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Land-Use Intensity Effects on Soil Organic Carbon Accumulation Rates and Mechanisms

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Abstract

Restoring soil C pools by reducing land use intensity is a potentially high impact, rapidly deployable strategy for partially offsetting atmospheric CO_2 increases. However, rates of C accumulation and underlying mechanisms have rarely been determined for a range of managed and successional ecosystems on the same soil type. We determined soil organic matter (SOM) fractions with the highest potential for sequestering C in ten ecosystems on the same soil series using both density- and incubation-based fractionation methods. Ecosystems included four annual row-crop systems (conventional, low input, organic and no-till), two perennial cropping systems (alfalfa and poplar), and four native ecosystems (early successional, midsuccessional historically tilled, midsuccessional never-tilled, and late successional forest). Enhanced C storage to 5 cm relative to conventional agriculture ranged from 8.9 g C m^{-2} y^{-1} in low input row crops to 31.6 g C m^{-2} y^{-1} in the early successional ecosystem. Carbon sequestration across all ecosystems occurred in aggregate-associated pools larger than 53 μm. The density-based fractionation scheme identified heavy-fraction C pools (SOM > 1.6 g cm^{-3} plus SOM < 53 μm), particularly those in macroaggregates (>250 μm), as having the highest potential C accumulation rates, ranging from 8.79 g C m^{-2} y^{-1} in low input row crops to 29.22 g C m^{-2} y^{-1} in the alfalfa ecosystem. Intra-aggregate light fraction pools accumulated C at slower rates, but generally faster than in inter-aggregate LF pools. Incubation-based methods that fractionated soil into active, slow and passive pools showed that C accumulated primarily in slow and resistant pools. However, crushing aggregates in a manner that simulates tillage resulted in a substantial transfer of C from slow pools with field mean residence times of decades to active pools with mean residence times of only weeks. Our results demonstrate that soil C accumulates almost entirely in soil aggregates, mostly in macroaggregates, following reductions in land use intensity. The potentially rapid destruction of macroaggregates following tillage, however, raises concerns about the long-term persistence of these C pools.

Key words: aggregates; agriculture; C-sequestration; forest C; organic; tillage; succession.

Introduction

Restoring some fraction of terrestrial soil C pools through changes in agricultural management is a high impact, rapidly deployable strategy for partially mitigating increases in atmospheric CO_2 (Caldeira and others 2004; CAST 2004; Pacala and Socolow 2004). Management strategies that may increase soil C storage include reducing tillage intensity and increasing residue inputs with cover crops, green manures, or perennial crops (West and

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Post 2002; Lal and others 2004). These practices modify decomposition dynamics by changing soil aeration, water dynamics, and aggregation, as well as the biochemistry and quantity of crop residues (Angers and Caron 1998; Martens 2000; Drinkwater and Snapp 2006). No-till annual cropping systems can sequester C at rates of 30–60 g C m^{-2} y^{-1} whereas perennial cropping systems and successional ecosystems can sequester C at higher rates (Davidson and Ackerman 1993; West and Post 2002). The rates of C sequestration and its underlying mechanisms, however, have rarely been determined in multiple, replicated, differently managed ecosystems on the same soil types.

Density fractionation methods that physically separate soil organic matter into light and heavy fractions, in conjunction with soil aggregation measurements, can provide considerable insight into the mechanisms underlying soil organic matter responses to ecosystem management (Elliott 1986; Strickland and Sollins 1987; Six and others 1998). Light fraction (LF) molecular chemistry resembles young plant materials, although fungal and faunal-derived compounds in various stages of decomposition may also be present (Molloy and Speir 1977; Golchin and others 1994). Its relatively short turnover time of several years can make LF more sensitive to changes in soil management than whole soils (Jenkinson and Rayner 1977; Wander and others 1994; Swanston and others 2002).

The incorporation of light fraction and other organic compounds into different sized aggregates can reduce their turnover time (Jastrow and others 1996; Balesdent and others 2000). Tisdall and Oades (1982) described a hierarchical conceptual model that explains relationships between stabilization of different sized aggregates and soil organic matter dynamics. They associated temporary organic materials such as polysaccharides with transient stabilization of macroaggregates (>250). Subsequent work using this model has demonstrated that during the decomposition of LF, the production of polysaccharides and other compounds can stimulate macroaggregate formation (Puget and others 1995) and the subsequent occlusion of LF within aggregates (intra-aggregate LF) reduces its decomposition rate (Elliott 1986; Jastrow and others 1996). The model by Tisdall and Oades (1982) associates microaggregates (<250 μm) with more recalcitrant compounds such as humic substances. Microaggregates respond very slowly to management changes whereas macroaggregates are rapidly destroyed following tillage and the intra-aggregate C pools thereupon released from protection may be rapidly lost (Oades 1984; Elliott 1986; Grandy and Robertson 2006a, b). Soil C accrual following afforestation, agricultural abandonment, and reducing tillage in agricultural soils occurs mainly in intra-aggregate C pools (Jastrow and others 1996; De Gryze and others 2004).

A potential limitation of light fraction methods is that aggregate characteristics such as pore space structure and bulk density, which affect the degree of physical protection conferred by aggregates, vary with ecosystem management (Puget and others 1995; Park and Smucker 2005). Additional information may, therefore, be gained by using respiration rates to quantify aggregate-associated C pools with different turnover times. Respiration rates reflect not only the amount of C but also its availability, and can be compared in crushed versus intact aggregates to directly assess the amount of C protected by aggregation.

One widely used method combines long-term respiration rates and acid hydrolysis to model active, slow and passive pools of C (Paul and others 2001). Active pool C has a turnover time of days to weeks, slow pool of years to decades, and the resistant pool of centuries (Paul and others 2001; Fortuna and others 2003). Modeling long-term respiration rates of crushed and intact aggregates into these three pools could provide a direct assessment of aggregate protection of C with different turnover times. The extent to which aggregate disruption transfers C from slow into active pools could have important implications for understanding C sequestration mechanisms and the effects of land use changes on C storage.

Quantifying aggregate protection is particularly important for predicting the effects of future changes in management intensity on C permanence (Paustian and others 2000; Marland and others 2001). Macroaggregates are highly susceptible to changes in plant communities and soil disturbance. Grandy and Robertson (2006b), for example, found that soil in the 2,000–8,000 μm aggregate size class declined from 0.34 to 0.19 g g^{-1} after plowing a previously uncultivated field once and that CO_2 emissions doubled over 3 years. If soil C primarily accumulates in intra-aggregate pools, and these pools are rapidly lost following aggregate destruction, sequestered C will be permanent only if management changes that increase aggregation are permanent. Very little land, however, is today permanently set aside, abandoned, converted to no-till or otherwise managed less intensively. Stored soil C dynamics, for example, might be rapidly changed by cultivating sites in the USDA

Conservation Reserve Program and other long-term set-aside lands (Bowman and others 1990; VandenBygaart and Kay 2004; Grandy and Robertson 2006b).

Robertson and others (2000) demonstrated the potential for cropping system management and succession to modify total soil C storage in ten ecosystems on the same soil type between 1989 and 1999 at a site in the northern US Corn Belt. They found that organic and no-till cropping systems increased C by 8 and 30 g C m^{-2} y^{-1}, respectively, whereas perennial and early successional systems increased surface soil C by 30–60 g C m^{-2} y^{-1}. Robertson and others (2000), however, did not investigate the processes underlying soil C responses to land-use intensity nor identify the C pools that may have high potential for sequestering soil carbon. Here, we investigate C fractions in these systems to identify pools with the greatest potential for C accumulation. We also assess the vulnerability of C in different soil aggregate size fractions to disturbance. Our specific objectives are to determine the effects of cropping system management (conventional, low input, organic, no-till, and perennial) and ecological succession (early, mid, and late old-field succession) on (1) stabilizing water-stable soil aggregates in different size classes; (2) enhancing C storage in physically protected, aggregate-associated C pools; and (3) controlling changes to the size and decay rates of physically-protected C pools following soil structural disturbance.

Materials and Methods

Experimental Site and Approach

Our experimental site is a series of ecosystems that differ in management intensity located at the W.K. Kellogg Biological Station (KBS) Long-Term Ecological Research (LTER) site (Table 1). KBS is located in SW Michigan and receives approximately 90 cm of precipitation annually, about half as snow; mean annual temperature is 9°C. All ecosystems are within 2 km of each other on the same or very similar soil series, mainly Kalamazoo (fine-loamy) and Oshtemo (coarse-loamy) mixed, mesic, Typic Hapludalfs developed on glacial outwash. These two series co-occur in all of these ecosystems and differ mainly in their Ap horizon texture, although variation within a series can be as great as variation between series (Crum and Collins 1995; Robertson and others 1997).

The ten experimental ecosystems include four annual cropping systems, two perennial cropping

Table 1. Cropping System and Successional Vegetation Effects on Soil C and N to 5 cm Soil Depth at the W.K. Kellogg Biological Station Long-Term Ecological Research Project in 2001

	Total C (%)	Total N (%)	Bulk density (g cm^{-3})	Total C (g m^{-2})	Total N (g m^{-2})	C/N ratio	pH	C change (g m^{-2} y^{-1})
Annual crops (corn–soybean–wheat rotation)								
Conventional	0.91 (0.08)	0.08 (0.01)	1.37 (0.01)	621 (51.1)	57.3 (5.31)	10.9 (0.35)	6.26 (0.04)	0.0
Low input w/legume cover	1.09 (0.05)	0.10 (0.01)	1.34 (0.03)	728 (46.0)	69.3 (4.54)	10.5 (0.17)	6.25 (0.05)	8.9
Organic w/legume cover	1.13 (0.04)	0.11 (0.00)	1.36 (0.04)	769 (44.5)	71.9 (3.21)	10.7 (0.26)	6.18 (0.04)	12.3
No-till	1.30 (0.08)	0.12 (0.01)	1.36 (0.03)	885 (55.1)	81.0 (4.66)	10.9 (0.19)	6.40 (0.05)	22.0
Perennial crops								
Alfalfa	1.42 (0.06)	0.13 (0.01)	1.35 (0.01)	962 (35.6)	85.8 (3.48)	11.2 (0.09)	6.63 (0.05)	28.4
Poplar	1.35 (0.10)	0.10 (0.01)	1.27 (0.03)	850 (43.4)	63.9 (2.68)	12.6 (0.19)	6.51 (0.10)	19.1
Successional ecosystems								
Early	1.66 (0.05)	0.14 (0.00)	1.21 (0.02)	1,001 (38.6)	86.1 (3.54)	11.6 (0.10)	6.39 (0.03)	31.6
Mid (historically tilled)	1.85 (0.02)	0.15 (0.01)	1.16 (0.02)	1,075 (31.0)	85.2 (4.09)	12.6 (0.37)	5.46 (0.12)	9.1
Mid (never-tilled)	3.49 (0.05)	0.28 (0.00)	0.93 (0.03)	1,626 (60.2)	128 (4.64)	12.7 (0.18)	5.93 (0.11)	0.0
Late (deciduous forest)	3.11 (0.18)	0.22 (0.02)	1.11 (0.01)	1,721 (108)	120 (12.9)	14.4 (0.61)	5.33 (0.06)	0.0

Means with standard errors in parentheses.

systems, and four successional ecosystems (Table 1). The annual cropping systems are corn–soybean–wheat rotations and include four management regimes: (1) conventional chemical management with tillage, (2) tilled, low chemical input, (3) tilled organic, and (4) conventional chemical management with no-till. Both low input and organic management systems have a leguminous winter cover crop (*Trifolium pretense* L.) to provide nitrogen in two out of every 3 years. No systems receive compost or manure and the standard input systems receive identical inorganic N fertilizers based on soil tests and best management practices, as described in detail by Grandy and others (2006a). The low input system receives an initial pulse of fertilizer at planting (ca. 29 kg N ha^{-1}) but no side-dress N applications (ca. 124 kg N ha^{-1} in the no-till and till systems).

The perennial crops include poplar trees (*Populus* × *euramericana* c.v. Eugenei.) on a ca. 10-year rotation cycle and alfalfa (*Medicago sativa*) on a 6–8 year rotation. The successional ecosystems include (1) recently abandoned, 12-year-old early successional old-fields; (2) historically tilled 50-year-old midsuccessional ecosystems; (3) a never-tilled 50-year-old midsuccessional ecosystem; and (4) a set of late successional oak-hickory forests that were never cleared or plowed. The annual and perennial cropping systems as well as the early successional ecosystem are replicated in six 1 ha plots (42 ha total) within the KBS LTER main experimental site. These treatments were all established in 1989 in a conventionally managed row-crop field. Midsuccessional historically tilled, midsuccessional never-tilled, and late successional ecosystems are replicated at different locations within a 2 km radius of the main site on the same soil series. The midsuccessional never-tilled sites were replicated four times within a 2 ha area 300 m from the cropping systems. These sites are mowed every year to maintain midsuccessional grasslands. The midsuccessional historically tilled and the forest ecosystems were each replicated three times. Within each of the six sites, a 1 ha sampling area was laid out in a similar manner to those in the main site. The midsuccessional historically tilled site consists of a mix of trees and shrubs with grass cover. These ecosystems have been organized along a management intensity gradient based on tillage, external inputs, and above-ground net primary productivity (Table 1).

Soil Sampling and Storage

Previous research at KBS (De Gryze and others 2004) and other studies (for example, West and Post 2002) have shown that C accumulates primarily near the soil surface following changes in tillage. To better understand the mechanisms underlying this accumulation and the persistence of accumulated C, we sampled to 5 cm. Soil samples were collected from five locations within each plot in June and July 2001. At each of the five sample locations, two subsamples with a diameter of 7.6 cm to a depth of 5 cm were taken by gently hammering a PVC core into the ground to minimize compression and the slicing of aggregates. In row-crop ecosystems, one of the subsamples at each location was taken in the row and the other between rows. In systems with a litter layer, all surface residues were pushed aside prior to sampling so that soil C values are for the mineral component only. All ten subsamples from each plot were combined to produce one representative sample for each of the 52 plots. Four separate samples for bulk density analysis were taken at the same time as those for aggregate analysis, using an 8 cm diameter Elkjamp root corer.

Field-moist soil samples were put into a cooler (4°C) prior to being broken along natural fracture planes and passed through an 8 mm sieve within 72 h of sampling. After sieving, soils were dried at room temperature in paper bags prior to storage in plastic bags. Care was taken throughout the study to minimize disturbance of the samples that might influence aggregate structure.

Water-Stable Aggregate Distribution

Aggregate distribution was determined on four replicate 100 g air-dried soil samples by wet-sieving in water through a series of 2,000, 250, and 53 μm sieves (Elliott 1986). Soil that was previously sieved to less than 8 mm was submerged for 5 min on the surface of the 2,000 μm sieve which was then moved up and down for over 2 min with a stroke length of 3 cm for 50 strokes (Grandy and Robertson 2006a). Sieving was repeated on the 250 μm (50 strokes) and 53 μm (30 strokes) sieves using the soil plus water that passed through the next larger sieve. Aggregates remaining on each sieve were dried at 60°C. Sand content was determined on an aggregate subsample after dispersing soil in sodium hexametaphosphate (0.5%) for 48 h on a rotary shaker at 190 rpm.

Aggregate-Associated Light Fraction Organic Matter

The method (Figure 1) we used to separate inter- and intra-aggregate light fraction (LF; organic matter of relatively low density) is based on

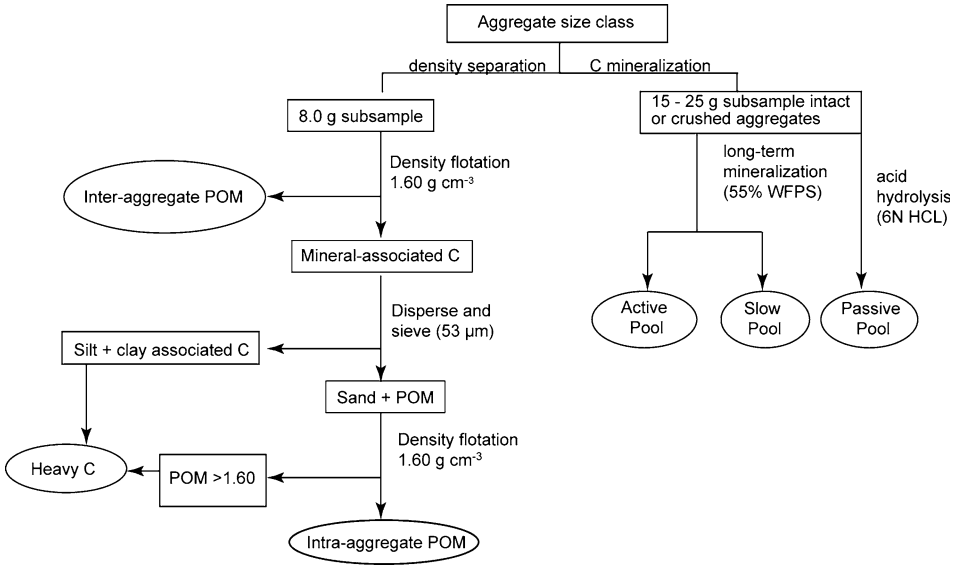

Figure 1. Outline of the soil organic matter pools (SOM) produced by density separation and long-term mineralization of different aggregate size classes. SOM pools that we quantify in this study are shown within *ovals*.

previously published protocols (Six and others 1998; Gale and others 2000). Aggregate subsamples were pre-wet prior to LF analysis to minimize aggregate destruction during LF separation. An 8 g subsample of aggregates was divided into half and placed on two membrane filters (47 mm diameter; Pall Supor-450) overlaying two paper filters (70 mm diameter; Whatman 42) in a 10 cm Petri dish. Four milliliters of deionized (DI) water were trickled onto the paper filters to slowly wet all of the aggregates by capillarity. After 16 h, aggregates were transferred from the membrane filters to 100 ml beakers with 5 ml aliquots of sodium polytungstate (NAPT) with a density of 1.62 g cm^{-3}. A total of 55 ml NAPT was used for each sample. A preliminary test showed that the final density of NAPT was about 1.60 g cm^{-3} following equilibration with the water contained in aggregates.

After 24 h on a lab bench at about 23°C, LF was aspirated from the surface of the NAPT and then rinsed on a hardened, ashless filter paper with at least 600 ml DI H_2O. We refer to this pool as inter-aggregate LF. After removal of this pool, we aspirated the remaining NAPT. Aggregates were then dispersed to release the intra-aggregate LF using sodium hexametaphosphate as described previously and resuspended in NAPT (d = 1.62 g cm^{-3}). The intra-aggregate LF was collected from the surface. The mineral-associated aggregate C plus POM with a density greater than 1.6 was determined by difference and is referred to as heavy-fraction C (HF). Organic C and total N concentrations of organic matter and whole soil samples were determined by dry combustion methods in a CHNS analyzer (Costech ECS 4010, Costech Analytical Technologies, Valencia CA.).

Laboratory Incubations

A subsample of aggregates (15–20 g) was transferred into a 60 ml glass serum vials with a 13 mm diameter opening. We estimated the bulk density of each of our samples after tamping down the serum vials ten times on a laboratory bench and from this determined the amount of water needed to bring them to 55% WFPS. Water applications were made slowly via 5 ml pipettes to minimize breakdown of aggregate structure following rewetting.

After wetting the samples, the serum vials were placed in a 237 cm^{-3} jar with approximately 60 ml of water in the bottom. These jars were covered with polyfilm that permits relatively free O_2 and CO_2 exchange but retains water. Jars were put into boxes and then into dark incubation chambers maintained at 25°C. Samples were periodically checked for water loss by weighing and were then rewetted, as necessary.

We added additional sand to the less than 53 µm size class to minimize O_2 depletion. The 2,000–8,000 µm size class contained an average of 45% sand and the 250–2,000 µm size class an average of 60% sand, whereas the less than 53 µm size class contained an average of 33% sand. Sand additions consisted of particles with a diameter between 250 and 1,000 µm and brought the average sand content in this size class up to 48%.

Respiration in all size classes was measured a minimum of 12 times over 205 d using a front-weighted sampling approach with greater sampling intensity early in the incubation (Figure 1). At each

sampling date serum vials were flushed for 45 s with a humidified air stream. After flushing, bottles were sequentially capped with a rubber septum. A 0.5 ml sample of headspace was immediately drawn with a syringe and then two additional samples were taken over a 90 min sampling interval. CO_2 content of each gas sample was analyzed using an infrared gas absorption (IRGA) analyzer, followed by calculation of the respiration potential for the time interval (Robertson and others 1999).

Active, slow and passive pool C associated with different aggregate size fractions were determined by modeling the long-term respiration data using exponential decay equations (Paul and others 2001). We used a differentiated version of a standard three-pool first order model to accommodate discontinuous sampling:

$$dC/dt = C_a \times k_a e^{(-k_a \times \text{days})} + (C_{soc} - C_r - C_a) \times k_s e^{(-k_s \times \text{days})} + C_r \times k_r e^{(-k_r \times \text{days})} \quad (1)$$

where C_a and k_a are the active C pool size and decay rate constant, k_s is the slow pool decay constant, and C_r and k_r are the resistant pool C size and decay rate constant. C_{soc} is total soil C. C_a, k_a, and k_s were determined by modeling; slow pool C (C_s) was determined by difference by subtracting C_a and C_r from C_{soc} and C_r was determined by acid hydrolysis. All detectable plant residues and POM were removed with tweezers prior to hydrolysis because of the potential for relatively young lignin to resist hydrolysis and inflate C_r estimates (Paul and others 2001). After removal of these materials, soil samples were ground with a mortar and pestle. Hydrolysis was carried out for 16 h at 110°C in 110 ml test tubes containing 2 g soil and 20 ml 6 N HCl. The k_r was assumed to be 8.3×10^{-6} d^{-1}, a previously used value for KBS soils (Paul and others 2001). Carbon dating of C_r in previous studies at our site has demonstrated that that this pool ranges from hundreds to thousands of years old (Paul and others 1997), resulting in a mean residence time so large and a k_r so small that deviations of the assumed value from the actual decay rate constant have little effect on the other parameters (Paul and others 2001; Fortuna and others 2003). Laboratory mean residence times were calculated as $1/k$. Field mean residence times were determined using a Q_{10} correction based on the difference in lab temperature (25°C) and mean field temperature at KBS (9°C) using the following equation: $2^{((25-9)/10)}$ (see Paul and others 2001).

To determine the potential for aggregate structure to control the distribution of C, an additional 15–20 g subsample of aggregates was crushed prior to performing the long-term mineralization assays. We based our crushing technique on field observations that tillage tends to release 53–250 μm aggregates from crushed 2,000–8,000 and 250–2,000 μm aggregates (Grandy and Robertson 2006a). Aggregates ranging in size from 2,000–8,000 and 250–2,000 μm were thus fractured to release microaggregates by passing them through a 250 μm sieve. The structure of aggregates in the 53–250 μm size class was destroyed by crushing aggregates in a mortar and pestle. Total potential physical protection of C by aggregates was estimated from increases in C_a associated with aggregate destruction where the difference in C_a between crushed and intact aggregates was positive. Samples where differences were negative were analyzed separately.

Statistical Analysis

Statistical analysis was performed using a completely random-design analysis of variance (ANOVA) with the Proc Mixed procedure in SAS (SAS Version 8.2, SAS Institute 1999). Data were analyzed by considering ecosystem and aggregate size class as fixed effects after log transformation to improve homogeneity of variance. Single degree of freedom comparisons were made using the LSD statistic to calculate a 95% confidence interval around the differences between means generated using the diff option in Proc Mixed. The LSD was carried out using the PDMIX800 algorithm (Saxton 1998). The texture of different aggregate size classes and treatments may differ due to tillage and soil textural heterogeneity. Very little soil C is associated with sand, and sand particles do not contribute to aggregate stabilization, so when comparing aggregate size distributions and C concentrations among treatments and size classes it is important to correct for sand content (Elliott and others 1991). We corrected aggregate size distributions and aggregate-associated SOM pools for sand larger than 53 μm.

Results

Total Soil C and N

Relative to conventional agriculture, increases in soil C concentrations from 0 to 5 cm occurred with no-till (43%), low input (17%) and organic (24%) management (Table 1). Perennial crops increased soil C concentrations relative to conventional management by 55% in alfalfa and 37% in poplar stands. In the early successional ecosystems soil C concentrations increased by 61% relative to

conventional agriculture. In both the early and midsuccessional historically tilled ecosystems there were substantially lower soil C concentrations than in the never-tilled midsuccessional systems or the deciduous forest. Carbon accumulation rates ranged from 8.9 g C m^{-2} y^{-1} in low input to 31.6 g C m^{-2} y^{-1} in the early successional ecosystems. Organic N concentrations also increased across the management intensity gradient. C/N ratios were similar among agricultural systems but increased in perennial cropping systems and successional ecosystems (Table 1).

Aggregate C

In all ecosystems except for the low input system, the mass of 2,000–8,000 μm size class aggregates increased relative to that in the conventional system (Figure 2). In the no-till system the 250–2,000 μm aggregate class increased and smaller size fractions decreased proportionately relative to conventional management (Figure 2). In the alfalfa, poplar, and successional ecosystems the 250–2,000 μm aggregate size class also increased relative to conventional management.

In all ecosystems except for the organic system, total C concentrations in the 2,000–8,000 μm aggregate size class increased (Figure 3). Total C in the 250–2,000 μm size class aggregates increased in the low input, perennial, and successional ecosystems relative to conventional management. Total C in the 53–250 μm size class aggregates also increased in perennial and successional ecosystems relative to the annual agricultural treatments. Carbon concentrations in the smaller than 53 μm size class were greater in the mid and late successional ecosystems than in the annual agricultural treatments (Figure 3). Carbon concentrations in macro (>250 μm) and microaggregates (<250 μm) were similar in the poplar, mid successional never-tilled, and late successional ecosystems and also between the 250–2,000 and 53–250 μm classes in the midsuccessional historically tilled system. In other ecosystems, C concentrations were lower in microaggregates than macroaggregates.

Aggregate Associated Light Fraction

In the 2,000–8,000 μm aggregate size class, the inter-aggregate LF concentrations were indistinguishable among the annual cropping systems and early successional ecosystems (Figure 4). In the midsuccessional historically tilled, midsuccessional never-tilled, and late successional ecosystems inter-aggregate LF increased by 301, 247, and 503%, respectively, compared to conventional agriculture

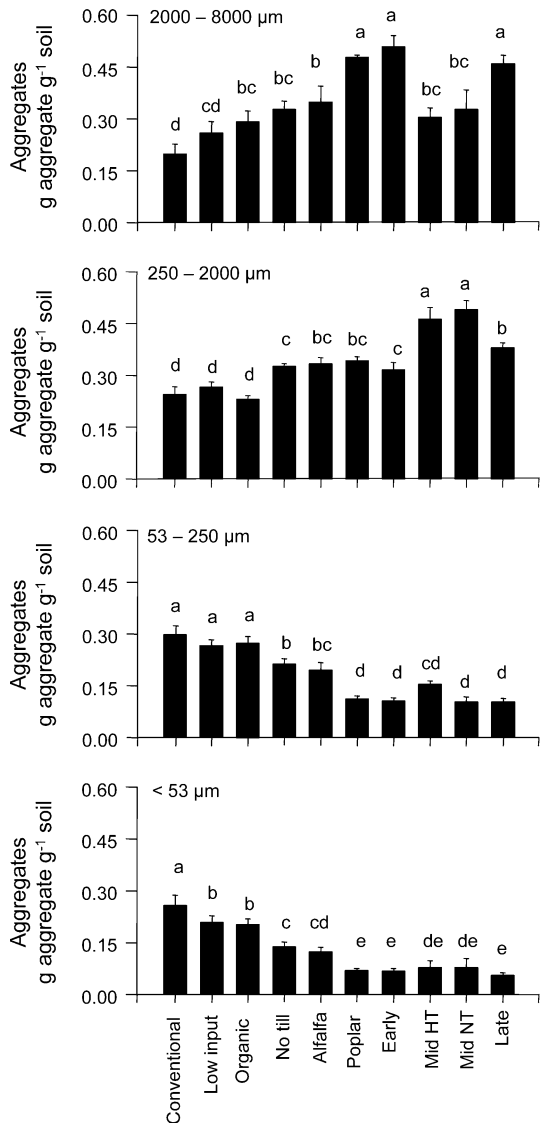

Figure 2. Ecosystem effects on the proportion of wet-sieved soil in different aggregate size fractions. Within an aggregate size class, ecosystems with different *lowercase letters* are significantly different ($P < 0.05$). Successional treatment abbreviations: early successional (*Early*), mid-successional historically tilled (*Mid HT*), midsuccessional never tilled (*Mid NT*), and late successional forest (*Late*). Bars are means ± SE (n = 3–6).

(Figure 4). In the 250–2,000 μm aggregate size class, inter-aggregate LF was generally similar among ecosystems, although the early successional, midsuccessional historically tilled, and late successional treatments increased C relative to alfalfa (Figure 4). In the 53–250 μm size class, inter-aggregate LF was similar among annual cropping systems. All four successional ecosystems had higher inter-aggregate LF than did the agricultural ecosystems.

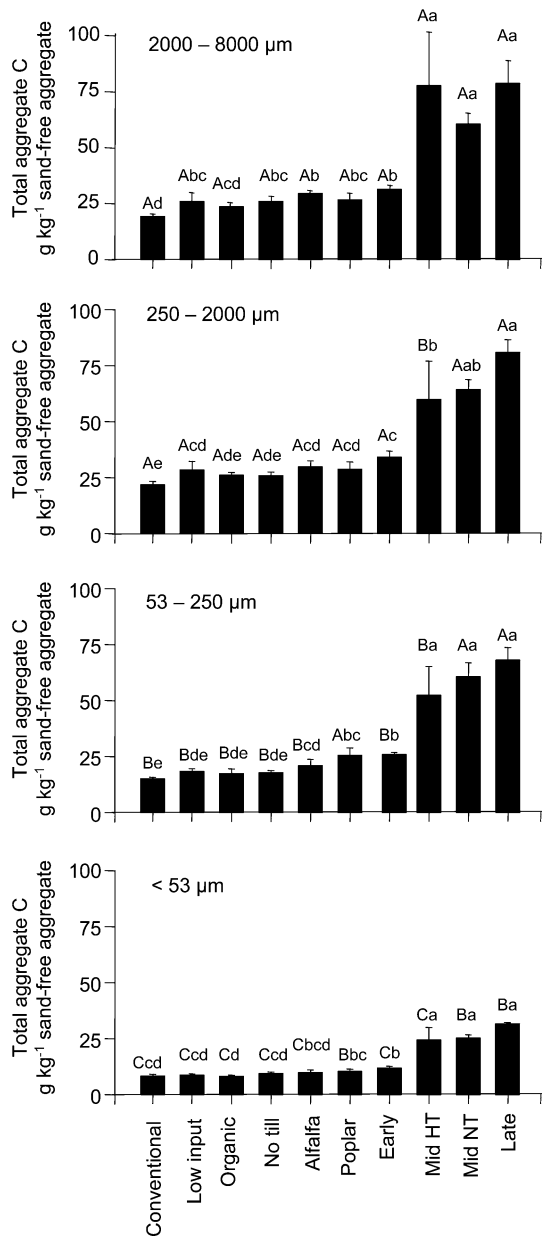

Figure 3. Ecosystem effects on total sand-free C concentrations in different aggregate size fractions. Within an aggregate size class, ecosystems with different *lowercase letters* are significantly different ($P < 0.05$). Within an ecosystem, size classes with different *uppercase letters* are significantly different. Bars are means ± SE.

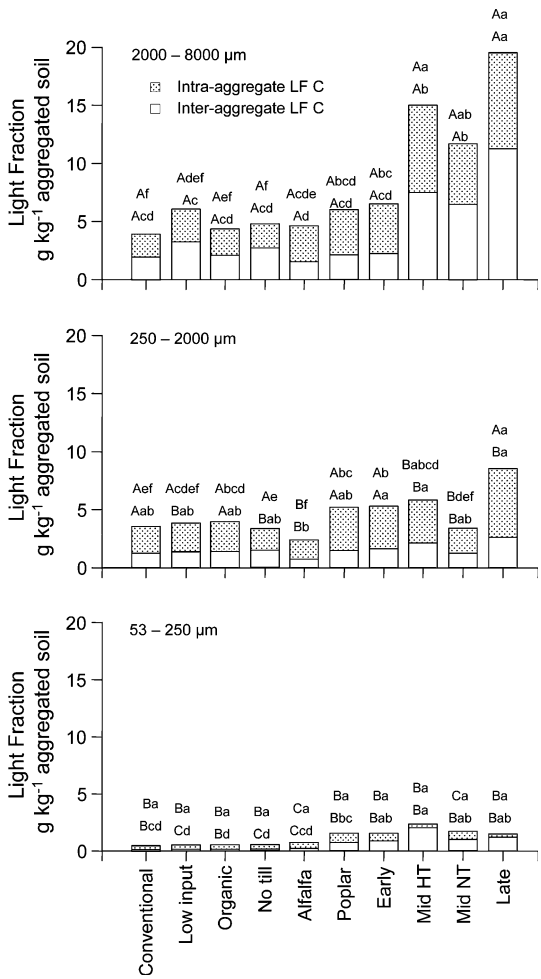

Figure 4. Ecosystem effects on the concentration of inter- and intra-aggregate light fraction (LF) C in aggregate size classes. Within a column, the results on top are from intra-aggregate LF and those on the bottom are for inter-aggregate LF. Within an aggregate size class, ecosystems with different *lowercase letters* are significantly different ($P < 0.05$). Within an ecosystem, size classes with different *uppercase letters* are significantly different. Statistical results and stacked bars for light fraction location are shown from top to bottom in the same order.

Intra-aggregate LF in the 2,000–8,000 µm size class was similar among agricultural systems; in the alfalfa, poplar, and early successional ecosystems LF increased relative to conventional agriculture. In the poplar system, intra-aggregate LF increased relative to conventional, organic, and no-till agriculture. The mid and late successional ecosystems had similar intra-aggregate LF but early successional ecosystems had lower intra-aggregate LF than did midsuccessional historically tilled and late successional systems. In the 250–2,000 µm size class, intra-aggregate LF was higher in organic than in no-till or conventional ecosystems. Intra-aggregate LF concentrations in poplar and early successional ecosystems were greater than those in conventional, no-till, and alfalfa systems.

Aggregate-Associated Active, Slow and Passive C

In the 2,000–8,000 µm aggregate size class, the active C pool sizes were similar among annual and perennial cropping systems and early successional

Table 2. Active (C_a), Slow (C_s) and Passive (C_r) Pool C Associated with Ecosystems and Intact Aggregate Size Classes

	C pool								
	Active				Slow				Resistant
	C_a (mg g^{-1})	k_a (10^{-2})(d^{-1})	LMRT (d)	FMRT (d)	C_s (mg g^{-1})	k_s (10^{-4}) (d^{-1})	LMRT (y)	FMRT (y)	C_r (mg g^{-1})
2,000–8,000 μm size class									
Conventional	0.545Ac	4.91Aa	20.7	62.8	11.4Ac	3.06Babc	10.3	31.3	7.36Ae
Low input	0.593Ac	5.43Aa	18.6	56.3	15.8Abc	2.56Abc	11.7	35.4	9.66Ade
Organic	0.568Ac	5.77Aa	17.4	52.8	13.4Abc	3.60Aab	8.29	25.1	9.67Ade
No-till	0.585Ac	5.22Aa	19.5	59.2	14.1Abc	3.78Aab	8.38	25.4	11.2Acd
Alfalfa	0.577Ac	4.34Ba	23.2	70.4	17.5Ab	1.73Ac	16.8	50.9	11.4Acd
Poplar	0.447Ac	5.01Aa	20.2	61.2	14.8Abc	4.70Ba	6.12	18.5	11.4Acd
Early	0.576Ac	5.05Aa	20.6	62.3	15.9Abc	4.00Aab	7.05	21.4	14.8Ac
Mid HT	2.17Aa	3.19Ba	32.1	97.2	47.0Aa	3.00Babc	9.42	28.6	28.8Ab
Mid NT	1.39Ab	3.36Ba	32.9	99.6	30.6ABa	3.95Aab	7.72	23.4	28.6ABb
Late	1.32Ab	3.07Aa	33.0	100	28.1ABa	3.20Aabc	9.27	28.1	49.4Aa
250–2,000 μm size class									
Conventional	0.353Abc	5.24Ab	23.1	70.0	8.16Bc	4.63Ab	9.49	28.8	9.67Ad
Low input	0.372ABbc	6.21Aab	17.1	51.8	16.9Ab	3.98Ab	7.33	22.2	11.1Acd
Organic	0.330ABbc	6.46Aab	16.6	50.5	13.9Ab	4.60Ab	6.11	18.5	11.9Acd
No-till	0.386Abc	6.22Aab	16.5	49.9	14.6Ab	3.82Ab	7.51	22.8	12.9Acd
Alfalfa	0.352ABbc	5.29Bb	20.9	63.3	17.5Ab	1.50Ac	19.2	58.1	11.9Acd
Poplar	0.251Ac	7.60Aa	15.7	47.7	13.1Ab	6.78Aa	4.20	12.7	15.3Abc
Early	0.356ABbc	6.14Aab	17.2	52.2	18.1Ab	5.00Aab	5.73	17.4	15.7Ab
Mid HT	1.26Ba	4.36ABb	32.8	99.5	34.1ABa	6.77Aa	4.54	13.7	24.6Aab
Mid NT	0.405Bbc	4.94ABb	22.8	69.0	44.2Aa	5.12Aab	6.58	20.0	19.3Bb
Late	0.686Bb	4.37Ab	23.5	71.2	40.4Aa	3.90Ab	7.53	22.8	39.6Aa
53–250 μm size class									
Conventional	0.177Bc	5.14Abc	20.9	63.5	5.31Cc	3.93ABbcde	7.20	21.8	9.64Ad
Low input	0.230Bbc	6.63Aab	17.5	53.1	7.94Bb	3.27Acde	9.17	27.8	10.2Ad
Organic	0.191Bbc	5.01Abc	20.4	61.7	7.53Bb	3.08Ade	10.7	32.6	9.46Ad
No-till	0.245Bbc	4.26Ac	40.7	123	7.52Bb	3.22Ade	12.6	38.1	10.1Ad
Alfalfa	0.142Bbc	8.29Aa	15.1	45.7	9.54Bb	2.82Ae	12.1	36.8	12.4Acd
Poplar	0.189Abc	6.60Aab	16.8	51.0	10.5Ab	4.66Bbcd	6.51	19.7	16.5Abc
Early	0.243Bbc	6.18Aabc	17.8	53.9	10.1Bb	4.80Abc	6.49	19.7	15.6Ac
Mid HT	0.588Cab	6.51Aabc	15.4	46.6	24.7Ba	4.47ABbcde	6.18	18.7	27.1Aab
Mid NT	0.476Babc	6.26Aabc	18.2	55.1	21.5Ba	6.33Aa	4.73	14.3	38.6Aa
Late	0.867Ba	5.57Aabc	20.0	60.7	24.7Ba	5.77Aab	4.79	14.5	42.5Aa

Within an aggregate size class, ecosystems with different lowercase letters are significantly different ($P < 0.05$). Within an ecosystem, size classes followed by different uppercase letters are significantly different. C_a and k_a represent active pool C and kinetics, C_s and k_s represent slow pool C and kinetics, and C_r and k_r represent resistant pool C and kinetics (see text for details). Laboratory mean residence time (LMRT) was calculated as 1/k. Field mean residence (FMRT) time was determined using a Q_{10} correction for the difference in lab temperature (25°C) and field mean temperature at KBS (9.0°C).

ecosystems whereas pool sizes in the mid and late successional ecosystems were greater than in the other ecosystems (Table 2). The mid and late successional ecosystems had greater C_s than other treatments across size fractions. The only annual crop management effect on C_r was that no-till had greater C_r than conventional till in the 2,000–8,000 μm size class. Poplar and early successional systems increased C_r relative to annual row crop systems in the 53–250 μm size class fractions.

The potential transfer of C from slow into active pools following aggregate destruction represents a large proportion of the active C pool in intact aggregates (Figure 5). There was no size class effect or size class by treatment interaction on the proportional increase in C_a due to aggregate crushing, so results are presented for the ecosystem main effects only. Crushing aggregates had no effect on k_a and effects on k_s were generally small or nonsignificant (data not shown). In each aggregate size

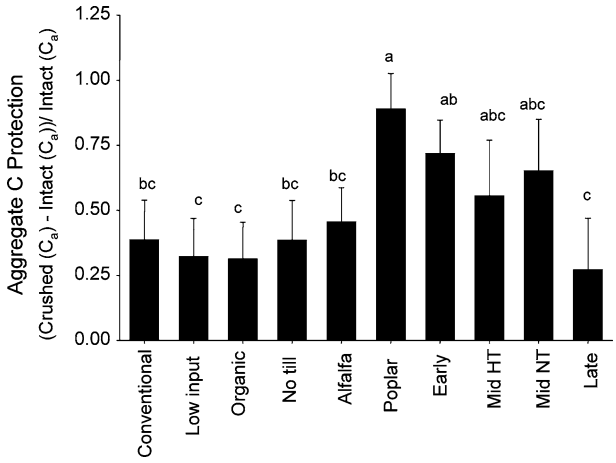

Figure 5. Ecosystem effects on the proportional increase in active C following destruction of aggregates. There were no aggregate size class or size class by treatment interactions for the proportional increase in active C so the results are presented for ecosystems averaged across size classes. Ecosystems with different *lowercase letters* are significantly different ($P < 0.05$).

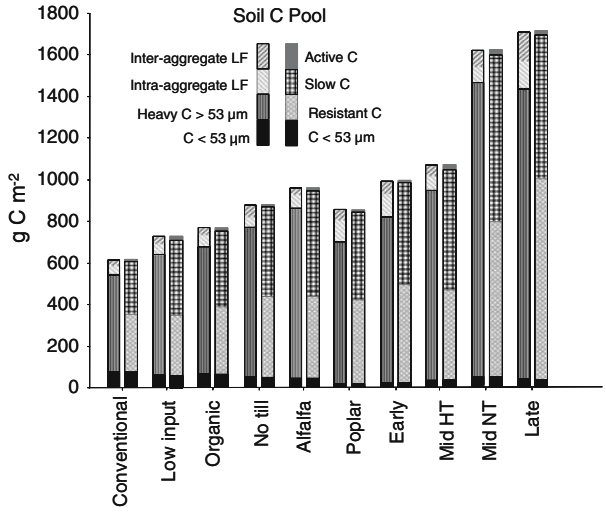

Figure 6. Comparison of whole soil C pools determined by light fraction and incubation-based methods. Aggregate-associated pools were summed across aggregate size classes. All pools listed, except for C smaller than 53 µm, are associated with aggregates larger than 53 µm.

class there was a total of 55 comparisons between crushed and intact aggregates. In the 2,000–8,000 µm size class three of these comparisons were negative, indicating a transfer of C from C_a to C_s following aggregate crushing (data not shown); in the 250–2,000 µm size class five comparisons were negative (data not shown); and in the 53–250 µm size class 29 were negative (data not shown).

Accumulation and Sequestration Rates of C Pools

In the physical fractionation scheme, C primarily accumulated in aggregate-associated HF pools (Figure 6) where rates ranged from 8.79 to 29.22 g C m^{-2} y^{-1} (Table 3). Intra-aggregate C increased from 0.55 g m^{-2} y^{-1} in the midsuccessional historically tilled system to 6.05 g C m^{-2} y^{-1} in the early successional system (Table 3). Inter-aggregate accumulation rates were generally similar or lower than intra-aggregate rates (with the exception of no-till). Carbon was lost from the smaller than 53 µm class in all systems relative to conventional agriculture (Table 3). In the incubation-based fractionation procedure, C accumulated primarily in resistant and slow pools.

Discussion

Soil C Storage and Sequestration Rates

Our results demonstrate the potential for no-till soil management, cropping intensity, and successional development to enhance total soil C storage (Table 1) and show that the rate of storage is related to changes in aggregation and the distribution of C in different aggregate size fractions (Figure 2). Among the management systems established from conventionally tilled row crops in 1989 and in place for 12 years, soil carbon (0–5 cm depth) accumulated most quickly in the early successional ecosystem (380 g m^{-2} C or 61% more carbon than in the conventionally managed annual cropping system), followed by the alfalfa (341 g m^{-2} C or 55% more), no-till (264 g m^{-2} C or 43% more), poplar (229 g m^{-2} C or 37% more), organic (148 g m^{-2} C or 24% more), and low-input (107 g m^{-2} C or 17% more) cropping systems. The deciduous forest and never-tilled mid-successional ecosystems had about 2.5 times more 0–5 cm soil C than the conventional system.

Rates of C accumulation appear related to changes in soil aggregate size classes. Accumulation was fastest in those ecosystems with the fastest accumulation of large aggregates (Figure 2): the no-till, alfalfa, poplar, and early successional systems had more soil in larger (250–2,000 µm) aggregates than more intensively managed systems, and the early successional and poplar systems had many more additional aggregates in the largest size class (2,000–8,000 µm).

Our no-till increases in soil C over 12 years are consistent with rates presented in recent reviews (Davidson and Ackerman 1993; Six and others 2004) and are similar to average accumulation

Table 3. Soil C Accumulation Rates in Different Pools and Ecosystems at the KBS LTER in 2001

	Light fraction-based pools				Incubation-based pools		
	C < 53 μm	Heavy C > 53 μm	Intra-aggregate LF (g C accumulation m^{-2} y^{-1})	Inter-aggregate LF (g C accumulation m^{-2} y^{-1})	Resistant	Slow	Active
Low input	−1.19	8.79	0.64	0.69	0.66	9.46	0.00
Organic	−1.01	11.70	1.03	0.57	3.78	9.46	0.06
No till	−2.23	21.37	0.59	2.25	9.30	14.61	0.30
Alfalfa	−2.66	29.22	1.85	0.01	9.53	21.40	0.15
Poplar	−4.59	17.04	4.93	1.69	10.18	13.54	−0.06
Early	−4.24	27.60	6.05	2.29	16.05	19.60	0.29
Mid HT	−0.87	8.91	0.55	0.48	3.15	6.54	0.24

rates for the Midwest of 30 g C m^{-2} y^{-1} (Franzluebbers and Steiner 2002), although lower than those found in some other some studies (for example, West and Post 2002). Our values are also consistent with those of Robertson and others (2000), who reported a no-till C accumulation rate of 30 g C m^{-2} y^{-1} for the 0–7 cm soil layer for this site between 1989 and 1999. Differences between our values and others, where they exist, may be primarily due to differences in sampling depth. We concentrated on the 0–5 cm layer because carbon change happens fastest in this portion of the soil profile and therefore offers advantages for observing mechanisms underlying change; however a complete understanding of soil carbon accumulation at this site requires a full-profile carbon analysis, not yet complete.

Our increases in soil C with organic and low input systems also demonstrate the potential for leguminous cover crops to increase soil C pools, although at slower rates than no-till. Carbon additions from leguminous cover crops are relatively small compared to cereal cover crops (Snapp and others 2005) and therefore may, at times, be insufficient to increase total soil C (MacRae and Mehuys 1985). Several studies, however, have found increases in soil C similar to ours with legume cover crops (for example, Drinkwater and others 1998; Grandy and others 2002), perhaps due to legume effects on microbial communities, the production of polysaccharides, and aggregate stabilization (Haynes and Beare 1996).

Aggregate Stability

Our results show a dramatic potential for ecosystem management to influence soil aggregate size distributions. Tillage decreases macroaggregation (for example, Six and others 2000; Mikha and Rice 2004; Wright and Hons 2004) and the destructive effects of tillage on soil structure begin to occur immediately after cultivation and are persistent (Grandy and Robertson 2006a). Opinions regarding the effects of plant communities on soil structure, however, remain varied, as residue quality and quantity as well as root growth may influence aggregation (Angers and Caron 1998; Martens 2000; Kavdir and Smucker 2005). Increasing C inputs to the soil can stimulate aggregation because of an increase in the production of microbial polysaccharides and other compounds that stabilize aggregates (Angers and Mehuys 1989; Roberson and others 1991). In the organic and low input systems, the quantity of aboveground biomass inputs were similar to those in our conventional systems (KBS LTER 2005), suggesting that differences in aggregation are due to root dynamics or the quality of residues rather than to aboveground biomass per se. Evidence from the poplar and early successional systems corroborates this notion: in both of these ecosystems there were more aggregates in the 2,000–8,000 μm size class than in the no-till system although in neither ecosystem were aboveground biomass inputs greater than in the no-till systems (De Gryze and others 2004). Roots can change aggregation directly by enmeshing soil particles into aggregates or indirectly by altering C inputs or wet-dry cycles. Perfect and others (1990) found that rates of structural improvement increased with the average weight and length of roots, and other investigators have found correlations between root growth and aggregate stability (Drury and others 1991). It is likely that differences in root dynamics were underlying some of the changes in aggregation that we measured.

The hierarchical model of aggregate formation and stabilization developed by Tisdall and Oades (1982) suggests that different C compounds are

associated with different aggregate size classes. Polysaccharides and other transient organic materials, as well as fungal hyphae and plant roots, stabilize macroaggregates. Because of the potential protection conferred by aggregates, the incorporation of labile C into macroaggregates and into microaggregates within macroaggregates decreases its turnover time (Denef and others 2001). Increases in soil C following decreases in tillage intensity (West and Post 2002; Puget and Lal 2005), changes in organic inputs (Sanchez and others 2004; Jarecki and others 2005), or altering cropping systems (Smith 2004; Wright and Hons 2004; Snapp and others 2005) are often associated with changes in aggregation, particularly macroaggregation. The differences in aggregation that we measured in response to tillage, plant communities, and successional stage, therefore, were likely important for building C.

The use of cover crops in the low-input and organic systems may contribute to some of the increase in aggregation associated with these systems relative to conventional systems. Legume decomposition may stimulate the production of polysaccharides and fungal hyphae capable of temporarily stabilizing soil aggregates (Haynes and Beare 1996; Martens 2000). Legume residue has been shown to double aggregation within days but these aggregates frequently have high turnover rates relative to the more persistent aggregates stabilized by corn residues and other more recalcitrant C. It seems possible that a mix of residues that includes legumes and more recalcitrant materials such as cereal straw or forage crops could result in the greatest stabilization of soil structure. Under these kinds of mixed cropping systems, a variety of compounds would be produced, some that could have a rapid and large effect on aggregation along with others that might contribute to the long-term stability of the aggregates produced.

Aggregate Associated Light and Heavy Fraction

Heavy-fraction (HF) organic matter, calculated as the difference between total aggregate C and light-fraction (LF) C, accounted for the largest proportion of the soil C gained across ecosystems. For example, in the no-till system differences in HF accounted for 82% of the C increase in 2,000–8,000 μm aggregates, and in midsuccessional never-tilled systems HF accounted for 80% of the difference in total C. Six and others (1999) found that between 50 and 66% of new C associated with macroaggregates was in the form of mineral-associated C, and Jastrow (1996) similarly found that C deposition in macroaggregates occurs principally in mineral-associated pools and that particulate soil organic matter accounted for less than 20% of C gain.

In contrast, within-ecosystem differences in HF among size classes were proportionately smaller than LF differences, and HF differences explained a smaller proportion of the variation in total C among size classes. For example, in the no-till system the difference in C concentration between the 2,000–8,000 and 53–250 μm size classes was 8.1 g kg^{-1} and 47% of this was accounted for by differences in HF. In early successional systems, HF was similar in the 2,000–8,000 (24.7 g kg^{-1}) and 53–250 (24.4 g kg^{-1}) μm size classes, so differences between size classes in total C concentration could be accounted for by entirely by changes in LF. Similarly, in midsuccessional historically-tilled, midsuccessional never-tilled, and late successional forest systems there were no differences in HF between size classes; there were, however, differences in LF. These results suggest that LF and HF C pools can be an important component of C differences among aggregate size classes, but that between ecosystems HF C accounts for most of the total C gain. Further, succession reduces differences in total C and HF C between size classes.

There was no accumulation of C in nonaggregated soil fractions smaller than 53 μm (Figure 6; Table 3) demonstrating the importance of aggregate-associated pools in sequestering C. Across ecosystems and aggregate size classes, aggregate associated heavy-fraction C pools showed the greatest potential for rapid sequestration, likely due to the stabilizing properties of clay minerals. Other studies have shown higher proportions of C in LF pools as well as greater potential for accumulating C in intra-aggregate LF pools in successional ecosystems and no-till agriculture (for example, De Gryze and others 2004). The relatively low rates of LF accumulation that we report here may be due to our using sodium polytungstate with a lower density (1.6 vs. 1.8 g cm^{-3}), which would have selected for LF materials in early stages of decomposition that are relatively free from mineral material. These materials are probably more susceptible to microbial colonization and decomposition following aggregate destruction than those LF components that are intimately associated with mineral particles.

The lack of agricultural management effects on inter-aggregate LF is consistent with other studies showing that reductions in agricultural management intensity do not quickly alter this pool and

that most C accumulation occurs in occluded pools (Wander and Yang 2000). The inter-aggregate LF pool is highly sensitive to agricultural disturbance and differences primarily occur between managed and unmanaged ecosystems (Arrouays and Pelissier 1994; Six and others 1999); its accumulation may occur slowly and is driven primarily by plant inputs, root dynamics, soil disturbance, and other activities that influence the decomposition environment (De Gryze and others 2004).

Aggregate-Associated Active, Slow and Passive C

When aggregate structure was left intact there were no differences in active pool C (C_a) among the annual or perennial agricultural treatments or early successional ecosystems (Table 2). There were differences, however, in the concentration of C in the slow (C_s) and resistant pools (C_r) of intact aggregates, demonstrating that C accumulation occurred principally in SOM pools that were chemically or physically protected (Figure 6; Table 3). Within aggregates, low O_2 concentrations and small and discontinuous pore spaces that restrict entry to some soil fauna reduce decomposition rates. Increases in active-pool C (Figure 5) following the breakdown of aggregates suggest that aggregate protection makes an important contribution to C accumulation across aggregate size classes. Within aggregates, there is a pool of C that is not chemically protected but is, to a degree, physically protected and thus part of the slow pool. Following tillage or other management practices that destroy aggregates, this C pool is released from physical protection and rapidly decomposes, as indicated by its transfer from the slow into the active pool.

The potential stimulation of C mineralization resulting from aggregate destruction that we report here is within range of that reported in other studies (Balesdent and others 2000). Elliott (1986), for example, found in a cultivated soil that breaking macroaggregates down to microaggregates increased C mineralization 19% in a cultivated soil and 4% in a previously uncultivated field. In a review of experimental comparisons of crushed and intact aggregates, Balesdent and others (2000) concluded that the protective capacity of aggregates increases with SOM concentration, clay content, and the absence of tillage. Our results support the hypothesis that potential protective capacity is related to the effects of management on aggregate SOM concentration. Because the proportional change in active pool SOM was similar among size classes, those aggregates with the highest C concentrations (generally the macroaggregates) provide the greatest C protection.

Long-term studies have demonstrated that tillage decreases soil C by 30–50% (Davidson and Ackerman 1993; Franzluebbers and Steiner 2002; West and Post 2002). Reductions in soil aggregation typically accompany these declines and several studies have found strong correlations between aggregate structure and organic matter (Chaney and Swift 1984; Shaver and others 2003). Our results suggest that potential C losses with soil disturbance and the role of aggregates therein are a function of aggregate C content, tillage intensity, and also aggregate size distribution.

Ecosystems with a high proportion of soil in macroaggregate size classes and high C concentrations within these aggregates will be particularly susceptible to C loss from soil disturbance. Successional ecosystems should thus be highly susceptible to C losses following cultivation as they have high SOM concentrations within macroaggregates that are highly susceptible to breakdown immediately following cultivation. In a related study we demonstrated that initial cultivation of the midsuccessional never-tilled ecosystem studied here reduced 2,000–8,000 μm aggregates within 60 days to levels indistinguishable from those in conventional agriculture (Grandy and Robertson 2006b). Associated with these changes were significant decreases in the proportion of LF protected within aggregates and CO_2 fluxes that increased an average of 1.0–1.9 g C m^{-2} day^{-1} over 3 years.

Organic matter within macroaggregates can be quickly incorporated into microaggregates (Denef and others 2001, 2004; Six and others 2004), and destroying these microaggregates also substantially increases respiration rates (Balesdent and others 2000). Although we did not trace the fate of individual aggregates, data generated in our lab and other studies suggest that microaggregates within macroaggregates are not immediately crushed by tillage but are released by tillage (Grandy and Robertson 2006a, b). Because of this, we did not pulverize our samples in the lab but tried to break them in a way that was consistent with what happens in the field. If tillage operations or other soil disturbance (for example, mining) were sufficiently intense to destroy microaggregates, additional C would undoubtedly be lost. What remains to be seen, however, is the effect of releasing microaggregates from within macroaggregates on long-term C dynamics. The free microaggregates from the row-crop agricultural systems had considerably less C content than the macroaggregates (Figure 3), suggesting that after

release, intra-macroaggregate microaggregates may rapidly lose C.

The potential for oxidation rates to decrease following aggregate destruction was demonstrated by samples where active-pool C in crushed aggregates was smaller than in intact aggregates. This principally occurred in the 53–250 μm aggregate size class. Other researchers have also reported decreases in respiration rates when soil structure is destroyed (Balesdent and others 2000). Although we added supplemental sand to this size class it is possible that anaerobic sites reduced respiration rates or that crushing facilitated organo-mineral interactions that protected C. Other studies have demonstrated that simulated tillage in some soils can increase aggregate turnover rates and that this is related to reduced CO_2 flux from soils (Plante and McGill 2002). Although the mechanisms have not been widely explored, Plante and McGill (2002) suggest that this phenomenon could be a function of changes in microbial biomass, or subsequent formation of new aggregates that may protect previously unprotected C. Supporting the possibility that changes in microbial community dynamics may be important, Calderón and others (2001) found that soil disturbance could reduce respiration rates and immediately alter microbial community structure. We did not attempt to measure changes in the microbial biomass following aggregate destruction or the formation of new aggregates; however, there was no observable formation of aggregates following aggregate destruction and the environmental processes that contribute to aggregate formation in the field (such as wetting–drying and freeze-thaw cycles) were absent from our microcosms. The possibility that disturbance in some soil types and ecosystems could increase C stabilization needs to be further explored.

Management Implications

Our results demonstrate that physical protection of C by aggregates is an important mechanism controlling SOM turnover in managed ecosystems and that 2,000–8,000 μm aggregates may reduce active pool C turnover—that is, increase carbon sequestration—by as much as 50%. The persistence of this aggregate-associated stored soil C, however, remains a major uncertainty due to its potential loss following increases in management intensity (Paustian and others 2000; Marland and others 2001; Pacala and Socolow 2004). No-till soil management in the US, although increasing, continues to be rotated with tillage because of concerns that no-till limits nitrogen availability, increases weed competition, and decreases yields. This practice increases aggregate turnover rates, oxidizes C, and reduces the potential for agricultural land to sequester C (Grandy and Robertson 2006a; Grandy and others 2006b). In a recent analysis of KBS LTER data, Grandy and others (2006a) demonstrated no negative effects of continuous no-till on yields, inorganic N availability, or N_2O fluxes over 12 years. Further, Six and others (2004) demonstrate that long-term no-till may decrease N_2O fluxes, which may be due to long-term soil structural improvements in no-till. Practices such as no-till and legume cropping and set-aside programs that increase soil C storage within aggregates must thus be maintained continuously and indefinitely to maximize potential ecosystem benefits.

Conclusions

Our results support theories that agricultural soil C losses near the soil surface can be partially reversed by using less intensive cultivation and manipulating plant community dynamics. We found that highest C accumulation rates occur in perennial cropping systems and early successional ecosystems. Across ecosystems, C accumulation relative to conventional agriculture principally occurred in heavy-fraction (density >1.6 g cm^{-3} or particle sizes <53 μm), slow-turnover, and acid-resistant pools of macroaggregates larger than 250 μm. The 2,000–8,000 μm size range demonstrated the greatest increases in active pool C following aggregate destruction. This suggests that macroaggregates have the greatest protective capacity across a range of ecosystems with contrasting histories of plant and soil management, but raises concerns about the persistence of sequestered C. The vulnerability of macroaggregates to destruction following tillage intensification and substantial shifts of C from physically protected slow pools into active pools following aggregate destruction demonstrates the need to protect stabilized SOM from tillage. Greatly increased macroaggregation and the enhanced protective capacity of macroaggregates in perennial crops and successional ecosystems underscore the need to protect these systems, in particular, from even occasional tillage and other increases in management intensity.

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