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Soil Aggregate Stabilization and Carbon Sequestration: Feedbacks through Organomineral Associations

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I. Introduction

Primary production (specifically, the rate and quality of C transfer belowground) and soil microbial activity (specifically, the rates of C transformation and decay) are recognized as the overall biological processes governing soil organic C (SOC) dynamics. These two processes and, hence, SOC cycling and storage are controlled by complex underlying biotic and abiotic interactions and feedbacks, most of which can be tied in one way or another to the influences of the five state factors related to soil formation (Jenny, 1941), and many of which are sensitive to management practices. Overall, C input rates and quality are largely dependent on climate (especially temperature and precipitation), vegetation type and landscape, soil type, and management practices. Decomposition processes and turnover rates, however, are greatly influenced by climate, the type and quality of organic matter (e.g., N content and the ratios of C:N and lignin:N), chemical or physicochemical associations of organic matter (OM) with soil mineral components, and the location of OM within the soil.

The mechanisms responsible for stabilizing SOC (Fig. 1) may be categorized as (1) biochemical recalcitrance, (2) chemical stabilization, and (3) physical protection (Christensen, 1996). Biochemical recalcitrance may be due to the chemical characteristics of the substrate itself — e.g., lignin derivatives (Stott et al., 1983) or melanins produced by fungi and other soil organisms (Martin and Haider, 1986) — or may result from transformations during decomposition, including incorporation into the excrement of soil meso- and microfauna (Kooistra and van Noordwijk, 1996). Chemical stabilization occurs because of chemical or physicochemical associations between what would otherwise be decomposable compounds and soil mineral components. For example, organic compounds sorbed to clay surfaces, often by polyvalent cation bridges, or those intercalated between expanding layers of clays are quite resistant to degradation (Martin and Haider, 1986; Christensen, 1996; Tisdall, 1996). In addition, the drying of organics may cause them to be denatured or polymerized, thereby protecting them chemically from decomposition (Dormaar and Foster, 1991). Soil structure, however, plays a dominant role in the physical protection of soil organic matter (SOM) by controlling microbial access to substrates, microbial turnover processes, and food web interactions (Elliott and Coleman, 1988; van Veen and Kuikman, 1990). Relatively labile material may become physically protected from decomposition by incorporation into soil aggregates (Oades, 1984; Gregorich et al., 1989; Golchin et al., 1994a,b) or by deposition in micropores inaccessible even to bacteria (Foster, 1985).

Because of the physical protection afforded by soil structure, significant interactions exist between SOC dynamics and the formation, stabilization, and degradation of soil aggregates. In soils where OM is the major aggregate binding agent, plant growth and the decomposition of organic inputs lead to the development of a hierarchical aggregate structure (Tisdall and Oades, 1982; Oades and Waters, 1991). The exact nature and

stability of this structure in a given soil depend on the relative amounts and strengths of various types of organomineral associations that function as aggregate binding and stabilizing agents at each hierarchical level of organization. At the same time, the nature of these organomineral associations and their spatial locations within the aggregate hierarchy determine the degree to which SOC is physically protected from decomposition and, consequently, result in organic pools with various input and turnover rates.

Thus, feedbacks between SOC cycling and aggregate cycling can occur. In aggrading systems, organic inputs lead to the formation and stabilization of aggregates, which in turn can protect SOM from decomposition, leading to further aggregate stabilization. In degrading systems, the disruption of aggregates exposes previously protected but relatively labile OM to decomposers, resulting in a loss of SOM and further destabilization of aggregates. In soils at or near equilibrium in terms of the amount of SOC in the whole soil, neither OM nor aggregates are static, and the turnovers of aggregates and various OM pools are still interrelated. In any case, the feedbacks between SOC cycling and aggregate cycling appear to be controlled by the formation or destruction of organomineral associations functioning as aggregate binding agents. Furthermore, in soils exhibiting a hierarchical aggregate structure, the feedbacks likely cross spatial scales affecting binding agents at different hierarchical levels of organization.

In this paper, we will examine the relationship between the function of various organomineral associations as aggregate binding agents and C sequestration in soils. Our discussions will focus on soils that exhibit an aggregate hierarchy in which aggregate stability is controlled primarily by organic materials. After briefly examining the nature and function of organomineral associations in macro- and microaggregates, we will present evidence from our own studies of restored prairies on Illinois mollisols as a case study to demonstrate the occurrence of feedbacks between aggregation and C accrual in an aggrading system.

II. Aggregate Hierarchy

Attempts to understand the formation and stabilization of aggregates in soils where OM is the major binding agent have been influenced considerably by the hierarchical view of the aggregation process proposed by Tisdall and Oades (1982) and elaborated by Dexter (1988), Kay (1990), and Oades and Waters (1991), among others. In this conceptual model (Fig. 2), the mechanisms of aggregate formation and stabilization and their relative importance change with spatial scale. Primary particles and clay microstructures are bound together with bacterial and fungal debris into extremely stable silt-sized microaggregates (2-20 μm in diameter), which may be bound together with fungal and plant debris and fragments into larger microaggregates (20-250 μm in diameter). The organic binding agents involved in stabilizing microaggregates are believed to be relatively persistent and to consist of humic materials or polysaccharide polymers strongly sorbed to clays, with the most persistent clay-

organic associations being strengthened by bridges of polyvalent metal cations (Tisdall and Oades, 1982; Tisdall, 1996). Microaggregates, in turn, are bound into macroaggregates (>250 μm in diameter) by (1) transient binding agents (i.e., readily decomposable organic materials, the most important being microbial- and plant-derived polysaccharides) and (2) temporary binding agents (i.e., fine roots, fungal hyphae, bacterial cells, and algae). As macroaggregates increase in diameter, transient binding agents appear to be less important, whereas temporary binding agents generally increase in importance.

All pools of organic binding agents are subject to the simultaneous effects of loss through decomposition and inputs from the creation of new materials. However, the long-term existence of persistent agents (perhaps tens to hundreds of years) may be due more to protection from decomposition by their physicochemical associations with inorganic soil components than to any inherent biochemical inertness (Kay, 1990).

The distinction between micro- and macroaggregates is based both on size and on susceptibility to slaking, i.e., rapid wetting (Edwards and Bremner, 1967; Tisdall and Oades, 1982). In soils exhibiting aggregate hierarchy, macroaggregates subjected to slaking break down into microaggregates, rather than primary particles. Stabilized microaggregates are not disrupted by rapid wetting and mechanical disturbance, including cultivation. In contrast, the stability of macroaggregates is generally controlled by management practices and other disturbances or by factors affecting root and hyphal growth and rhizosphere organisms (Tisdall and Oades, 1980, 1982).

A consequence of aggregate hierarchy is the porosity exclusion principle outlined by Dexter (1988). If aggregate hierarchy exists, then smaller aggregates should have smaller pores, greater contact between particles, and higher bulk densities than larger aggregates because the latter also contain larger pores between the smaller aggregates that comprise them (Oades and Waters, 1991; Oades, 1993). As such, the effectiveness of various binding mechanisms will depend on their physical dimensions relative to those of the pores (i.e., planes of weakness) being bridged (Kay, 1990).

Although it is helpful to think of aggregate hierarchy in the sense of the binding together of increasingly larger aggregated units, in most cases aggregates are probably not formed sequentially. In fact, evidence exists to suggest that although plant roots and fungal hyphae provide the mechanical framework for the formation of macroaggregates, it is the decomposition process that leads to the development of microaggregates and an aggregate hierarchy (Elliott and Coleman, 1988; Tiessen and Stewart, 1988; Oades and Waters, 1991; Beare et al., 1994b). Hence, microaggregates may form as a result of biological activity within or on the edges of relatively stable macroaggregates or may develop when macroaggregates turn over or fragment as the roots or hyphae binding them together are decomposed. Of course, in cultivated or other disturbed systems a significant proportion of macroaggregates may be reformed from relatively intact microaggregates as a result of root and hyphal growth.

All levels of aggregate development, however, may occur simultaneously as each aggregate size class forms and turns over at its own rate, depending on management practices and on the degree of protection from decomposition afforded the organic binding agents of each size class. Oades (1993) speculated that aggregate hierarchy occurs in soils as a legacy of long-term exploration by roots, particularly those of grasses, and that it is not likely to occur in very young soils (e.g., polders) or to apply in soils where inorganic cements predominate (e.g., oxisols).

III. Organomineral Associations

Organomineral associations can occur at a variety of spatial scales with varying degrees of stability against physical, chemical, or biological disruption or degradation. In his extensive review of the subject, Christensen (1996) divided organomineral complexes into primary and secondary associations. He defined primary organomineral complexes as those related to the primary structure of soils and associated with primary particles isolated after complete dispersion of the soil. Secondary organomineral complexes were defined as consisting of aggregates of primary organomineral complexes that form the secondary structure of soils. We will consider here secondary organomineral associations within macroaggregates (but external to microaggregates) and those within microaggregates 2-250 μm in diameter and also how these organomineral associations promote the stabilization of both soil aggregates and SOM.

A. Macroaggregates

Because of the porosity exclusion principle, the stabilization of hierarchically formed macroaggregates requires organomineral associations large enough to bridge the gaps and pores between the microaggregates and primary particles composing macroaggregates. Larger macroaggregates can also be composed of smaller macroaggregates, making the size of the gaps to be stabilized even larger. Organomineral associations at this scale are largely related, either directly or indirectly, to the growth and decomposition of plant roots and the hyphae of mycorrhizal fungi (Tisdall, 1996; Jastrow et al., 1997).

The lengths of roots and mycorrhizal hyphae are often directly related to the percentage of soil in water-stable macroaggregates, particularly in aggrading systems (Tisdall and Oades, 1980; Miller and Jastrow, 1992a). The direct effects of living roots and hyphae (Fig. 2) may be conceptualized by viewing the three-dimensional network of roots and hyphae as a "sticky string bag" that physically entangles or enmeshes smaller aggregates and particles, creating rather stable macroaggregates (Oades and Waters, 1991). Not only do roots and hyphae form a network that can serve as a framework for macroaggregate formation, but extracellular mucilage coatings on root and hyphal surfaces can strongly sorb to inorganic materials, helping to stabilize aggregates (Tisdall and Oades, 1979; Gupta and Germida, 1988; Tisdall, 1991; Dorioz et al., 1993). Furthermore, encrustation of roots and

hyphae with inorganics is believed to physically slow decomposition, thereby preserving the enmeshing framework for a time even after the roots and hyphae senesce (Oades and Waters, 1991). The pressures exerted by growing roots and by localized drying caused by plant water uptake are physical forces that promote both the formation and the degradation of aggregates (Kay, 1990). Hence, the types of roots produced by different plants and their densities and architectures can influence macroaggregate size distributions (Miller and Jastrow, 1990).

The evidence for the role of extracellular mucilage coatings (the "sticky" part of the string bag) is based largely on microscopy and selective staining of ultrathin sections (e.g., Tisdall and Oades, 1979; Gupta and Germida, 1988; Oades and Waters, 1991; Foster, 1981, 1994). These mucilages are generally believed to consist mainly of polysaccharides but may also contain polyuronic acids and amino compounds (Foster, 1981; Tisdall, 1996). However, recent studies suggest that arbuscular mycorrhizal fungi produce a previously undescribed class of aggregate binding agents (R.M. Miller, S.F. Wright, J.D. Jastrow, and A. Upadhyaya, unpublished data). As identified by using immunofluorescent monoclonal antibody techniques, arbuscular mycorrhizal hyphae produce a hydrophobic glycoproteinaceous substance, named glomalin, on the surfaces of both internal and external hyphae (Wright et al., 1996). Glomalin is also deposited on soil surfaces, where its resistance to extraction suggests it might be relatively persistent (Wright and Upadhyaya, 1996). The amounts of glomalin extracted from soils of a prairie restoration chronosequence were directly related to both external hyphal lengths and the mean weight diameter of slaked, water-stable aggregates (R.M. Miller, S.F. Wright, J.D. Jastrow, and A. Upadhyaya, unpublished data). Glomalin may polymerize and develop its hydrophobicity in response to drying and air exposure (Wessels, 1996), thereby protecting the hyphae from desiccation. However, this polymerization process may extend to and incorporate contacts with other soil components, essentially adhering fungal walls to soil and particulate organic matter (POM) surfaces. In addition to the glue-like properties of glomalin, its hydrophobicity may contribute indirectly to aggregate stability by dampening the disruptive forces of rapid water movement into the pores between and within aggregates.

Most of the indirect effects of roots and hyphae are related to decomposition processes. The exudates and rhizodeposits of growing roots are rapidly turned over by active microbial populations that are dominated by gram-negative bacteria (Foster, 1983), resulting in the deposition of extracellular microbial polysaccharides in the rhizosphere. Furthermore, as roots and hyphae die, organic substrate is deposited throughout the macroaggregate structure of the soil, where the activities of soil fauna, saprophytic fungi, and bacteria reduce this material to POM, resulting in further deposition of microbial polysaccharides. In addition, colonization of POM or fecal pellets by saprophytic fungi and the consequent proliferation of hyphae (Fig. 2) contribute to stabilizing the pores between microaggregates and other particles (Haynes and Beare, 1996). The coating of aggregate surfaces and intramacroaggregate pores with microbially derived polysaccharides and other transformation products, such as

aliphatic compounds, helps to stabilize macroaggregates (Haynes and Swift, 1990; Martens and Frankenberger, 1992; Haynes and Francis, 1993). However, because of the lability of most of these materials as a substrate for further microbial attack, the persistence of this mechanism depends on the balance between production and degradation and the extent of chemical or physical stabilization (Haynes and Beare, 1996).

The OM binding microaggregates and other particles together into macroaggregates is believed to be physically protected from decomposition. Evidence for the protection of relatively labile, intramacroaggregate OM and its function as an intermicroaggregate binding agent comes from observations of the loss of both aggregate stability and OM following the cultivation of undisturbed soils (e.g., Tisdall and Oades, 1980; Carter, 1992; Cambardella and Elliott, 1993) and from laboratory mineralization studies of intact and crushed macroaggregates (Elliott, 1986; Gupta and Germida, 1988; Beare et al., 1994a).

Cambardella and Elliott (1992, 1993, 1994) suggested that much of the SOM lost when long-term grasslands are cultivated is POM or a relatively labile, silt-sized organomineral fraction (2-20 μm) with a density of 2.07-2.22 g cm^{-3}, which together may account for about 40% of the total SOC. Because large shares of both of these organic pools were found within small macroaggregates (250-2000 μm), these authors proposed that both pools serve as intermicroaggregate binding agents. Furthermore, they suggested that together the two SOM fractions account for a significant portion of the conceptually defined intermediate (or slow) pool of current SOM models (Parton et al., 1996).

Theoretically, aggregate hierarchy predicts that the organic C (OC) content of macroaggregates should be greater than that of microaggregates because the former are composed of the latter plus organic intermicroaggregate binding agents. In summarizing a range of studies, Angers and Carter (1996) concluded, however, that the associations between aggregate size and C contents are not clear or consistent. Direct, inverse, and nonexistent relationships have been documented. The results apparently depend both on operational differences between studies (e.g., aggregate separation procedures, whether POM is removed, or whether concentrations are corrected for sand content) and on actual differences between systems (e.g., vegetation and soil types, management practices, and climatic conditions).

Hypothetically, the OM in macroaggregates also should be younger and more labile. In most studies, the relationships between the C:N ratio of aggregate OM and aggregate size support this contention, as do most of the laboratory mineralization studies (Angers and Carter, 1996). Recent studies using the natural abundance of stable C isotopes following a switch in the photosynthetic pathway of the vegetation as a tracer of recent organic inputs demonstrate that macroaggregates have a higher proportion of C derived from the most recent vegetation than do microaggregates (Skjemstad et al., 1990; Puget et al., 1995; Angers and Carter, 1996). Similarly, Jastrow et al. (1996) observed that the proportion of recent C in large macroaggregates (>1 mm) was greater than in

microaggregates, but unlike the other studies, they also found the proportion of recent C in microaggregates (53-212 μm) was essentially equal to the proportions in small macroaggregates (up to 1 mm). The differing results may be due to management differences; Jastrow et al. (1996) studied an aggrading temperate pasture, whereas Puget et al. (1995) and Angers and Carter (1996) worked in temperate cultivated systems. Skjemstad et al. (1990) also studied a pasture (although under wet, subtropical conditions), but they separated and analyzed all macroaggregates as one size class.

B. Microaggregates

As noted earlier, the decomposition process is probably the driving force that leads to the development of microaggregates and an aggregate hierarchy. The stability of microaggregates depends mostly on the strength by which clays and other inorganic components of the soil are sorbed to POM, microbial debris, and a variety of other organic colloids and compounds primarily of microbial origin. Sorption occurs via a variety of organomineral associations, such as polyvalent cation bridges, H-bonding, van der Waals forces, and interactions with hydrous oxides and aluminosilicates (Edwards and Bremner, 1967; Oades, 1984; Haynes and Beare, 1996; Tisdall, 1996). Clays are generally the mobile component, with much of their movement and reorientation around organics resulting from localized drying and the mechanical actions of plant and fungal growth. Drying also appears to play an important role in increasing the stability of organomineral associations by enhancing bonding forces and the polymerization and denaturing of the organics (Oades, 1984; Chenu, 1989; Dormaar and Foster, 1991; Dorioz et al., 1993).

A hierarchy of microaggregates, based on the scale of the organic nucleating agents, develops in many soils (Fig. 2). The C:N ratios of both the light (<2 g cm^{-3}) and mineral-associated fractions of microaggregates from a mollisol generally decreased with aggregate size, indicating increasing levels of decomposition (Baldock et al., 1992). Particulate OM (mostly plant and fungal debris) is often found at the core of microaggregates 90-250 μm in diameter, where it is protected from rapid decomposition by encrustation with inorganic material (Oades and Waters, 1991; Waters and Oades, 1991). This POM is eventually decomposed, often leaving cavities surrounded by smaller microaggregates believed to be stabilized by the metabolic products and bodies of microbes that used the POM as a substrate. Plant fragments are more difficult to recognize in microaggregates less than 90 μm in diameter. The cores of microaggregates 20-90 μm in diameter may include the resistant remnants of plant debris, such as lignin particles, or may be empty. Microaggregates less than 20 μm in diameter appear to consist of clay microstructures stabilized by microbially derived polymers, hyphal fragments, and bacterial cells or colonies encrusted with clay particles. Baldock et al. (1992) found that both the light and mineral-associated

fractions of aggregates 2-20 μm in diameter had C:N ratios (11.5 and 8.8, respectively) within the range measured for soil microbial biomass (8-12).

Golchin et al. (1994b) proposed a conceptual model of the changes OM undergoes during decomposition, from its entry into the soil through its incorporation into microaggregates to its eventual rendering into microbial metabolites and association with clay minerals (Fig. 3). These authors proposed that when plant (surface and root) debris enters the soil, it is initially colonized by soil microbes and begins to adsorb mineral particles. As plant fragments become encrusted with mineral particles, they become the organic cores of stable microaggregates and are protected from rapid decomposition. While these organic cores are still rich in carbohydrates and chemically attractive to microorganisms, microbially produced mucilages and metabolites permeate the encrusting mineral particles, resulting in very stable aggregates. However, once the more labile portions of the organic cores are consumed, decomposition of more resistant plant structural materials proceeds more slowly. Eventually, decomposition of the organic cores renders the aggregates unstable, and relatively recalcitrant POM is released from intimate association with mineral particles, because the production of stabilizing microbial products declines as the organic cores become less palatable. Mineral particles and organomineral associations that coated the cores along with adsorbed microbial products may then become associated with more labile POM.

This model was developed from studies employing ultrasonic dispersion and sequential density fractionation techniques to isolate (1) free POM located between aggregates, (2) occluded POM from within aggregates, and (3) colloidal or clay-associated (amorphous) OM (Golchin et al., 1994a,b). The chemical composition of the isolated fractions was characterized by solid-state ^{13}C nuclear magnetic resonance spectroscopy, and the degree of mineral association of each fraction was determined on the basis of density, C and N contents, and scanning electron microscopy. Additional support for the model was obtained from subsequent studies using the natural abundance of stable C isotopes as a tracer of OM cycling through fractions isolated from soils sampled 35 and 83 years after a switch in the photosynthetic pathway of the vegetation (Golchin et al., 1995).

IV. Interrelationships between Aggregation and Organic Carbon Sequestration: A Case Study

Our studies of a chronosequence of prairie restorations on mollisols that were cultivated for over 100 yr can be used as a case study to examine the interrelationships of aggregation and OC sequestration in an aggrading system. Because the restoration chronosequence provides gradients of water-stable macroaggregate formation and total SOC (Fig. 4), along with gradients of root and hyphal proliferation and of various other SOC pools (Cook et al., 1988; Miller and Jastrow, 1992b; Jastrow, 1996; Jastrow et al., 1997), the site allows us not only to investigate how different organic binding mechanisms interact to promote the development of soil aggregate hierarchy, but also to determine how and where OC is sequestered within this hierarchy. Similarly, we believe that the site

provides evidence for the existence of feedbacks between the formation and stabilization of soil aggregates and SOC sequestration.

A. Organomineral Associations and Development of Soil Aggregate Hierarchy

The relative contributions of roots, mycorrhizal hyphae, SOM, microbial biomass, and microbially derived polysaccharides to the direct and indirect mechanisms of water-stable macroaggregate formation were investigated by using path analysis techniques (Jastrow et al., 1997). Path analysis enables the heuristic examination of causal processes underlying observed relationships. After constructing a conceptual model of the interrelationships among multiple independent and dependent variables (Fig. 5), the total correlations between independent and dependent variables can be partitioned into causal (direct and indirect effects) and noncausal components (Asher, 1983).

In the restoration chronosequence, external mycorrhizal hyphae had the strongest direct effect on the percentage of water-stable macroaggregates (Table 1). Roots exhibited the next strongest direct effects on aggregation, with essentially equal contributions for each of two measured diameter size classes. However, the indirect effects of the two size classes differed substantially, with fine roots (0.2-1 mm in diameter) having the overall largest total effect of all binding agents evaluated. The indirect effects of fine roots on macroaggregates was due primarily to strong positive associations of fine roots with mycorrhizal hyphae and microbial biomass. Interestingly, the strongest indirect contribution of veryfine roots (<0.2 mm in diameter) was via SOC, probably as the major source of accruing POM. Hence, the path analysis approach strongly supported the importance of the various contributions of roots and mycorrhizal hyphae to the stabilization of macroaggregates in aggrading systems. The roles of microbially derived extracellular polysaccharides (as measured by hot-water soluble carbohydrate C) and of POM (best represented by the indirect effects of roots through SOC) in stabilizing macroaggregates were overwhelmed by the contributions of roots and hyphae via the "sticky string bag" mechanism in this system.

The results of further separate path analyses for each of three macroaggregate size fractions (Jastrow et al., 1997) support the role of the porosity exclusion principle as a factor controlling the types of organic binding agents that function at different spatial scales within aggregates (Tisdall and Oades, 1982; Oades and Waters, 1991; Dorioz et al., 1993). In general, the relative importance of the binding mechanisms for each aggregate size fraction was related to the physical size of the mechanism and the strength of its associations with other mechanisms. For example, fine roots had their greatest effects on aggregates greater than 2 mm in diameter, whereas veryfine roots exerted their strongest effects on smaller aggregates. Also as expected, the strongest direct effect in the smallest macroaggregate size fraction was due to microbial biomass. However, in contrast to what

their physical size would suggest, mycorrhizal hyphae were of greatest relative importance in the two largest aggregate size fractions, because of their strong associations with fine roots.

B. Aggregate-Associated Carbon Sequestration

Because of the high densities of roots and hyphae occurring in restored prairie (Cook et al., 1988; Miller and Jastrow, 1992b), the formation of macroaggregates stable enough to withstand slaking and wet sieving is rapid. At the same time, OC is accumulating across the chronosequence at a much slower rate (Fig. 4). In fact, the rate constant (k) of the exponential model describing changes in aggregation (0.438 yr^{-1}) is more than 35 times the k for total SOC (0.012 yr^{-1}). Consequently, the calculated average turnover time ($1/k$) for macroaggregates is 2.3 yr compared with 83 yr for total SOC. Given that the longevity of a majority of prairie grass roots is about three growing seasons (Weaver and Zink, 1946), the rapid turnover time for macroaggregates is not surprising.

The relatively rapid turnover time for macroaggregates suggests that physical protection of intermicroaggregate binding agents (such as POM) inside macroaggregates may not be a major mechanism influencing C sequestration in this system. However, the lack of major seasonal changes in aggregation for older restorations (J.D. Jastrow and R.M. Miller, unpublished data) indicates that new macroaggregates are probably being formed just as rapidly as old macroaggregates are being degraded. Hence, the majority of intermicroaggregate binding agents are not likely to be unprotected for lengthy periods of time.

An increase in the C:N ratios of macroaggregates with time since planting to prairie also suggested that the accumulating OM is not highly processed and could include relatively large quantities of POM trapped inside macroaggregates (Jastrow, 1996). However, the C content of the light-fraction POM (<1.85 g cm^{-3}) released by relatively low ultrasonic energy from within macroaggregates was a relatively constant proportion of the total OC in whole soils across the chronosequence. Rather, C accrual with time since planting to prairie occurred in the heavy fraction (>1.85 g cm^{-3}), suggesting that C was accumulating as organic cores of undispersed microaggregates located within macroaggregates and/or as microbially produced mineral-associated complexes (Jastrow, 1996). These findings are consistent with the conceptual model of OM cycling through microaggregates proposed by Golchin et al. (1994b).

Other studies from the same site also support this conceptual model. The inputs and turnover of OC in different size classes of water-stable aggregates were estimated by using the natural abundance of stable C isotopes following a switch in vegetation from long-term corn (C4) on soils formed under tallgrass prairie (dominated by C4 grasses) to C3 pasture grasses (Jastrow et al., 1996). The average turnover time for old (C4-derived) C was 412 yr for microaggregates, compared with an average turnover time for macroaggregates of 140 yr, indicating that old C associated with microaggregates may be more biochemically recalcitrant and better physically protected than

that associated with macroaggregates. Net inputs of new (C3-derived) C increased with aggregate size (0.73 to 1.13 g kg^{-1} yr^{-1}). Together, these data support the concept of an aggregate hierarchy. The faster turnover times for old C and greater inputs of new C in macroaggregates suggest that they are composed of a mixture of microaggregates (with much longer turnover times) and of other C pools (such as intermicroaggregate binding agents) that are both turning over and accumulating more rapidly than the C associated with microaggregates. However, net inputs to microaggregates were equal to those for small macroaggregates (up to 1 mm in diameter), suggesting (1) that the formation and degradation of microaggregates may be more dynamic than predicted by their resistance to mechanical dispersion or by the turnover times for old C and (2) that at least two different OC pools characterized by differing turnover rates exist within microaggregates. Golchin et al. (1995) also hypothesized, on the basis of changes in the natural abundance of stable C isotopes, that microaggregates contain two C pools with differing turnover rates.

For soils *in situ*, microaggregates whose stability is weakened by the lack of microbial activity may be more susceptible to degradation caused by chemical dispersion or by physical stresses. Thus, as microbial activity slows, clays associated with microaggregate surfaces may be released and dispersed, enabling them to become reoriented around and sorbed to the mucilages and metabolites on the surfaces of new (in our case, C3-derived) chemically attractive POM supporting an active microbial population. At the same time, the slow turnovers observed for old (C4-derived) C occur because (1) additional time is needed for all of the C4-derived POM contained within microaggregates to degrade and (2) significant quantities of C4-derived microbial metabolites likely remain strongly associated with mineral particles encrusting new (C3-derived) microaggregate cores.

Alternatively, a significant proportion of the C3-derived C associated with microaggregates may be located on aggregate surfaces. In soils with very stable macroaggregates, such as those in this study, the few microaggregates released by slaking were probably bound into macroaggregates *in situ* but were not stabilized sufficiently to survive the slaking process. Hence, they could be coated with intermicroaggregate binding agents of relatively new origin. This scenario is consistent with the observed deposition of glomalin by mycorrhizal hyphae on aggregate surfaces (Wright and Upadhyaya, 1996; R.M. Miller, S.F. Wright, J.D. Jastrow, and A. Upadhyaya, unpublished data), as discussed in Section IIIA. The scenario may also be related to the relatively labile, silt-sized organomineral fraction (density = 2.07-2.22 g cm^{-3}) isolated by Cambardella and Elliott (1994) from within macroaggregates, which they hypothesized is of microbial origin and functions as an intermicroaggregate binding agent.

C. Demonstration of Feedbacks

Thus, we have demonstrated for our system that the rapid formation of water-stable macroaggregates is followed by the sequestration and accrual of SOC, and we have examined how and where the C is accumulating. However, because of the rapid incorporation of over 90% of the soil into macroaggregates able to survive slaking and wet sieving (Fig. 4), the demonstration that C sequestration feeds back to enhance aggregate stability requires a method capable of assessing greater levels of stability. Hence, we combined wet sieving with turbidimetric techniques in an approach to aggregate stability assessment that differs somewhat from the combined method developed by Pojasok and Kay (1990). For aggregates that have survived slaking and wet sieving, their stabilities should be related to the amounts of clays dispersed by the higher energy and abrasive forces associated with end-over-end rotation (compared with wet sieving).

Size fractions of water-stable macro- and microaggregates were collected by slaking of air-dry soil followed by wet sieving as described by Jastrow et al. (1996). After sieving, all size fractions were air-dried. For each size fraction, 0.25-g subsamples of intact aggregates were weighed into spectrophotometer tubes, 7 ml of deionized water were added, and the tubes were covered with Parafilm. After 5 min in water, the tubes were spun end-over-end about their centers (30 rpm) for 2 min and allowed to settle undisturbed for 30 min. The percent light transmission was measured at a wavelength of 630 nm on a Spectronic 20 spectrophotometer. Two subsamples were measured and averaged for each size fraction from each of five randomly collected cores for each sampled plot.

For each size fraction, the increases in percent transmission observed across the chronosequence indicate relatively lower amounts of dispersed clays and greater aggregate stability with time since disturbance (Fig. 6). Improvements in aggregate stability were also associated with increasing SOC ($r \geq 0.83$, $P \leq 0.0001$ for each size fraction). Interestingly, macroaggregates from the cultivated field were significantly more stable than microaggregates, but substantial increases in the stability of microaggregates and small macroaggregates (212-500 μm) occurred only 4 yr after planting to prairie. For larger aggregates (>500 μm), significant improvement in stability was not observed until 15 yr of prairie.

These findings, coupled with those presented in Fig. 4, suggest that relatively stable macroaggregates can be formed rapidly in response to the proliferation of roots and hyphae associated with grassland vegetation but that improvements in stability resulting from concomitant increases in SOC appear to occur initially at smaller spatial scales. Presumably this occurs through the deposition of microbial byproducts and the sorption of clays to OM during decomposition.

V. Conclusions

Soil aggregation and OM storage are intimately associated with each other. Consequently, changes in either of these processes often result in feedbacks on the other. These feedbacks are mediated through organomineral associations, which function as aggregate binding and stabilizing agents. The nature of various organomineral associations and their spatial locations within soil aggregate structure determine the extent to which SOC is physically protected and chemically stabilized, resulting in organic pools with varying input and turnover rates (Table 2). Similarly, when OM is the major stabilizing agent and aggregate structure is hierarchical, different types of aggregates are being formed and turned over at different rates related to the turnover rates of their organomineral binding agents.

Thus, better information on the nature and dynamics of organomineral associations will lead to a greater understanding of soil structural dynamics and of C cycling and sequestration in soils. Consequently, such information will also contribute to improved approaches to soil management. Similarly, a better understanding of organomineral associations may provide a key to better defining or quantifying the conceptual pools used by SOM simulation models and could serve as the basis for development of a new generation of such models.

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Table 1. Observed correlations between the percentage of water-stable macroaggregates (>212 μm) and measurements of selected organic binding agents and their partitioning into direct, indirect, and total causal effects on the basis of path analysis ($n = 49$). The difference between the correlation and the total effect is due to conceptually noncausal relationships between variables (see text). Data from Jastrow et al. (1997).

Measured parameter	Correlation (r)	Direct effect	Indirect effect	Total effect
Fine root length	0.91	0.25	0.47	0.72
Veryfine root length	0.85	0.26	-0.04	0.22
External hyphal length	0.89	0.38	0	0.38
Soil organic C	0.43	0	0.09	0.09
Microbial biomass C	0.65	0.14	0.03	0.17
Hot-water soluble carbohydrate C	0.55	0.05	0	0.05

Table 2. Estimated ranges in the amounts and turnover times of various types of organic matter stored in agricultural soils. From Carter (1996) with permission.

Type of organic matter	Proportion of total organic matter (%)	Turnover time (yr)
Litter	—	1-3
Microbial biomass	2-5	0.1-0.4
Particulate	18-40	5-20
Light fraction	10-30	1-15
Intermicroaggregate [a]	20-35	5-50
Intramicroaggregate [b]		
Physically sequestered	20-40	50-1000
Chemically sequestered	20-40	1000-3000

[a] Within macroaggregates but external to microaggregates, including particulate, light fraction, and microbial C.

[b] Within microaggregates, including sequestered light fraction and microbially derived C.

Figure Legends

Fig. 1. Mechanisms of soil organic matter stabilization.

Fig. 2. Conceptual diagram of soil aggregate hierarchy.

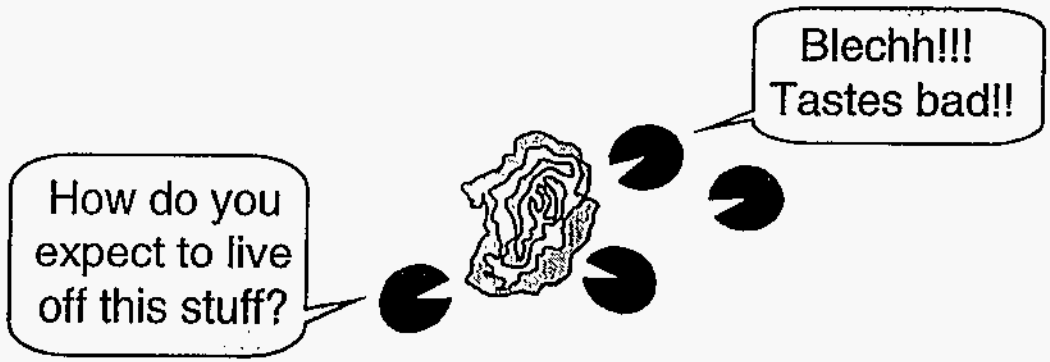
Fig. 3. Conceptual model of microaggregate turnover as proposed by Golchin et al. (1994b).

Fig. 4. Changes in percentage of macroaggregates and accumulation of total soil organic carbon with time since last cultivation and planting to grassland. Error bars indicate standard errors ($n = 10$). Reprinted with permission from Jastrow (1996).

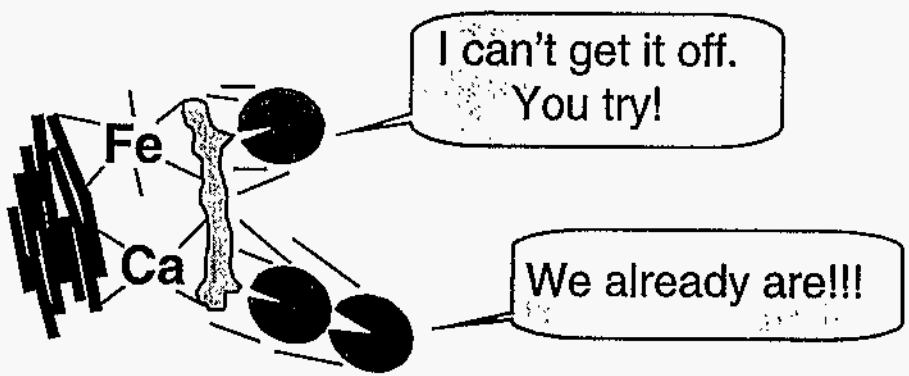
Fig. 5. Conceptual path model of hypothesized causal relationships among roots, the external hyphae of mycorrhizal fungi, soil organic carbon, microbial biomass, and microbially derived polysaccharides (hot-water soluble carbohydrate carbon) and their effects on the formation of water-stable macroaggregates. Causal relationships are indicated by single-headed arrows, and existing but unanalyzed correlations are indicated by double-headed arrows. Adapted from Jastrow et al. (1997).

Fig. 6. Results of the combination of wet sieving and turbidimetric techniques as an approach to assessing the relative stability of different size classes of aggregates in a chronosequence of restored tallgrass prairie on long-term cultivated soils ($n = 5$). Within each size fraction, bars indicated by the same letter are not significantly different on the basis of Fisher's protected least significant difference ($P \leq 0.05$).

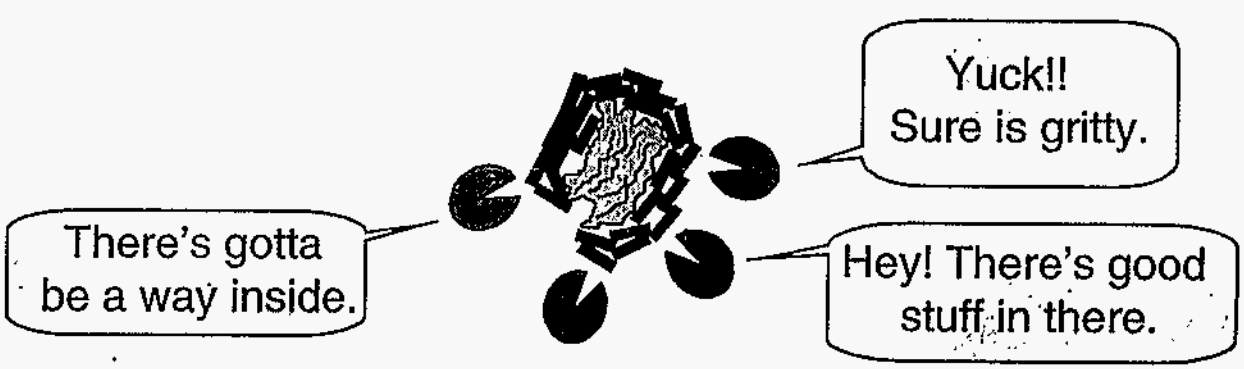
Biochemical Recalcitrance



Chemical Stabilization



Physical Protection



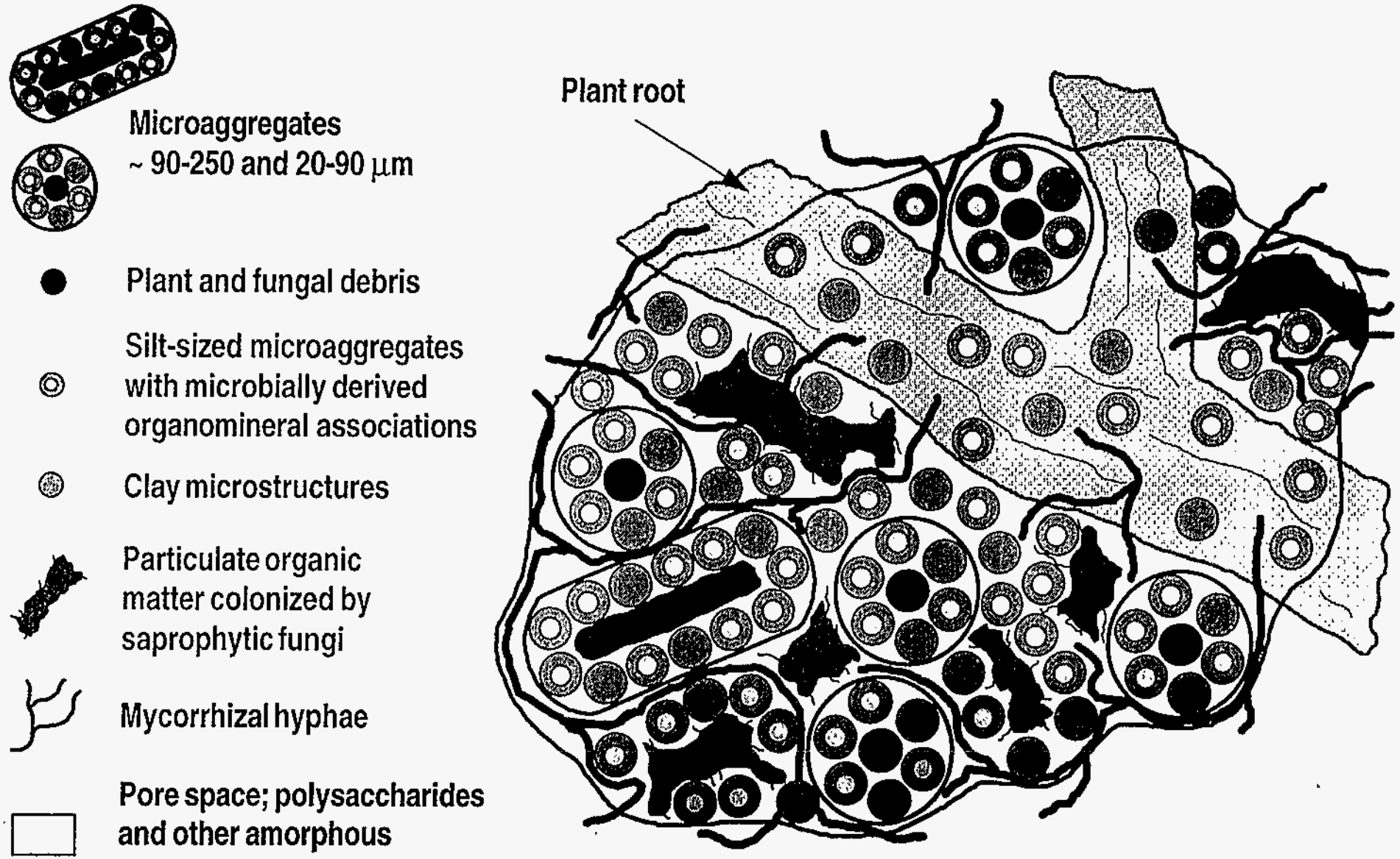
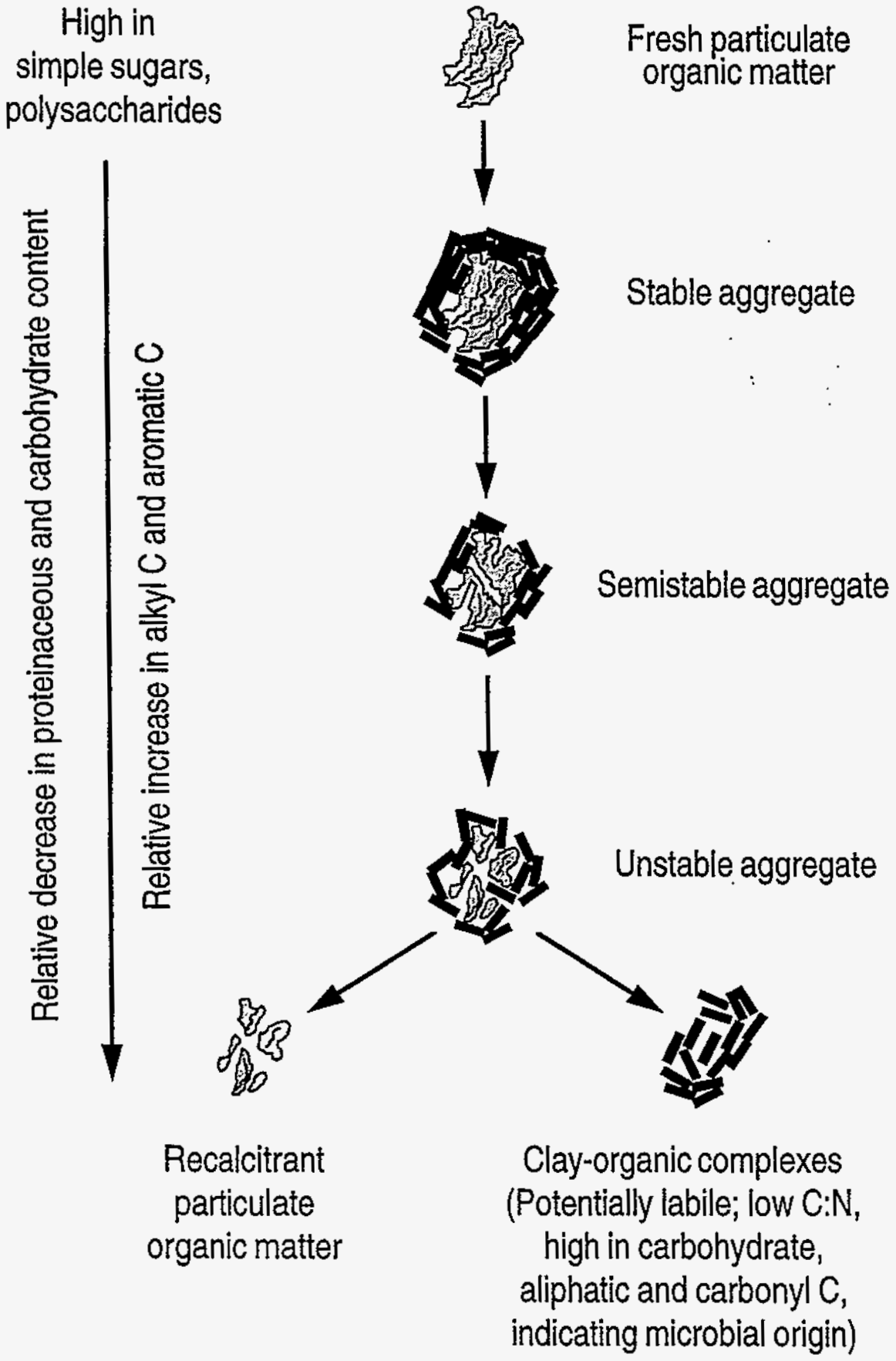

Microaggregates
~ 90-250 and 20-90 μm
Plant and fungal debris
Silt-sized microaggregates with microbially derived organomineral associations
Clay microstructures
Particulate organic matter colonized by saprophytic fungi
Mycorrhizal hyphae
Pore space; polysaccharides and other amorphous interaggregate binding agents
Plant root

Fig. 2

Fig. 3


High in
simple sugars,
polysaccharides
Relative decrease in proteinaceous and carbohydrate content
Relative increase in alkyl C and aromatic C
Fresh particulate
organic matter
Stable aggregate
Semistable aggregate
Unstable aggregate
Recalcitrant
particulate
organic matter
Clay-organic complexes
(Potentially labile; low C:N,
high in carbohydrate,
aliphatic and carbonyl C,
indicating microbial origin)

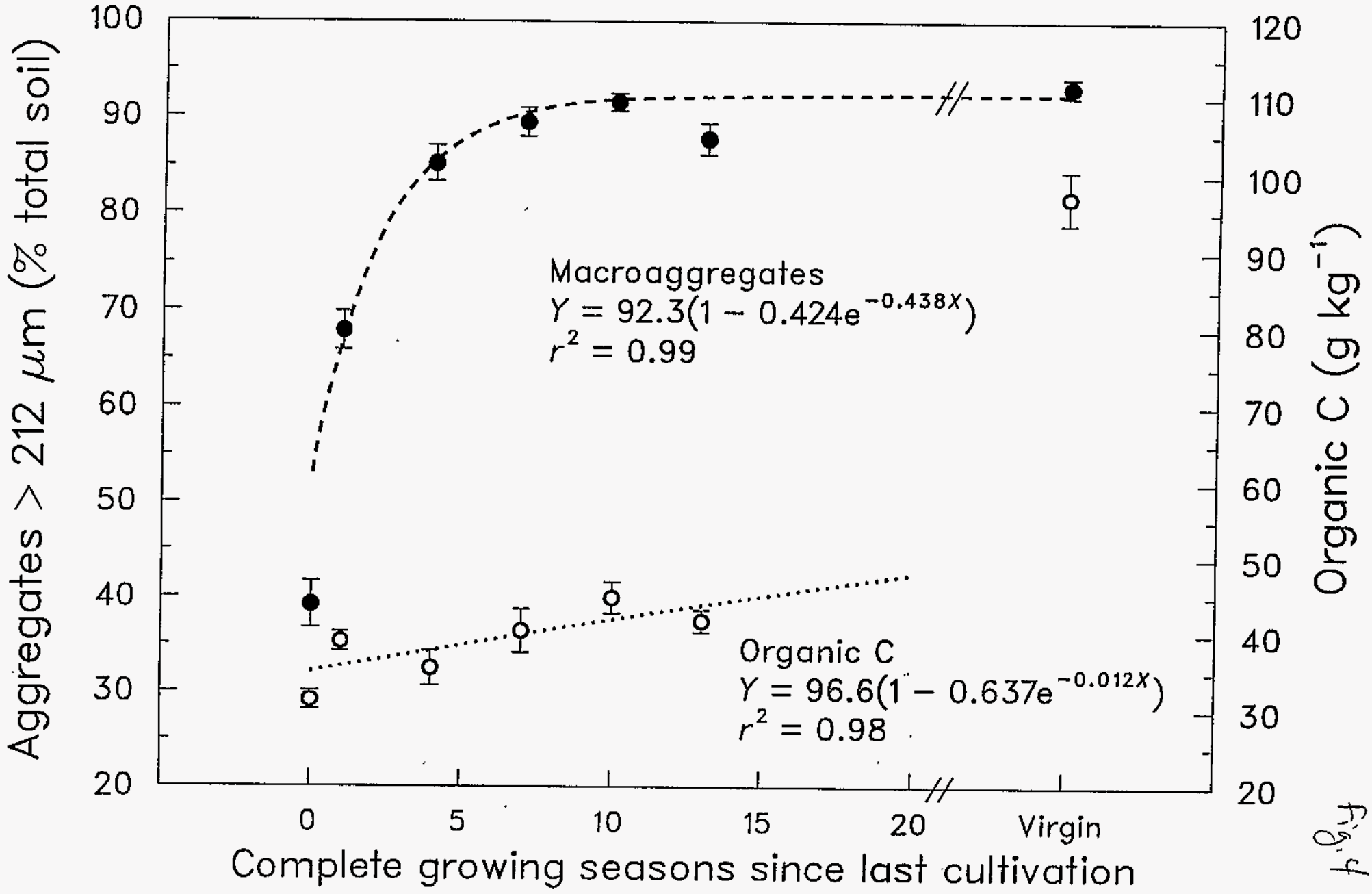

Aggregates > 212 μm (% total soil)
Organic C (g kg⁻¹)
Complete growing seasons since last cultivation
Macroaggregates
Y = 92.3(1 − 0.424e^−0.438X)
r² = 0.99
Organic C
Y = 96.6(1 − 0.637e^−0.012X)
r² = 0.98
100
90
80
70
60
50
40
30
20
120
110
100
90
80
70
60
50
40
30
20
0
5
10
15
20
Virgin

Fig. 9.4

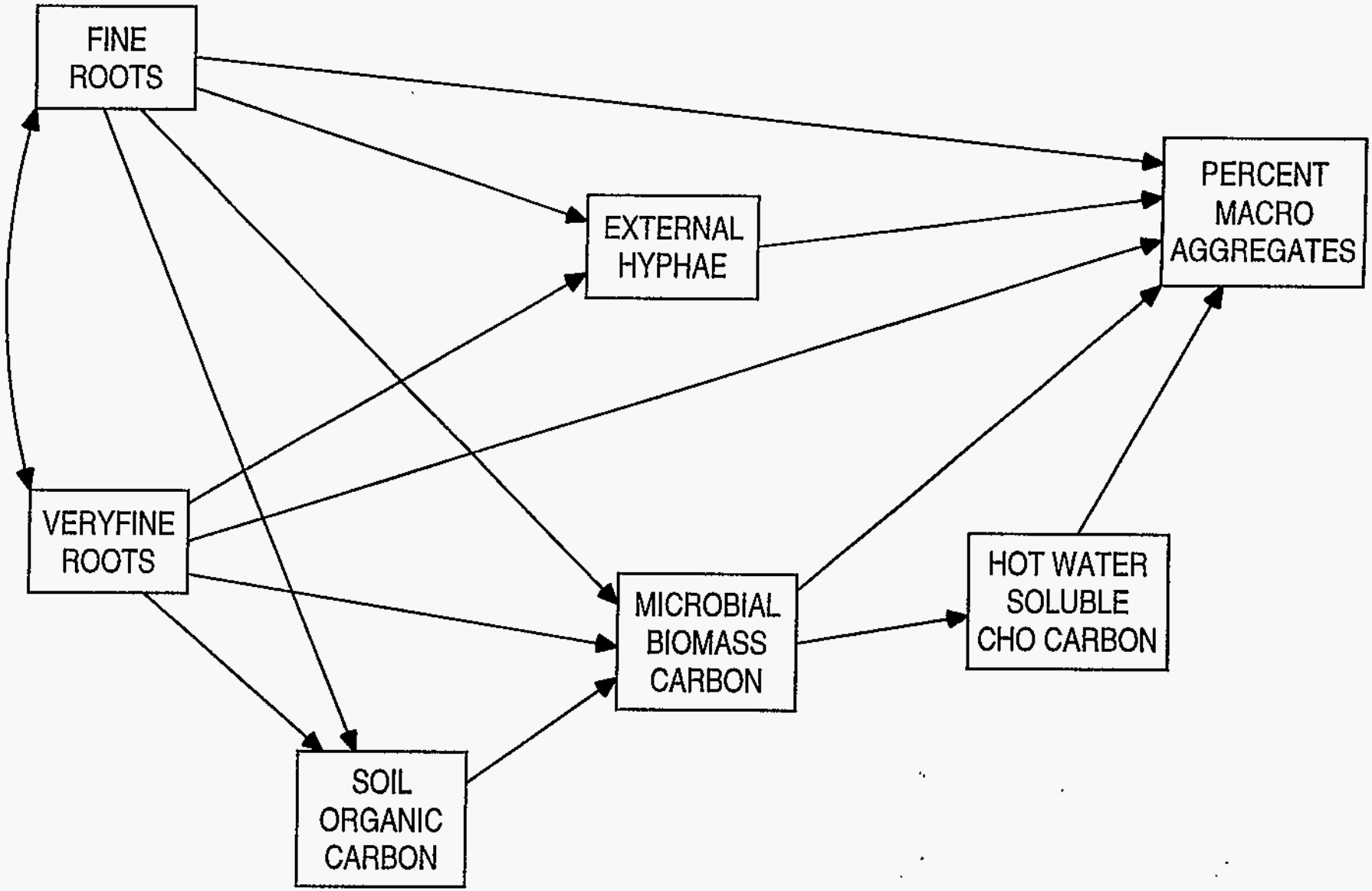

FINE ROOTS
EXTERNAL HYPHAE
PERCENT MACRO AGGREGATES
VERYFINE ROOTS
MICROBIAL BIOMASS CARBON
HOT WATER SOLUBLE CHO CARBON
SOIL ORGANIC CARBON

Fig. 5

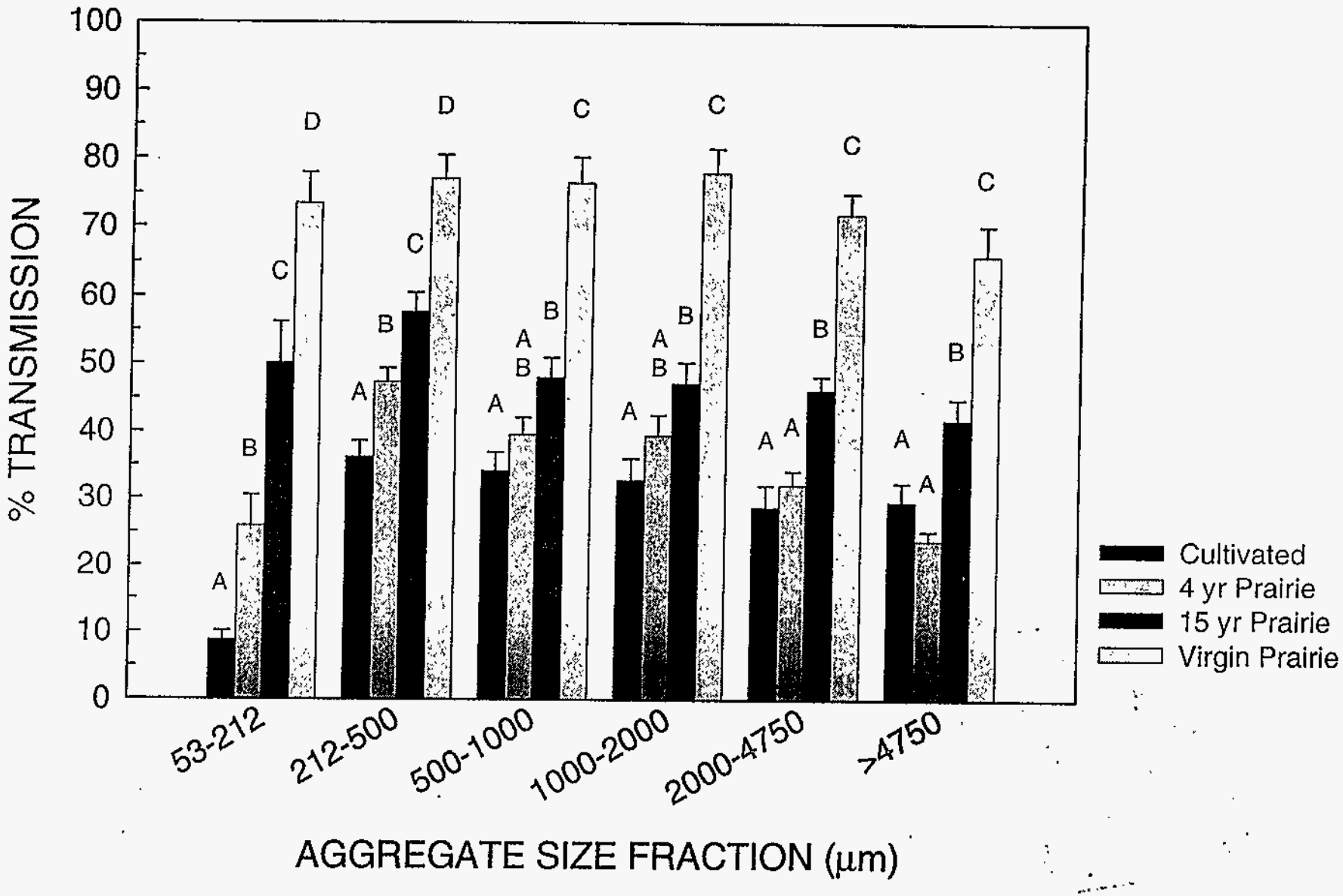

100
90
80
70
60
50
40
30
20
10
0
% TRANSMISSION
A
B
C
D
A
B
C
D
A
A
B
B
A
A
B
B
A
A
B
C
A
A
B
C
53-212
212-500
500-1000
1000-2000
2000-4750
>4750
AGGREGATE SIZE FRACTION (µm)
Cultivated
4 yr Prairie
15 yr Prairie
Virgin Prairie

Fig. 6