ELSEVIER

Geoderma 74 (1996) 65–105

GEODERMA

Stabilization and destabilization of soil organic matter: mechanisms and controls

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Received 1 December 1993; revised 26 July 1995; accepted 3 April 1996

Abstract

We present a conceptual model of the processes by which plant leaf and root litter is transformed to soil organic C and CO_2. Stabilization of a portion of the litter C yields material that resists further transformation; destabilization yields material that is more susceptible to microbial respiration. Stability of the organic C is viewed as resulting from three general sets of characteristics. *Recalcitrance* comprises molecular-level characteristics of organic substances, including elemental composition, presence of functional groups, and molecular conformation, that influence their degradation by microbes and enzymes. *Interactions* refers to the inter-molecular interactions between organics and either inorganic substances or other organic substances that alter the rate of degradation of those organics or synthesis of new organics. *Accessibility* refers to the location of organic substances with respect to microbes and enzymes. Mechanisms by which these three characteristics change through time are reviewed along with controls on those mechanisms. This review suggests that the following changes in the study of soil organic matter dynamics would speed progress: (1) increased effort to incorporate results into budgets for whole soil (e.g., converting to a kg/ha basis) so that the relative importance of processes can be judged; (2) more attention to effects of inter-molecular interactions (especially Al complexation) on enzyme activity and substrate degradation; (3) increased effort to experimentally manipulate soils, preferably across a range of soil types; (4) study of stabilization and destabilization mechanisms under conditions that are well defined yet more relevant to soil environments than those used previously; and (5) experiments better designed to isolate mechanisms so results are not confounded by effects of other mechanisms operating simultaneously.

1. Introduction

After nearly a century of study, the dynamics of soil organic matter (SOM) remain imperfectly understood. It is widely assumed, for example, that fresh plant detritus is converted gradually to more stable forms (sometimes termed "humus"), and that this

PII S0016-7061(96)00036-5

stabilization involves a variety of physical, chemical, faunal, and microbial processes. Most of these stabilization mechanisms are not well understood, their rates cannot be measured in the soil, and there is no way to construct budgets of the carbon and nutrient fluxes that result from them. Indeed, for many stabilization processes, we lack even the most basic information on the factors controlling them. As a result, most models of SOM dynamics do not deal with stabilization processes. Instead, they divide SOM into several compartments based on assumed turnover times, and define dynamics in terms of transfers from one such compartment to another (e.g., Parton et al., 1987, 1988; Jenkinson, 1990).

In this paper, we suggest a conceptual model of the processes involved in the stabilization of fresh plant material into SOM, and the concomitant process of destabilization, building on earlier conceptual models (Anderson, 1979; Smith, 1979; Van Veen and Paul, 1981; McGill et al., 1981; Oades, 1988). We review factors that may determine rates of these processes (process controls) and some of the more important interactions among those controls. Carbon dynamics are emphasized here, although we recognize that N, S, and P are components of SOM and important modifiers of its dynamics. And, although we cite literature on these controls, we make no claim here to have exhaustively reviewed the literature.

2. Conceptual model of SOM stabilization and destabilization

The C flows and transformations upon which the conceptual model is based are shown in Fig. 1. We assume that most C enters as fresh plant material, either aboveground or belowground, and is lost via respiration. Smaller amounts of C can enter in throughfall (drip from plants) and as sediment from upslope and can exit in leachate or via sediment movement downslope. Within the soil (including the surface litter layer), the plant material becomes *stabilized* at varying rates and to varying degrees through time.

2.1. Preliminary definitions

By SOM we mean all dead materials in or lying on the soil that contain organic C. *Detritus* refers to SOM still recognizable as dead plant or animal material, including leaf litter, coarse woody debris, and dead roots.

By *stabilization*, we mean a decrease in the potential for SOM loss by respiration, erosion or leaching. Stabilization may begin before plant tissues reach the ground, or even before they die, but we focus here on those processes that involve detritus in or in contact with the soil. *Destabilization* is the inverse of stabilization, that is the increase in the potential for SOM loss by respiration, etc.

Degradation we define by analogy to cellular metabolism (cf. Leninger, 1970, p. 273) as including all processes, mainly depolymerization and oxidative reactions, by which relatively large molecules such as poly-aromatics, carbohydrates, lipids, and proteins, arising both within cells and free in the soil environment, are converted into smaller, simpler molecules such as carboxylic acids, amino acids, and CO_2.

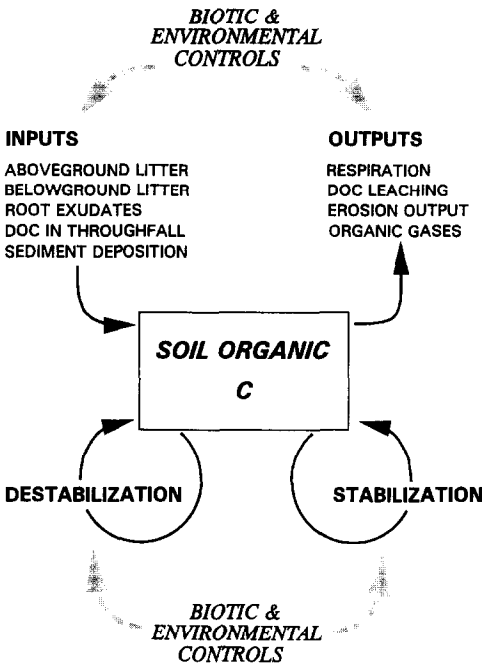


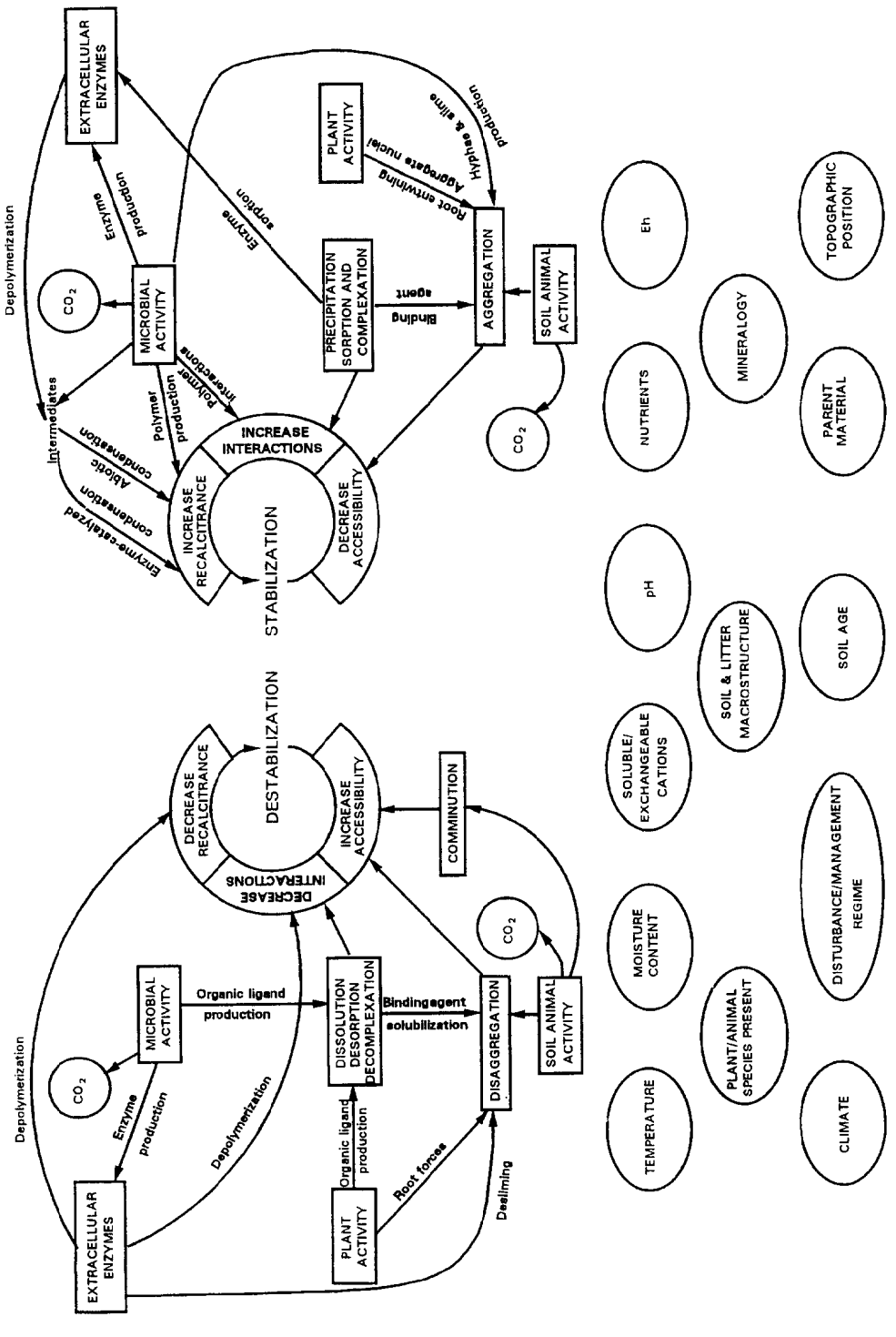
Fig. 1. The amount of organic C in soil results from the difference between long-term organic C additions and losses. Outputs are increased by destabilization processes, which increase the potential for organic C to be respired, eroded, or leached, and decreased by stabilization processes. All processes are influenced by biotic controls, such as abundance of microbial and plant species, and environmental controls, such as temperature, moisture, and soil texture.

Synthesis, the inverse of degradation, includes all processes by which simple precursor molecules become linked to form larger molecules, such as poly-aromatics, polysaccharides, nucleic acids, proteins, and lipids. Precursors can arise from degradative processes outside or inside cells, either before or after the cells die. When synthesis occurs outside cells, we refer to it here as *condensation.*

2.2. Controls diagram

Potential controls on stabilization and destabilization are diagrammed in Fig. 2. This figure focuses specifically on stabilization and destabilization as they relate to respiration. Controls on stabilization and destabilization could also be defined with respect to erosion and leaching, but the diagram might then be somewhat different.

Fig. 2 has been drawn with stabilization and destabilization as separate but analogous circles, each divided into the same three parts: change in recalcitrance, change in interactions, and change in accessibility (see also Cheshire et al., 1974; Ladd et al., 1993). This parallel representation of stabilization and destabilization is intended to highlight the many similarities between their controls.


Depolymerization
EXTRACELLULAR ENZYMES
MICROBIAL ACTIVITY
CO2
Enzyme production
Organic ligand production
DISSOLUTION DESORPTION DECOMPLEXATION
Binding agent solubilization
DISAGGREGATION
SOIL ANIMAL ACTIVITY
PLANT ACTIVITY
Organic ligand production
Root forces
Depolymerization
Desliming
DECREASE INTERACTIONS
DECREASE RECALCITRANCE
DESTABILIZATION
INCREASE ACCESSIBILITY
COMMINUTION
Depolymerization
EXTRACELLULAR ENZYMES
Enzyme production
MICROBIAL ACTIVITY
CO2
Enzyme sorption
PRECIPITATION SORPTION AND COMPLEXATION
Binding agent
PLANT ACTIVITY
Root entwining
Aggregate nuclei
Hyphae & elfins production
AGGREGATION
SOIL ANIMAL ACTIVITY
CO2
Intermediates
Enzyme-catalyzed condensation
Abiotic condensation
Polymer production
Polymer interactions
INCREASE INTERACTIONS
INCREASE RECALCITRANCE
STABILIZATION
DECREASE ACCESSIBILITY
TEMPERATURE
MOISTURE CONTENT
PLANT/ANIMAL SPECIES PRESENT
CLIMATE
DISTURBANCE/MANAGEMENT REGIME
SOLUBLE/ EXCHANGEABLE CATIONS
pH
SOIL & LITTER MACROSTRUCTURE
SOIL AGE
NUTRIENTS
Eh
MINERALOGY
PARENT MATERIAL
TOPOGRAPHIC POSITION

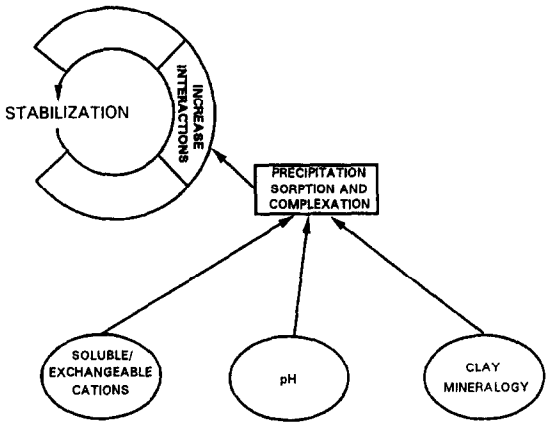


Fig. 3. Interaction of soil organic C with other substances can increase stabilization with respect to microbial respiration. Through precipitation, sorption, and complexation reactions, organics may interact with other organics or with inorganic materials, such as clay surfaces or dissolved aluminum and iron, thereby lowering their potential to be acted upon by microorganisms and their extracellular enzymes. The reactions are influenced by the chemical environment and by the surface properties of clay minerals.

Recalcitrance comprises molecular-level characteristics of organic substances, including elemental composition, presence of functional groups, and molecular conformation, that influence their degradation by microbes and enzymes.

Interactions refers to the inter-molecular interactions between organics and either inorganic substances or other organic substances, that alter the rate of degradation of those organics or synthesis of new organics.

Accessibility refers to the location of organic substances as it influences their access by microbes and enzymes.

Stability is the integrated effect of recalcitrance, interactions, and accessibility. By definition, it increases with recalcitrance and decreases with accessibility. Whether it increases with interactions is an important issue that we explore further here.

The immediate (proximal) factors controlling stabilization and destabilization are shown in Fig. 2 to the right or left of the circles. Distal controls are arranged hierarchically toward the bottom of Fig. 2, with the first row comprising intermediate factors that provide links from the second row, and so on. Arrows connecting the distal controls to the more proximal ones, as well as many feedbacks from proximal factors to more distal ones, have been left out for simplicity. Some of these connections are discussed as we review the proximal controls, and shown in accompanying illustrations (Fig. 7), but thorough discussion is beyond the scope of this paper.

Fig. 2. The stability of soil organic C with respect to microbial respiration is determined by inherent recalcitrance of organic compounds, interaction with stabilizing substances, and accessibility to microorganisms. Proximal controls directly influence these characteristics, and distal factors, shown at the bottom of the figure, affect the proximal controls. Note that the same proximal controls and distal factors affect both destabilization and stabilization processes. Also note that respiration of some organic C occurs during the stabilization of other organic C.

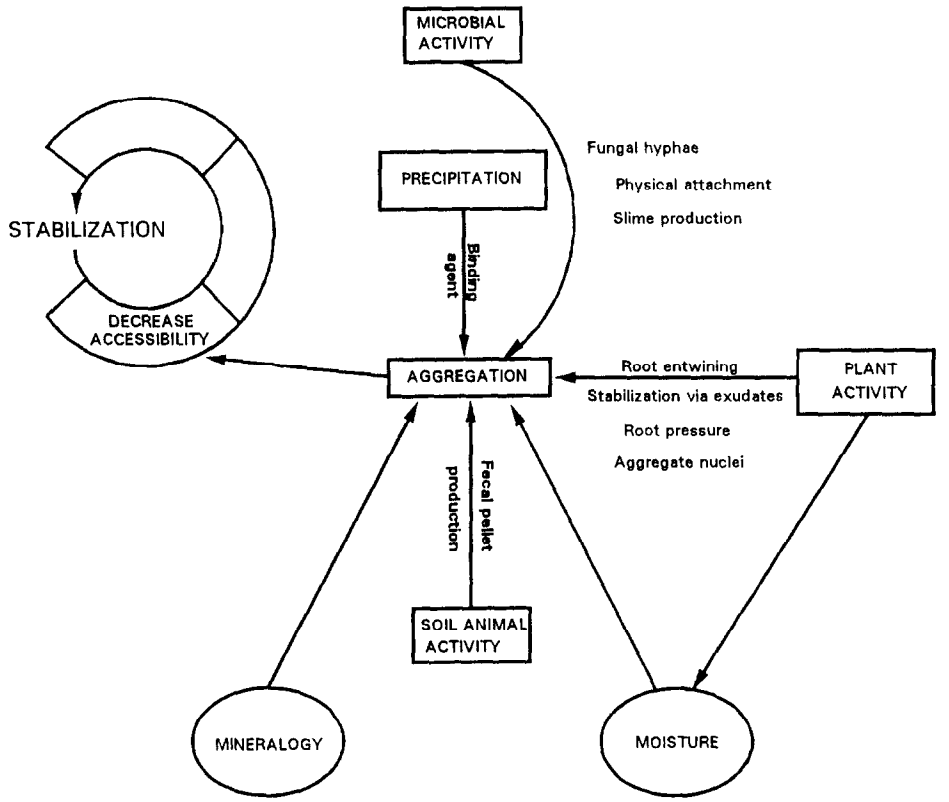


Fig. 4. Accessibility of organic C to microbes may be decreased by incorporation within aggregates, where small or tortuous pores may restrict entry by microorganisms or their extracellular enzymes, or oxygen levels may so low as to support only limited microbial activity. Aggregation is promoted by a variety of chemical, microbial, and higher-plant controls.

At the bottom of Fig. 2 are shown the ultimate factors determining SOM dynamics at a specific site — essentially Hans Jenny's (1941) factors of soil formation, except that we have substituted management/disturbance for biota. Plant/animal species composition (essentially the gene pool at a given site) has been placed in an intermediate level of control as it is determined in turn by the ultimate factors, notably management/disturbance in combination with climate.

2.3. Plant litter composition

A large body of literature deals with effects of litter composition (so-called litter quality) on mass loss during several years of decomposition. For example, degradation rate can decrease with lignin: N ratio (Aber et al., 1990; Anderson, 1991) and with tannin content (Palm and Sanchez, 1991). Studying mass loss from pine litter of differing N concentration, Berg (1986) proposed that degradation of cellulose and other more labile components increased with N concentration, but that degradation of lignin

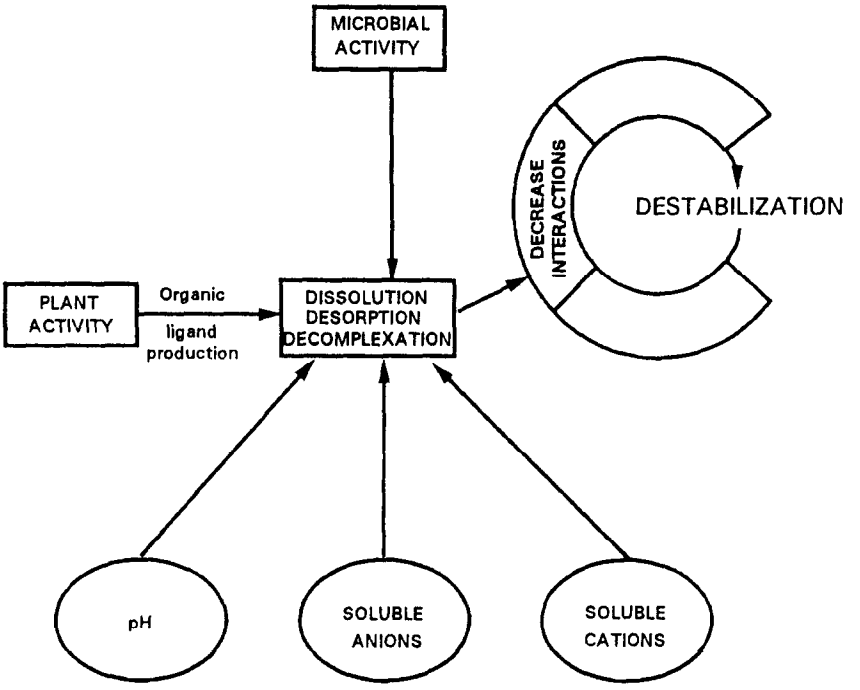


Fig. 5. Decreased interactions with other substances are hypothesized to destabilize soil organic C with respect to microbial respiration. Dissolution, desorption, and decomplexation reactions that yield free organics for microbial uptake or enzymatic breakdown are influenced by several chemical, microbial, and higher-plant controls.

decreased with increasing N concentration. Molecular-scale interactions between constituents of detritus may also influence mass-loss rates. For example, cellulose loss may be slowed if the cellulose is encrusted with lignin (Oades, 1988; Blanchette, 1991).

How initial composition affects the stability of the residue remaining after several years of decomposition is less clear. Melillo et al. (1989) suggested that the composition of the residue remaining after several years, as indicated by cellulose : lignin ratio, was unrelated to initial composition. There is some evidence that N content of the long-term residue may correlate well with that of the initial material (Aber et al., 1990), but how this relates to long-term stability is unclear. In general, these studies provide important information on possible factors influencing initial degradation rates and on changes in the composition of residue over time. However, they focus on results of the stabilization and destabilization processes, rather than on the processes themselves, which are the focus of our review.

3. Stabilization

Here we consider each process or factor that controls the rate of stabilization (each of the arrows leading to the stabilization wheel). We define the mechanisms involved,

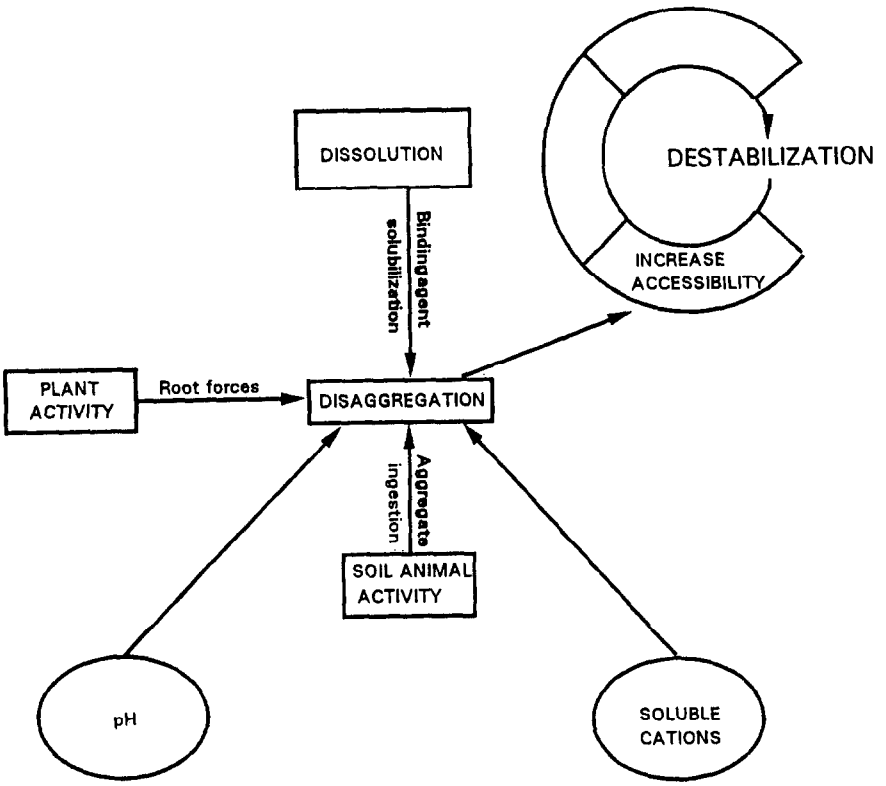


Fig. 6. Disaggregation increases accessibility of soil organic C to microorganisms and extracellular enzymes, thereby promoting microbial respiration. Note that plant activity and soil animal activity are active in both disaggregation and aggregation (Figs. 3–6 and 4) processes.

review the immediate controls on the process or factor, and discuss known or potential effects on stability.

3.1. Controls that increase recalcitrance

3.1.1. Changes in chemical characteristics of SOM

Microbes selectively degrade the less recalcitrant compounds and thus gradually increase the average recalcitrance of the non-respired C. Such *selective degradation* increases only the average recalcitrance of the residue, not the recalcitrance of any particular C atom. This process has been referred to by many as "selective preservation", but we consider that a misnomer as there is no preservation mechanism at work.

^{13}C-NMR techniques allow quantification of relative amounts of *o*-alkyl (–C–O–C–), aromatic (⬡), carboxyl (–COOH), and alkyl (–C–C–C–) carbon in the soil. The correspondence between *o*-alkyl as measured by ^{13}C-NMR spectroscopy and carbohydrate as measured by various wet chemistry methods is not entirely clear. Several

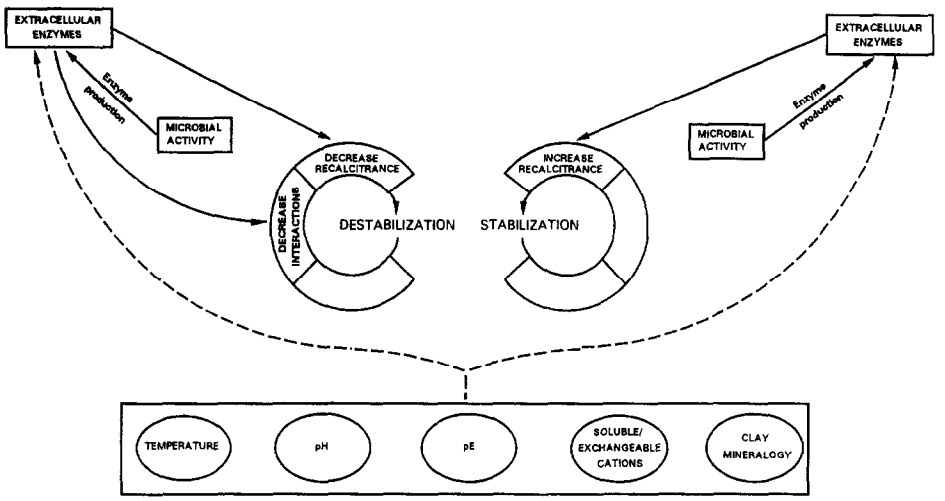


Fig. 7. Distal factors influence the proximal controls of destabilization and stabilization of soil organic C. The same factor can simultaneously promote destabilization and stabilization, which makes it difficult to examine and quantify individual processes.

studies suggest that ^{13}C-NMR may overestimate concentrations of carbohydrate (Cheshire et al., 1992; Zech et al., 1992; Guggenberger et al., 1996).

Based largely on ^{13}C-NMR, it is now thought that alkyls constitute a large part of the SOM (Hayes and Himes, 1986; Hempfling et al., 1987; Oades, 1988, 1989; Theng et al., 1989; Ziegler and Zech, 1989; Newman and Tate, 1991; Zech et al., 1992). Some soil alkyl material is thought to derive directly from plant and mycorrhizal tissues (Hempfling et al., 1991; Baldock et al., 1992; Baldock and Preston, 1995) and so not be the result of C stabilization processes operating in the soil. Other alkyls result from microbial synthesis, as described next.

Baldock et al. (1989, 1990a,b) found that, when uniformly ^{13}C-labelled glucose was added to whole soil, the ^{13}C appeared successively in materials that were dominantly *o*-alkyl, then aromatic, then alkyl. Comparing ^{13}C-NMR spectra across eight soils, Baldock et al. (1992) found that alkyls were most dominant in the two tropical Oxisols; presuming microbial degradation to be fastest in tropical soils, they interpreted this as indicating that the alkyls constitute the most stable soil C. Capriel et al. (1990), however, found that a hexane-extracted alkyl fraction was intermediate in degradability between glucose and corn straw, and suggested that inaccessibility rather than recalcitrance might account for the stability of the alkyls.

A 34-yr pot experiment followed changes in SOM composition as grass was grown in humus-free marl (Schulten et al., 1992). The first 7 years were marked by relative accumulation of lignin dimers, whereas later stages showed slight enrichment of carbohydrates, alkanes/alkenes, fatty acids and N heterocycles. Alkylaromatics increased sharply between years 13 and 19, then remained steady. It is thus possible that alkyls accumulate in part because they occur in combination with aromatics, as suggested earlier by Schnitzer and Neyroud (1975).

Kögel-Knabner et al. (1992) reported that concentrations of large rigid alkyl molecules

increased with depth in forest soil profiles. They concluded that these rigid alkyls were most likely not inherited unchanged from microbial or plant cells, but resulted instead from in situ alteration of the alkyl polymer structure — most likely from an increase in cross-linking.

Kinchesh et al. (1995) used ^{13}C-NMR to analyze composition of unfractionated SOM from long-term plots at Rothamsted, England. They found that the *o*-alkyl fraction varied markedly with management treatment and vegetation whereas the aromatic and methoxyl alkyl fractions varied hardly at all, and that amounts of carbohydrate were largest where inputs of organic matter were largest. The relative amount of alkyl C did not decrease after 20 years of bare fallow. These results are consistent with the Baldock/Oades model of conversion of C from carbohydrate to aromatic and alkyl, although they could equally well indicate selective degradation of the carbohydrate. Additional ^{13}C-NMR studies of unfractionated SOM in soils of varying age, mineralogy, and vegetation or management history are needed.

3.1.2. Microbial synthesis and extracellular condensation

As microbes assimilate low molecular-weight compounds (organic acids, sugars, amino acids), some C is respired to produce energy, and the rest is synthesized into either new tissues (growth) or metabolites that are released to the extracellular environment. Released metabolites can include simple organic acids, polysaccharides, polyaromatic melanoid pigments, and extracellular enzymes.

The products of microbial synthesis vary markedly in recalcitrance. In Tables 1–4, we have compiled reports of in vitro degradation of a wide range of mono- and polymeric molecules and microbial products and tissues. In all studies degradation was expressed as the percent of ^{14}C-labeled substrate released as CO_2 during a soil incubation. This measure of degradation provides an index of recalcitrance, although some caution is needed as experimental conditions were not the same in all studies. In many studies substrates were treated or amended in order to gain insight into potential stabilization processes. For example, incorporating the substrate into a model humic-acid polymer or adding allophane consistently stabilized both simple and complex substrates.

Several patterns emerge from Tables 1–4. Whole microbial cells and cell walls generally decompose more slowly than the free amino acids, sugars and phenolics used for growth. Groups of microbes differ, however, in the recalcitrance of their cellular constituents. Fungi and actinomycetes degrade more slowly than bacteria and, within the fungi, those with melanized cell walls degrade more slowly than those with hyaline cells.

Saprophytic fungi and bacteria, especially actinomycetes, and even some ectomycorrhizal fungi, have been shown to synthesize dark-colored humic-like polymers in vitro (Tan et al., 1978; Stevenson, 1982; Martin and Haider, 1986; Oades, 1989; Paim et al., 1990). The polymers may be incorporated into cell walls (e.g., fungal melanins — Bell and Wheeler, 1986) or released as metabolites during growth or stationary phase and by autolysis after cell death. Such polymers in general degrade slowly relative to other products of microbial metabolism (Tables 1–4).

Microbes mediate extracellular synthesis reactions by releasing extra-cellular peroxidases and phenoloxidases that oxidize phenols to quinones, which then react with O, N,

and S nucleophiles in other phenols, amino acids, or peptides to yield aromatic polymers (Stevenson, 1982; Stott and Martin, 1990).

Quinones are also produced during abiotic reactions catalyzed by oxides of Al, Fe(III), Mn(IV) and Si, and can then initiate condensation reactions that produce polyphenols (Wang et al., 1986; Huang, 1991).

In general, one would expect the structure of polymers formed by extra-cellular enzymes or by abiotic condensation to be more random than those formed within microbial cells, and that a more randomly arranged structure would be more recalcitrant than a regularly repeating structure (Swaby and Ladd, 1962, 1966; Oades, 1988), but we know of no studies in which the recalcitrance of the humic polymers formed by these three pathways was actually compared.

3.2. Controls that increase interactions

3.2.1. Microbial polysaccharides

Many bacteria and fungi release diverse polysaccharides into their immediate environment. While long implicated in aggregate formation and stabilization (see Section 3.3.1), such microbial slime can also increase interactions by binding metabolically active cells and extra-cellular enzymes to detrital and mineral particles (Dickerson and Baker, 1979; Martens and Frankenberger, 1991). Interactions between the slime and the particle surface may affect the rate of slime degradation but we located no studies of this.

3.2.2. Sorption and precipitation

As much of the terminology in this field is muddled, some definitions are prerequisite to efficient discussion. *Sorption* is the transfer of a solute (the *sorbate*) from solution to an existing solid phase (the *sorbent*). *Adsorption* is the net accumulation of sorbate at the interface between the soil solution and the sorbent (a two-dimensional process). *Absorption* is the accumulation of sorbate *within* an existing sorbent. *Precipitation* is the accumulation of a solute as a *new* solid phase (a three-dimensional process). In reality, however, adsorption, adsorption, and precipitation can be virtually indistinguishable in soil (Sposito, 1984, p. 123).

Effects of sorption and precipitation on degradation: Degradation of the sorbate may be affected by its interaction with the sorbent, but the evidence to date is indirect and conflicting. For example, adding clays to soil or soil suspensions alters rates of degradation of organics, but Stotsky (1986) in reviewing the literature found that degradation rates increased in some experiments and decreased in others. In all of these laboratory experiments, effects of sorption may have been confounded with other interactions (Stotsky, 1986). For example, clays may also (1) interact directly with microbes, thus altering the rate and pathways of microbial metabolism; (2) modify the solution environment (e.g., by buffering pH, which affects microbial and enzyme activity); and (3) bind extracellular enzymes and thus modify their activity. Moreover, since sorption also tends to promote aggregation (Section 3.3.1), effects of sorption and aggregation are difficult to separate.

Much indirect evidence suggests that clay somehow stabilizes SOM. An effect of clay content can be inferred, for example, from studies on stabilization of crop residues

Table 1
In vitro degradation of monomeric and polymeric compounds, microbial products, and microbial whole cells and tissues, with treatments affecting substrate stability: different substrates in same soil

Substrate	Substrate treatment	Soil	% degradation (incubation time in weeks)				Reference
			1	4	12	52	
Monomers							
glycine	none	Greenfield sandy loam [a]	75	86	89	–	Verma et al. (1975)
leucine	none	Greenfield sandy loam	64	77	81	–	Verma et al. (1975)
glucose	none	Greenfield sandy loam	63	73	77	–	Zunino et al. (1982)
glucosamine	none	Greenfield sandy loam	55	65	73	–	Bondietti et al. (1972)
benzoic acid	none	Greenfield sandy loam	68	78	82	–	Haider et al. (1977)
p-hydroxybenzoic acid	none	Greenfield sandy loam	52	65	73	–	Haider et al. (1977)
vanillic acid	none	Greenfield sandy loam	47	64	71	–	Haider et al. (1977)
protocatechuic acid	none	Greenfield sandy loam	32	65	68	–	Haider and Martin (1975)
catechol	none	Greenfield sandy loam	7	11	18	–	Martin et al. (1979)
emodin (anthraquinone)	none	Greenfield sandy loam	49	65	69	–	Linhares and Martin (1979)
Polymers							
glycyl–alanine	none	Greenfield sandy loam	44	89	–	–	Verma et al. (1975)
glycyl–leucine	none	Greenfield sandy loam	48	84	–	–	Verma et al. (1975)
glycyl–glycyl–leucine	none	Greenfield sandy loam	58	80	–	–	Verma et al. (1975)
protein from *Chlorella*	none	Greenfield sandy loam	49	59	67	–	Zunino et al. (1982)
cellulose	none	Greenfield sandy loam	27	52	78	–	Zunino et al. (1982)
chitosan	none	Greenfield sandy loam	20	45	–	–	Bondietti et al. (1972)
model lignin $-OCH_3$ group	none	Greenfield sandy loam	–	12	–	56	Martin et al. (1982)
model lignin aromatic ring	none	Greenfield sandy loam	–	6	–	27	Martin et al. (1982)
model humic acids —							
hydroxyphenols	none	Greenfield sandy loam	< 1	1	–	–	Bondietti et al. (1972)
hydroxybenzoic acids	none	Greenfield sandy loam	0	2	–	–	Bondietti et al. (1972)

Bacterial polysaccharides							
Anabaena flos-aquae	none	Greenfield sandy loam	32	59	70	–	Verma and Martin (1976)
Azotobacter chroococcum	none	Greenfield sandy loam	62	73	–	–	Martin et al. (1966)
Chromobacterium violaceum	none	Greenfield sandy loam	2	28	–	–	Martin et al. (1966)
Leuconostoc dextranicus	none	Greenfield sandy loam	53	71	79	–	Zunino et al. (1982)
Mostoc muscorum	none	Greenfield sandy loam	24	40	60	–	Verma and Martin (1976)
Fungal melanins							
Aspergillus glaucus	none	Greenfield sandy loam	–	2	4	9	Martin et al. (1982)
Hensonula toruloidea	none	Greenfield sandy loam	–	3	5	9	Martin et al. (1982)
Stachybotrys atra							
from cells	none	Greenfield sandy loam	< 1	3	6	–	Linhares and Martin (1978)
from growth medium	none	Greenfield sandy loam	< 1	5	10	–	Linhares and Martin (1978)
Microbial cells and tissues							
Actinomycetes							
Micromonospora chalceae cells	none	Greenfield sandy loam	10	–	57	–	Kassim et al. (1981)
Streptomyces halstedii cells	none	Greenfield sandy loam	24	–	57	–	Kassim et al. (1981)
Bacteria							
Anabaena flos-aquae							
cells	none	Greenfield sandy loam	38	51	66	–	Verma and Martin (1976)
cell walls	none	Greenfield sandy loam	25	45	55	–	Verma and Martin (1976)
cytoplasm	none	Greenfield sandy loam	53	67	73	–	Verma and Martin (1976)
Bacillus subtilis							
cell wall	none	Greenfield sandy loam	54	71	79	–	Nelson et al. (1979)
cytoplasm	none	Greenfield sandy loam	60	69	76	–	Nelson et al. (1979)
Chromobacterium violaceum cells	none	Greenfield sandy loam	45	57	67	–	Verma and Martin (1976)
Pseudomonas aeruginosa							
cells	none	Greenfield sandy loam	52	68	77	–	Nelson et al. (1979)
cell wall	none	Greenfield sandy loam	48	66	74	–	Nelson et al. (1979)
cytoplasm	none	Greenfield sandy loam	53	64	71	–	Nelson et al. (1979)

Table 1 (continued)

Substrate	Substrate treatment	Soil	% degradation (incubation time in weeks)				Reference
			1	4	12	52	
Fungi (hyaline)							
Mucor rouxii							
cells	none	Greenfield sandy loam	31	45	58	–	Nelson et al. (1979)
cell wall	none	Greenfield sandy loam	22	35	50	–	Nelson et al. (1979)
cytoplasm	none	Greenfield sandy loam	56	68	76	–	Nelson et al. (1979)
Fungi (melanic)							
Hensonula toruloidea cells	none	Greenfield sandy loam	13	–	39	–	Kassim et al. (1981)
Stachybotrys atra cells	none	Greenfield sandy loam	2	–	44	–	Kassim et al. (1981)
Fungi (hyaline)							
Polystictus versicolor cells	none	Mexico silt loam	–	–	63	–	Hurst and Wagner (1969)
Schizophyllum commune cells	none	Mexico silt loam	–	–	69	–	Hurst and Wagner (1969)
Fungi (melanic)							
Cenococcum graniforme	none	Mexico silt loam	–	–	45	–	Hurst and Wagner (1969)
Cladosporium sp cells	none	Mexico silt loam	–	–	47	–	Hurst and Wagner (1969)
Mycelium radicis-atrovirens cells	none	Mexico silt loam	–	–	40	–	Hurst and Wagner (1969)

[a] Greenfield sandy loam (Mollic Haploxeralf), pH 7.0, 1.02% OM, 0% allophane.

in soils of differing texture (Sørensen, 1975, 1981; Jenkinson, 1977; Ladd et al., 1977, 1981, 1985, 1993). Amato and Ladd (1992) found strong correlations between clay content (and its various correlates, such as CEC) and accumulation of microbial biomass derived from ^{14}C-glucose. Correlations between clay and SOM content can be quite good, at least over regions of similar mineralogy (e.g., Burke et al., 1989). Oades (1988) points to several sequences of soils in which the percentage loss of SOM upon cultivation correlated inversely with clay content. He noted, however, that cross-site correlations between clay content and SOM dynamics can be difficult to interpret because clay content correlates well with other factors, such as moisture retention and cation exchange capacity, that in turn influence plant detrital production (and, one might add, microbial activity).

Effects of precipitation are harder to document, in part because it is difficult to know that precipitation has occurred. A clear example may be inositol polyphosphates, a major form of organic phosphorus that is stabilized against enzymatic hydrolysis by formation of insoluble Al or Fe compounds (McKeague et al., 1986).

Controls on sorption: Sorption is influenced by the nature of the sorbent, the sorbate, and the bathing solution from which it is sorbed (Fig. 3). Laboratory studies have shown that hydrophobic substances are sorbed more readily than hydrophilic (Jardine et al., 1989; Vance and David, 1989; Varadachari et al., 1994), although a field study by Qualls and Haines (1991) showed no such difference.

Clays, including layer aluminosilicates, amorphous aluminosilicates, and the so-called sesquioxides (oxides, hydroxides, and oxyhydroxides of Al and Fe), provide the vast majority of sorbent surface area in soil. Clay surfaces can be divided into two fundamentally distinct types (cf. Uehara and Gillman, 1981; Sollins et al., 1988; Oades et al., 1989; McBride, 1989). On hydroxylated surfaces, net surface charge varies, becoming increasingly negative as pH increases. Such variable-charge surfaces occur on kaolinite, sesquioxides, and amorphous aluminosilicates. Permanent charge arises from substitution of ions of lower valence for ones of higher valence within the crystal structure of clays. The resulting negative charge is a permanent feature of the clay and is largely unaffected by pH. Permanent-charge surfaces occur on smectite, illite, and other layer silicate clays.

Bonding mechanisms differ depending on the nature of the sorbate and sorbent. Sorption of negatively charged organic groups (e.g., dissociated carboxylic acid groups) can occur through replacement of surface hydroxyl groups (ligand exchange) (e.g., Parfitt et al., 1977; Mott, 1981). Since surface hydroxyls are restricted to variable-charge surfaces, sorption of negatively charged organics by ligand exchange should be most important in oxide-rich and allophanic soils. Positively charged organic groups (i.e., organic bases such as protonated amines) should sorb readily on negative surfaces by cation exchange, but such groups are relatively uncommon in soil and litter solution (Qualls and Haines, 1991), perhaps in fact because they are sorbed rapidly. Sorption of organic anions by electrostatic interaction (anion exchange) would require positive surface charge, which is encountered mainly in the subsurface horizons of variable-charge soils (Uehara and Gillman, 1981; Sollins et al., 1988). Sorption of negatively charged organic groups through cation bridging should also be possible (Tate and Theng, 1980; Varadachari et al., 1995).

Table 2
In vitro degradation of monomeric and polymeric compounds, microbial products, and microbial whole cells and tissues, with treatments affecting substrate stability: effect of different soils, including those differing in allophane content

Substrate treatment	Substrate	Soil	% degradation (incubation time in weeks)				Reference
			1	4	12	52	
Monomers							
glucose	none	Greenfield sandy loam [a], 0% allophane	63	73	77	–	Zunino et al. (1982)
glucose	none	Pillan, 0% allophane	59	67	74	–	Zunino et al. (1982)
glucose	none	Corte Alto, 15% allophane	25	46	58	–	Zunino et al. (1982)
glucose	none	Puerto Octay, 26% allophane	15	39	52	–	Zunino et al. (1982)
glucose	none	Ohinepanea sandy loam, 1.5% allophane	50	63	–	–	Saggar et al. (1994)
glucose	none	Katikati sandy loam, 6% allophane	48	59	–	–	Saggar et al. (1994)
glucose	none	Horotiu silt loam, 9% allophane	44	54	–	–	Saggar et al. (1994)
glucose	none	Otorohanga silt loam, 13% allophane	44	54	–	–	Saggar et al. (1994)
glucosamine	none	Greenfield sandy loam	55	65	73	–	Bondietti et al. (1972)
glucosamine	none	Steinbeck loam [b]	36	65	67	–	Kassim et al. (1981)
Polymers							
protein from *Chlorella*	none	Chino loam	43	53	63	–	Martin and Haider (1979)
protein from *Chlorella*	none	San Jacinto sandy loam	18	42	58	–	Martin and Haider (1979)
protein from *Chlorella*	none	Greenfield sandy loam, 0% allophane	49	59	67	–	Zunino et al. (1982)
protein from *Chlorella*	none	Pillan, 0% allophane	42	52	63	–	Zunino et al. (1982)
protein from *Chlorella*	none	Corte Alto, 15% allophane	4	25	35	–	Zunino et al. (1982)
protein from *Chlorella*	none	Puerto Octay, 26% allophane	15	27	38	–	Zunino et al. (1982)

cellulose	none	German chernozem	39	64	72	–	Azam et al. (1985)
cellulose	none	Chino loam	26	51	65	–	Martin and Haider (1979)
cellulose	none	San Jacinto sandy loam	4	29	54	–	Martin and Haider (1979)
cellulose	none	Greenfield sandy loam	27	52	78	–	Zunino et al. (1982)
cellulose	none	Pillan, 0% allophane	41	61	78	–	Zunino et al. (1982)
cellulose	none	Corte Alto, 15% allophane	2	7	42	–	Zunino et al. (1982)
cellulose	none	Puerto Octay, 26% allophane	1	6	23	–	Zunino et al. (1982)
model lignin –OCH3 group	none	Steinbeck loam, 0% allophane	–	6	–	42	Martin et al. (1982)
model lignin –OCH3 group	none	Greenfield sandy loam, 0% allophane	–	12	–	56	Martin et al. (1982)
model lignin –OCH3 group	none	Pillan, 0% allophane	–	25	–	59	Martin et al. (1982)
model lignin –OCH3 group	none	Puerto Octay, 26% allophane	–	13	–	46	Martin et al. (1982)
model lignin aromatic ring	none	Steinbeck loam, 0% allophane	–	3	–	26	Martin et al. (1982)
model lignin aromatic ring	none	Greenfield sandy loam, 0% allophane	–	6	–	27	Martin et al. (1982)
model lignin aromatic ring	none	Pillan, 0% allophane	–	6	–	24	Martin et al. (1982)
model lignin aromatic ring	none	Puerto Octay, 26% allophane	–	1	–	11	Martin et al. (1982)
Bacterial polysaccharides							
Leuconostoc dextranicus	none	Greenfield sandy loam, 0% allophane	53	71	79	–	Zunino et al. (1982)
Leuconostoc dextranicus	none	Pillan, 0% allophane	31	48	69	–	Zunino et al. (1982)
Leuconostoc dextranicus	none	Corte Alto, 15% allophane	7	37	51	–	Zunino et al. (1982)
Leuconostoc dextranicus	none	Puerto Octay, 26% allophane	2	16	33	–	Zunino et al. (1982)
Fungal melanins							
Aspergillus glaucus	none	Greenfield sandy loam, 0% allophane	–	2	4	9	Martin et al. (1982)
Aspergillus glaucus	none	Puerto Octay, 26% allophane	–	< 1	< 1	3	Martin et al. (1982)
Hensonula toruloidea	none	Greenfield sandy loam, 0% allophane	–	3	5	9	Martin et al. (1982)
Hensonula toruloidea	none	Puerto Octay, 26% allophane	–	< 1	1	4	Martin et al. (1982)

[a] Greenfield sandy loam (Mollic Haploxeralf), pH 7.0, 1.02% OM, 0% allophane.
[b] Steinbeck loam (Mollic Haploxeralf), pH 5.0, 1.48% OM, 0% allophane.

Table 3
In vitro degradation of monomeric and polymeric compounds, microbial products, and microbial whole cells and tissues, with treatments affecting substrate stability: effect of humic acid and other organics

Substrate	Substrate treatment	Soil	% degradation (incubation time in weeks)				Reference
			1	4	12	52	
Monomers							
glucosamine	none	Greenfield sandy loam [a]	55	65	73	–	Bondietti et al. (1972)
glucosamine	mixed with HA [b]	Greenfield sandy loam	51	62	70	–	Bondietti et al. (1972)
glucosamine	complexed with HA	Greenfield sandy loam	5	8	15	–	Bondietti et al. (1972)
glucosamine	complexed with HA	Greenfield sandy loam	–	9	15	20	Martin et al. (1982)
protocatechuic acid	none	Greenfield sandy loam	32	65	68	–	Haider and Martin (1975)
protocatechuic acid	complexed with HA	Greenfield sandy loam	1	3	4	–	Haider and Martin (1975)
catechol	none	Greenfield sandy loam	7	11	18	–	Martin et al. (1979)
catechol	polymerized with with peroxidase	Greenfield sandy loam	2	5	7	–	Martin et al. (1979)
emodin (anthraquinone)	none	Greenfield sandy loam	49	65	69	–	Linhares and Martin (1979)
emodin (anthraquinone)	polymerized with catechol	Greenfield sandy loam	10	37	55	–	Linhares and Martin (1979)
Polymers							
glycyl–alanine	none	Greenfield sandy loam	44	89	–	–	Verma et al. (1975)
glycyl–alanine	complexed with HA	Greenfield sandy loam	9	14	–	–	Verma et al. (1975)
glycyl–leucine	none	Greenfield sandy loam	48	84	–	–	Verma et al. (1975)
glycyl–leucine	complexed with HA	Greenfield sandy loam	8	14	–	–	Verma et al. (1975)
glycyl–glycyl–leucine	none	Greenfield sandy loam	58	80	–	–	Verma et al. (1975)
glycyl–glycyl–leucine	complexed with HA	Greenfield sandy loam	14	21	–	–	Verma et al. (1975)
protein from *Chlorella*	none	Greenfield sandy loam	49	59	67	–	Zunino et al. (1982)
protein from *Chlorella*	complexed with HA	Greenfield sandy load	–	6	11	14	Martin et al. (1982)
protein from *Chlorella*	none	Puerto Octay, 26% allophane	15	27	38	–	Zunino et al. (1982)
protein from *Chlorella*	complexed with HA	Puerto Octay, 26% allophane	–	1	4	10	Martin et al. (1982)
chitosan	none	Greenfield sandy loam	20	45	–	–	Bondietti et al. (1972)
chitosan	complexed with HA	Greenfield sandy loam	16	27	–	–	Bondietti et al. (1972)

Microbial cells and tissues

Bacteria							
Anabaena flos-aquae							
cell walls	none	Greenfield sandy loam	25	45	55	–	Verma and Martin (1976)
	complexed with HA	Greenfield sandy loam	9	17	28	–	Verma and Martin (1976)
cytoplasm	none	Greenfield sandy loam	53	67	73	–	Verma and Martin (1976)
	complexed with HA	Greenfield sandy loam	8	12	17	–	Verma and Martin (1976)
Bacillus subtilis							
cell wall	none	Greenfield sandy loam	54	71	79	–	Nelson et al. (1979)
	complexed with HA	Greenfield sandy loam	1	6	13	–	Nelson et al. (1979)
cytoplasm	none	Greenfield sandy loam	60	69	76	–	Nelson et al. (1979)
	complexed with HA	Greenfield sandy loam	18	31	40	–	Nelson et al. (1979)
Pseudomonas aeruginosa							
cell wall	none	Greenfield sandy loam	48	66	74	–	Nelson et al. (1979)
	complexed with HA	Greenfield sandy loam	5	11	15	–	Nelson et al. (1979)
cytoplasm	none	Greenfield sandy loam	53	64	71	–	Nelson et al. (1979)
	complexed with HA	Greenfield sandy loam	21	31	39	–	Nelson et al. (1979)
Fungi (hyaline)							
Mucor rouxii							
cells	none	Greenfield sandy loam	31	45	58	–	Nelson et al. (1979)
	complexed with HA	Greenfield sandy loam	16	26	34	–	Nelson et al. (1979)
cell wall	none	Greenfield sandy loam	22	35	50	–	Nelson et al. (1979)
	complexed with HA	Greenfield sandy loam	10	18	25	–	Nelson et al. (1979)
cytoplasm	none	Greenfield sandy loam	56	68	76	–	Nelson et al. (1979)
	complexed with HA	Greenfield sandy loam	16	26	34	–	Nelson et al. (1979)

[a] Greenfield sandy loam (Mollic Haploxeralf), pH 7.0, 1.02% OM, 0% allophane.
[b] HA = model humic acid.

Table 4
In vitro degradation of monomeric and polymeric compounds, microbial products, and microbial whole cells and tissues, with treatments affecting substrate stability: effect of Al and Fe

Substrate	Substrate treatment	Soil	% degradation (incubation time in weeks)				Reference
			1	4	12	52	
Bacterial polysaccarides							
Azotobacter chroococcum	none	Greenfield sandy loam [a]	62	73	–	–	Martin et al. (1966)
Azotobacter chroococcum	complexed with Al	Greenfield sandy loam	51	66	–	–	Martin et al. (1966)
Azotobacter chroococcum	complexed with Fe	Greenfield sandy loam	9	23	–	–	Martin et al. (1966)
Chromobacterium violaceum	none	Greenfield sandy loam	2	28	–	–	Martin et al. (1966)
Chromobacterium violaceum	complexed with Al	Greenfield sandy loam	7	29	–	–	Martin et al. (1966)
Chromobacterium violaceum	complexed with Fe	Greenfield sandy loam	6	31	–	–	Martin et al. (1966)

[a] Greenfield sandy loam (Mollic Haploxeralf), pH 7.0, 1.02% OM, 0% allophane.

Other bonding mechanisms involved in sorption include water bridging, hydrogen bonding, and van der Waals forces (Burchill et al., 1981). In addition, Jardine et al. (1989) concluded that sorption of humic substances on soil was "by physical sorption driven by favorable entropy changes". Due to the diversity of sorbents and sorbates in soils, several mechanisms will likely be involved simultaneously (Jardine et al., 1989).

The composition of the bathing solution affects sorption. For example, pH affects the surface charge on variable-charge clays and the extent of dissociation of carboxylic acid groups in organic compounds, and should therefore affect sorption of the organics on the clays. But again, trends are not clear. Sorption of humic and fulvic acids on synthetic gibbsite peaked at pH 5 (Evans and Russell, 1959) whereas sorption on K-saturated smectite and on synthetic lepidocrocite decreased continuously over the range pH 3.2 to 7.0 (Evans and Russell, 1959). In other studies with humic substances, sorption on gibbsite, montmorillonite, illite, mordenite, and amorphous silica decreased over this same pH range, whereas it decreased or stayed constant for kaolinite, and increased for δ-Al_2O_3 (Tipping, 1981; Inoue et al., 1990; Schulthess and Huang, 1991).

Adding cations increases sorption of organics on clay surfaces. For example, sorption of humic acid on illite, montmorillonite, and kaolinite varied with the cation added, decreasing in the order Al > Ca > Mg > K, Na (Varadachari et al., 1991). Addition of Ca and Mg to synthetic goethite increased adsorption of humic substances (Tipping, 1981). The cations are assumed to provide a bridge between the negatively charged clay surface and the negatively charged organic functional group, but we know of no spectroscopic evidence for this.

Unfortunately, the relevance of most sorption studies to questions of SOM dynamics is unclear. Although virtually all soil mineral particles are coated with amorphous organomineral materials, which presumably alter the surface properties of the particles and thus their sorption capacity, sorption has been studied mainly with artificially prepared or cleaned clays that were free of such organomineral coatings. The few attempts to study effects of coatings on sorption have yielded conflicting results (e.g., Fusi et al., 1989; Inoue et al., 1990). Further, the sorption of humic materials on organic coatings or organic particles already present in the soil has not been adequately explored, although sorption of well defined organics such as pesticides (Morrill et al., 1982) and nitrification inhibitors (Jacinthe and Pichtel, 1992) is known to occur.

Amounts of sorbed material in soil: The quantitative importance of sorption in SOM stabilization and accumulation is even less well understood than the mechanisms and controls of sorption. How much of the OM in soil might be sorbed? A commonly used fractionation technique separates particles on the basis of density — the denser particles are those in which the OM is associated with larger amounts of mineral material (Young and Spycher, 1979). But whether the OM in the denser particles is actually sorbed on mineral particles, rather than trapped within aggregates, is unclear.

Mayer (1994a,b) has calculated that, with monolayer coverage of mineral surfaces by typical soil organics, 500 μg C would be retained per m^2 of surface area; he in fact observed a strong correlation between surface area and C content (after removal of light-fraction detritus) in both marine sediments and A horizons of soils, although with large variability in the latter. For most samples, C values were near those predicted by the monolayer model. Moreover, many samples falling below the monolayer line were

from highly unproductive sites (low OM inputs), while many falling above the line were from sites with unusually high OM inputs or where interactions and lack of accessibility might be expected to slow degradation. In the laboratory, amounts of humic substances sorbed are generally less than 500 μg C/m^2, but it is possible that the contact time between organics and surfaces in these studies (generally < 24 h) was insufficient to saturate the surfaces.

3.2.3. Complexation reactions

Complexation of transition metals, such as Al(III) and Fe(III), by organic substrates is perhaps the clearest example of an interaction that increases substrate stability. Major complexation sites on organic substrates include, in order of affinity, –C–OH > $-NH_2$ > –N=N– > –COOH > –C–O–C– ≫ –C=O (Stevenson, 1982). For aromatics at least, the order of affinity varies with the cation: for Al, –COOH–OH > –OH–OH > –COOH–COOH > –COOH, whereas for Ca, –COOH–COOH > –COOH–OH > –COOH > OH–OH (Tam and McColl, 1990). Ester-bonded phosphate and sulfate groups can also serve as complexation sites. We found no information on complexation by soil alkyls, although it is well known that fatty acids form salts with metal ions (e.g., soaps).

Al complexation affects degradation rates. Addition of $Al(OH)_3$ gel decreased the rate of decomposition of ^{14}C-glucose and ground corn stalks added to an Al-humus rich soil (Jacquin et al., 1978). Microbial utilization of ^{14}C-citrate and fulvic and humic acids was greatly reduced upon adding Al at amounts calculated so that toxic effects of inorganic Al species were unlikely to have caused the decrease in citrate degradation (Boudot et al., 1986, 1989). In Tables 1–4, the bacterial polysaccharides most stabilized by Al and Fe were those containing uronic acid groups.

A role for Al-complexation in SOM dynamics is supported further by the observation that SOM accumulates in very large amounts in certain soils that lack even amorphous alumino-silicate clays such as allophane and imogolite. These soils, now placed in the Melanic and Fulvic great groups within the Andisol order of Soil Taxonomy (Soil Survey Staff, 1992), have low ratios of oxalate-extractable Si to oxalate-extractable Al suggesting that the Al occurs mainly as Al–OM complexes rather than as a constituent of clay or clay-like minerals (Wada and Higashi, 1976; see also Wada, 1980; Martin et al., 1982; Boudot and Chone, 1985; Boudot et al., 1988). The genesis of such soils is unclear, but it is widely assumed that the formation of Al–OM complexes promotes OM accumulation by somehow stabilizing the OM (Duchaufour, 1976; Monreal et al., 1981; Zunino et al., 1982; Martin and Haider, 1986; Oades, 1988).

Recent ^{13}C-NMR comparisons across soil types offer further evidence that Al-complexation may slow the accumulation of alkyl carbon. Working with two Mollisols, two Oxisols, two Alfisols, an Andisol, and a Histosol, Baldock et al. (1992) obtained spectra for clay and silt size-classes and for the lighter particles in coarser size-classes. They found that the Andisol differed from all the others in that there was less variation in composition with particle size and comparatively less accumulation of alkyl carbon in the soil as a whole. They concluded that this was due to the tendency for the Andisol to form Al complexes that protect the OM from microbial degradation.

Based on the limited data available, the aromatics would be expected to interact more

strongly though complexation reactions than would the *o*-alkyl or alkyl fractions. Soil humic–acid fractions, for example, have been shown to provide more –COOH complexation sites than soil polysaccharides (~ 300 vs. 50–100 $cmol_c/kg$), although the polysaccharide data refer only to uronic acids (Cheshire, 1979), which would neglect any contribution by amino sugars and *cis*-di-OH groups (e.g., mannose). No similar data was found for alkyl compounds in two major reviews of soil lipids (Stevenson, 1982; Dinel et al., 1990). Assuming though that soil alkyl compounds are fairly large molecular weight, little tendency to form complexes would be expected.

One other line of evidence may relate to whether dissolved Al interacts with organics to alter their degradation rate. A series of papers in the early 1970s showed that inorganic salts, especially $AlCl_3$, increased net *N* mineralization in soils rich in allophane and Al–OM complexes but had much less effect in other soils (Singh et al., 1969; Broadbent and Nakashima, 1971; Heilman, 1975). Al was more effective than Ca or K, and Cl was more effective than CO_3 or HPO_4. The relation, if any, between these increases in net N mineralization and changes in OM stability remains unclear.

3.3. Controls that decrease accessibility

3.3.1. Aggregation

Aggregates are simply particles composed of smaller particles, which may themselves be aggregates (Tisdall and Oades, 1982; Elliott, 1986; Emerson et al., 1986). Aggregates range in size from microns to millimeters (Muneer and Oades, 1989b) and are often classified according to their ability to resist slaking in water (Kemper and Chepil, 1986). Both particles and the materials that bind them together (the binding agents) can be either mineral or organic (Tisdall and Oades, 1982; Oades, 1984; Lynch and Bragg, 1985; Chaney and Swift, 1986b; Bartoli et al., 1988; Bartoli and Philippy, 1990; Capriel et al., 1990; Haynes and Swift, 1990; Dinel et al., 1991).

Effects of aggregation on OM stability: Aggregation can influence accessibility of substrate to microbes and fauna and rates of diffusion of reactants and products of extracellular synthesis reactions. Theoretical calculations suggest that aggregation should limit access to organic matter. For example, Van Veen and Kuikman (1990) calculated that 95% of the pore space in a silt loam was accounted for by pores too small to be accessible to bacteria. Similarly, Adu and Oades (1978) noted that, if one assumes that enzyme diffusion in soil is too slow to be significant, then some 90% of the surface area of a clay or clay loam would be inaccessible to organisms and extracellular enzymes.

Direct evidence for effects of aggregation on accessibility is limited. Adu and Oades (1978) produced synthetic aggregates that were labelled uniformly with ^{14}C substrates. Aggregates of a sandy loam soil respired less starch than did unaggregated soil, which they took as evidence of the presence of inaccessible micropores in the aggregates. This pattern was not observed for a clayey soil, or when the substrate was glucose. Bartlett and Doner (1988) incorporated lysine and leucine either homogeneously throughout sterilized synthetic aggregates or only on their surfaces. After adding inoculum, more of the amino acid was respired from aggregate surfaces than from within aggregates indicating delay in microbial access to substrate within the aggregates. Priesack and

Kisser-Priesack (1993) sterilized large (1.8 cm) aggregates with gamma-radiation, then added ^{13}C-glucose and showed that the rate of glucose utilization decreased with distance into the aggregate interior. Also, Killham et al. (1993) found that ^{14}C-glucose turned over faster when introduced into larger pores (6–30 μm) than into small pores (< 6 μm neck diameter). This and other recent studies, however, suggest that aggregation may serve as much to protect microbes from predation as to protect substrate from degradation (see Sect. 5.2).

Indirect evidence that aggregation can limit substrate accessibility is that respiration increases when aggregates are disrupted (see Sect. 4.3.2). This evidence is not conclusive, however, because aggregation affects factors in addition to accessibility. For example, oxygen concentrations are low in the middle of aggregates (Sexstone et al., 1985), which may limit respiration even if substrate is accessible.

Mechanisms and controls: Aggregation is affected by chemical, microbial, plant, animal, and physical processes (Fig. 4). Microbes promote aggregation by several mechanisms: (1) fungal hyphae bind solid grains and aggregates together to create larger aggregates; (2) bacteria attach to soil particles (or vice-versa, depending on relative size), thus forming bridges between particles; (3) fungi and bacteria release polysaccharides that serve as a binding agent (review by Lynch and Bragg, 1985). Plants play various roles in aggregation. Root exudates may flocculate colloids and bind or stabilize aggregates (Glinski and Lipiec, 1990). Root exudates may also influence aggregation indirectly through effects on microbial activity (Section 5.2). Pressure exerted by developing roots may induce aggregation, and water uptake by roots may dehydrate soil colloids, thus causing shrinkage and eventual stabilization of soil aggregates (Glinski and Lipiec, 1990).

Many soil animals (including collembola, earthworms, millipedes, isopods, termites, ants and beetles) promote aggregation by forming fecal pellets and excreting binding agents (Hole, 1981; Pawluk, 1987; Lavelle, 1988). Improved aggregation by earthworms was demonstrated by MacKay and Kladivko (1985), who found that the presence of earthworms increased the proportion of soil in water-stable aggregates (> 0.21 mm diam.).

Fe-oxide rich soils (e.g., many Oxisols) and allophanic soils are among the most stably micro-aggregated (El-Swaify, 1980; Warkentin and Maeda, 1980; Churchman and Tate, 1986, Churchman and Tate, 1987; Strickland et al., 1988). This is generally interpreted as evidence that oxides and hydroxides of Al and Fe, as well as amorphous aluminosilicates, are important in aggregation.

Evidence for the importance of various materials as binding agents comes from studies of disaggregation upon exposure to chemical extractants (e.g., Bartoli and Philippy, 1990; Wierzchos et al., 1992), correlation of aggregate stability with soil properties (Molope et al., 1987), and addition of binding agents to soil. Aggregation was increased by adding exudates from corn and bromegrass roots (Pojasok and Kay, 1990), fungal polysaccharides (Chenu, 1989), glucose, humic acid (Chaney and Swift, 1986a,b), Ca^{2+} (Muneer and Oades, 1989a), and dissolved humic materials (Caillier and Visser, 1988). Tannins stabilize polysaccharide binding agents (Griffiths and Burns, 1972). If solid organic matter is added, microbial activity must occur before aggregation will increase; effectiveness of microbes in improving aggregate stability increases in the

following order: fungi > actinomycetes > bacteria, although there is much variation within each group (Lynch and Bragg, 1985).

Different binding agents and mechanisms are thought to come into play at different size scales. Based on results of electron microscopy, aggregate disruption by sonication, and elemental analysis, Tisdall and Oades (1982) hypothesized that, for a Calcixeroll, amorphous aluminosilicates and oxides serve as binding agents for submicron aggregates; resistant aromatic compounds associated with polyvalent metal cations for aggregates up to 250 μm; and roots, hyphae and transient polysaccharides of plant or microbial origin for aggregates > 250 μm.

Tiessen and Stewart (1988) used light and electron microscopy to study a variety of aggregate types in a Mollisol and an Alfisol. They emphasized the importance of microbial polysaccharides in stabilizing microaggregates (1–20 μm) and of plant detritus as nuclei for development of larger aggregates (100–300 μm). In contrast, solid silt- to sand-size mineral grains appeared to provide the nuclei for aggregate development in soils derived from volcanic mudflows (Spycher et al., 1986).

4. Destabilization

Destabilization is the overall process by which soil organic substances become less resistant to degradation. By definition, it occurs by decreasing recalcitrance or by increasing accessibility. Decreasing interactions may also promote destabilization.

4.1. Controls that decrease recalcitrance

4.1.1. Depolymerization

Depolymerization mechanisms are well studied for plant or microbial constituents, such as cellulose and lignin, but not for most soil organic matter. The process can be assumed to be dominantly extra-cellular since the molecules involved are large. Many studies show decolorization of soil humic–acid fractions in vitro (Hurst et al., 1962; Bhardwaj and Gaur, 1971; Domsch et al., 1981; Mishra and Srivastava, 1986) but there is little information on mechanisms. One possible humic depolymerization mechanism involves ligninase-like peroxidase enzymes (Blondeau, 1989), as suggested earlier by work of Hurst et al. (1962) on the ability of white-rot fungi to degrade the soil humic-acid fraction.

Only one study of degradation of alkyl polymers was located (Capriel et al., 1990) and it did not address mechanisms. Depolymerization by enzymes that hydrolyze soil polysaccharides could reasonably be expected to be a key process in destabilization, but this has apparently not been studied.

4.2. Controls that decrease interactions

4.2.1. Dissolution / desorption reactions

Influence of desorption on degradation: In laboratory experiments, soil carbohydrate extracted and then reintroduced to soil was degraded rapidly over the course of a 1–6 yr incubation, whereas levels of carbohydrate in untreated soils changed little over the

same period (Cheshire et al., 1974). The authors concluded that inaccessibility or molecular interactions, not recalcitrance, was responsible for the slow degradation of carbohydrate in the untreated soil.

Smith et al. (1992) used ^{14}C labelling in combination with fluorescence to determine that desorption of quinoline from clay surfaces was prerequisite to microbial utilization; desorption rather than microbial processes limited degradation of quinoline to CO_2. Similar studies of naturally occurring organics could not be located. Furthermore, information on the degradability of natural organics in soil solutions is limited (e.g., Zsolnay and Steindl, 1991; Qualls and Haines, 1992) and it is unclear if their presence in solution vs solid phase affects their degradation rate.

Recent work with marine sediments, building on the C monolayer model of Mayer (1994a,b), showed that simple desorption of organics with distilled water was sufficient to increase rates of degradation some 30–40 fold (Keil et al., 1994).

Controls on dissolution / desorption (Fig. 5): Information on controls on dissolution/desorption of organics is often conflicting, probably because several mechanisms are at work simultaneously. A lower solution pH caused extraction of less organic C from an O horizon but more from a spodic B horizon (Vance and David, 1989). Decreasing ionic strength increased the amount of DOC extracted from three mineral soil horizons (Evans et al., 1988) and from O horizons (Vance and David, 1989). Solution $p\epsilon$ could affect desorption/adsorption of organics by influencing Fe solubility but we found no studies of this.

Anions differ in their desorbing power. Based on the physical chemistry of the ligand exchange reaction, desorption power "should" decrease in the order: phosphate > sulfate > nitrate = chloride, a trend partially confirmed for three mineral horizons by Evans et al. (1988).

4.3. Controls that increase accessibility

4.3.1. Communution

The physical breakdown of detritus into smaller pieces can promote degradation. Fyles and McGill (1987), for example, found that cutting pine needles into 1-cm lengths doubled the initial degradation rate. Neal et al. (1965) determined that small particles of red alder and Douglas-fir sawdust degraded faster than large ones. One possible cause of the increased degradation is greater exposure of surface area to microbial attack. However, in this last study, increasing the surface area more than 300-fold increased degradation less than 3-fold, indicating the importance of other controls on degradation. Swift et al. (1979) found that comminution of oak litter produced an immediate but transitory increase in fungal catabolism; particle size of detritus also influenced dominance by surface-growing unicellular vs penetrative mycelial microbes. Lastly, it should be noted that the effect of comminution on degradation is not always positive. For example, Scheu and Wolters (1991) found that mechanical fragmentation *slowed* degradation of beech leaf litter. In general, the importance of such structural controls on degradation may limit the usefulness of litter chemistry as a predictor of degradation rates.

4.3.2. Disaggregation

Effects on degradation rates: We located no in situ studies in which both disaggregation and rates of CO_2 evolution were measured. Balesdent et al. (1990) compared till and no-till cultivation on fields planted continuously to C_4 crops for 17 years after nearly continuous planting of C_3 crops. From the difference in ^{13}C abundance through the two profiles, they concluded that tillage *per se* about doubled the rate of disappearance of the soil organic C that had accumulated under the C_3 crops.

Laboratory studies have shown that disaggregation brought about by sonication, grinding, or crushing increases rates of CO_2 evolution (Rovira and Greacen, 1957; Craswell and Waring, 1972a,b; Gregorich et al., 1989; Ladd et al., 1993; Beare et al., 1994) and net N mineralization (Hiura et al., 1976; Strickland et al., 1992). Fine sieving caused an increase in CO_2 evolution and net N mineralization that correlated well with fine pore volume across a range of loams, clays, and sandy soils (Hassink, 1992).

Field studies suggest a relation between disaggregation and increased SOM degradation rates. Cultivation of OM-rich soils can cause rapid decreases in OM content (Mann, 1986; Ladd et al., 1993), even OM that has been present in soil for > 40 years (Ladd et al., 1993). In soils low in OM, continued cropping can increase OM content (Mann, 1986), but this may reflect more the effect of increased detrital inputs to the soil, rather than any increase in OM due to cultivation *per se*. Some of the decrease with continued cropping is due to erosion, but a large part is thought to be due to increased respiration promoted by disruption of aggregates (Van Veen and Kuikman, 1990).

Mechanisms and controls: Biological, chemical, and physical processes all serve to disrupt aggregates (Fig. 6). Continued tillage is well known to decrease the degree of aggregation, more so in some soils than in others. The variation reflects differences in the stability of the aggregates, with Oxisols and Andisols being some of the most stably aggregated soils worldwide (Sanchez, 1976; Uehara and Gillman, 1981). Addition of strongly hydrated cations such as Na^+ deflocculates clays. As pH of variable-charge clays increases, their net negative surface charge increases also until at some point the clays deflocculate due simply to electrostatic repulsion. This phenomenon has been demonstrated in the laboratory (El-Swaify, 1980) but its importance in situ appears not to have been studied. Exposure to a solution dominated by Na^+ or H^+ caused disaggregation of aggregates and concomitant release of Al and organic C, which was interpreted as dissolution of Al–OM complexes that act as binding agents (Bartoli and Philippy, 1990). Reducing conditions should promote disaggregation where Fe(III) compounds are important binding agents, but we found no studies of this.

Microbial activity in general should play a major role in disaggregation. Degradation of microbial slime for example should be a powerful disaggregative force but this does not appear to have been studied.

The role of plant activity is better studied. Growth of roots and root hairs produces lines of weakness along which the clod or soil mass may break (Glinski and Lipiec, 1990). Maize roots decreased structural stability by chelating iron and aluminum, thus destroying chemical bonds with organic matter (Kobayashi and Otake, 1977); such an effect may fall in an area of overlap between "decreasing interactions" and "increasing accessibility".

Animals presumably promote not just aggregation, but also disaggregation. For

example, some fecal pellets are foraged upon and in some cases disrupted by smaller fauna. Earthworms were noted to have broken down friable granular structure into a structureless sticky mass (Hole, 1981) but effects on degradation rates were not measured.

5. Effects of distal factors

The previous discussion has reviewed the proximal factors influencing SOM stabilization and destabilization. As part of that discussion, we examined how two of the proximal factors, sorption/precipitation/complexation and aggregation (and their counterparts for destabilization), are influenced by the more distal factors (those toward the bottom of Fig. 2). In this section, we consider the distal controls on two more of the major proximal controls — activity of extra-cellular enzyme and of microbes. Controls on animal activity, the remaining proximal control, are not reviewed, because effects of animal activity on stabilization and destabilization are more tenuous (see Section 3.3.1, 4.3.1, 4.3.2) than those of the other proximal controls.

5.1. Controls on activity of extra-cellular enzymes

Many of the distal factors toward the bottom of Fig. 2 can affect soil enzyme activity (Fig. 7). McClaugherty and Linkins (1990) found that temperature influenced cellulase activity more in litter layers than in mineral soil and that activity of chitinase was affected less than that of cellulase. Pulford and Tabatabai (1988) found that water-logging had variable effects on various soil enzymes, although it was unclear whether enzyme activity or concentration had in fact been affected. Extracellular phenoloxidases and peroxidases (see Section 3.1.2) require oxygen and hydrogen peroxide, respectively, as electron acceptors, and these can be limiting in microaerophilic environments (Burns, 1978). Several studies suggest that the activity of enzymes involved in nutrient mineralization may decrease with increasing levels of inorganic forms of that nutrient (Dick, 1994; Gregorich et al., 1994).

Metal ions in solution can have variable effects on enzyme activity (Iwai et al., 1970; Juma and Tabatabai, 1977; Al-Khafaji and Tabatabai, 1979; Mathur and Sanderson, 1980; Mathur et al., 1980; Frankenberger and Bingham, 1982; Dick and Tabatabai, 1983; Stott et al., 1985). The role of Al^{3+} and Fe^{3+} is of special interest: these ions can occur naturally in the soil in relatively high concentrations, and there is some evidence that complexation with Al^{3+} may inhibit SOM decomposition (see Section 3.2.3). Al^{3+} strongly inhibited activity of mannanase (Takahashi et al., 1984), alpha-glucuronidase (Uchida et al., 1992), and phytase (Shimizu, 1992); although the concentrations used (1–5 mM) were much higher than occur naturally in the soil, the nearly complete inhibition of enzyme activity warrants experiments with lower concentrations. Earlier work (Juma and Tabatabai, 1977) showed that the degree of inhibition of phosphatase by Al or Fe in three soils increased with increasing acidity. It should be noted also that reported decreases in enzyme activity with increased acidity (Lähdesmäki and Piispanen, 1992) could be due in part to increased solution Al^{3+}. Gianfreda et al. (1993) in fact

showed that invertase activity decreased with increasing concentrations of OH–Al species, especially in the presence of tannic acid, although again the concentrations of Al^{3+} used were higher than one would expect to occur naturally.

Binding of enzymes to clays most often reduces enzyme activity while stabilizing the enzyme against thermal denaturation and proteolytic degradation (e.g., Lähdesmäki and Piispanen, 1992), but there are exceptions (Burns, 1986). Adsorption of cellulase to montmorillonite increased the pH of optimum activity from 4.8 to 6 (Pflug, 1982). Fusi et al. (1989) and Gianfreda et al. (1991, Gianfreda et al., 1992) used amorphous Fe and Al oxyhydroxide coatings on clays to more closely simulate the soil matrix in examining the adsorption of proteins, including enzymes; the presence of such coatings significantly altered controls on enzyme activity. A later paper showed that tannic acid and Al–OH species interacted to increase sorption of invertase to montmorillonite without decreasing its activity (Gianfreda et al., 1993).

5.2. *Controls on microbial activity*

Microbial activity is influenced by many factors. Direct effects of temperature, moisture, and $p\epsilon$ on microbial activity are well known (Paul and Clark, 1989; Anderson, 1991; Gregorich et al., 1994) and will not be discussed further here. Temperature and moisture also influence the microbial community by their effect on vegetation. For example, depending largely on the plant community and nature of detrital inputs, the belowground microbial community can be dominated by either bacteria or fungi (Holland and Coleman, 1987; Ingham et al., 1989). SOM degradation rates are affected by the presence of plants (Jenkinson, 1977; Reid and Goss, 1982; Sparling et al., 1982; Martin, 1987) and mycorrhizae (Read, 1991). Basidiomycete fungi are more abundant and play a more important role in forest ecosystems than in grasslands (Frankland et al., 1982; Ingham et al., 1989). The significance of this for any of the microbial controls on stabilization or destabilization is unknown.

Ambient nutrient levels (as opposed to nutrient levels in a degrading substrate) can affect microbial processes. Where nutrients limit microbial growth, adding nutrients can stimulate microbial populations and activity and increase the rate at which organic C is degraded to CO_2 and transformed to microbial products. For example, adding ammonium nitrate increased the rate of mass loss from Douglas-fir needles (Homann and Cole, 1990). However, N addition can also decrease microbial activity and CO_2 evolution, especially for recalcitrant materials (Fog, 1988); possible mechanisms of this effect include influence on competition between different types of decomposers, repression of enzyme formation, and promotion of condensation of amino and phenolic compounds into recalcitrant substances. A potentially important, but largely unstudied, effect of nutrient levels on microbial activity is through slime production — in fungi, for example, slime production increases with increasing C : N ratio of the substrate (Pielken et al., 1990). Nitrogen limitation also increased microbial production of a humic precursor (Carlile, 1956). Finally, adding nutrients can influence microbial activity indirectly, as by changing soil pH (Kelly and Henderson, 1978).

Aggregation may affect SOM stabilization and destabilization indirectly by influencing microbial activity. Effects of aggregation on microbial biomass and turnover have

seen increasing study. Hassink et al. (1993), working across soils of varying texture, found a strong positive correlation between bacterial biomass and volume of pores with 0.2–1.2 μm diameter; no such relation was found for fungi. Ladd et al. (1992) found that microbial biomass ^{14}C turned over more slowly in a well structured, clay-rich Vertisol than in a lighter textured, weakly aggregated Alfisol. Ladd et al. (1993) review other papers showing that survival of microbes added to soils correlates directly with soil clay content.

In addition, the chemical environment within aggregates is distinctive (e.g., Sexstone et al., 1985), which may affect microbial processes and extra-cellular or abiotic synthesis reactions (Allison, 1968; Hattori and Hattori, 1976). This may in turn affect processes of OM synthesis within aggregates, but studies of such effects are lacking.

6. Effects of factors of soil formation

Tracing the causal links from proximal controls, such as aggregation and enzyme and microbial activity, all the way to the factors of soil formation, shown at the bottom of Fig. 2, is perhaps best left as an exercise for the reader. Nonetheless, the concept of factors of soil formation has been critical in the development of soil science, and it may be useful to look briefly at how they relate to stabilization and destabilization.

For the most part the soil formation factors affect SOM stabilization and destabilization through the intermediate controls. Parent material and soil age probably influence stabilization and destabilization mainly through effects on mineralogy and soil macrostructure. As discussed already, mineralogy is especially important in allophanic and other soils lacking crystalline clays, perhaps because Al stabilizes the OM by forming complexes.

The five factors of soil formation are not entirely independent of each other or of the more proximal factors. For example, management/disturbance regime depends on the fertility and erosivity of the soil. Likewise, management/disturbance regime and erosion rate can combine over the long term to alter topographic position. Also, at a global scale, SOM can affect climate strongly by serving as a source or sink for CO_2 (Jenkinson et al., 1991; Eswaran et al., 1993) and other gases (Moore and Knowles, 1989; Steudler et al., 1989). But in general, these five most distal factors are remarkably independent, both of each other and of the more proximal controls, which helps explain why Jenny's insight has been so useful in ecosystem studies.

7. Future directions

The fate of organic C in soil is determined by simultaneous and often competing chemical, physical, and microbial processes. The conceptual model presented here provides a framework for integrating information on these processes, for identifying areas of insufficient knowledge, and for guiding future experimentation. It is not

intended as a final product but rather as a template to be amended as new findings are made.

As indicated throughout the review, much knowledge is lacking and experimental results are often conflicting. We suggest that the following changes in the study of SOM dynamics would help fill gaps and resolve inconsistencies:

- Increased effort to convert results into budgets for whole soil so that the relative importance of processes can be judged. Often this could be accomplished simply by converting results to a kg/ha or other areal basis.
- More attention to effects of inter-molecular interactions (especially Al complexation) on enzyme activity and substrate degradation rates.
- Increased effort to experimentally manipulate soils, preferably across a range of soil types.
- Increased use of conditions that are well defined yet relevant to soil environments. For example, in sorption studies, clays can be used that have organic or amorphous mineral coatings rather than clean clays.
- Experiments better designed to isolate mechanisms so results are not confounded by effects of other mechanisms operating simultaneously. For example, sterile conditions should be assured for sorption studies, so results will not be confounded by effects of microbial activity.

The model presented here focuses on destabilization and stabilization of SOM with respect to conversion to CO_2. Conceptual models of stabilization and destabilization with respect to leaching, erosion, and nutrient mineralization might also be helpful. Such models would parallel to some extent the model presented here. Sorption, for example, affects not just respiration but also leaching, and aggregation affects erosion. However, the models might have to include additional control mechanisms.

Conceptual models can provide a basis for mathematical simulation models that may be useful in evaluating ecosystem response to disturbances, such as changes in climate and land-management practices (Ågren et al., 1991; Anderson, 1991). Several existing mathematical models of SOM dynamics operate over months to centuries (see Jenkinson, 1990), but whether these models will adequately forecast response to future impacts is not clear. Long-term field studies must be initiated, and existing soil chrono-, topo-, and climo-sequences must be utilized in order to test these models. If the models prove inaccurate, new simulation models may be needed in which processes are represented more mechanistically than in current models. Conceptual models, such as that presented here, may provide a basis for such new simulation models of SOM dynamics.

Acknowledgements

We thank J.A. Baldock, C.V. Cole, and D.S. Jenkinson for helpful comments, and J. Powers for help with graphics and literature review. Many ideas presented here came into clearer focus as a result of the senior author's participation in a workshop organized by G. Ruark, M. Proe, and W. Dick for the Bioenergy Subgroup of the International Energy Agency. A contribution from the Andrews Long-Term Ecological Research program (NSF BSR 9011663).

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