Review

A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics☆

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Abstract

Since the 1900s, the link between soil biotic activity, soil organic matter (SOM) decomposition and stabilization, and soil aggregate dynamics has been recognized and intensively been studied. By 1950, many studies had, mostly qualitatively, investigated the influence of the five major factors (i.e. soil fauna, microorganisms, roots, inorganics and physical processes) on this link. After 1950, four theoretical mile-stones related to this subject were realized. The first one was when Emerson [Nature 183 (1959) 538] proposed a model of a soil crumb consisting of domains of oriented clay and quartz particles. Next, Edwards and Bremner [J. Soil Sci. 18 (1967) 64] formulated a theory in which the solid-phase reaction between clay minerals, polyvalent cations and SOM is the main process leading to microaggregate formation. Based on this concept, Tisdall and Oades [J. Soil Sci. 62 (1982) 141] coined the aggregate hierarchy concept describing a spatial scale dependence of mechanisms involved in micro- and macroaggregate formation. Oades [Plant Soil 76 (1984) 319] suggested a small, but very important, modification to the aggregate hierarchy concept by theorizing the formation of microaggregates within macroaggregates. Recent research on aggregate formation and SOM stabilization extensively corroborate this modification and use it as the base for furthering the understanding of SOM dynamics. The major outcomes of adopting this modification are: (1) microaggregates, rather than macroaggregates protect SOM in the long term; and (2) macroaggregate turnover is a crucial process influencing the stabilization of SOM. Reviewing the progress made over the last 50 years in this area of research reveals that still very few studies are quantitative and/or consider interactive effects between the five factors. The quantification of these relationships is clearly needed to improve our ability to predict changes in soil ecosystems due to management and global change. This quantification can greatly benefit from viewing aggregates as dynamic rather than static entities and relating aggregate measurements with 2D and 3D quantitative spatial information.
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1. Introduction

The interest in long-term sustainability and reduction of environmental costs of agricultural ecosystems have emerged and only recently augmented. To achieve this interest, soil organic matter (SOM) dy-

namics and nutrient cycling need to be better under-
stood and subsequently managed. In trying to further
our understanding of these important dynamic soil
properties, recent research focuses often on the role
played by the soil matrix, the soil biota and their mul-
tiple interactions. It is this multitude of interactions
that makes it a very complex research subject to be
elucidated.

Studies tackling this complexity often use aggre-
gate measurements as surrogates of the, in itself, com-
plex soil matrix. Aggregates not only physically pro-
tect soil organic matter (e.g. Tisdall and Oades, 1982),
but also influence microbial community structure (e.g.
Hattori, 1988), limit oxygen diffusion (e.g. Sexstone
et al., 1985), regulate water flow (e.g. Prove et al.,
1990), determine nutrient adsorption and desorption
(e.g. Linquist et al., 1997; Wang et al., 2001), and
reduce run-off and erosion (e.g. Barthes and Roose,
2002). All of these processes have profound effects on
SOM dynamics and nutrient cycling.

The objective of the first section of this review is to
give a historical account of the development of theories
related to aggregate–SOM interactions. In the second
section influences and interactions between the major
factors controlling aggregation are synthesized with a
special reference to microaggregation and macroag-
gregate turnover.

2. Historical development of theoretical aggregate–SOM models

2.1. Before 1950

All major factors playing a role in aggregate for-
mation and stabilization were already identified in the
early 1900s. By then, it was already clear that the
following factors influenced soil aggregation: (1) soil
fauna; (2) soil microorganisms; (3) roots; (4) inor-
ganic binding agents; and (5) environmental variables
(Fig. 1). The most extensively studied group of soil
fauna in relation to aggregation is the earthworms. Re-
cently, termites have received a well-deserved greater
attention for their significant involvement in soil struc-
tural building. Mycorrhizal and saprophytic fungi are
the most important soil microorganisms involved in
the formation and stabilization of aggregates, but also
bacteria can have profound influences on aggregation,

especially at the microscale. Penetrating roots can me-
chanically break up existing aggregates, but they also
stabilize surrounding aggregates through drying the
soil and root exudation with its associated microbial
activity. Most studies investigating the relationship be-
tween inorganic binding agents and aggregation have
focused on calcium and oxyhydroxides. The promi-
nent impact of the physical processes of drying and
wetting plus freezing and thawing on both the forma-
tion and the degradation of aggregation is well known.

The impact of these five factors on aggregation and
the interactions and feedbacks between the five factors
are described in some very comprehensive reviews
published in the 1950s–early 1960s: Martin et al.
(1955), Henin et al. (1958), Greenland (1965a,b),
Harris et al. (1966), Kemper and Koch (1966). Their
excellent syntheses will not be repeated in this review,
but a short summary will be provided as a referral.
Martin et al. (1955) described in detail the positive
influence of organic residues, microbial activity, syn-
thetic soil conditioners and exchangeable cations on
soil aggregation. Henin et al. (1958) reviewed different
methodologies to measure aggregate stability and used
them to develop an instability index strongly related
to soil functioning (i.e. the instability index of a soil
is directly related to its infiltration rate). An in depth
description of the interactions between clays and or-
ganic compounds with specific reference to the influ-
ence of mineralogy and oxides is given by Greenland
(1965a,b). Harris et al. (1966) focused on the biologi-
cal (i.e. microbial activity and earthworms) and envi-
ronmental factors and how they are affected by agri-
cultural practices. They also gave a detailed account
of the chemical reactions involved in the formation of
aggregates. One of the very few attempts to quantify
the relationships between these factors and aggregate
stability was done by Kemper and Koch (1966).

It is evident from these reviews that before 1950,
very little effort was made to develop theoretical
frameworks of aggregate formation and the relation-
ships between SOM, roots, soil fauna, soil microor-
ganisms, physical processes and inorganic binding
agents were little or not at all quantified.

2.2. After 1950

In this section, all studies considered critical for
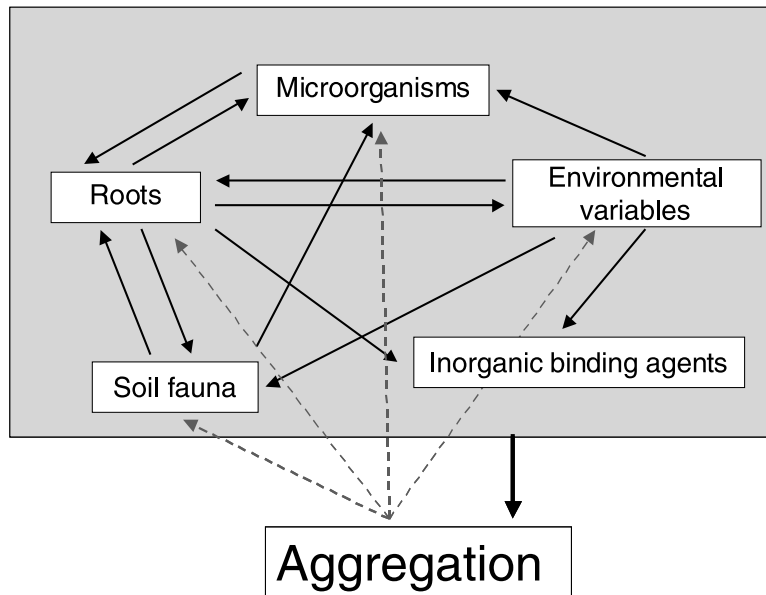our current understanding of aggregate–SOM dynam-

Fig. 1. The multiplicity of interactions and feedbacks between the five major factors influencing aggregate formation and stabilization.

ics are chronologically described (Fig. 2). The first aggregate–SOM conceptual model, based on the current theory at that time, was proposed by Emerson (1959). Emerson (1959) described how a soil crumb consisted of domains of oriented clays and quartz particles. According to the Emerson model, SOM increased the stability of a soil crumb by linking together domains of oriented clays and quartz particles. The process of slaking was consequently understood as the breaking of quartz-domain bonds by the crystalline swelling of clay domains upon wetting. Emerson (1977), based on his model, argued that the amount of protected SOM is proportional to the surface area of the domains. In other words, only a monolayer of SOM can be associated with the domain surface. This monolayer of SOM is stabilized between clay domains by being cross-linked through Al, Fe and hydrogen bonds.

Edwards and Bremner (1967) proposed the next major theoretical stepping stone. They presented the microaggregate theory in which the formation of microaggregates was envisioned as a solid-phase reaction between organic matter, polyvalent metals and electrically neutral clays. They rejected Emerson's model of aggregates containing sand grains as primary building blocks. According to Edwards and Bremner (1967),

the only highly stable aggregates are fine sand- and silt-sized microaggregates ($<250\,\mu\text{m}$) consisting of clay–polyvalent metal–organic matter complexes. Microaggregates are formed by bonding of C–P–OM clay sized units, where C: clay particle, P: polyvalent metal (Fe, Al, Ca) and OM: organo-metal complex, and are represented as $[(\text{C–P–OM})_x]_y$. It is evident that the C–P–OM units are equivalent to the clay domains of Emerson. However, Edwards and Bremner (1967) envisioned C–P–C and OM–P–OM units too. They also postulated that the organic matter complexed into the microaggregates would be inaccessible to microorganisms and physically protected.

The aggregate hierarchy concept proposed by Tisdall and Oades (1982) is probably the most significant theoretical advancement in the understanding of aggregate–SOM interactions. In the aggregate hierarchy concept it is postulated that the different binding agents (i.e. transient versus temporary versus persistent binding agents) act at different hierarchical stages of aggregation. Free primary particles and silt-sized aggregates ($<20\,\mu\text{m}$) are bound together into microaggregates ($20\text{–}250\,\mu\text{m}$) by persistent binding agents (i.e. humified organic matter and polyvalent metal cation complexes), oxides and highly disordered aluminosilicates. These stable microaggregates, in turn,

Soil crumb consists of domains of oriented clays and quartz particles — Emerson (1959)

Microaggregate theory — Edwards and Bremner (1966)

Aggregate hierarchy theory — Tisdall and Oades (1982)

Postulation of microaggregate formation within macroaggregates — Oades (1984)

The soil organic matter that binds together microaggregates into macroaggregates is lost upon cultivation — Elliott (1986)

Four hierarchical pore categories form the mirror image for the aggregate hierarchy — Elliott and Coleman (1988)

Earthworm activity induces the formation of microaggregates within casts — Shipitalo and Protz (1989)

Porosity exclusion principle defines scale of effectiveness of binding agents — Dexter (1988); Kay (1990)

Aggregate hierarchy exists only in soils where organic matter is the major binding agent — Oades and Waters (1991)

Mechanisms involved in the formation, stabilization and degradation of microaggregates — Golchin et al. (1994a)

Corroboration of microaggregate formation within macroaggregates — Angers et al. (1997)

Disturbance increases macroaggregate turnover, which diminishes carbon stabilization in newly formed microaggregates within macroaggregates — Six et al. (1998)
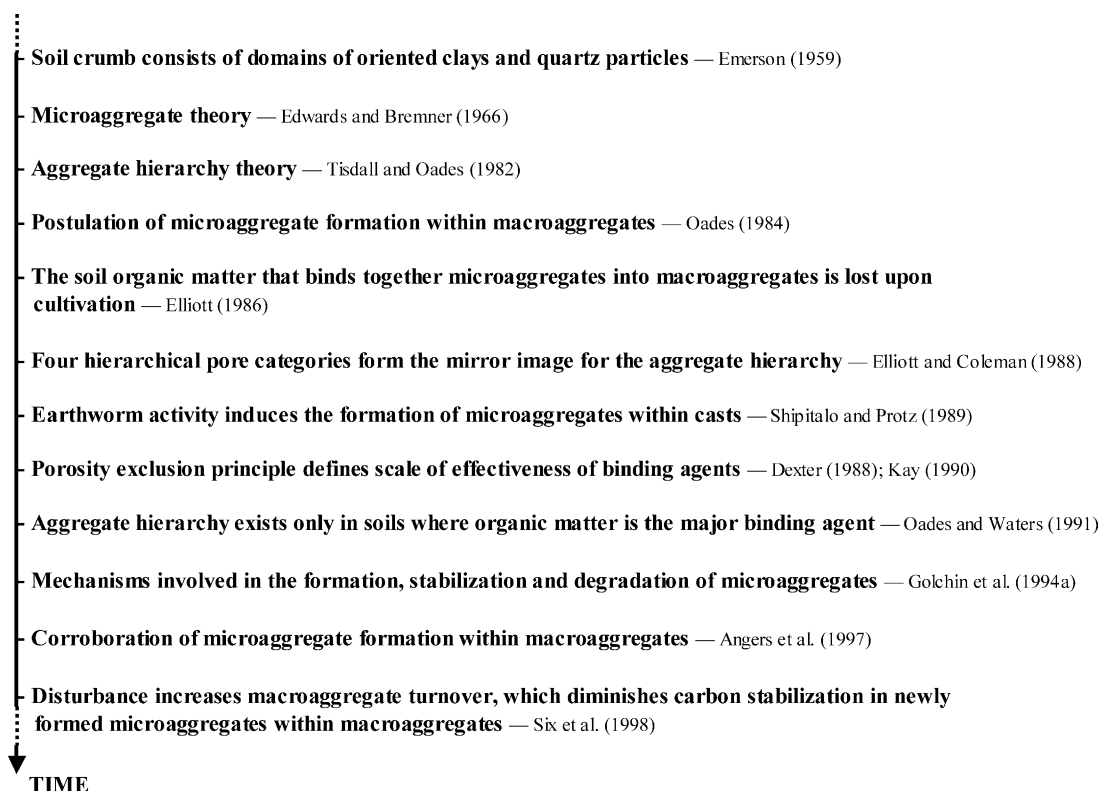
TIME

Fig. 2. A time line of the critical advancements in the understanding of soil organic matter–aggregation interactions.

are bound together into macroaggregates ($>250\,\mu$m) by temporary (i.e. fungal hyphae and roots) and transient (i.e., microbial- and plant-derived polysaccharides) binding agents. However, the polysaccharides are believed to mostly exert their binding capacity on a scale $<50\,\mu$m within the macroaggregates. Because of this hierarchical order of aggregates and their binding agents, microaggregate stability is higher and less dependent on agricultural management than macroaggregate stability.

Two years after the publication of the aggregate hierarchy theory, Oades (1984) formulated a small, but later to be found very important, modification to the concept of the hierarchical build up of aggregates (Fig. 3). In the hierarchical aggregate model of Tisdall and Oades (1982), it was implicitly understood that aggregates are sequentially formed, i.e. microaggregates are first formed free and then serve as the building blocks for the formation of macroaggregates. Oades (1984), on the other hand, postulated that the roots

and hyphae holding together the macroaggregate form the nucleus for microaggregate formation in the center of the macroaggregate. Since roots and hyphae are temporary binding agents, they do not persist and decompose into fragments. These fragments coated with mucilages produced during decomposition become en-
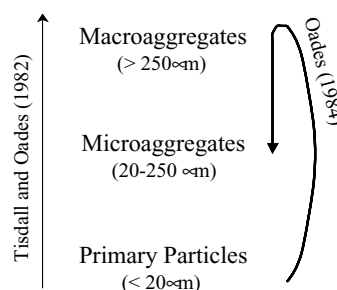

Fig. 3. The opposing chronology of the formation of the hierarchical aggregate orders implicitly described by Tisdall and Oades (1982) vs. postulated by Oades (1984).

crusted with clays resulting in the inception of a microaggregate within a macroaggregate.

Elliott (1986) tested the aggregate hierarchy model for North American grassland soils and applied it to explain the loss of SOM upon cultivation. As a direct consequence of the concept of microaggregates being bound together by SOM into macroaggregates, Elliott (1986) hypothesized that macroaggregates contain more labile and less highly processed SOM than microaggregates and that this SOM is lost upon cultivation. His hypothesis was corroborated and it identified for the first time the direct link between agricultural disturbance, decreased aggregation and loss of labile SOM. Based on these concepts, two sets of observations can be used to identify the existence of an aggregate hierarchy in a soil: (1) an increase in C concentration with increasing aggregate-sized class; and (2) a higher content of new and more labile (e.g. having a higher C:N ratio) C in macroaggregates than in microaggregates.

Elliott and Coleman (1988) adopted the concept of microaggregate formation within macroaggregates from Oades (1984) and ascribed this microaggregate formation to the anaerobic and resulting reducing conditions in the center of the macroaggregates. They also described, as a mirror image of the aggregate hierarchy, four hierarchical pore categories: (1) macropores; (2) pore space between macroaggregates; (3) pores between microaggregates but within macroaggregates; and (4) pores within microaggregates. This hierarchical pore structure facilitates the understanding of how pore networks determine the links between organisms in a soil food web. The macropores house microarthropods; nematodes move through the pores between macroaggregates; protozoa, small nematodes and fungi inhabit the pore space between microaggregates; bacteria are protected within the pores of the microaggregates.

Based on the hierarchical order of soil aggregation by Hadas (1987), which is very similar to the one of Tisdall and Oades (1982), Dexter (1988) formulated the "porosity exclusion principle". The porosity exclusion principle states that the aggregates of a lower hierarchical order exclude the pore spaces between the building blocks of the aggregates of a higher hierarchical order. Because pores form cavities and failure planes, the excluded porosity in aggregates of a lower order causes their greater density and internal strength compared to aggregates in a higher order. This "porosity exclusion principle" is similar to that given by Currie (1966). Kay (1990) took the "porosity exclusion principle" a step further by arguing that the effectiveness of different binding agents would depend on their dimensions relative to the size of the pores or failure planes that need to be bridged to bind particles together. Hence, inorganic and organic stabilizing compounds with their small dimensions are able to stabilize microaggregates, but roots and hyphae will have to act as binding agents between particles separated by greater distances or pores. It is evident that the pore exclusion principle and the hierarchical aggregate model both lead to the same hierarchical relationship between binding agents and aggregate orders.

Shipitalo and Protz (1989) presented a model for microaggregate formation within worm casts. This model contrasts with others models of aggregate formation because it describes how earthworms directly promote the formation of organic matter-cored microaggregates. Soil and litter ingestion and subsequent peristalsis by earthworms fragments litter and completely destroys the pre-existing microstructure of a soil. During gut transit, however, clay minerals and organic materials are intimately mixed and become encrusted with mucus to create a new nucleus for microaggregate formation. Within the excreted casts, drying and aging (i.e. thyxotropic hardening) facilitate the strengthening of the bonds between organic materials, mucus and minerals to stabilize the newly formed microaggregates.

In addition to the two tests for aggregate hierarchy based on the concepts of Elliott (1986) (see above), an elegant third test was developed by Oades and Waters (1991). They argued that if a soil expresses an aggregate hierarchy, macroaggregates will gradually break down into microaggregates before they dissociate into primary particles, as an increasing dispersive energy is applied to the soil. They utilized this line of thought by measuring the water-stable aggregate distribution of a soil after exposing it to a gradient of increasing dispersive energy: (1) slow wetting; (2) fast wetting; (3) 16 h shaking; and (4) sonication. The methodology was employed to two Alfisols, a Mollisol and an Oxisol and resulted in the confirmation of an aggregate hierarchy for the two Alfisols and the Mollisol, but not for the Oxisol. Oades and Waters (1991) con-

cluded that aggregate hierarchy exists in soils where aggregate formation and stabilization are directed by organic matter but is not found in oxide-rich soils (e.g. Oxisols). In oxide-rich soils, rather the oxides than organic materials are the dominant binding agents and diminish the expression of an aggregate hierarchy.

In a series of studies, Golchin et al. (1994a,b, 1995) gathered corroborative results for a conceptual model of interactions between organic matter, soil biota, and primary particles leading to the formation, stabilization and degradation of microaggregates (Golchin et al., 1994b). Golchin et al. (1994b) proposed that when fresh plant material (as surface residues or roots) enters the soil, it induces the formation of aggregates because it stimulates the production of microbial-derived binding agents by being a C source for microbial activity. During decomposition, plant material fragments or particulate organic matter (POM) gradually become encrusted with clay particles and microbial products to form the core of stable microaggregates. Microbial mucilages and metabolites further impregnate the mineral crust surrounding the still decomposing organic cores to form very stable microaggregates. Eventually, the organic cores are depleted of available SOM resulting in a cessation of microbial activity and production of mucilages. The halting of production of binding agents and the use of them as substrate leads to a loss of stability of the microaggregates. Upon breakdown of the microaggregates, the mineral crusts impregnated with microbial byproducts are released to form stable silt-sized organo-mineral complexes.

Some corroborating results were presented by Beare et al. (1994) and Jastrow (1996) for the formation of microaggregates within macroaggregates (Oades, 1984) according to the processes described by Golchin et al. (1994b). However, Angers et al. (1997) presented the most convincing quantitative data in corroboration of the concept of microaggregate formation within macroaggregates. They traced C and N in macro- and microaggregates during decomposition of $^{13}C^{15}N$-labeled wheat straw under field conditions. During the initial decomposition period, ^{13}C was accumulated in the macroaggregates but the ^{13}C enrichment of the macroaggregates decreased thereafter. Concomitant with the decrease in ^{13}C enrichment of the macroaggregates a stabilization of ^{13}C was observed in the microaggregates. This redistribution of C from macroaggregates to microaggregates with time clearly indicates that microaggregates are formed within macroaggregates and then released upon breakdown of the macroaggregates.

Since the study of Angers et al. (1997), numerous studies have proposed small variants of conceptual models presenting the role SOM and especially POM play in the formation of microaggregates within macroaggregates (Jastrow and Miller, 1998; Six et al., 1998; Gale et al., 2000; Puget et al., 2000). It is emphasized that root-derived POM plays an important role in the formation of microaggregates (Gale et al., 2000; Wander and Yang, 2000; Puget and Drinkwater, 2001) and that microaggregate formation is crucial for the storage and stabilization of soil C in the long term (Jastrow and Miller, 1998; Six et al., 1998; Gale et al., 2000).

Based on the above-described tight feedback between POM and macro- and microaggregate dynamics and additional data collected in native grassland, no-tillage and conventional tillage agroecosystems, Six et al. (1998) developed a conceptual model (Fig. 4) to explain the influence of disturbance (e.g. tillage) on soil C stabilization rates. Their model links a proportion of the C lost upon disturbance to the increased turnover of macroaggregates. A disturbance-induced increase in macroaggregate turnover inhibits the formation of microaggregates within macroaggregates and the long-term sequestration of C within microaggregates. Within the model, the rate of macro- and microaggregate formation, stabilization and degradation are directly related to the dynamics of POM-C. Following the incorporation of fresh residue in the soil, soil fungi and other soil microorganisms utilize the more easily available C and produce mucilages resulting in the formation of macroaggregates around coarse (>250 μm) intra-aggregate POM (coarse iPOM). Coarse iPOM is further decomposed and fragmented into fine (53–250 μm) iPOM. The fine iPOM and associated mucilages become encrusted with minerals to form the stabilized organic core of a newly developed microaggregate within macroaggregate. The latter process is cut short if the macroaggregate turnover is increased by disturbance, resulting in a reduced sequestration of C (Six et al., 2000a).
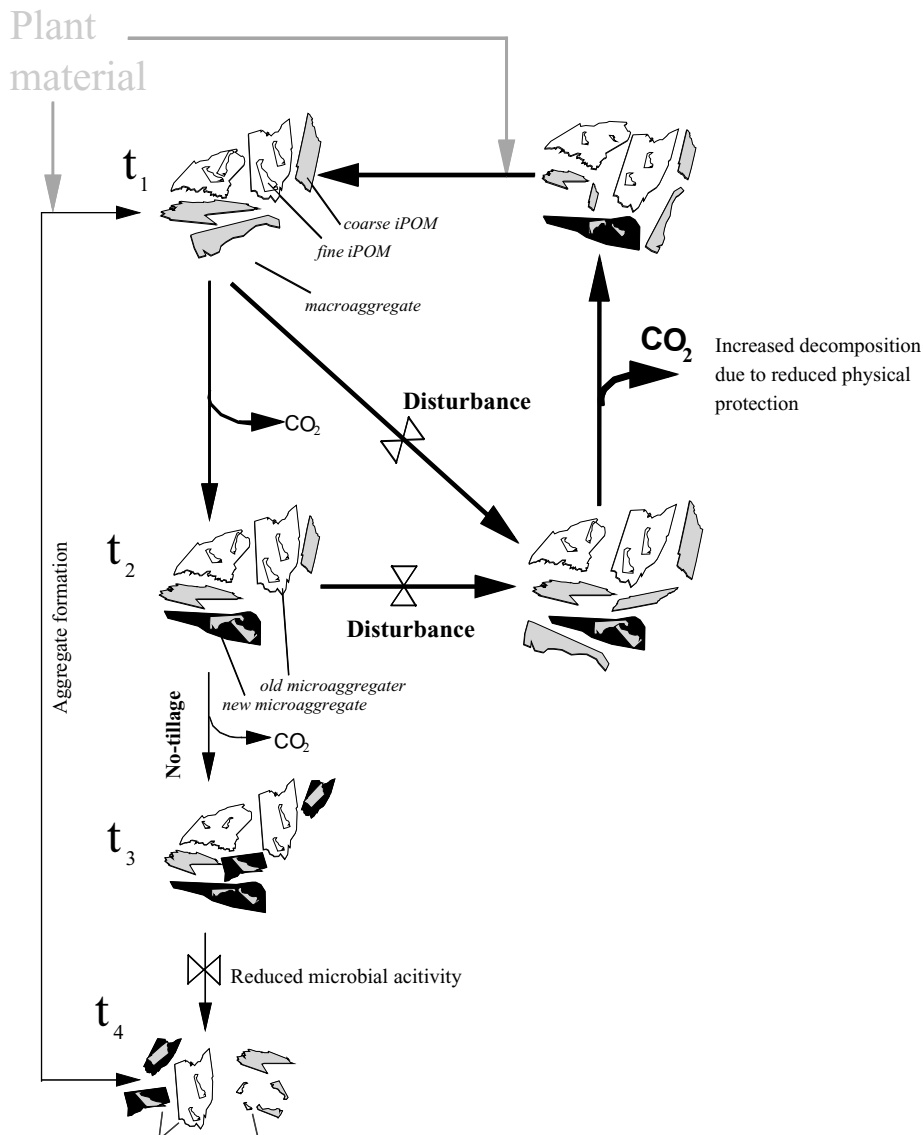
Fig. 4. This conceptual model of the 'life cycle' of a macroaggregate illustrates the formation of new microaggregates within macroaggregates and the accumulation vs. mineralization of aggregate-associated organic C. As aggregate turnover takes place an aggregate forms and stabilizes around particulate organic matter encrusted with microbial products and earthworm mucus, it becomes unstable due to a cessation of microbial activity and eventually disrupts. Disturbances such as tillage enhance macroaggregate turnover, which diminishes the formation of new microaggregates within macroaggregates and the protection of soil organic matter in these microaggregates. Figure is adopted from Six et al. (2000a).

2.3. Recent developments related to macroaggregate turnover

Plante and McGill (2002a,b) suggested that the relationship between physical protection of SOM and the turnover of macroaggregates differs for fresh residue versus stabilized SOM. For stabilized SOM, the slower the macroaggregate turnover the higher the protection level. An intermediate aggregate turnover would be optimal for newly incoming fresh residue because a
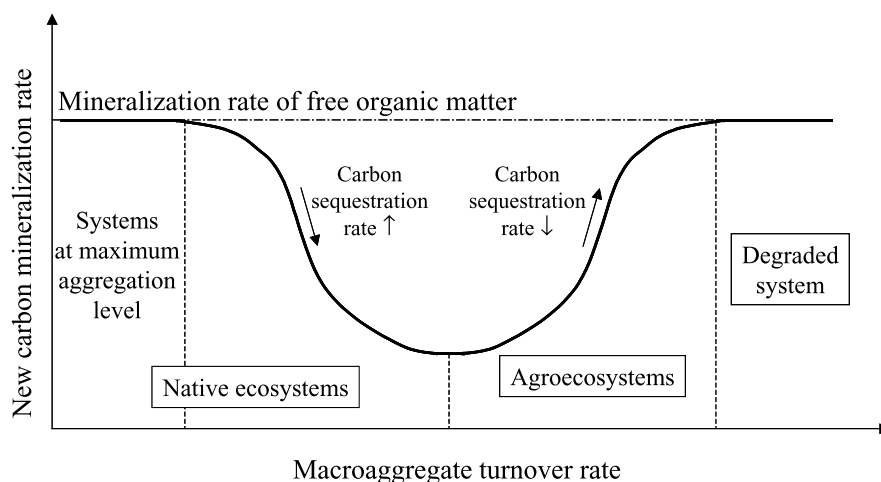
Fig. 5. Change in aggregate turnover and mineralization of newly added C input across ecosystems representing a range of disturbance regimes. Figure based on Plante and McGill (2002a).

certain aggregate turnover is needed to have aggregate formation and occlusion and subsequent protection of C within the aggregates. However, we suggest that macroaggregate turnover in most ecosystems is never so slow that it hinders the stabilization of C (see Fig. 5). In most ecosystems and especially agroecosystems, macroaggregation shows great seasonal dynamics (Angers and Mehuys, 1988; Coote et al., 1988; Perfect et al., 1990a,b) and the mean residence time of macroaggregates has been estimated to average 27 days with estimates as low as 5 days (Plante et al., 2002). Consequently, there is a great discrepancy between the time scales of macroaggregate turnover and the annual input of new C after harvest in agroecosystems; macroaggregates form and break down at a much faster rate than the rate of major input of new C in agroecosystems. Nevertheless, the concept of intermediate macroaggregate turnover might be applicable in some extreme cases in which aggregate breakdown is so slow that no aggregate formation occurs (Fig. 5). In this situation, new C will mineralize at a similar rate of free organic matter and no aggregate formation occurs because the aggregation level is at its maximum (Kemper and Koch, 1966; Six et al., 2002a). The latter prevents the new C to be a nucleation site for the formation of new aggregates. Therefore, in some rare ecosystems, there may be no aggregate formation so that the stabilization of new C is prevented. In contrast, disturbance is frequent in most other systems and

expected to induce a fast enough aggregate turnover for stabilization of new C.

As shown by Oades and Waters (1991), an aggregate hierarchy is expressed in soils dominated by 2:1 minerals where SOM forms bridges between negatively charged clay minerals, while in oxide dominated soils, electrostatic interactions between clay minerals and oxides prevents the expression of an aggregate hierarchy. Consequently, the coupling between SOM and aggregate dynamics is less evident and the loss of labile SOM upon cultivation cannot be explained according to Elliott (1986) and Six et al. (2000c). Since C concentrations do not increase with increasing aggregate size in oxide dominated soils (Elliott et al., 1991; Feller et al., 1996; Six et al., 2000c), an increase in labile C-depleted microaggregates upon a breakdown of labile C-rich macroaggregates by cultivation cannot be used as an explanation (Elliott, 1986; Six et al., 2000c). However, the data presented in Fig. 6 suggest that the link between disturbance, macroaggregate turnover and SOM dynamics (see Six et al., 1998) holds across soils with different mineralogies. In Fig. 6, the Mollisol is dominated by 2:1 clay minerals (Six et al., 2000b), whereas the Alfisol is characterized by a mixed mineralogy (i.e. 2:1 and 1:1 clay minerals and oxides) (Six et al., 2000b) and the Oxisol is dominated by 1:1 minerals and oxides (Denef et al., 2002). All three soils were collected from long-term agricultural experiments comparing no-tillage (NT) and con-
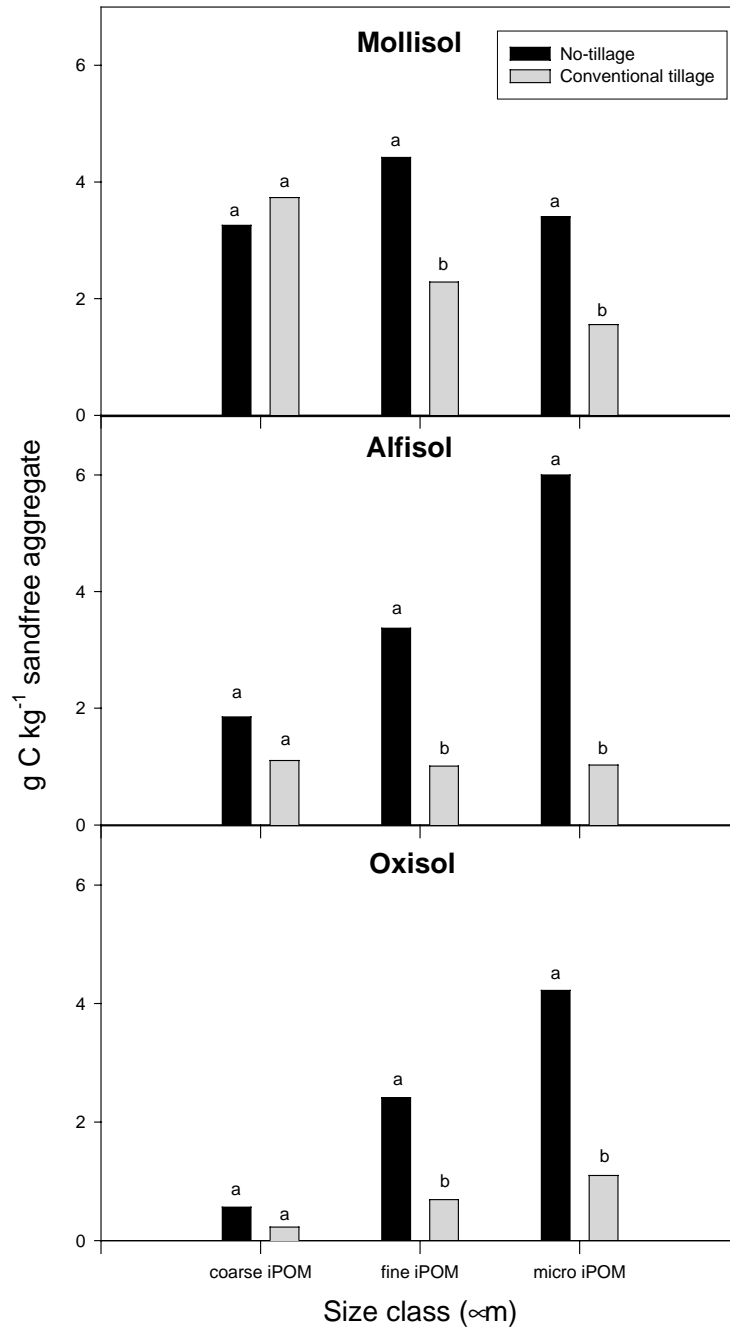
Fig. 6. Effect of tillage on intra-aggregate particulate organic matter (iPOM) C (g kg^{-1} aggregate on a sand-free basis) in slaked macro- and microaggregates from a Mollisol dominated by 2:1 minerals, an Alfisol with a mixed (2:1 plus 1:1 plus oxides) mineralogy, and an Oxisol dominated by 1:1 minerals and oxides (coarse iPOM = 250–2000 μm sized iPOM inside a macroaggregate; fine iPOM = 53–250 μm sized iPOM in a macroaggregate; micro iPOM = 53–250 μm sized iPOM in a microaggregate). Values followed by a different lowercase letter within an iPOM size class are significantly different between tillage treatments. Data adopted from Six et al. (1998, 1999) and Blauwet and Leyssens (2002).

ventional tillage (CT) management practices. Within a tillage treatment, an increasing C concentration with increasing aggregate size class was observed in the Mollisol, but not in the Alfisol and the Oxisol (Six et al., 2000c; Blauwet and Leyssens, 2002). Therefore, the aggregate hierarchy was only expressed in the Mollisol. Nevertheless, fine iPOM and microaggregate occluded POM (micro iPOM) concentrations were lower in NT compared to CT and coarse iPOM was not significantly different between NT and CT in all three soils (Fig. 6). These data indicate that a decreased macroaggregate turnover under NT compared to CT leads to a stabilization of POM in stable microaggregates (Six et al., 1998, 1999, 2000a) in all three soils. In addition, Denef et al. (2004) studied the same three soils and found that C associated with the microaggregates within macroaggregates accounted for 20–47% of total C content in the NT systems but explained 45–87% of the difference in total C differences between NT and CT. In conclusion, the link between macroaggregate turnover, microaggregate formation and C stabilization seems to be valid across soils with different mineralogies.

3. Major factors controlling macroaggregate turnover and microaggregation

In this section, we review and synthesize the research progress since 1950 related to the five major factors (see Fig. 1) influencing aggregation. We focus on the controls of formation and stabilization of microaggregates and the formation and breakdown of macroaggregates. We opted for these two focuses because microaggregates are the structural units within the soil where SOM is predominantly stabilized in the long term and the balance between formation and breakdown of macroaggregates determines macroaggregate turnover, having an indirect effect on microaggregate formation.

3.1. Soil fauna: earthworms and termites

3.1.1. Earthworms
The importance of earthworms in soil systems and the formation of soil structure has been recognized since the time of Charles Darwin. In his book, 'The formation of vegetable mould, through the action of

worms with observations on their habits', Darwin (1881) described the fine soil particles of dark color 'which cover the whole surface of the land in every moderately humid country' as 'vegetable mould'. He stated that this mould has passed many times through the 'intestinal canals' of earthworms and could therefore better be called 'animal mould'.

After Darwin, more and more researchers focused on the activity of earthworms in soil ecosystems. Of special interest has been the earthworms' key role in the formation and stability of soil aggregates and the cycling of nutrients (see Lee and Foster, 1991; Edwards and Bohlen, 1996) by removing plant litter and other organic materials from the soil surface and their incorporation into soil aggregates (Martin, 1991). Earthworms ingest organic matter, mix it with inorganic soil material, pass the mixture through their gut and excrete it as a cast. Early researchers (Ponomareva, 1950; van de Westeringh, 1972) have stated that up to 50% of surface layer soil aggregates in temperate pastures are earthworm casts. In mull-type forest soils (Kubiena, 1953) and in wooded savanna soils at Lamto, Ivory Coast (Lavelle, 1978), the soil top layer consists almost entirely of earthworm casts. Lee (1985) estimated that in an average temperature pasture and grasslands, earthworms cast 40–50 t ha^{-1} year^{-1} on the surface and even more below the surface.

There are two ways in which earthworms mediate soil aggregates: (1) burrowing and (2) cast formation (Brown et al., 2000). During burrowing a pressure is exerted on the surrounding soil and external mucus is deposited on the burrow walls (Edwards and Bohlen, 1996). Hence, the burrow walls are often lined with oriented clays and organic mucilage, which can form a stable structure (Jeanson, 1964). Numerous studies showed a higher stability in earthworm casts than in the surrounding soil aggregates (Monnier and Jeanson, 1964; van Rhee, 1977; De Vleesschauwer and Lal, 1981; McKenzie and Dexter, 1988; Shipitalo and Protz, 1988; Marinissen, 1994). However, the casting activities only enhance aggregate stability if the casts are dried or aged (Shipitalo and Protz, 1988; Marinissen and Dexter, 1990). In addition, the stability of the casts depends on the quality of the ingested organic matter (Shipitalo and Protz, 1988) and the amount of castings also depends on the feeding activity. When food supply is limited, earthworms seem to

ingest more soil in an effort to obtain sufficient food, and consequently cast more frequently (Abbott and Parker, 1981; Martin, 1982).

Earthworm activity does not only mediate macroaggregate formation but also microaggregate formation (Shipitalo and Protz, 1989; Barois et al., 1993). Based on thin sections of the earthworm gut, casts and control soil from earthworm microcosms, several studies have shown that during gut transit organic materials are intimately mixed and become encrusted with mucus to create new nuclei for microaggregate formation (Shipitalo and Protz, 1988, 1989; Barois et al., 1993). The presence of microstructures within casts was confirmed for field soils (Blanchart et al., 1993; Winsome and McColl, 1998). In addition, biogenic macroaggregates from pasture soils had a four times greater proportion (∼20%) than biogenic macroaggregates of an arable soil (∼5%) (Jongmans et al., 2001; Pulleman et al., 2004b). Greater amounts of fine POM were occluded within these microaggregates within biogenic macroaggregates compared to microaggregates occluded within physicogenic macroaggregates (Pulleman et al., 2004a). After 12 days of an incubation study with ^{13}C-labeled plant material, Bossuyt et al. (2004a,b) found a four times greater mass of microaggregates containing more new and protected C inside large macroaggregates (>2000 μm) in the presence of earthworms than in the absence of earthworms (i.e. 25 versus 6% microaggregates). The above-described results indicate that earthworms have a direct and fast impact on microaggregate formation and the stabilization of new C within these microaggregates.

There are several mechanisms to explain the increase of micro- and macroaggregate stability by earthworms. Stability might arise from mechanical binding by vascular bundles from ingested plant material or from fungal growth after excretion of the casts (Marinissen and Dexter, 1990). Stability might also originate from the microorganisms which proliferate in ingested materials in the gut (Parle, 1963; Arthur, 1965) and in the earthworm casts (Brown, 1995; Edwards and Bohlen, 1996; Brown et al., 2000). The microbial-derived polysaccharides deposited within the casts strengthen bonds between organic and mineral components (Shipitalo and Protz, 1989; Martin, 1991). Within days of cast excretion, a decline of microbial activity is detected and is correlated with the disappearance of labile C and available N (Lavelle et al., 1989; Scheu and Wolters, 1991). After the decline of these labile materials, more recalcitrant organic materials (e.g. hemicellulose and lignin) become integrated into compact structures as organo-mineral microaggregates (Shipitalo and Protz, 1989; Lavelle et al., 1997). It is also suggested that aggregate stability is induced by the cementing of soil particles in the worm's gut by calcium humate formed from decomposing organic material and calcite excreted by the worm's calciferous glands (Satchell, 1983).

Not all earthworm species have as profound influences on aggregation and SOM dynamics and their overall influence depends on the interactions between different earthworm categories. The different earthworm categories are divided according to their feeding or casting strategies. Bouché (1977) recognized three morpho-ecological groups: (1) epigeic species; (2) anecic species; and (3) endogeic species. Epigeic species are defined as litter dwellers. They live above the mineral soil surface, mainly in the litter layer of forest soils. Their activity has little or no effect on soil structure or aggregation. Anecic species live in burrows in the mineral soil and bring dead leaves from the soil surface into their burrows to feed (Lee, 1985). The organic materials are mixed with minerals and lead to a formation of stable organo-mineral structures within the casts (see above). Anecic species also form an extensive network of burrows, contributing to aggregate formation and stabilization. Endogeic species live in mineral soil horizons and feed on soil enriched with organic matter. They are considered major agents of aggregation and SOM stabilization (Lavelle and Spain, 2001).

Lee and Foster (1991) suggested that a mix of anecic and endogeic earthworm species is the most beneficial for soil structural health. In tropical agroecosystems, the interaction between endogeic earthworm species with different influences on soil structure appears to be necessary to sustain physical soil fertility (Blanchart et al., 1997). Large endogeic species, such as *Pontoscolex corethrurus* or *Millsonia anomala*, egest large and compact casts (>5 mm) (Blanchart et al., 1999). They are called 'compacting species' and are known to increase the soil bulk density and proportion of macroaggregates. The increase in bulk density is caused by: (1) the formation of organo-mineral bonds after mixing and chemical

transformations in the gut; (2) the reabsorption of water in the latter part of the earthworm intestine; and (3) the strong compaction by the tail muscles when casts are expelled (McKenzie and Dexter, 1988). Casts of compacting species might create anaerobic conditions slowing down decomposition (Blanchart et al., 1993). Smaller decompacting earthworm species (e.g. Eudrilidae) feed on these large casts and form smaller and more delicate casts (0.5–5 mm) (Blanchart et al., 1999). Decompacting earthworms decrease the soil bulk density and the proportion of large, compact aggregates. When decompacting species ingest casts of compacting species, previously physically protected C can be mineralized. When, on the other hand, compacting species ingest casts of decompacting species, mineralizable C can be protected in their large casts (Dickschen and Topp, 1987; Blanchart et al., 1999). The activity of only compacting earthworm species can cause the formation of a compact surface crust. This might impede water infiltration when no organic residues are present, but in the presence of organic residues, a favorable macroaggregate soil structure can develop (Blanchart et al., 1997, 1999). Barros et al. (2001) described a site after forest clearing where a single species, *P. corethrurus*, became very abundant. This species formed a continuous compacted layer, impermeable to water. This layer reached a thickness of 20 cm. The compacting effects here appeared "more pronounced than that of a bulldozer" (Chauvel et al., 1999).

Earthworms have not only opposite effects on soil structure, but their influence on ecosystem C stocks shows temporal variability (Martin, 1991). Lierman and Woomer (unpublished data, cited by Lavelle et al. (1997)) found that the C stock first declined after earthworm introduction but was 28% greater than initial C stock levels after 30 years of earthworm presence. McCartney et al. (1997) reported an increase of 0.18% soil C after 3 years of a reduction in the earthworm population by electroshocking. Similarly, initial decreases in SOM levels and acceleration of SOM turnover have been observed in the presence of earthworms (Gilot-Villenave et al., 1996; Pashani et al., 1996). This temporal change in C stocks might be related to the initial fast decomposition rates associated with the newly formed casts (Martin, 1991) versus the longer-term stabilization of C within microaggregates formed within the casts.

3.1.2. Termites

As pointed out by Lee and Foster (1991), there is very little quantitative information available about the role termites can play in soil structural building. However, it is evident that some termite species influence the structural stability of soils, especially the microstructure (Lobry de Bruyn and Conacher, 1990; Holt and Lepage, 2000; Bignell and Holt, 2002). Soil-feeding termites form microaggregates either by passing soil material through their intestinal system and depositing it as fecal pellets or by mixing the soil with saliva using their mandibles (Jungerius et al., 1999; Bignell and Holt, 2002). The stable microstructures have been mostly found within the termite mounds, but how widely these microstructures are eventually dispersed throughout the surrounding soils is unknown (Holt and Lepage, 2000). In addition, it is only the termite species that enrich their materials with organic materials and exchangeable cations who will improve soil structural stability. In conclusion, further research is needed to investigate the true soil structural building capacity of termites.

3.2. Microorganisms

The contribution of microbial activity to aggregate formation, stabilization and eventually degradation has been extensively reviewed before (e.g. Lynch and Bragg, 1985; Oades, 1993; Degens, 1997). Therefore, only a brief synthesis is given in this review. Even though the link between microorganisms and aggregation is pertinent, microbial biomass and water-extractable carbohydrates have been correlated to varying degrees with aggregation (see Degens, 1997 for an overview of studies). The varying degrees of correlation between aggregation and microbial biomass or microbial products are related to: (1) the different scales (i.e. macro versus microaggregate scale) of influence of fungi versus bacteria; (2) soil texture; and (3) soil mineralogy. The fungal mycelium has been described as a 'sticky string bag' because it entangles particles within the hyphae network and cements particles together through extracellular polysaccharide production (Oades and Waters, 1991). In accordance with the aggregate hierarchy theory and the pore exclusion principle, the enmeshment of particles by the 'sticky string bag' is a major factor in the formation of macroaggregates (Tisdall et al.,
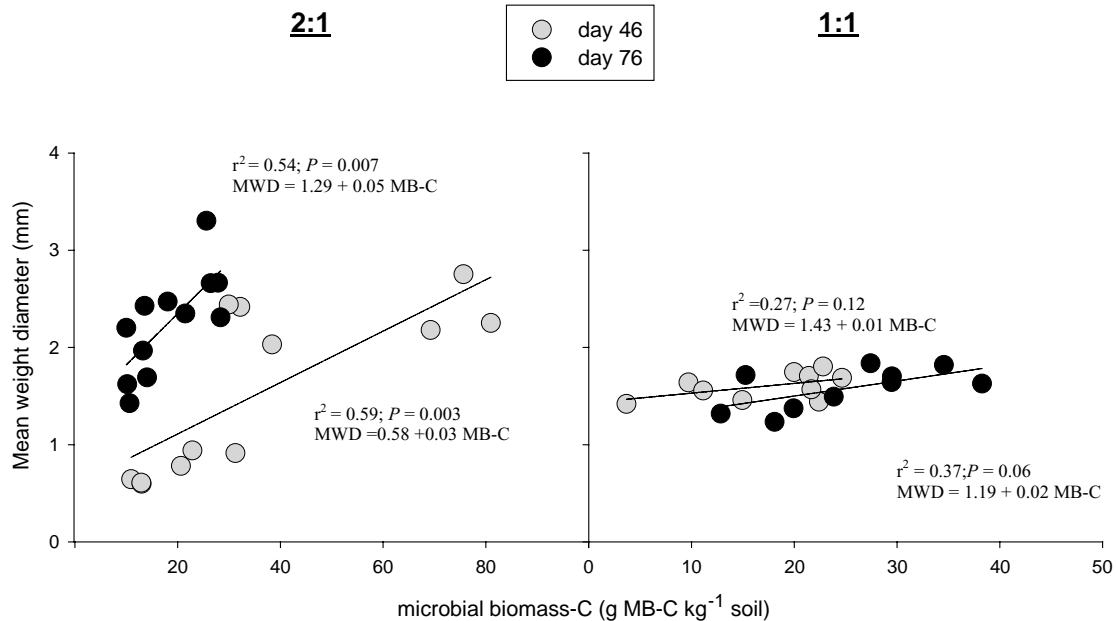
2:1   ○ day 46   **1:1**
                        ● day 76

Fig. 7. Relationship between microbial biomass C (g MB-C kg^{-1} soil) and aggregation (expressed in mean weight diameter) in a Mollisol dominated by 2:1 minerals and an Oxisol dominated by 1:1 minerals and oxides. Data adopted from Denef and Six (2003).

1997; Bossuyt et al., 2001). In contrast, the production of mucilages by bacteria and fungi enhances only the formation of microaggregates (Chenu, 1989; Oades, 1993). In coarse textured sandy soils, aggregation is weakly related to microbial biomass and products (Degens et al., 1994; Degens and Sparling, 1996) because only the hyphal network is able to cross-link the abundant sand particles to form stable aggregates. In clayey soils, on the other hand, both bacteria and fungi and their products play a role in aggregation. The influence of mineralogy is illustrated in Fig. 7. Denef and Six (2003) investigated under greenhouse conditions the influence of root-versus shoot-derived wheat C on macroaggregation in a Mollisol, dominated by 2:1 minerals, and an Oxisol, dominated by kaolinite and oxides. The different treatments caused a range in aggregation and microbial biomass. In the Mollisol, significant regressions were found between aggregation and microbial biomass at both sampling dates (Fig. 7). In contrast, aggregation was found to be independent from the microbial biomass content in the Oxisol. The fact that the sandy soil investigated by Degens and Sparling (1996) was a kaolinitic soil might also have played

a role in their observed non-significant relationship between aggregation and microbial biomass and products.

Since fungi stabilize macroaggregates, they counteract disruptive forces leading to a breakdown of macroaggregates. Therefore, fungi are expected to slow down macroaggregate turnover and indirectly enhance the formation of microaggregates. However, this link between fungal abundance, macroaggregate turnover and microaggregate formation has not been directly investigated.

In contrast to the wealth of knowledge about the impact of microbial activity on microaggregation, the degree to which the microaggregate structure dictates the microbial community is much less known. Several studies have reported on the spatial compartimentalization of protozoa and bacteria by aggregates (Elliott et al., 1980; Vargas and Hattori, 1986; Hattori, 1988; Kuikman et al., 1990). However, a low predation is not the only characteristic for a definable habitat for microorganisms within the microaggregate structure (Ranjard and Richaume, 2001); other characteristics are relative stable water potential, low nutrient and oxygen availability, and low accessibility for

exogenous toxic elements (Ranjard and Richaume, 2001). Phillipot et al. (1997) demonstrated that denitrifying bacteria with a nitrite-reductase gene had a competitive advantage over wild strains to colonize the center of a artificial remolded aggregate. Ranjard et al. (1997, 2000) reported that bacteria occluded within microaggregates were not exposed to the same level of the toxicant Hg(II) as the bacteria on the outer side of aggregates. Poly et al. (2001) showed that the composition of the diazotropic communities differed across microaggregate fractions. These few available studies clearly indicate that physicochemical characteristics of microaggregates determine the ecology of various microbial populations and therefore warrant further investigations relating biological functioning of microbes to microaggregates.

3.3. Roots

The influence of roots and plants in general on soil structure has been reviewed by Angers and Caron (1998) and Degens (1997). Root-related processes affecting soil structure can be grouped into five categories: (1) root penetration; (2) changed soil water regime; (3) root exudation; (4) dead root decomposition; and (5) root entanglement.

The compressing action of growing roots decreases soil porosity in the zone between roots and re-orientates clay particles along the root surface (Dorioz et al., 1993). Near the root surfaces, bulk density can be increased from 12 to 35% compared with that of the bulk soil (Young, 1998). These modifications occur mostly within a 50–200 μm zone around the roots (Dorioz et al., 1993), inducing the formation of microaggregates. In contrast, a decrease in macroaggregation after plant growth is partially due to the penetrating effect of roots into macropores. Materechera et al. (1994) found that, even at constant water potentials, roots decreased the proportions of already formed large water stable aggregates by 20–50%. Similar results were reported by Monroe and Kladivko (1987); they observed a fast decrease in aggregation the first 7 days after planting followed by an increase after 3 weeks. Reid and Goss (1982) found a decrease of 10–20% in water unstable aggregates with maize, tomato and wheat roots after 25 days of incubation. However, water stable aggregation

increased after air-drying the soil and nullified the disruptive effect of roots. Denef et al. (2002) observed similar changes in aggregation associated with wheat roots. In conclusion, root penetration decreases the proportion of relatively unstable macroaggregates but increases the proportion of relatively stable microaggregates. However, differences in the root architecture (e.g. degree of branching, thickness of roots, etc.) will determine the overall influence of root penetration on aggregation (Carter et al., 1994).

Soil roots also influence aggregation through modifying the soil water status in several ways. First, plant water uptake causes a localized drying of the soil, which promotes the binding of root exudates on clay particles (Reid and Goss, 1982). Second, root exudation reduces the wetting rate by occluding pores or increasing pore tortuosity, thereby reducing slaking of aggregates (Caron et al., 1996). Third, water flows preferentially along living roots due to the presence of a saturated film of water along the roots. For example, Rasse et al. (2000) found an increase of K_{sat} of 57% due to the presence of an alfalfa root system. The three above-described processes lead to a change in the frequency and the amplitude of dry–wet cycles (Reid and Goss, 1982). Ten to 20% less aggregation has been observed in planted soils that are kept continuously wet compared to planted soils in which the plants are allowed to periodically dry (20–50% reduction in water content (w/w)) the soil and induce dry–wet cycles (Reid and Goss, 1982; Materechera et al., 1992, 1994).

As plant roots release organic material within the rhizosphere, they directly and indirectly (through microbial stimulation; see Section 3.2) affect soil structure. Mucilages produced by roots may stick soil particles directly together. Adding extracted maize root mucilage to soils led to an instantaneous aggregate formation, without any interference of microbial activity (Morel et al., 1991). However, the effect of mucilage on aggregation lasted for only 14 days in a soil with 17% clay, 30 days in a soil with 25% clay and 42 days in a soil with 45% clay (Morel et al., 1991; Traore et al., 2000). Baldock and Kay (1987) found that roots stabilize aggregates through exudation of materials (mainly polysaccharides) sensitive to periodate destruction. Nevertheless, these materials could not account for all the increases in soil aggregation induced by plant roots. Traore et al. (2000) could mimic

the influences of soluble mucilages on aggregate formation by using a mixture of glucose, amino acids and organic acids.

The degree of influence by roots on soil structure through root exudation is very variable as production and composition of mucilages depend on: (1) water regime, e.g. low soil moisture stimulates maize mucilage production (Watt et al., 1994; Czarnes et al., 2000); (2) plant species, e.g. maize roots exude more than wheat roots (Hutsch et al., 2002) and lupin exudates stimulate fungal growth more than wheat exudates (Haynes and Beare, 1997); (3) time, e.g. greater production has been observed in earlier development stages (Gransee and Wittenmayer, 2000); and (4) soil depth, e.g. larger production near the surface (Merbach et al., 1999).

During the decomposition of dead roots, soil structure will be promoted. The magnitude of the effect is related to the amount and the decomposability of the material (Robinson and Jacques, 1958). Puget and Drinkwater (2001) found that remaining roots were more important than shoots of a leguminous green manure in promoting aggregation. Likewise, Gale et al. (2000) found that most stable aggregates were formed after senescence and not during the vegetative phase.

The entanglement of particles by roots to form and stabilize macroaggregates has been emphasized in many studies (e.g. Tisdall and Oades, 1982; Miller and Jastrow, 1990; Jastrow et al., 1998). However, it is difficult to separate the influence of entanglement versus exudation by roots. In addition, arbuscular mycorrhizal (AM) fungi are often associated with root systems, further complicating the separation of the effects of roots versus AM fungi and their exudates. Nevertheless, Thomas et al. (1993) tried to separate the influence of AM fungi from soybean roots by using a screen only permeable for hyphae and not for roots. They concluded that both fungi and roots increased aggregation. Similar results were obtained by Andrade et al. (1998) and Bethlenflavay et al. (1999). Rillig et al. (2002b), on the other hand, concluded that the positive effect of roots on aggregation was mainly due to the excretion of a soil protein glomalin by AM fungi. They found an increase in root weights concomitant with a decrease both in macroaggregation and in soil glomalin following an artificial increase of temperature.

Path analysis has been used in attempts to separate direct and indirect effects of roots, hyphae and their exudates on macroaggregate formation and stabilization (Miller and Jastrow, 1990; Jastrow et al., 1998; Bearden and Petersen, 2000; Rillig et al., 2002a). Bearden and Petersen (2000) concluded that the mechanisms of aggregate stabilization depended on the size of the aggregates. Whereas formation of aggregates between 1 and 2 mm was associated with hyphal length and not with root growth, roots and hyphae were involved in the formation of aggregates >2 mm. Jastrow et al. (1998) found that the strongest total influence on the proportion of macroaggregates was caused by a direct effect of fine roots plus an indirect effect by the association of the fine roots with external hyphae. In contrast, the strongest direct effect on the amount of macroaggregates was caused by external hyphae. Although there were significant linear correlations between soluble carbohydrates and macroaggregation, the path analysis showed no effect of soluble carbohydrates on macroaggregate formation.

3.4. Inorganic binding agents

3.4.1. Oxides

The aggregating and SOM stabilizing effect of oxides has been emphasized in many studies (e.g. Oades et al., 1989; Six et al., 2002b) and oxides have been reported as being the dominant binding agent in oxide-rich soils (Lamar and Bresson, 1989; Oades and Waters, 1991; Rhoton et al., 1998). The aggregating effect of oxides is mainly at the microaggregate level (Oades et al., 1989; Igwe et al., 1999; Muggler et al., 1999) but also macroaggregation has been related to oxide content (Arduino et al., 1989; Six et al., 2000b; Imhoff et al., 2002). Shang and Tiessen (1997, 1998) reported that the stabilization of C in tropical soils is highest in stable microaggregates consisting of oxides, soil organic matter and minerals. Oxides can act as binding agents in three ways: (1) organic materials adsorb on oxide surfaces (Oades et al., 1989); (2) an electrostatic binding occurs between the positively charged oxides and negatively charged clay minerals (El-Swaify and Emerson, 1975); and (3) a coat of oxides on the surface of minerals forms bridges between primary and secondary particles (Fordham and Norrish, 1983; Kitagawa, 1983; Muggler et al., 1999).

The latter process is probably mostly responsible for a greater stability of macroaggregates in Oxisols compared to temperate soils with low oxide levels. In a kaolinitic soil, this binding of oxides to minerals will reduce the cation exchange capacity of the kaolinite and increases the positive charge property of the kaolinite, further promoting the aggregation through electrostatic binding (Dixon, 1989).

3.4.2. Calcium

It is generally accepted that calcium is a critical element for the stabilization of SOM and aggregates through its role in the formation clay–polyvalent cation–organic matter complexes (Peele, 1936; Myers, 1937; Peterson, 1947; Muneer and Oades, 1989b; Clough and Skjemstad, 2000). Because calcium exerts its influence at the scale of the organo-mineral complexation, its stabilization effect is mostly observed at the microaggregate level (Grant et al., 1992; Baldock et al., 1994), but it can also indirectly increase macroaggregation through a stimulation of microbial activity in acidic soils (Chan and Heenan, 1999). Additions of calcium to field soils, in the form of lime or gypsum, increased ($\sim$10%) the aggregation level (e.g. Muneer and Oades, 1989a; Chan and Heenan, 1998, 1999). However, an initial temporary decrease (1–3%) in aggregate stability has been observed upon the application of lime to variable charged soils (Ghani et al., 1955; Roth and Pavan, 1991; Chan and Heenan, 1998). This temporal decrease in aggregation has been related to an increase in soil pH (Roth and Pavan, 1991) and microbial activity (Chan and Heenan, 1998, 1999) upon lime application to these acidic soils. An increase in pH of a variable charge soil leads to an increase of negative charges (Roth and Pavan, 1991), resulting in a dominance of repulsive forces over edge-to-face flocculation of kaolinite or oxide–kaolinite coagulation (see above). The dominance of repulsive forces causes dispersion. Nevertheless, this decrease in aggregation seems to be reversed in the longer-term (Roth and Pavan, 1991; Chan and Heenan, 1998) and is more pronounced if the calcium is added together with an organic matter source (such as wheat straw) (Baldock et al., 1994). The latter suggests that the process of calcium bridging is the dominant factor for the long-term positive effect of calcium addition on the structural stability of a soil.

3.5. Environmental variables: freeze–thaw cycles, dry–wet cycles, and fire

3.5.1. Freeze–thaw cycles

It has been observed that frost leads to breakdown (Chepil, 1954; Sillanpaa and Webber, 1961; Edwards, 1991) and formation (Bisal and Nielsen, 1964; Bryan, 1971; Lehrsch et al., 1991; Lehrsch, 1998) of soil aggregates. In addition, Lehrsch et al. (1993) emphasized the non-uniformity of structural changes induced by frost: by freezing a soil sample, some parts of the sample always become wetter and others get drier (e.g. near and below ice lenses). In wetter parts, frost disrupts aggregates because ice crystals expanding in pores break the particle-to-particle bonds. In contrast, drying is believed to cause a shrinkage of the soil mass and precipitation of bonding agents at particle-to-particle contacts (Lehrsch et al., 1991). These contrasting processes result in parts of the sample with respectively decreased and increased aggregate stability. Therefore, aggregate stability measurements on the whole sample yields only the average of these opposing changes.

One general consistent trend is that the disruptive effects of frost are enhanced with increasing water content. Sillanpaa and Webber (1961) reported a decrease in mean weight diameter (MWD) of larger aggregates with increasing moisture content (i.e. >0.20 kg kg^{-1}). Bullock et al. (1988) suggested that at low water contents (i.e. <0.20 kg kg^{-1}), ice crystals are formed fast and complete their growth in soil pores before they can create significant disruptive force on the walls of these pores. Staricka and Benoit (1995) and Hinman and Bisal (1968) studied the influence of water content on the susceptibility of aggregates to freeze–thaw (FT) cycles followed by air-drying versus freeze-drying. Freeze-drying occurs when a frozen soil surface is exposed to air temperatures of $\sim$0 °C and high (1–2 m s^{-1}) wind speeds (Bullock et al., 1988; de Jong and Kachanoski, 1988). At low water contents (i.e. <0.20 kg kg^{-1}), both freezing methods had no appreciable effect on aggregate stability. However, at high water contents (i.e. >0.20 kg kg^{-1}), aggregates >4 mm were only slightly disrupted by FT followed by air-drying, whereas freeze-drying resulted in a complete aggregate disruption. They suggested that while freezing of moist soil results in aggregation disruption, cohesion during

thawing and drying reverses the destruction to some degree. In contrast, freeze-drying removes water from the soil by sublimation, avoiding cohesion-induced recovery of aggregate stability.

Macroaggregates are more susceptible to the disruptive forces of frost than microaggregates (Chepil, 1954). Some studies even showed increased microaggregate stability upon freezing at high moisture levels (Sillanpaa and Webber, 1961; Hinman and Bisal, 1968). However, Sillanpaa and Webber (1961) observed only an increase in <0.25 mm sized aggregates when crushed, whereas original <0.25 mm sized aggregates did not show any increase upon FT. They suggested that this was attributed to higher availability of SOM and free clay particles in the crushed versus the original aggregate fraction.

Macroaggregates are less vulnerable to FT forces when the soil has higher contents of clay (Edwards and Bremner, 1967) and/or SOM (Sillanpaa and Webber, 1961; Lehrsch et al., 1991) and/or Fe-oxide (Russell, 1973). Lehrsch et al. (1991) and Lehrsch (1998) observed the highest macroaggregate stability in the soil with highest clay content. Moreover, in the clay-rich soil (41% clay), the effect of FT on aggregate stability was not affected by moisture content and number of FT cycles. In clay poor soils (∼15% clay), macroaggregate stability generally decreased with increased moisture content at the time of freezing (Lehrsch et al., 1991) and with increasing number of FT cycles (Lehrsch, 1998). Low OM soils (OM contents of 2.21% or less) tended to decrease in stability or increase initially then decrease as FT cycles continued to accrue beyond three cycles (Lehrsch et al., 1991). Lehrsch et al. (1991) suggested that elevated OM content (>3% OM content) (is effective in stabilizing frozen aggregates, but only at lower moisture contents ($<0.20\,\mathrm{kg\,kg^{-1}}$). They hypothesized that OM provides elasticity, which at low water contents, enables aggregates to withstand ice-lens expansion pressures. At high water contents, this elasticity is insufficient to prevent fracture.

In conclusion, macroaggregate turnover will be increased by FT cycles but to a lesser degree in dry soil with a high clay content, OM level and Fe-oxide concentration. The possibility of the formation and stabilization of microaggregates needs to be further investigated.

3.5.2. Drying and wetting

Soils are continually exposed to drying and wetting (DW) through wind, rainfall and snow. In general, drying and wetting are counteracting processes and it is the relative impact of these processes that is responsible for observed decreases as well as increases in aggregation upon DW. In addition, the response of a soil to DW is also attributed to soil properties and management, and methods for simulating DW or measuring aggregation.

Drying and wetting has been related to the formation of soil aggregates in non-aggregated soils (Utomo and Dexter, 1982): non-aggregated soils (e.g. compacted arable soils) will respond to DW by a break up of soil clods and an aggregation of smaller particles (Chaney and Swift, 1986). Dorioz et al. (1993) also observed a formation of microaggregates after one dry–wet cycle. In aggregated soils, DW generally decrease the proportion of aggregates (Soulides and Allison, 1961; Denef et al., 2001) due to: (1) non-uniform hydration and swelling of the clay fraction upon wetting; and (2) compression of occluded air in the capillary pores when water rapidly enters the soil pores (Grant and Dexter, 1990). Aggregate breakdown will therefore depend on the wetting rate. Upon capillary wetting, entrapped air is allowed to escape, leading to minimal disruption (Kemper and Rosenau, 1986). Aggregates seem to be more resistant to wetting after prolonged air-drying compared to short-term drying (Kemper and Rosenau, 1984), due to a greater release of organic substances and consequently more possible associations between organics and mineral particles (Haynes and Swift, 1990). According to Denef et al. (2001), frequent exposure of soil to DW can induce aggregate stabilization rather than aggregate disruption. They suggested that disintegration of aggregates allows the particles to settle into more packed configurations which results in a greater cohesion upon the next drying event (Kemper and Rosenau, 1984).

Haynes and Swift (1990) observed a reduction of ∼50% in aggregate stability for air-dried arable soil samples but an increase of ∼10% in aggregate stability for air-dried pasture soil samples, compared to their field-moist counterparts. Pasture soils have a high SOM content, which results in a reduced wettability because of the hydrophobic characteristics of SOM (Caron et al., 1996) and the formation of many addi-

tional intermolecular associations upon drying. In contrast, arable soils have a lower SOM content and are rewetted much faster. Therefore, in arable soils, the disruptive effect of wetting outweighs the stabilizing effect of drying.

Soil mineralogy also influences the effect of DW on aggregation. Soils dominated by swelling clays are characterized by low aggregate stability, whereas oxides and kaolin clays are responsible for highly stable aggregation. Burroughs et al. (1992) observed that about 50% more aggregate breakdown occurred in soils rich in swelling clays versus soils rich in kaolin clays upon wetting. Similar observations were made by Mermut et al. (1997): splash upon rainfall (RF) was about four times greater for smectic soils than for soils rich in Fe-oxyhydroxides.

Most studies investigating DW effects on aggregation are based on immersion wetting of dry aggregates. However, in order to study best the behavior of soil in the field under RF action, the impact of raindrops on dry soil has to be included. Briggs (1974) showed that aggregate breakdown induced by RF is partly explained by wetting and partly by drop impact. The relative impact of both forces depends on soil cover, texture, moisture content and mineralogy. Soil cover (mulch or dense herbage) can prevent the surface soil from air-drying and quick submergence in water, and reduce the impact by falling raindrops. Cernuda et al. (1954) observed higher vulnerability of aggregates to raindrops with decreasing moisture content, except for completely saturated aggregates that were easily destroyed upon RF compared to moderately moist aggregates, indicating the cohesive action of interfacial water films. Glanville and Smith (1988) observed that upon RF, soils rich in sesquioxides were 3–6 times more disrupted by the raindrop impact than by slaking.

As for the FT cycles, the faster macroaggregate turnover induced by DW cycles and RF will be less in soils with high Fe-oxide, kaolinite and SOM contents and the formation of microaggregates by DW cycles needs to be further elucidated.

3.5.3. Fire

Studies on the effect of fires on aggregation and SOM have shown contrasting results. Generally, after a severe forest fire, SOM and aggregation decrease, due to combustion of cementing organic substances (Giovannini et al., 1988; Fernandez et al., 1997). According to Giovannini and Lucchesi (1997), soil physicochemical changes are related to the temperature reached during fire. Heating of a soil up to 600 °C resulted in decreased OM content, but increased macroaggregation (Giovannini and Lucchesi, 1997; Guerrero et al., 2001). This heat-induced aggregation has been attributed to a dehydration of soil gels and thermal transformations of the cementing Fe and Al oxides with temperatures >220 °C (Giovannini et al., 1990). Loss in soil organic C (SOC) was shown to differ among aggregate size fractions: fire mainly reduced SOC pools associated with macroaggregates whereas microaggregate-associated C was not affected (Garcia-Oliva et al., 1999). They suggest that while heat induces macroaggregate formation during the fire, the macroaggregate-C loss by combustion will weaken biological aggregate stabilization mechanisms in the long term. Arocena and Opio (2003) also suggested to weigh the short-term benefits of a fire versus the long-term losses due to the observed cracks in soil aggregates after a fire.

4. Conclusions

Major progress has been made in the understanding of the link between aggregates, soil biota and soil organic matter dynamics. This is evident from the continuous evolving of the conceptual models depicting our theoretical understanding of this link. The most important concepts constituting our current understanding are: (1) a hierarchical order of aggregates exists in soil where SOM is the major binding agent; (2) microaggregates are formed within macroaggregates; (3) root-derived POM plays an important role in aggregate dynamics; (4) the activity of earthworms has a decisive role in the formation of macro- and microaggregates; (5) SOM is predominantly stabilized in stable microaggregates; and (6) changes in the rate of macroaggregate turnover influence SOM stabilization across soil types and disturbance regimes.

Although the five major factors (Fig. 1) affecting soil structure were known well before 1950, the quantification of the single influences and involved feedback mechanisms remain lacking. The remaining lack of quantification probably originates from: (1)

the manifold of interactions and feedbacks between soil fauna, microbes, roots, inorganic binding agents, environmental factors and structure; (2) the different scales and dimensions on which many mechanisms operate; and (3) the natural heterogeneity of the soil as a three-dimensional porous system. Furthermore, most experiments focusing on mechanisms are designed to yield simple correlations between the factors and aggregation. Simple correlations do not inform about the importance of single factors and the interactive effects between factors. Promising solutions could be: (1) integrating aggregation measurements with morphological characterization and with 2 and 3D spatial information; (2) viewing aggregates rather as dynamic than static entities; (3) exploring novel statistical techniques (path analysis, envelope analysis, etc.); (4) employing spatial explicit models that represent the soil as a 3D body to predict experimental data (Young, 1998); and (5) integrating all five major factors (Fig. 1) influencing soil structure in modeling exercises with a focus on the interactions and feedbacks.

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