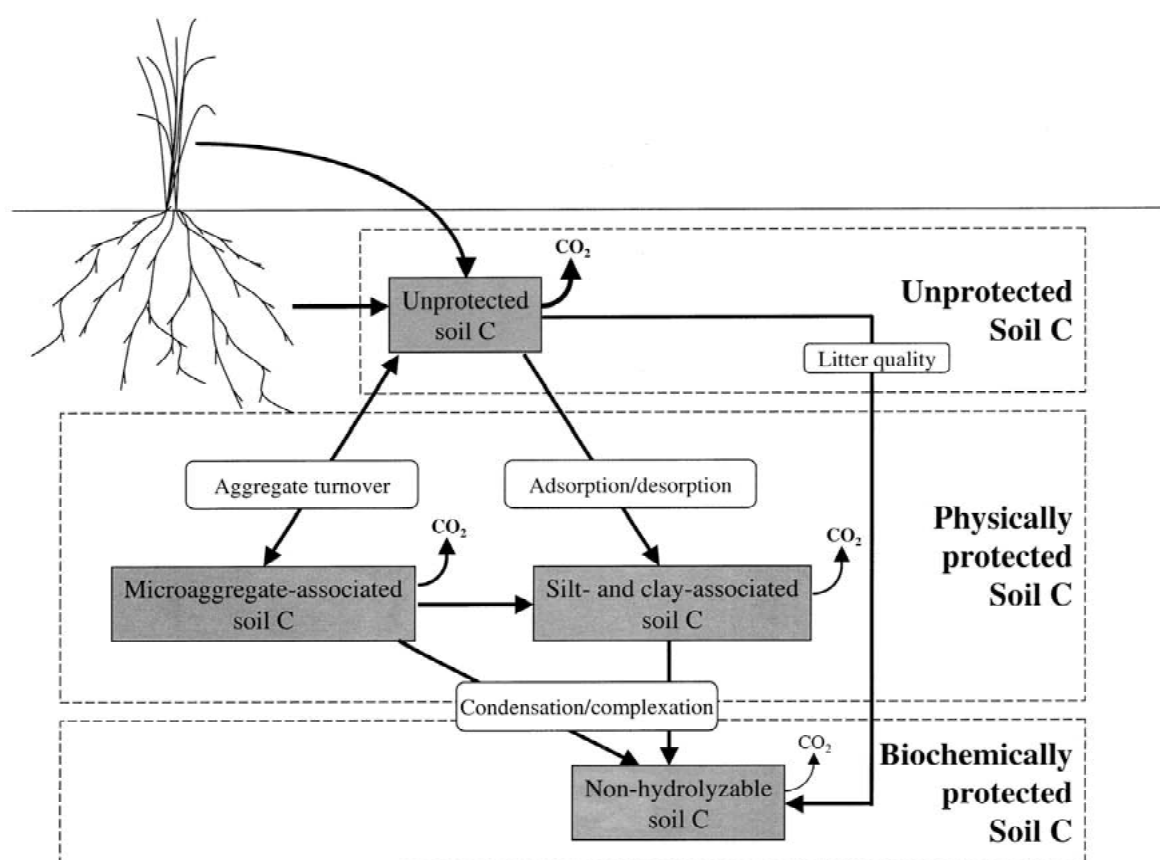
Figure 3. Conceptual model of soil organic matter (SOM) dynamics with measurable pools. The soil processes of aggregate formation/degradation, SOM adsorption/desorption and SOM condensation/complexation and the litter quality of the SOM determine the SOM pool dynamics.

ials and humified organic matter of the LF is confirmed by its amino acid composition (Greenland and Ford, 1964; Turchenek and Oades, 1979) and it has been observed that microorganisms are associated with the LF (Chotte et al., 1998; Jocteur Monrozier et al., 1991). In addition, amino sugar, glucosamine, and muramic acid analyses indicate a significant microbial contribution to POM, which is mostly fungal (Six et al., 2001; Solomon et al., 2001). Consequently, POM and LF or the unprotected SOM fraction is a mixture of compounds caused by a regenerating plant residue pool and partial microbial decomposition.

Unprotected SOM as a nutrient source

The LF and POM have a high C/N ratio and a low net N mineralization (N_{min}) potential (Catroux and Schnitzer, 1987; Chichester, 1969; Greenland and Ford, 1964; Lowe and Hinds, 1983; Sollins et al., 1984; Tiessen and Stewart, 1983; Turchenek and Oades, 1979). For example, Boone (1994) measured the N_{min} potential of LF for a cornfield, pine stand and maple stand and found that LF only represented 11% (maize), 13% (pine) and 2% (maple) of the N_{min} potential of the whole mineral soil. The net N_{min} of the LF and POM has been directly related to its N concentration and inversely related to its C:N ratio (Barrios et al., 1996; Hassink, 1995; Sollins et al., 1984), indicating the importance of the net N immobilization process, resulting from the N demand associated with initial microbial growth, for the decomposition of these fractions (Recous et al., 1999).

It has been suggested that the LF and POM are good indicators for labile organic matter (Janzen et al., 1992). Research has shown a strong correlation between LF C and/or N amount and soil respiration and/or mineralizable N (Alvarez et al., 1998; Curtin and Wen, 1999; Janzen et al., 1992, Sierra, 1996). For example, LF content explained 40–50% of the field variation in N_{min} of a maize field in the Argentine Pampa (Sierra, 1996). As the LF, POM is a significant contributor to N mineralization and turnover. A highly significant relationship between POM N and N uptake by maize was observed in a bioassay study (Vanlauwe et al., 1998) and in field trials (Vanlauwe et al., 1999).

Influence of management on inprotected SOM

Since LF and POM are labile organic matter pools, they are sensitive to management practices (Balesdent, 1996; Biederbeck et al., 1994; Bremer et al., 1994; Janzen, 1987; Janzen et al., 1992; Tiessen and Stewart, 1983; Solomon et al., 2000) and consequently highly influenced by the cultivation history of the soil (Greenland and Ford, 1964). Examples are: (1) the N pool size of the LF was significantly different between no-tillage, chisel tillage and plough tillage, whereas there were no differences in the heavy fraction among these treatments (Alvarez et al., 1998); (2) the frequency of fallow in wheat rotations in southwestern Saskatchewan was found to be the dominant factor affecting the LF-C and LF-N content (Biederbeck et al., 1994); and (3) the amounts of LF-N were significantly different between tree fallow systems with different tree species after 2 and 3 years of establishment (Barrios et al., 1997). Bremer et al. (1994) concluded that the LF is the most robust indicator of management-induced changes in SOM. They calculated the sensitivity of total C, light fraction and mineralized C to different spring wheat crop rotations by subtracting the value of the treatment with the lowest level of the respective parameters from the value of the treatment with the highest level and dividing it by the lowest value. The results were 0.2, 2.5 and 1.5 for total C, light fraction and mineralizable C respectively.

Using ^{13}C natural abundance techniques, Balesdent (1996) concluded that POM has a short mean residence time relative to C associated with clay- and silt-sized organomineral complexes, indicating the relative high lability of POM. Tiessen and Stewart (1983) observed a strong decrease in POM after 60 years of cultivation; the biggest reduction of SOM was observed in the floatable POM. Others have reported that coarse organic matter (>100 μm or >250 μm) was the SOM pool mostly influenced by type of management (Quiroga et al., 1996; Solomon et al., 2000). These results indicate that POM, especially floatable and coarse POM, provides an earlier indication of the consequences of different soil managements than did total organic matter (Dalal and Mayer, 1986a,b).

New conceptual SOM model with measurable pools

The information reviewed here suggests that SOM behaves in ways that can be explained by generalizing basic physicochemical soil processes and that a model structure relating these processes is capable of describing the behavior of measurable SOM pools (Figure 3). The model (currently at a conceptual stage) integrates traditional first order decomposition dynamics of SOM with the main SOM stabilization mechanisms that have been identified. An important ramification of this model is the concept that storage capacity of soils may become saturated with respect to C. Indications for a carbon saturation level in soils were given by Campbell et al. (1991) and Solberg et al. (1997). Both studies found no increase in soil C content with a two to three fold increase in C inputs. In addition, by relating C inputs with C content for 48 agricultural systems across 11 sites (Paul et al. 1997b), we found that an asymptotic relationship explained slightly more of the observed variability than a linear relationship (Figure 4).
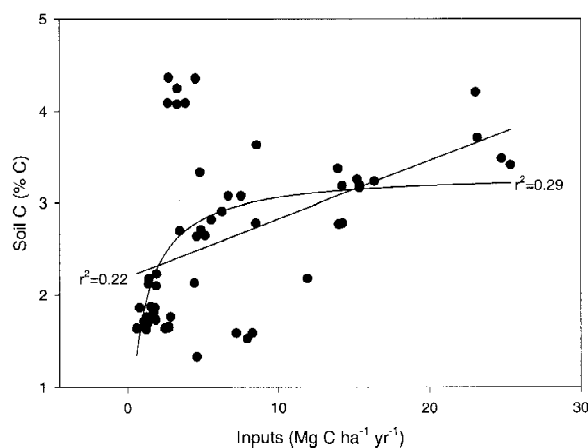
Figure 4. Relationship between carbon inputs (Mg C ha^{-1} yr^{-1}) and total soil organic carbon (Mg C ha^{-1}) across 11 agricultural field experiment sites with an array of experimental units (Paul et al., 1997b).

Figure 5. Relationship between carbon inputs (Mg C ha^{-1}) and light fraction C (g C kg^{-1} soil) in an agricultural field experiment at Melfort, Saskatchewan, Canada (Campbell et al., 1991; Janzen et al., 1992).

Basic, mechanistic soil processes are incorporated in the model but the conceptual pools (active, slow and passive) developed elsewhere (Jenkinson and Rayner, 1977; Parton et al., 1987) are still reflected within the structure of the model (Figure 3). We hypothesize that the microaggregate-protected C plus silt- and clay-protected C represents part of the slow pool whereas the unprotected pool represents the active fraction and part of the slow pool. The non-hydrolyzable fraction of the silt- and clay-associated C represents the biochemically protected pool (Figure 3) and is hypothesized to be comparable to the passive pool. The unprotected C pool is POM or LF not occluded within microaggregates whereas the microaggregate-protected C pools is fine POM occluded within microaggregates.

The processes of microaggregate formation/degradation (i.e. microaggregate turnover), adsorption/desorption, and condensation/complexation are the main mechanisms of protection and release of SOM (Figure 3). The direct transformation of unprotected soil C to the biochemically stabilized non-hydrolyzable soil C is mainly determined by litter quality. Incorporation of the processes of desorption and adsorption was used by Hassink and Whitmore (1997) to model silt- and clay-protection of SOM. Condensation and complexation dynamics have been studied and information is available in the literature (Stevenson, 1994). Microaggregate formation and degradation are beginning to be understood, but more detailed information about microaggregate behavior must be obtained to accurately model these processes.
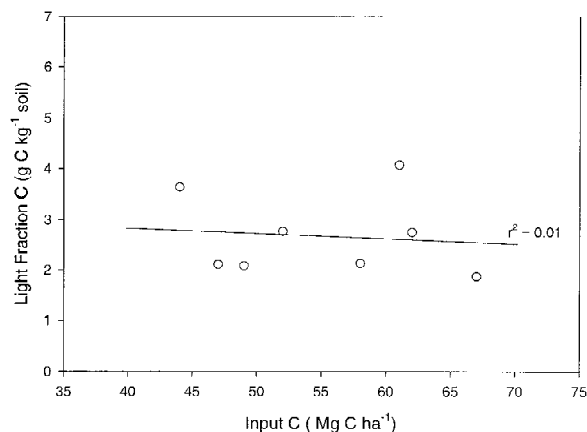
Finally, the size of the unprotected SOM pool is a function of C inputs and the specific decomposition rate of the various C components. The decomposition rate of the unprotected C pool is, by definition, independent of the level of chemical and physical protection, but it is related to soil moisture, temperature, intrinsic biodegradability and N availability as principal controls on microbial activity. There are indications that the unprotected C pool also becomes saturated. Solberg et al. (1997) found a higher amount of LF-C when 25 kg N ha^{-1} was added to a barley cropping system than when no fertilizer was added, but there was no additional increase in LF-C with 50 and 75 kg N ha^{-1} additions even though yield responses were observed. Based on data presented by Janzen et al. (1992) and Campbell et al. (1991) for the seemingly C saturated soil at Melfort, we related LF-C to C inputs and found no relationship (Figure 5).

In Figure 6, we present a fractionation scheme that could isolate the four SOM pools forming the basis of our new conceptual model, making it a model with measurable pools (Figure 3). In a first step, coarse non-protected POM, microaggregates, and silt+clay associated C are isolated from 2 mm air-dried sieved soil. These fractions can be isolated with a recently developed method by Six et al. (2000b). The method accomplishes a complete break up of macroaggregates without breaking up microaggregates, which are then separated by sieving. In a second step, fine non-protected POM that was collected together with the microaggregates on the sieve is isolated by density flotation (Six et al., 2000b). Subsequently, microag-
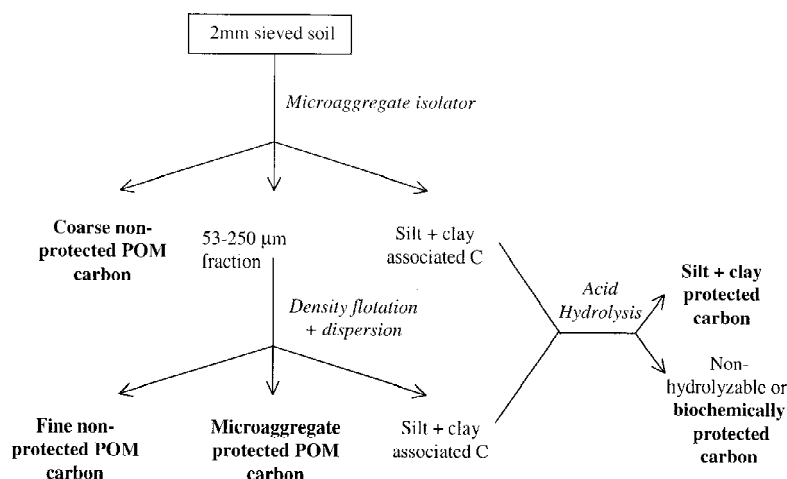
Figure 6. Fractionation scheme to isolate SOM fractions used in conceptual SOM model.

gregates are dispersed to isolate microaggregate protected POM versus silt and clay associated C (Six et al., 2000b). The silt and clay associated C fractions from step 1 and 2 are then hydrolyzed to differentiate the silt+clay protected C versus biochemically protected carbon.

Summary and conclusion

From a synthesis of knowledge on stabilization mechanisms for different soil organic matter pools we have conceptualized a model of SOM dynamics based on four measurable pools: (1) a biochemically-protected C pool, (2) a silt- and clay-protected C pool, (3) a microaggregate-protected C pool, and (4) an unprotected C pool. Each pool has its own dynamics and stabilizing mechanisms, which we hypothesize to determine a level at which soil C becomes saturated.

The silt and clay protected C pool is the C that is protected by association with the mineral particles and is by our definition hydrolyzable. The size of the pool depends on the silt and clay proportion in soil and the relationship between the silt and clay proportion differs between forest and grassland ecosystems. With the same proportion of silt and clay particles, 2:1 clay mineral dominated soils have a greater silt- and clay-protected C pool than 1:1 clay mineral dominated soils. Upon cultivation, silt- and clay-protected C is lost.

The physical protection of SOM exerted by aggregates is indicated by a positive influence of aggregation on the accumulation of SOM. In addition, cultivation has been found to result in a loss of SOM by breaking up the aggregates. Along with the accumulation of SOM by inclusion in aggregates, a qualitative change in the chemical structure of SOM has been found. The physical protection of SOM exerted by aggregates is predominantly at the microaggregate level. Therefore our second protected SOM pool is the microaggregate-protected C pool.

The biochemically-protected C pool turns over very slowly and is often equated to the non-hydrolyzable fraction. It is the inherent and attained complex chemical composition of the non-hydrolyzable fraction that inhibits decomposition.

The unprotected C pool is isolated as LF or POM not occluded within microaggregates. The Nmin in soil has been positively related to the N content of the unprotected C and negatively to the C/N ratio of the unprotected C because of immobilization during initial stages of incubation. The unprotected C pool is labile, is an important nutrient source and is very sensitive to management practices.

In order to develop a quantitative model based on our conceptual model the controls on the dynamics and sizes of our proposed pools need to be better quantified. The formation and degradation processes of microaggregates are less understood than that of macroaggregates and minimal quantitative data is available for these processes. Even though we delineated the four pools as conceptually different pools with different stabilization mechanisms because we believe that they are the main stabilization mechanisms for them, there might be some overlap in stabilization mechanisms between the different pools. For example, it is conceivable that the non-hydrolyzable fraction is not only biochemically stabilized but is also partially sta-

bilized by association with clay and silt particles or the silt and clay protected pool is also partially stabilized by incorporation in microaggregates. The relative importance of the different mechanisms should be investigated. One of the major gaps in knowledge and consequently a research priority is the mechanistic explanation of a saturation level, if it exists, for the unprotected and biochemically protected pools.

Acknowledgements

References

Alvarez R, Alvarez C R, Daniel P E, Richter V and Blotta L 1998 Nitrogen distribution in soil density fractions and its relation to nitrogen mineralisation under different tillage systems. Aust. J. Soil Res. 36, 247–256.

Amelung W, Zech W, Zhang X, Follett R F, Tiessen H, Knox E and Flach K W 1998 Carbon, nitrogen, and sulfur pools in particle-size fractions as influenced by climate. Soil Sci. Soc. Am. J. 62, 172–181.

Amelung W, Zhang X, Flach K W and Zech W 1999 Lignin in particle-size fractions of native grassland soils as influenced by climate. Soil Sci. Soc. Am. J. 63, 1222–1228.

Anderson D W, Saggar S, Bettany J R and Stewart J W B 1981 Particle size fractions and their use in studies of soil organic matter: I. The nature and distribution of forms of carbon, nitrogen, and sulfur. Soil Sci. Soc. Am. J. 45, 767–772.

Anderson D W and Paul E A 1984 Organo-mineral complexes and their study by radiocarbon dating. Soil Sci. Soc. Am. J. 48, 298–301.

Angers D A and Mehuys G R 1990 Barley and alfalfa cropping effects on carbohydrate contents of a clay soil and its size fractions. Soil Biol. Biochem. 22, 285–288.

Angers D A and Ndayegamiye A 1991 Effects of manure application on carbon, nitrogen, and carbohydrate contents of a silt loam and its particle-size fractions. Biol. Fert. Soils 11, 79–82.

Angers D A, Ndayegamiye A and Cote D 1993 Tillage-induced differences in organic matter of particle-size fractions and microbial biomass. Soil Sci. Soc. Am. J. 57, 512–516.

Angers D A, Recous S and Aita C 1997 Fate of C and nitrogen in water-stable aggregates during decomposition of $^{13}C^{15}N$-labelled wheat straw in situ. Eur. J. Soil Sci. 48, 295–300.

Arah J 2000 Modelling SOM cycling in rice-based production systems *In* Carbon and Nitrogen Dynamics in Flooded Soil. Eds. G J D Kirk and D C Olk. pp 163–179. International Rice Research Institute, Philippines.

Balesdent J 1996 The significance of organic separates to carbon dynamics and its modeling in some cultivated soils. Eur. J. Soil Sci. 47, 485–493.

Balesdent J, Besnard E, Arrouays D and Chenu C 1998 The dynamics of carbon in particle-size fractions of soil in a forest-cultivation sequence. Plant Soil 201, 49–57.

Balesdent J, Chenu C and Balabane M 2000 Relationship of soil organic matter dynamics to physical protection and tillage. Soil Tillage Res. 53, 215–230.

Barrios E, Buresh R J and Sprent J I 1996 Nitrogen mineralization in density fractions of soil organic matter from maize and legume cropping systems. Soil Biol. Biochem. 28, 185–193.

Barrios E, Kwesiga F, Buresh R J and Sprent J I 1997 Light fraction soil organic matter and available nitrogen following trees and maize. Soil Sci. Soc. Am. J. 61, 826–831.

Barrow N J 1969 The accumulation of soil organic matter under pasture and its effect on soil properties. Aust. J. Exper. Agric. Animal Husb. 9, 437–445.

Bartlett J R and Doner H E 1988 Decomposition of lysine and leucine in soil aggregates: adsorption and compartimentalization. Soil Biol. Biochem. 20, 755–759.

Bates J A R 1960 Studies on a Nigerian forest soil I. The distribution of organic matter in the profile and in various soil fractions. J. Soil Sci. 11, 246–256.

Beare M H, Cabrera M L, Hendrix P F and Coleman D C 1994 Aggregate-protected and unprotected organic matter pools in conventional- and no-tillage soils. Soil Sci. Soc. Am. J. 58, 787–795.

Besnard E, Chenu C, Balesdent J, Puget P and Arrouays D 1996 Fate of particulate organic matter in soil aggregates during cultivation. Eur. J. Soil Sci. 47, 495–503.

Biederbeck V O, Janzen H H, Campbell C A and Zentner R P 1994 Labile soil organic matter as influenced by cropping practices in an arid environment. Soil Biol. Biochem. 26, 1647–1656.

Bonde T, Christensen B T and Cerri C C 1992 Dynamics of soil organic matter as reflected by natural ^{13}C abundance in particle size fractions of forested and cultivated oxisols. Soil Biol. Biochem. 24, 275–277.

Boone R D 1994 Light fraction soil organic matter: origin and contribution to net nitrogen mineralization. Soil Biol. Biochem. 26, 1459–1468.

Bosatta E and Agren G I 1996 Theoretical analyses of carbon and nutrient dynamics in soil profiles. Soil Biol. Biochem. 28, 1523–1531.

Bossuyt H, Six J and Hendrix P F 2002 Aggregate protected carbon in no-tillage and conventional tillage agroecosystems using ^{14}C-labeled plant residue. Soil Sci. Soc. Am. J., Submitted.

Bremer E, Janzen H H and Johnston A M 1994 Sensitivity of total, light and mineralizable organic matter to management practices in a Lethbridge soil. Can. J. Soil Sci. 74, 131–138.

Cadisch G and Giller K E 1997 Driven by Nature: Plant litter quality and decomposition. CAB International, Wallingford, Oxon, UK. 409 p.

Cambardella C A and Elliott E T 1992 Particulate soil organic matter across a grassland cultivation sequence. Soil Sci. Soc. Am. J. 56, 777–783.

Cambardella C A and Elliott E T 1993 Carbon and nitrogen distribution in aggregates from cultivated and native grassland soils. Soil Sci. Soc. Am. J. 57, 1071–1076.

Campbell C A, Bowren K E, Schnitzer M, Zentner R P and Townley-Smith L 1991 Effect of crop rotations and fertilization on soil biochemical properties in a thick Black Chernozem. Can. J. Soil Sci. 71, 377–387.

Catroux G and 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.

Chantigny M H, Angers D A, Prévost D, Vézina L-P and Chalifour F-P 1997 Soil aggregation and fungal and bacterial biomass under annual and perennial cropping systems. Soil Sci. Soc. Am. J. 61, 262–267.

Cheshire M V and Mundie C M 1981 The distribution of labeled sugars in soil particle size fractions as a means of distinguishing plant and microbial carbohydrate residues. J. Soil Sci. 32, 605–618.

Chichester F W 1969 Nitrogen in soil organo-mineral sedimentation fractions. Soil Sci. 107, 356–363.

Chotte J L, Ladd J N and Amato M 1998 Sites of microbial assimilation and turnover of soluble and particulate ^{14}C-labelled substrates decomposing in a clay soil. Soil Biol. Biochem. 30, 205–218.

Christensen B T 1985 Carbon and nitrogen in particle size fractions isolated from Danish arable soils by ultrasonic dispersion and gravity-sedimentation. Acta Agric. Scand. 35, 175–187.

Christensen B T 1986 Straw incorporation and soil organic matter in macro-aggregates and particle size separates. J. Soil Sci. 37, 125–135.

Christensen B T 1987 Decomposability of organic matter in particle size fractions from field soils with straw incorporation. Soil Biol. Biochem. 19, 429–435.

Christensen B T 1996 Carbon in primary and secondary organomineral complexes. In Structure and Organic Matter Storage in Agricultural Soils. Eds. M R Carter and B A Stewart. pp 97–165. CRC Press, Inc, Boca Raton, FL.

Collins H P, Elliott E T, Paustian K, Bundy L G, Dick W A, Huggins D R, Smucker A J M and Paul E A 2000 Soil carbon pools and fluxes in long-term corn belt agroecosystems. Soil Biol. Biochem. 32, 157–168.

Curtin D and Wen G 1999 Organic matter fractions contributing to soil nitrogen mineralization potential. Soil Sci. Soc. Am. J. 63, 410–415.

Dalal R C and Henry R J 1988 Cultivation effects on carbohydrate contents of soil and soil fractions. Soil Sci. Soc. Am. J. 52, 1361–1365.

Dalal R C and Mayer R J 1986a Long term trends in fertility of soils under continuous cultivation and cereal cropping in southern Queensland. III distribution and kinetics of soil organic carbon in particle-size fractions. Aust. J. Soil Res. 24, 293–300.

Dalal R C and Mayer R J 1986b Long term trends in fertility of soils under continuous cultivation and cereal cropping in southern Queensland. IV Loss of organic carbon from different density functions. Aust. J. Soil Res. 24, 301–309.

Denef K, Six J, Bossuyt H, Frey S D, Elliott E T, Merckx R and Paustian K 2001 Influence of wet-dry cycles on the interrelationship between aggregate, particulate organic matter, and microbial community dynamics. Soil Biol. Biochem. 33, 1599–1611.

Dixon J B 1989 Kaolin and Serpentine group minerals. In Minerals in Soil Environments. Ed. J B Dixon and S B Weed. pp 467–525. SSSA Book Series No. 1. SSSA, Madison, WI.

Donigian A S, Patwardhan A S, Chinnaswamy R V and Barnwell T O 1997 Modeling soil carbon and agricultural practices in the U.S.: An update of preliminary study results. In Soil Processes and the Carbon Cycle. Eds. R Lal, J M Kimble, R F Follett and B A Stewart. pp 499–518. CRC Press, Inc, Boca Raton, FL.

Edwards A P and Bremner J M 1967 Microaggregates in soils. J. Soil Sci. 18, 64–73.

Elliott E T 1986 Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. Soil Sci. Soc. Am. J. 50, 627–633.

Elliott E T and Coleman D C 1988 Let the soil work for us. Ecological Bulletins 39, 23–32.

Elliott E T, Anderson R V, Coleman D C and Cole C V 1980 Habitable pore space and microbial trophic interactions. Oikos 35, 327–335.

Elliott E T, Paustian K and Frey S D 1996 Modeling the measurable or measuring the modelable: A hierarchical approach to isolating meaningful soil organic matter fractionations. In Evaluation of Soil Organic Matter Models. Eds. D S Powlson, P Smith and J U Smith. pp 161–179. NATO ASI Series, Springer-Verlag.

Elustondo J, Angers D A, Laverdiere M R and N'Dayegamiye A 1990 Itude comparative de l'agrégation et de la matiére organique associée aux fractions granulométriques de sept soils sous culture de maïs ou en prairie. Can. J. Soil Sci. 70, 395–402.

Feller C and Beare M H 1997 Physical control of soil organic matter dynamics in the tropics. Geoderma 79, 69–116.

Feller C, Albrecht A and Tessier C 1997 Aggregation and organic matter storage in kaolinitic and smectitic tropical soils. In Structure and Organic Matter Storage in Agricultural Soils. Eds. M R Carter and B A Stewart. pp 309–359. CRC Press, Boca Raton, FL.

Follett R F, Paul E A, Leavitt S W, Halvorson A D, Lyon D and Peterson G A 1997 Carbon isotope ratios of Great Plains soils and in wheat-fallow systems. Soil Sci. Soc. Am. J. 61, 1068–1077.

Franzluebbers A J and Arshad M A 1996 Water-stable aggregation and organic matter in four soils under conventional and zero tillage. Can. J. Soil Sci. 76, 387–393.

Franzluebbers A J and Arshad M A 1997 Particulate organic carbon content and potential mineralization as affected by tillage and texture. Soil Sci. Soc. Am. J. 61, 1382–1386.

Gale W J, Cambardella C A and Bailey T B 2000 Root-derived carbon and the formation and stabilization of aggregates. Soil Sci. Soc. Am. J. 64, 201–207.

Golchin A, Oades J M, Skjemstad J O and Clarke P 1994 Study of free and occluded particulate organic matter in soils by solid state ^{13}C CP/MAS NMR spectroscopy and scanning electron microscopy. Aust. J. Soil. Res. 32, 285–309.

Golchin A, Clarke P, Oades J M and Skjemstad J O 1995 The effects of cultivation on the composition of organic matter and structural stability of soils. Aust. J. Soil Res. 33, 975–993.

Greenland D J 1965 Interactions between clays and organic compounds in soils. Part I. Mechanisms of interaction between clays and defined organic compounds. Soils and Fertilizers 28, 415–532.

Greenland D J and Ford G W 1964 Separation of partially humified organic materials from soils by ultrasonic vibration. Transactions of the eight International Congress of Soil Science 3, 137–148.

Gregorich E G, Kachanoski R G and Voroney R P 1989 Carbon mineralization in soil size fractions after various amounts of aggregate disruption. J. Soil Sci. 40, 649–659.

Guggenberger G, Christensen B T and Zech W 1994 Land-use effects on the composition of organic matter in particle-size separates of soil: I. Lignin and carbohydrate signature. Eur. J. Soil Sci. 45, 449–458.

Guggenberger G, Zech W, Haumaier L and Christensen B T 1995 Land-use effects on the composition of organic matter in particle-size separates of soil: II. CPMAS and solution ^{13}C NMR analysis. Eur. J. Soil Sci. 46, 147–158.

Guggenberger G, Frey S D, Six J, Paustian K and Elliott E T 1999 Bacterial and fungal cell-wall residues in conventional and no-tillage agroecosystems. Soil Sci. Soc. Am. J. 63, 1188–1198.

Hassink J 1995 Density fractions of soil macroorganic matter and microbial biomass as predictors of C and N mineralization. Soil Biol. Biochem. 27, 1099–1108.

Hassink J 1997 The capacity of soils to preserve organic C and N by their association with clay and silt particles. Plant Soil 191, 77–87.

Hassink J and Whitmore A P 1997 A model of the physical protection of organic matter in soils. Soil Sci. Soc. Am. J. 61, 131–139.

Hattori T 1988 Soil aggregates as microhabitats of microorganisms. Rep. Inst. Agr. Res. Tohoku Univ. 37, 23–36.

Ismail I, Blevins R L and Frye W W 1994 Long-term no-tillage effects on soil properties and continuous corn yields. Soil Sci. Soc. Am. J. 58, 193–198.

Janzen H H 1987 Soil organic matter characteristics after long-term cropping to various spring wheat rotations. Can. J. Soil Sci. 67, 845–856.

Janzen H H, Campbell C A, Brandt S A, Lafond G P and Townley-Smith L 1992 Light fraction organic matter in soils from long-term crop rotations. Soil Sci. Soc. Am. J. 56, 1799–1806.

Jastrow J D 1996 Soil aggregate formation and the accrual of particulate and mineral-associated organic matter. Soil Biol. Biochem. 28, 656–676.

Jastrow J D, Boutton T W and Miller R M 1996 Carbon dynamics of aggregate-associated organic matter estimated by carbon-13 natural abundance. Soil Sci. Soc. Am. J. 60, 801–807.

Jenkinson D S and Rayner J H 1977 The turnover of soil organic matter in some of the Rothamsted classical experiments. Soil Sci. 123, 298–305.

Jocteur Monrozier L, Ladd J N, Fitzpatrick R W, Foster R C and Raupach M 1991 Components and microbial biomass content of size fractions in soils of contrasting aggregation. Geoderma 49, 37–62.

Kemper W D and Koch E J 1966 Aggregate stability of soils from Western United States and Canada. pp 1–52. Colorado Agric. Exp. Stn. Bull. 1355.

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

Kononova M M 1966 Soil Organic Matter, Its Nature, Its role in Soil Formation and in Soil Fertility. Pergammon Press, Oxford, 252 p.

Ladd J N, Amato M and Oades J M 1985 Decomposition of plant material in Australian soils. III. Residual organic and microbial biomass C and N from isotope-labeled legume material and soil organic matter, decomposing under field conditions. Aust. J. Soil Res. 23, 603–611.

Ladd J N, Jocteur-Monrozier L and Amato M 1992 Carbon turnover and nitrogen transformations in an alfisol and vertisol amended with [U-^{14}C] glucose and [^{15}N] ammonium sulfate. Soil Biol. Biochem. 24, 359–371.

Larson W E, Clapp C E, Pierre W H, Morachan Y B 1972 Effects of increasing amounts of organic residues on continuous corn: II. Organic carbon, nitrogen, phosphorus and sulfur. Agronomy J. 64, 204–208.

Leinweber P and Reuter G 1992 The influence of different fertilization practices on concentrations of organic carbon ant total nitrogen in particle-size fractions during 34 years of a soil formation experiment in loamy marl. Biol. Fert. Soils 13, 119–124.

Leavitt S W, Follett R F and Paul E A 1996 Estimation of slow- and fast-cycling soil organic carbon pools from 6N HCl hydrolysis. Radiocarbon 38, 231-239.

Lowe L E and Hinds A A 1983 The mineralization of nitrogen and sulphur from particle size separates of gleysolic soils. Can. J. Soil Sci. 63, 761–766.

Magid J, Gorissen A and Giller K E 1996 In search of the elusive 'active' fraction of soil organic matter: three size-density fractionation methods for tracing the fate of homogeneously ^{14}C labeled plant materials. Soil Biol. Biochem. 28, 89–99.

McGill W B 1996 Review and classification of ten soil organic matter models. In Evaluation of Soil Organic Matter Models. Eds. D S Powlson, P Smith and J U Smith. pp. 111–132. NATO ANSI Series, Springer Verlag.

McKeague J A 1971 Organic matter in particle-size fractions and specific gravity fractions of some Ah horizons. Can. J. Soil Sci. 51, 499–505.

Meijboom F W, Hassink J and Van Noordwijk M 1995 Density fractionation of soil macroorganic matter using silica suspensions. Soil Biol. Biochem. 27, 1109–1111.

Merckx R, Den Hartog A and van Veen J A 1985 Turnover of root-derived material and related microbial biomass formation in soils of different texture. Soil Biol. Biochem. 17, 565–569.

Metherell A K 1992 Simulation of soil or oranic matter dynamics and nutrient cycling in agroecosystems. Ph.D. Diss. Colorado State University, Fort Collins.

Molloy L F and Speir T W 1977 Studies on a climosequence of soils in tussock grassland. 12. Constituents of the soil light fraction. New Zealand J. Soil Sci. 20, 167–177.

Monreal C M and Kodama H 1997 Influence of aggregate architecture and minerals on living habitats and soil organic matter. Can. J. Soil Sci. 77, 367–377.

Motavalli P P, Palm C A, Parton W J, Elliott E T and Frey S D 1994 Comparison of laboratory and modeling simulation methods for estimating carbon pools in tropical forest soils. Soil Biol. Biochem. 26, 935–944.

Murayama S, Cheshire M V, Mundie C M, Sparling G P and Shepherd H 1979 Comparison of the contribution to soil organic matter fractions, particularly carbohydrates, made by plant residues and microbial products. J. Sci. Food Agric. 30, 1025–1034.

Nacro H B, Benest D and Abbadie L 1996 Distribution of microbial activities and organic matter according to particle size in a humid savanna soil (Lamato, Cote D'Ivoire). Soil Biol. Biochem. 28, 1687–1697.

Oades J M, Vassallo A M, Waters A G and Wilson M A 1987 Characterization of organic matter in particle size and density fractions from Red-Brown Earth by solid-state ^{13}C NMR Aust. J. Soil Res. 25, 71–82.

Oades J M and Waters A G 1991 Aggregate hierarchy in soils. Aust. J. Soil Res. 29, 815–828.

Parton W J, Schimel D S, Cole C V and Ojima D S 1987 Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci. Soc. Am. J. 51, 1173–1179.

Parton W J, Ojima D S, Cole C V and Schimel D S 1994 A general model for soil organic matter dynamics: Sensitivity to litter chemistry, texture and management. In Quantitative Modeling of Soil Forming Processes. pp 147–167. SSSA Special Publication 39, Madison, WI.

Paul E A, Horwath W R, Harris D, Follett R, Leavitt S W, Kimball B A and Pregitzer K 1995 Establishing the pool sizes and fluxes in CO$_2$ emissions from soil organic matter turnover. In Soils and Global Change. Eds. R Lal, J Kimble, E Levine and B A Stewart. pp 297–304. CRC Press, Boca Raton, FL.

Paul E A, Follett R F, Leavitt S W, Halvorson A, Peterson G A and Lyon D J 1997a Radiocarbon dating for determination of soil organic matter pool sizes and dynamics. Soil Sci. Soc. Am. J. 61, 1058–1067.

Paul E A, Paustian K, Elliott E T and Cole C V 1997b Soil Organic Matter in Temperate Agroecosystems. CRC Press, Boca Raton. 414 p.

Paul E A, Harris D, Collins H P, Schulthess U, Robertson G P 1999 Evolution of CO$_2$ and soil carbon dynamics in biologically managed, row-crop agroecosystems. Appl. Soil Ecol. 11, 53–65.

Paul E A, Collins H P and Leavitt S W 2001 Dynamics of resistant soil carbon of Midwestern agricultural soils measured by naturally occurring ^{14}C abundance Geoderma 104, 239–256.

Paustian K, Parton W J and Persson J 1992 Modeling soil organic matter in organic-amended and N-fertilized long-term plots. Soil Sci. Soc. Am. J. 56, 476–488. Paustian K 1994 Modelling soil biology and biogeochemical processes for sustainable agriculture. In Management of Soil Biota in Sustainable Farming Systems. Eds. C Paknjurst, B M Doube and V V S R Gupta. pp 182–196. CISRO Publ., Melbourne.

Paustian K, Collins H P and Paul E A 1997 Management controls on soil carbon. In Soil Organic Matter in Temperate Agroecosystems. Eds. E A Paul, K Paustian, E T Elliott and C V Cole. pp 15–49. CRC Press, Boca Raton, FL.

Paustian K, Six J, Elliott E T and Hunt H W 2000 Management options for reducing CO$_2$ emissions from agricultural soils. Biogeochemistry 48, 147–163.

Powlson D S, Smith P and Smith JU 1996 Evaluation of Soil Organic Matter Models. NATO ANSI Series, Springer Verlag. 429 p.

Priesack E and Kisser-Priesack G M 1993 Modelling diffusion and microbial uptake of ^{13}C-glucose in soil aggregates. Geoderma 56, 561–573.

Puget P, Chenu C and Balesdent J 1995 Total and young organic matter distributions in aggregates of silty cultivated soils. Eur. J. Soil Sci. 46, 449–459.

Puget P, Besnard E and Chenu C 1996 Une méthode de fractionnement des matières organiques particulaires des sols en fonction de leur localisation dans les agrégats. C.R. Acad. Sci. Paris, t. 322, sJrie II a, pp. 965–972

Puget P, Angers D A and Chenu C 1999 Nature of carbohydrates associated with water-stable aggregates of two cultivated soils. Soil Biol. Biochem. 31, 55–63.

Pulleman M M and Marinissen J C Y 2001 Carbon mineralization as affected by natural aggregation in pasture versus arable soil. Soil Biol. Biochem. submitted.

Quiroga A R, Buschiazzo D E and Peinemann N 1996 Soil organic matter particle size fractions in soils of the semiarid argentinian pampas. Soil Sci. 161, 104–108.

Recous S, Aita C and Mary B 1999 In situ changes in gross N transformations in bare soil after addition of straw. Soil Biol. Biochem. 31, 119–133.

Ridley A M, Helyar K R and Slattery W J 1990 Soil acidification under subterranean clover (*Trifolium subterraneaum* L.) pastures in North-Eastern Victoria. Aust. J. Exper. Agric. 30, 195–201.

Russell J S 1960 Soil fertility changes in the long term experimental plots at Kybybolite, South Australia. I. Changes in pH, total nitrogen, organic carbon and bulk density. Aust. J. Agr. Res. 11, 902–926.

Schnitzer M and Khan S U 1972 Humic Substances in the Environment. Marcel Dekker, New York. 379 p.

Schofield R K and Samson H R 1954 Flocculation of kaolinite due to the attraction of oppositely charged crystal faces. Faraday Discussions 18, 135–145.

Schulten H R, Leinweber P and Sorge C 1993 Composition of organic matter in particle size fractions of an agricultural soil. J. Soil Sci. 44, 677–691.

Sexstone A J, Revsbech N P, Parkin T B and Tiedje J M 1985 Direct measurement of oxygen profiles and denitrification rates in soil aggregates. Soil Sci. Soc. Am. J. 49, 645–651.

Shang C and Tiessen H 1997 Organic matter lability in a tropical oxisol: Evidence from shifting cultivation, chemical oxidation, particle size, density, and magnetic fractionations. Soil Sci. 162, 795–807.

Sierra J 1996 Nitrogen mineralisation and its error of estimation under field conditions related to the light-fraction soil organic matter. Aust. J. Soil Res. 34, 755–767.

Six J, Elliott E T, Paustian K and Doran J W 1998 Aggregation and soil organic matter accumulation in cultivated and native grassland soils. Soil Sci. Soc. Am. J. 62, 1367–1377.

Six J, Elliott E T and Paustian K 1999 Aggregate and soil organic matter dynamics under conventional and no-tillage systems. Soil Sci. Soc. Am. J. 63, 1350–1358.

Six J, Paustian K, Elliott E T and Combrink C 2000a Soil structure and soil organic matter: I. Distribution of aggregate size classes and aggregate associated carbon. Soil Sci. Soc. Am. J. 64, 681–689.

Six J, Elliott E T and Paustian K 2000b Soil macroaggregate turnover and microaggregate formation: A mechanism for C sequestration under no-tillage agriculture. Soil Biol. Biochem. 32, 2099–2103.

Six J, Guggenberger G, Paustian K, Haumaier L, Elliott E T and Zech W 2001 Sources and composition of soil organic matter fractions between and within aggregates. Eur. J. Soil Sci. 52, 607–618.

Skjemstad J O, Dalal R C and Barron P F 1986 Spectroscopic investigation of cultivation effects on organic matter of Vertisols. Soil Sci. Soc. Am. J. 50, 354–359.

Skjemstad J O, Le Feuvre R P and Prebble R E 1990 Turnover of soil organic matter under pasture as determined by ^{13}C natural abundance. Aust. J. Soil Res. 28, 267–276.

Skjemstad J O, Clarke P, Taylor J A, Oades J M and McClure S G 1996 The chemistry and nature of protected carbon in soil. Aust. J. Soil Res. 34, 251–271.

Solberg E D, Nyborg M, Izaurralde R C, Malhi S S, Janzen H H and Molina-Ayala M 1997 Carbon Storage in soils under continuous cereal grain cropping: N fertilizer and straw. In Management of Carbon Sequestration in Soil. Eds. R. Lal, J M Kimble, R F Follett and B A Stewart. pp 235–254. CRC Press, Boca Raton, FL.

Sollins P, Spycher G and Glassman C A 1984 Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. Soil Biol. Biochem. 16, 31–37.

Sollins P, Hofmann P and Caldwell B A 1996 Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74, 65–105.

Solomon D, Lehmann J and Zech W 2000 Land use effects on soil organic matter properties of chromic Luvisols in semi-arid northern Tanzania: carbon, nitrogen, lignin and carbohydrates. Agr. Ecosys. Environ. 78, 203–213.

Solomon D, Lehmann J and Zech W 2001 Land use effects on amino sugar signature of chromic Luvisols in the semi-arid part of northern Tanzania. Biol. Fert. Soils 33, 33–40.

Sorensen L H 1972 Stabilization of newly formed amino acid metabolites in soil by clay minerals. Soil Sci. 114, 5–11.

Stemmer M, Von Lutznow M, Kandeler E, Pichlmayer F and Gerzabek M H 1999 The effect of maize straw placement on

mineralization of C and N in soil particle size fractions. Eur. J. Soil Sci. 50, 73–85.

Stevenson F J 1994 Humus Chemistry: Genesis, Composition, Reactions. John Wiley & Sons, New York. 496 p.

Tiessen H and Stewart J WB 1983 Particle-size fractions and their use in studies of soil organic matter: II Cultivation effects on organic matter composition in size fractions. Soil Sci. Soc. Am. J. 47, 509–514.

Tisdall J M and Oades J M 1982 Organic matter and water-stable aggregates in soils. J. Soil Sci. 33, 141–163.

Torn M S, Trumbore S E, Chadwick O A, Vitousek P M and Hendricks D M 1997 Mineral control of soil organic carbon storage and turnover. Nature 389, 170–173.

Trumbore S E 1993 Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. Glob. Biogeochem. Cycles 7, 275–290.

Trumbore S E, Chadwick O A and Amundson R 1996 Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science 272, 393–396.

Turchenek L W and Oades J M 1979 Fractionation of organomineral complexes by sedimentation and density techniques. Geoderma 21, 311–343.

Vanlauwe B, Sanginga N and Merckx R 1998 Soil organic matter dynamics after addition of nitrogen-15-labeled Leucena and Dactyladenia residues. Soil Sci. Soc. Am. J. 62, 461–466.

Vanlauwe B, Aman S, Aihou K, Tossah B K, Adebiyi V, Sanginga N, Lyasse O, Diels J and Merckx R 1999 Alley cropping in the moist savanna of West-Africa III. Soil organic matter fractionation and soil productivity. Agroforestry Systems 42, 245–264.

van Veen J A and Kuikman P J 1990 Soil structural aspects of decomposition of organic matter by micro-organisms. Biogeochemistry 11, 213–233.

Young J L and Spycher G 1979 Water-dispersible soil organicmineral particles: I. Carbon and nitrogen distribution. Soil Sci. Soc. Am. J. 43, 324–328.

Zhang H, Thompson M L and Sandor H A 1988 Compositional differences in organic matter among cultivated and uncultivated Argiudolls and Hapludalfs derived from loess. Soil Sci. Soc. Am. J. 52, 516–222.

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Appendix A. Silt plus clay (0–20 μm) content and silt- and clay-associated C concentration for various soils arranged by land use

Author	Year	Clay type	Silt+clay (%)	Silt+clay C (g C kg soil^{-1})
Cultivated				
Balesdent et al.	1998	2:1	57.7	13.8
			62.5	25.8
Bonde et al.	1992	1:1	70.3	16.5
			70.5	15.5
Christensen	1985	2:1	28.3	8.9
			29.0	15.8
			60.4	14.6
			78.4	13.2
			97.6	17.2
Christensen	1986	2:1	36.8	14.9
			36.8	13.8
Christensen	1987	2:1	13.3	21.7
			13.6	22.4
			30.1	10.7
			30.2	11.1
Feller and Beare	1997	1:1	12.5	3.7
			15.2	3.9
			10.1	3.2
			12.3	3.5
			13.3	3.8
			13.6	3.5
			15.6	4.7
			26.9	9.7
			28.4	7.2
			69.4	14.8
			70.1	12.6
			71.6	13.3
			80.5	16.9
			86.9	33.3
			87.1	27.4

Appendix A. Continued

Author	Year	Clay type	Silt+clay (%)	Silt+clay C (g C kg soil^{-1})
Feller and Beare	1997	2:1	11.7	2.7
			70.5	25.4
Guggenberger et al.	1994	2:1	58.5	24.2
Hassink	1997	2:1	3.6	3.6
			6.2	7.4
Schulten et al.	1993	2:1	21.0	16.3
Turchenek and Oades	1979	2:1	83.0	45.2
Turchenek and Oades	1979	Mixed	46.5	8.4
			80.2	59.1
Zhang	1988	2:1	49.0	14.3
			53.0	19.2
Forest				
Balesdent et al.	1998	2:1	61.4	47.4
Bates	1960	1:1	9.7	7.1
Bonde et al.	1992	1:1	62.9	24.8
Feller and Beare	1997	1:1	11	5.5
			22.7	13.1
			29.4	9.8
			61.4	18.0
			62.9	26.1
			61.4	34.2
Feller and Beare	1997	2:1	12.0	3.9
Guggenberger et al.	1994	2:1	63.2	71.7
			63.7	46.4
McKeague	1971	2:1	43.0	20.8
			43.8	30.3
			60.0	26.1
Grassland				
Amelung et al.	1998	2:1	19.9	7.4
			26.1	7.0
			28.0	7.5
			32.5	12.6
			32.6	9.9
			33.6	9.9
			35.1	27.6
			38.7	15.1
			41.3	22.6
			45.3	18.7
			45.7	16.1
			47.3	23.1
			48.6	27.0
			49.6	22.2
			51.4	39.9
			53.7	19.8
			57.8	12.6
			59.7	24.2
			59.8	29.4

Appendix A. Continued

Author	Year	Clay type	Silt+clay (%)	Silt+clay C (g C kg soil^{-1})
			64.6	48.2
			77.4	41.8
Dalal and Mayer	1986a	2:1	52.1	13.2
			55.8	14.8
			65.2	14.0
Dalal and Mayer	1986a	Mixed	27.4	6.7
			82.3	11.5
			86.8	14.0
Elustondo et al.	1991	2:1	15.4	15.7
			16.7	17.9
			34.8	19.9
			43.7	21.3
			61.2	23.7
			63.5	24.1
			65.8	37.6
Feller and Beare	1997	1:1	4.9	1.5
			11.9	5.0
			17.4	6.0
			19.3	7.5
			19.3	7.8
			25.2	9.7
			28.4	12.7
			30.5	10.7
			72	9.8
			82.3	30.1
			82.9	36.1
Feller and Beare	1997	2:1	70.1	32.7
			59.4	19.4
Guggenberger et al.	1995	1:1	56.0	22.3
			56.1	19.6
			56.5	22.6
Guggenberger et al.	1994	2:1	60.1	52.0
Hassink	1997	2:1	1.9	4.1
			2.8	0.9
			3.5	3.6
			3.6	1.0
			4.4	7.5
			5.4	3.0
			5.8	10.2
			8.9	3.6
			13.3	11.1
			35.6	18.6
			36.5	27.5
			42.6	19.9
			45.5	13.5
			76.0	31.0
Leinweber and Reuter	1992	2:1	37.6	14.8
			41.0	8.9
			41.5	10.6
			41.9	7.4

Appendix A. Continued

Author	Year	Clay type	Silt+clay (%)	Silt+clay C (g C kg soil^{-1})
McKeague	1971	2:1	37.0	22.4
			45.0	34.3
			48.3	43.1
			52.1	47.9
			59.4	50.6
			62.4	47.4
			70.0	37.2
			70.2	70.7
			70.3	48.0
			73.3	28.1
Nacro et al.	1996	1:1	16.0	6.0
Turchenek and Oades	1979	Mixed	50.7	19.7
Zhang et al.	1988	2:1	54.7	28.2
			56.3	32.0
Unknown				
Feller and Beare	1997	1:1	5.2	1.2
			6.5	1.4
			20.8	7.9
			24.2	8.4
			27.4	11.8
			67.8	20.3
			68.5	16.3

Appendix B. Silt plus clay (0–50 μm) content and silt- and clay-associated C concentration for various soils arranged by land use

Author	Year	Clay type	Silt+clay (%)	Silt+clay C (g C kg soil^{-1})
Cultivated				
Anderson et al.	1981	2:1	68.0	16.0
			70.5	18.9
Angers et al.	1993	2:1	65.0	23.3
			67.0	29.7
			69.0	29.9
Angers and Ndayegamiye	1991	2:1	73.0	17.1
			73.0	17.1
			73.0	14.0
Balesdent et al.	1998	2:1	88.1	14.1
			91.4	26.3
[a]Catroux and Schnitzer	1987	2:1	69.5	26.7

Appendix B. Continued

Author	Year	Clay type	Silt+clay (%)	Silt+clay C (g C kg soil^{-1})
Elustondo et al.	1990	2:1	9.0	11.7
			24.4	17.8
			41.0	19.8
			44.4	18.0
			64.6	71.4
			71.6	24.2
			72.3	39.3
Shang and Tiessen	1997	1:1	22.8	7.9
[c]Stemmer et al.	1999	2:1	52.2	14.1
			82.1	11.2
Tiessen and Stewart	1983	1:1	68.0	18.9
Tiessen and Stewart	1983	2:1	21.0	9.8
			26.0	21.8
			26.0	15.6
			26.0	13.7
[b]Turchenek and Oades	1979	2:1	92.4	46.2
[b]Turchenek and Oades	1979	Mixed	80.6	20.7
			96.5	61.9
Young and Spycher	1979	2:1	52.0	7.9
			88.0	8.0
Zhang et al.	1988	2:1	92.3	15.8
			94.0	21.1
Forest				
Balesdent et al.	1998	2:1	87.6	48.2
Bates	1960	1:1	38.4	30.9
McKeague	1971	2:1	61.0	21.3
			63.8	30.6
			65.7	39.9
			75.0	26.3
			90.6	32.9
Shang and Tiessen	1997	1:1	19.7	8.7
Young and Spycher	1979	2:1	18.0	31.6
			77.0	37.6
Grassland				
McKeague	1971	2:1	28.3	43.2
			55.0	23.1
			58.0	36.5
			69.1	48.7
			71.3	43.5
			75.4	53.3
			78.4	47.6
			81.2	71.4
			87.0	38.0
			89.3	48.4
			94.3	28.3
			97.0	56.9
Nacro et al.	1996	1:1	20.3	6.5

Appendix B. Continued

Author	Year	Clay type	Silt+clay (%)	Silt+clay C (g C kg soil[−1])
[c]Stemmer et al.	1999	2:1	59.5	11.6
Tiessen and Stewart	1983	1:1	68.0	21.8
Tiessen and Stewart	1983	2:1	21.0	14.1
			26.0	20.5
[b]Turchenek and Oades	1979	Mixed	80.6	20.7
Young and Spycher	1979	1:1	73.0	10.6
			87.0	13.5
Zhang et al.	1988	1:1	91.0	36.7
			92.3	32.3
Unknown				
Young and Spycher	1979	Allophanic	71.0	67.5

[a]Particles less than 45 μm.
[b]Particles less than 53 μm.
[c]Particles less than 63 μm.