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¹⁴C Cycling in lignocellulose-amended soils: predicting long-term C fate from short-term indicators

Received: 3 July 2004 / Revised: 16 May 2005 / Accepted: 16 May 2005 / Published online: 28 June 2005
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Abstract We compared lignocellulose (the second most abundant component of plant material) degradation over 8 months in contrasting soils from each of five sites across the United States with the aim of assessing which soils are likely to store more C. The soils were collected from a tallgrass prairie restoration (farmland, and plots restored in 1993 and 1979), the semiarid shrub-steppe (cool, moist upper slope and warm, dry lower slope soils), long-term farmland (no-till and conventional-till), and from two forest soils (loblolly pine and Douglas fir; fertilized and non-fertilized). Soils that rapidly metabolized freshly added C exploited endogenous and newly transformed C to a lesser degree over the course of the incubation (lower slope shrub-steppe, nonfertilized Douglas fir, and tallgrass prairie farmed and 1993 restorations). We also pooled the data to find a strong relationship between sand content and lignocellulose C remaining in the soil after 8 months ($R=0.68$) and also between short-term storage of lignocellulose C (at 7 days) and lignocellulose C remaining after 8 months ($R=0.94$). To predict C storage, models of C and soil properties must be modified to reflect the structure and function of microbial communities. Communities in richer soils may be more competent to use native C following fresh C additions when compared with communities in poorer soils.

Keywords C sequestration · Lignocellulose degradation · Soil properties · Predictors of C storage

Introduction

Lignocellulose is a major structural component of vascular plants and the second most abundant biopolymer on the planet, a complex substrate composed of aromatic lignitic and cellulosic components. Even though cellulose can be protected from decomposition by clays and lignins, cellulosic components tend to be decomposed much more readily than the lignitic components, making the lignin the most biologically recalcitrant part of the substrate (Crawford et al. 1977). The slower decomposition rate of lignin and possibly physically protected cellulose may be associated with a more efficient storage of C, as soil microorganisms may respire less of the substrate as CO₂ (Smith 1994). To investigate C storage in complex C systems, it is advantageous to use ¹⁴C lignin to follow decomposition products into various C fractions to estimate the ultimate fate of recalcitrant material.

Lignocellulose degradation is primarily, but not always, mediated by fungi (Cox et al. 2001). Fungal inoculation can accelerate this process, but may be unsuccessful when introduced to natural soils (Lang et al. 1998). It is possible that indigenous species of fungi may be best adapted to partition lignin efficiently into more recalcitrant fractions of the organic matter pool than introduced species; therefore, the study and stimulation of native organisms may lead to best practices to enhance C sequestration. Fungi that were associated with the lignitic substrate were able to use the solubilized organic C and released less of it to the surrounding bulk soil for other organisms (fungi and bacteria) to use (Lang et al. 2000). This provides further incentive to identify soils that are actively storing C and to study the processes by which this occurs.

Land management practices will affect C dynamics and storage; practices that are best for traditional agricultural may not be best for C sequestration (Paul et al. 2004). Much effort has been invested in identifying practices that favor C sequestration. Agricultural soils managed with no, or minimum tillage, are more likely to sequester C than conventionally tilled soils (Saber and Mrabet 2002; Six et al. 1998; Yang and Kay 2001). This is also true for soils

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in which tillage ceased and the land had reverted back to native systems (Jastrow 1996). There is a strong association of N with C cycling. However, N additions do not always increase C storage (Paul et al. 2004), because it has been found to stimulate mineralization of labile C pools, such as those found in the litter layers of some Swiss forest soils, thus decreasing the total C contained in the soil profile (Jandl et al. 2003).

In addition to identifying soils that actively store C, identifying simple, or short-term, measurements or predictors that may provide information about the long-term disposition of C in a soil is a paramount challenge. The range of characteristics that can be used to organize soils is vast, and the suite of predictive traits almost endless. However, some features are more promising than others. For example, much effort has been spent on using soil textures as indicators of various biochemical rates and processes (Côté et al. 2000; Hook and Burke 2000). Other characteristics that have been found to be associated with C dynamics include microbial activity (Bailey et al. 2002), particulate organic C (Franzluebbers and Arshad 1997), and mineralizable N and C contents (Chantigny et al. 2002). In other studies, substrate preference may govern the differential decomposition of newly added materials compared with endogenous C sources (Girisha et al. 2003). Most of these studies have focused on a single soil or a single contrasting pair of soils, making broad inferences from these relationships difficult.

The purpose of this research was twofold: (1) to search for differences in lignocellulose metabolism in forest, grassland, prairie and agricultural soils, differing in management or state, and (2) to identify short-term indicators of long-term C distribution. Specifically, we hypothesized that N fertilized soils, restored prairie, and grassland soils and soils under no-tillage mediated would be most likely to retain more freshly added C.

Materials and methods

Soils

Soils were collected from the five locations across the United States in the spring of 2001, using a uniform depth increment of 0–5 cm. The five different ecosystems are:

Semiarid shrub-steppe. Two locations were sampled: an upper (840 m ASL) and a lower (313 m ASL) position on Rattlesnake Mountain at the Arid Lands Ecology Reserve (Richland, WA). These locations differ in that the lower site has a hotter, drier climate than the upper site, with a mean annual temperature ~6°C (5°C) warmer and ~90 mm (50 mm) less precipitation annually than the upper site (Link et al. 2003; Smith et al. 2002). The soils at this site are Xerollic Camborthids.

Tall grass prairie. Three locations within the tallgrass prairie restoration chronosequence at the Fermi National Laboratory (Batavia, IL) were sampled: plots

reverted to tallgrass prairie in 1979 and 1993, and farmland that has been in long-term rotation with row crops (J. Jastrow, personal communication). All soils were Typic Endoaquolls.

Douglas fir forest. Two locations of a previously established research program (1980) in a Douglas fir forest near Buckley, WA, were sampled: control (no fertilizer) and N-fertilized plots (200 kg N ha⁻¹, previously applied in 1997). These soils are of volcanic origin and classified as Typic Hapludands.

Loblolly pine plantation. Similar to the Douglas fir forest, two established research plots (1990) were sampled in a loblolly pine plantation near Atmore, AL: control (no fertilizer) and N-fertilized plots (diammonium phosphate in 1990). These soils are classed as Rhodic Kandudults.

Agricultural land. Two farmed fields near Palouse, WA, that have been managed with contrasting tillage practices were sampled: conventional tillage (CT) and 25 years of no tillage (NT). The soils are in fields adjacent to each other on the same soil series (Palouse silt loam). The typical crop rotation is winter wheat and dry peas. Conventional tillage consisted of plowing (moldboard) and harrowing, either in the spring or the fall, but at least once a year. The no-till field is planted with a one-pass drill with no cultivation. The soils are classified as Pachic Haploxerolls.

Selected characteristics of the 11 soils are presented in Table 1. All soils were sieved (2 mm), with removal of visible plant material, and subsequently stored at 4°C until conditioning or analysis. Total C and N were determined by combustion (Leco Corp., St. Joseph, MI), pH by analysis in a 1:2 (w:w) soil/water slurry, and particle size by the hydrometer method (Bouyoucos 1962). The F:B ratio was determined using the selective inhibition method in previously published research (Bailey et al. 2002).

Incubation and respiration

¹⁴C-labeled lignocellulose with a specific activity of 478 dpm mg⁻¹ lignocellulose (1,541 dpm mg⁻¹ C; D. Crawford, University of Moscow, Idaho, USA) was used in all soil incubations. This material was ground to >53 μm, making it part of the particulate organic matter (POM) C fraction. Soils (10 g, oven-dry equivalent) were weighed into 50-ml tubes and conditioned at 21°C at a water content of -0.03 MPa for 1 week before lignocellulose was added (Bailey et al. 2002). The incubation with lignin was maintained at the same temperature (21°C) and moisture content (-0.03 MPa). ¹⁴C-labeled lignocellulose was added to soils from each site such that the amount of C added as lignocellulose approximated the amount of C that, when added as glucose, stimulated the maximum respiratory response as reported by Bailey et al. (2002). Therefore, the soils from the semiarid shrub-steppe received 3 mg lignocellulose g⁻¹ soil, the soils from the tallgrass prairie received 4 mg

Table 1 Selected characteristics of the studied soils

Site	Soil	Total C (mg g ⁻¹ soil)	Total N (mg g ⁻¹ soil)	POM-C (mg g ⁻¹ soil)	Texture			pH	F:B ^a
					Sand %	Clay %	Silt %		
Tallgrass prairie	Ag	36.0	3.4	ND	21	35	44	5.6	0.85
	R93	50.2	3.9	7.3	39	29	32	6.6	10.7 ^b
	R79	49.9	4.6	6.7	17	19	64	7.3	13.5
Douglas fir forest	FC	88.8	5.3	19.3	71	4	24	4.9	0.97
	FN	130.4	6.8	45.2	77	6	16	5.4	2.45
Shrub-steppe	DL	8.5	0.8	1.9	41	17	42	6.9	1.64
	DU	16.1	1.6	5.5	39	11	50	6.8	1.97
Palouse	AT	24.4	2.0	5.2	23	22	54	6.2	2.61
	AN	46.6	3.7	12.5	37	12	50	6.0	1.26
Loblolly pine	LC	18.3	0.6	6.0	63	17	20	5.1	1.09
	LN	17.3	0.5	6.6	67	17	16	4.8	1.06

POM-C Particulate organic matter—carbon, ND no data

^aData from Bailey et al. (2002)

^bUnpublished data

lignocellulose g⁻¹ soil, the soils from the Douglas fir forest and the farm soils from Washington received 8 mg lignocellulose g⁻¹ soil, and the soils from the loblolly pine plantation received 2 mg lignocellulose g⁻¹ soil. Incubation units were replicated to allow triplicate destructive analysis of particulate organic matter C (POM-C) of each soil at selected times (7 days, 2 months, 8 months) during the incubation.

Prior to the tubes being sealed, a vial containing 1 ml of 1 M KOH was added to each tube to trap CO₂. The traps were replaced at days 1, 3, and 7, and thereafter approximately weekly. A 0.25-ml aliquot from each collected trap was added to 10 ml of Optifluor scintillation cocktail (Packard Scientific, USA) and counted on a Packard Scintillation System for ¹⁴C activity. The remaining 0.75 ml was titrated according to the method described by Zibilske (1994) to quantify total CO₂ evolved. The traps were only counted for the first 193 days of the incubation. After that, the activities evolved did not exceed background levels for counting. Titrations were conducted on traps collected for the duration of the incubation (230 days).

Particulate organic matter

POM-C and POM-¹⁴C were determined on 3-g subsamples from each replicate for each treatment. The soils were weighed into small bottles and 9 ml of sodium hexametaphosphate (0.5%) were added. The bottles were sealed and laid flat on a reciprocating shaker and agitated for 24 h. The POM was collected by filtering the soil suspension through a 53-μm screen positioned above a large funnel. A spray bottle of distilled water was used to rinse all of the non-POM (NPOM) material through the screen. The NPOM fraction was collected in a preweighed collection beaker under the funnel. As soon as the rinse water ran clear into the NPOM collection beaker, the beaker was set aside. The POM materials collected on the surface of the sieve were then quantitatively rinsed with distilled water into another preweighed beaker.

The beakers containing POM and NPOM were oven-dried in a forced-air oven set to 70°C for several days until a constant weight was reached, to calculate the size of the POM and NPOM fractions. The dried fractions were ground and 0.1-g subsamples were combusted at 900°C in a stream of oxygen in an RJ Harvey Biological Oxidizer (New Jersey, USA), and the resulting ¹⁴CO₂ was trapped in the RJ Harvey Scintillation cocktail. The trapped ¹⁴CO₂ was counted to determine the quantity of ¹⁴C in each fraction.

Soil microbial biomass

Soil microbial biomass was measured using the chloroform fumigation-extraction procedure (Vance et al. 1987) as described by Voroney et al. (1993). Samples (3 g) of each soil were divided into nonfumigated and fumigated samples, and the nonfumigated subsamples were immediately extracted with 0.5 M K₂SO₄. The fumigated samples were incubated overnight in an atmosphere of chloroform which was then removed through several exchanges of air in the incubation apparatus. After the complete removal of chloroform, these samples were extracted with 0.5 M K₂SO₄. The increased amount of ¹⁴C released by fumigation (e.g., fumigated C–nonfumigated C) is attributed to the lysis of soil microbial biomass and reported here as the increased flush of ¹⁴C.

Statistical analyses

All statistics were conducted in Systat 10 (SPSS, Inc., Chicago, IL). Means separation was done for all POM and biomass data using a one-way ANOVA with Bonferroni pairwise comparisons to detect significant differences. Comparisons were conducted within sites, across all three sampling times. Carbon dioxide evolution curves were compared within sites using the General Linear Models procedure with repeated measures analyses.

Results and discussion

Total ^{14}C respired

The specific activity of the CO_2 evolved is a way to assess the degree to which the microbial community in a soil metabolizes the newly added ^{14}C relative to the endogenous soil organic ^{12}C . High specific activities reflect a preferential exploitation of the new, labeled C, while lower specific activities indicate an increased exploitation of the endogenous C. In this study, these specific activities corresponded to the mineralization of 22–38% of the added ^{14}C from all soils. The prairie restoration chronosequence soils mineralized 33% (Ag), 36% (R93), and 34% (R79) of the applied ^{14}C during the experiment (Fig. 1). The forest soils mineralized 31% (FC), 26% (FN), 28% (LC), and 22% (LN) of the added ^{14}C (Fig. 1). Finally, the shrub-steppe and agricultural soils respired 32% (DL), 37% (DU), 32% (AT), and 38% (AN) (Fig. 1). These numbers are in good agreement with the proportion of a model lignocellulose compound (1,4-DHP) that was degraded by single strains of white rot fungi in soil after 56 days: *Pseudomonas sordida* respired 44%, *Trametes versicolor* (23%), and pure cultures of *Trametes hirsuta* (30%) of the added substrate (Tuomela et al. 2002).

We had hypothesized that one of the soils collected from each location would be more likely to enhance C storage than the other, based on its long-term management history. Specifically, we speculated that the older restored prairie (R79), the N-fertilized forest soils (FN and LN), the shrub-steppe upper slope position (DU), and the no-till agricultural soil (AN) would be likely to retain more added C than the other same-site soil over the duration of the incubation. What we observed was that soils that were not predicted to favor C storage (DL, FC, Ag and R93; Fig. 1) evolved CO_2 with a higher specific activity than soils speculated to retain added C. This indicates that higher C retention in the soils likely to retain C (R79, DU, AN, FN, LN) is attributable to the greater metabolic efficiency in incorporating added C into secondary metabolites and SOM.

The addition of substrates (plant material or C compounds) to soil may cause an increase or decrease in C respired from native SOM, the so-called priming effect (Jenkinson 1966; Sauerbeck 1966). Compounds such as glucose can cause a negative priming effect (Bingeman et al. 1953), but most plant material additions cause a positive priming effect (Sorensen 1963) likely due to microbial stimulation and enzyme production. In this study, the soils with the higher retention of added C had lower amounts of primed ^{12}C from native SOM. Thus the results discussed above, that the soils predicted to store C had lower specific activity of respired C, was not attributable to dilution by primed SOM C, but was due to greater use efficiency.

The total CO_2 respired showed interesting differences between ecosystems and treatments, which delineates the complex interactions between microbial biomass and SOM. For the grassland systems (Fig. 1a–c), the soils hypothesized to retain more added C evolved the same or greater

amounts of CO_2 than the soils thought to be less retentive. In the case of the prairie soils (Ag, R93, R79), the greater CO_2 respired by the R79 soil was not simply attributable to higher SOM-C (Table 1), but was possibly confounded by the increasing fungal to bacterial ratios (F:B) of 0.85, 10.7, and 13.5 for Ag, R93, and R79, respectively, as reported elsewhere for these soils (Bailey et al. 2002). However, for the desert soils (Fig. 1b) with similar microbial biomass concentrations, the twofold difference in total soil C probably did account for the difference in total CO_2 evolved. For the tilled (AT) and no-tilled (AN) soils, there was less ^{14}C decomposition in the no-till soil but higher priming of native SOM, thus showing equal amounts of total CO_2 evolved. This similarity of CO_2 production occurs in spite of the fact that the AN soil has twice the total soil C as the AT soil; again, as with the prairie soil, there is a large difference in the F:B ratios of these two soils.

The two forest soils showed opposite patterns of total CO_2 evolved in the control versus the N fertilized soils (Fig. 1d, e). The Douglas fir fertilized soil (FN) had significantly greater total CO_2 production than the control soil (FC) even though it decomposed less added ^{14}C lignocellulose. The explanation is complicated by the fact that the FN soil has an F:B ratio of 2.45 compared to the FC F:B ratio of 0.97, but there is also a large disparity in total soil C (Table 1). In contrast, the N-fertilized loblolly pine plantation soil (LN) respired less C than the corresponding non-fertilized soil (LC) which can mostly be attributed to the priming of SOM C, since both soils have a similar F:B ratio of 1.1.

The soils identified as having a greater potential for C sequestration had lower CO_2 -specific activity, but generally higher total CO_2 than the comparison soils. The greater-potential soils also had less primed $^{12}\text{CO}_2$ from the addition of lignocellulose. These measurements point to the conclusion that community structure, such as the F:B ratio, in the soil is important when comparing treatments, management, and ecosystems, because the interaction of these parameters can make simple comparisons invalid.

Particulate organic matter-C

All of the lignocellulose used in this study was ground to $>53\ \mu\text{m}$ and initially classified as POM-C. The ^{14}C enrichment of the POM fraction decreases through the duration of this experiment (Fig. 2) and accounted for 80–90% loss after 7 days. This is a reasonable trajectory, as no new ^{14}C or POM was added through the experiment. It does, however, indicate that there was little to no recycling of freshly added C or its metabolites into the POM fraction. The rapid loss can be expected from material that is ground to less than $100\ \mu\text{m}$. As suggested by the C dynamics in Fig. 1, the soils speculated to store more C rapidly metabolized C out of the POM fraction with little change over time. Across all soils, 10–25% of the ^{14}C loss from the POM fraction was evolved as $^{14}\text{CO}_2$. The most dynamic C cycling was seen in the AT and NT soils, where there was an exponential decline in the ^{14}C POM in the AT soil and faster

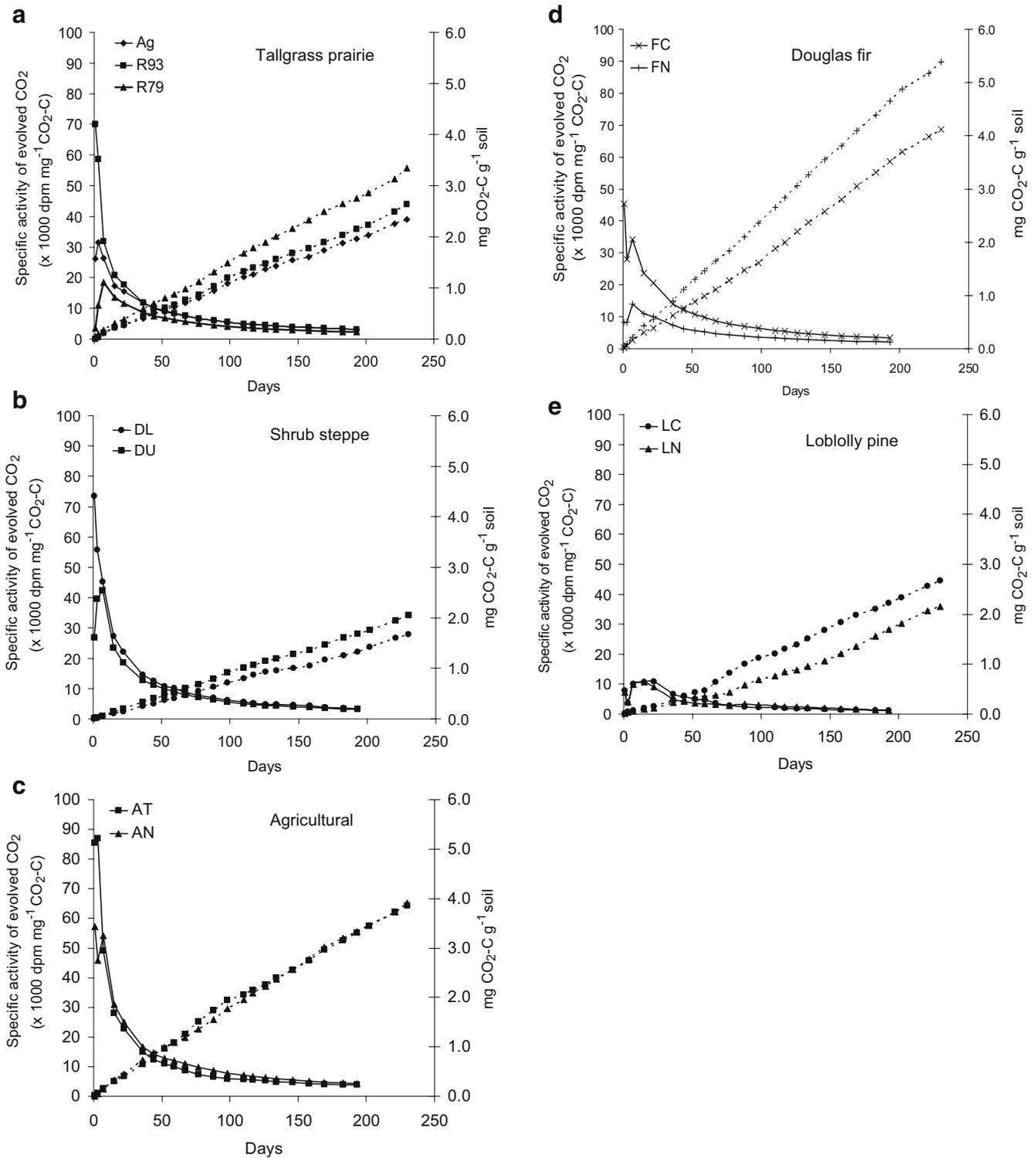


Fig. 1 Specific activity (—) of CO_2 evolved during incubation. Total CO_2 evolved during incubation (- - -). Soils from each site are presented together. Within each site, specific activity curves differ significantly from one another ($P < 0.05$), except for the shrub-steppe

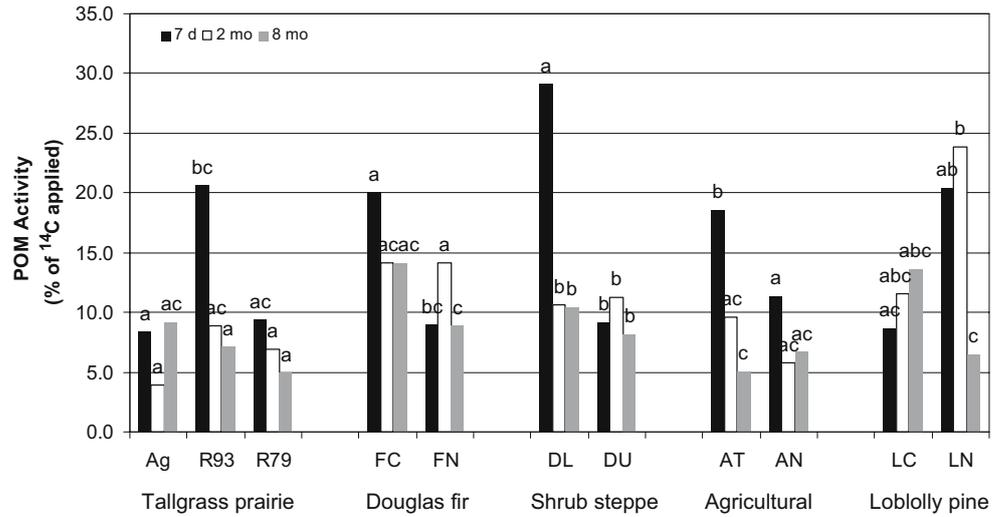
soils (*DL*, *DU*), for which no significant difference was detected. Within each site, CO_2 evolution curves differ significantly from one another ($P < 0.05$), except for the agricultural soils (*AN*, *AT*) for which no significant difference was detected

initial decomposition in the NT soil. This is consistent with Fig. 1 and with the explanation of greater priming in the NT soil. The size of the total POM-C fractions did not change during the course of the experiment (data not shown).

Soil microbial biomass

At the three time points analyzed, ^{14}C enrichment of the biomass never exceeded 3% of the amount of ^{14}C applied

Fig. 2 Enrichment of the POM fraction with ¹⁴C at 7 days, 2 months, and 8 months during incubation. Bars topped by the same letter are not significantly different (Bonferroni, *P*<0.05). Comparisons are only valid within sites



to a soil (Fig. 3), and confirmed what has been observed in other studies concerning the degradation of complex ¹⁴C substrates (Bailey and McGill 2002). What is intriguing is the stability of the newly added ¹⁴C in the microbial biomass of some of the soils, particularly R79, DU, AT, AN, and LC; the enrichment of the biomass does not change significantly over the times measured (Fig. 3). The R79, DU, and LC soils all respired more total C than their corresponding site-pair soil, and AT and AN respired the same amount of C. The low and consistent amount of ¹⁴C in the microbial biomass coupled with the evidence of greater efficiency suggest that soils with more potential for C storage are cycling the lignocellulose substrate into more recalcitrant forms of SOM.

Predictors of C storage

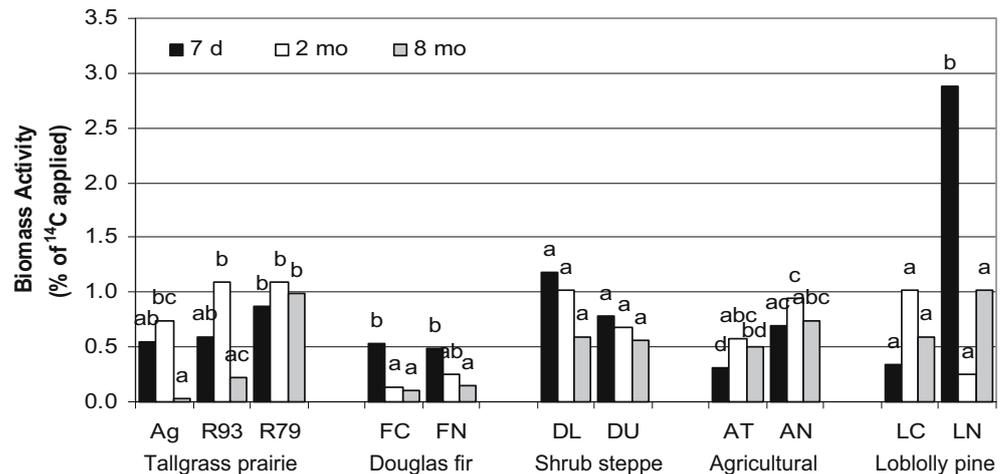
We sought to identify predictors of the long-term fate of this freshly added C from two perspectives. The first was to take advantage of this diverse suite of soils and associate the amount of C remaining in the soils after 8 months with an easily measured soil characteristic. The second per-

spective was to examine the short-term C dynamics for insights into the long-term C fate.

We attempted to relate a number of characteristics to the amount of C remaining in the soils after 8 months of incubation. Soil texture was strongly associated with C remaining in the soils at all three dates (only day 7 and month 8 are shown; Fig. 4). The ¹⁴C remaining in the soil at 8 months showed a strong positive association with the amount of sand in the soil (*P*=0.006), whereas no significant relationship was detected between clay content and soil ¹⁴C. It is interesting that the clay component, which is widely regarded as being the most active soil texture component with respect to stabilization and protection of soil C (Ladd et al. 1996), had no significant relationship with C storage at any time that we sampled—which is contrary to much of the literature relating soil texture and C dynamics (Amato and Ladd 1992; Franzluebbers and Arshad 1997).

The main body of literature would indicate that the residual C added should correlate with clay content. However, Gregorich et al. (1991) (glucose), Sorensen et al. (1996) (clover), and Saggari et al. (1996) (ryegrass) found no relationship between residual C and clay content. The conclusion of these studies was that clay had a far more

Fig. 3 Enrichment of the soil microbial biomass with ¹⁴C at 7 days, 2 months, and 8 months during the incubation. Bars topped by the same letter are not significantly different (Bonferroni, *P*<0.05). Comparisons are only valid within sites



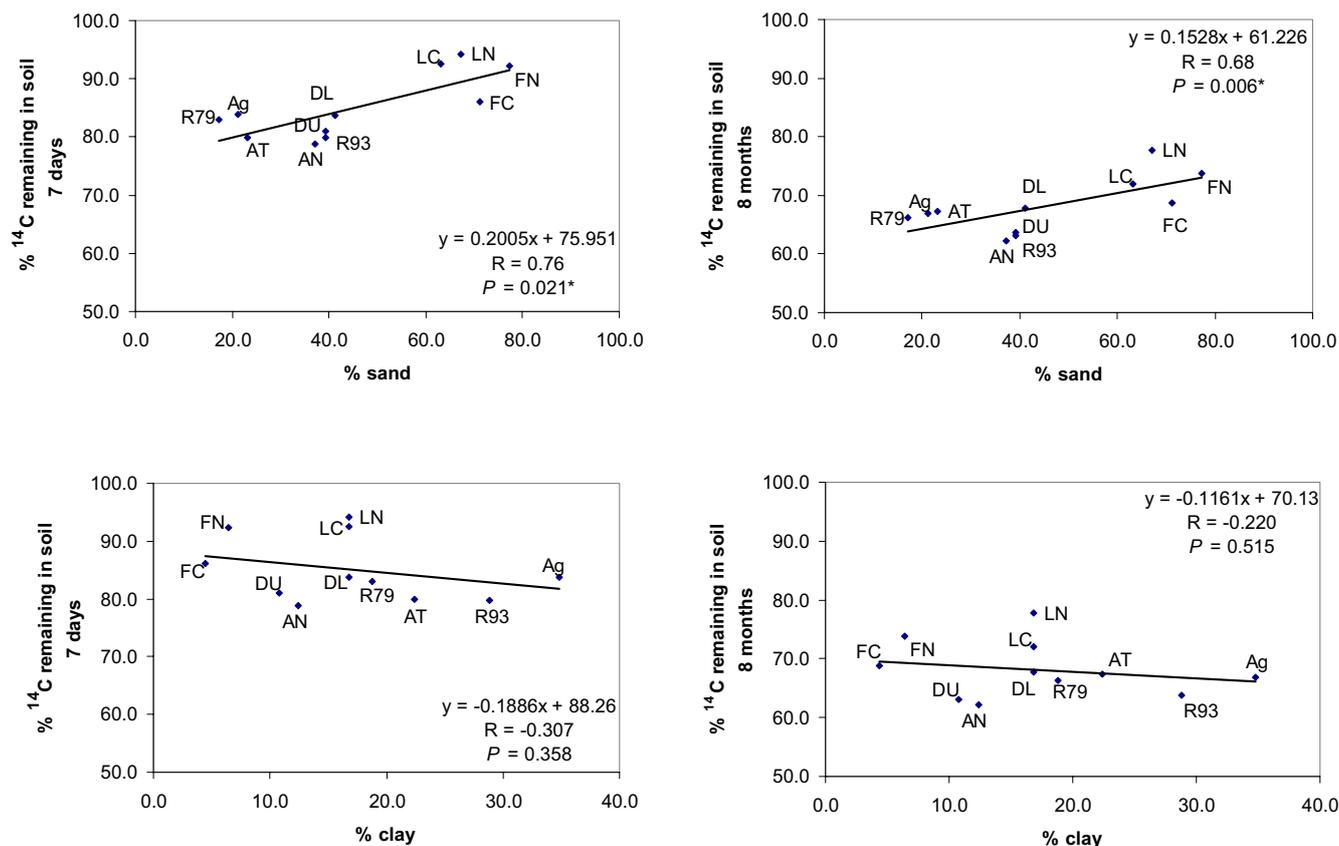


Fig. 4 Prediction of C storage at 7 days and 8 months using soil clay and sand contents

stabilizing effect on microbial biomass C rather than non-biomass residual C. In addition, Ladd et al. (1992) found that the decay of microbial biomass ^{14}C was 2–3 times faster in a sandy loam soil compared to a clay soil, but that the nonbiomass C decayed only 1–1.2 times faster in the sandy loam soil; similar results are discussed in Ladd et al. (1996). A difficulty in these studies is the use of soluble to very soluble substrates such as glucose and plant material that contains water-soluble compounds. In a comparable study, Stott et al. (1983) found similar residual lignin residues in soils of 9 and 20% clay contents incubated for 6 to 12 months.

In this study the incubation conditions of all soils were the same and we suggest that the substrate and its proximity to decomposer populations is the reason for more residual ^{14}C in the sandy soils. The rapid mineralization of lignin in the finer textured soils was followed by diffusion of decomposition products throughout the soil matrix enhancing secondary mineralization. This process was retarded in the sandier soils due to microbial population distribution and diffusional constraints. The four soils from the two forest sites (LC, LN, FC, FN) had the highest sand contents, and these four soils retained the greatest portion of the ^{14}C applied in the soil matrix after 8 months of incubation. For the ecosystems included in this study, the soil clay contents ranged from 4 to 35%.

We also found a strong ($R=0.94$), significant ($P<0.001$) positive relationship between the short-term retention of

C (7 days) and the long-term storage of C at 8 months (Fig. 5). This is encouraging, because it indicates that short-term metabolic rates are predictive of long-term rates for complex substrates such as lignocellulose. This relationship would not, perhaps, be true for simpler substrates such as glucose, for which metabolism is rapid, and once complete, the ensuing ^{14}C dynamics are predicated on the more complex forms of assimilated ^{14}C , causing later dynamics to be much slower.

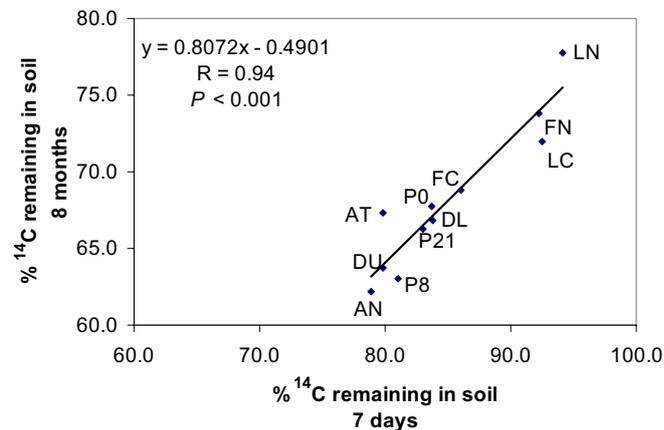


Fig. 5 Prediction of longer-term storage of new C (8 months) using short-term (7 days) storage of newly added C

Conclusions

All of the soil-site pairs we studied showed a marked difference in either, or both, the total amount of C mineralized over 8 months, or in the specific activity of the evolved CO₂ in the first 2 months. These differences clearly indicate that the soils of these pairs are differentially using either endogenous soil C or the freshly added C. The soils that rapidly metabolized freshly added C exploited endogenous and newly transformed C to a lesser degree over the course of the incubation. These also tended to be the soils that had been hypothesized to not favor C storage, and in fact, had lower amounts of soil C compared to their contrasting paired soil from the same site. The microbial communities of these soils may be less able to metabolize the recalcitrant endogenous C remaining in the soil, whereas those communities in the richer soils at the same site may be more diverse or competent to use the native C following stimulation of the biomass by the freshly added C.

We identified two possible predictors of longer-term C storage. Soil sand content was correlated with the amount of freshly added C remaining in the soils after 8 months. The short-term mineralization of lignocellulose C (measured as C remaining in the soil) was also found to be predictive of the longer-term storage of C, after 8 months. Both of these predictors may be valuable tools in C management systems. Predicting 8-month C storage with the 7-day metric was a strong, significant function; however, the association of sand with C storage is a rapid assessment that can be made based on standard soil characterization analyses.

Acknowledgements The Consortium for Research on Enhanced Carbon Sequestration in Terrestrial Ecosystems is supported by the US Department of Energy (DOE), Office of Science, as part of the Terrestrial Carbon Sequestration program in the Office of Biological and Environmental Research. Additionally, we were also supported by the United States Department of Agriculture, Consortium for Agricultural Soils Mitigation of Greenhouse Gases. Pacific Northwest National Laboratory is operated for the DOE by Battelle Memorial Institute under contract number DE-AC05-76RL01830. We thank D. Bikfasy, S. Fansler, and H. Kostandarithes for their assistance on this project.

References

- Amato M, Ladd JN (1992) Decomposition of ¹⁴C-labeled glucose and legume material in soils: properties influencing the accumulation of organic residue C and microbial biomass C. *Soil Biol Biochem* 24:455–464
- Bailey VL, McGill WB (2002) Fate of ¹⁴C-labeled pyrene in a creosote- and octadecane in an oil-contaminated soil. *Soil Biol Biochem* 34:423–433
- Bailey VL, Smith JL, Bolton H Jr (2002) Fungal-to-bacterial ratios in soils investigated for enhanced carbon sequestration. *Soil Biol Biochem* 34:1385–1389
- Bingeman CW, Varner JE, Martin WP (1953) The effect of the addition of organic materials on the decomposition of an organic soil. *Soil Sci Soc Am Proc* 17:34–38
- Bouyoucos G (1962) Hydrometer method improved for making particle size analysis of soils. *Agron J* 54:464–465
- Chantigny MH, Angers DA, Rochette P (2002) Fate of carbon and nitrogen from animal manure and crop residues in wet and cold soils. *Soil Biol Biochem* 34:509–517
- Côté L, Brown S, Paré D, Fyles J, Bauhus J (2000) Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. *Soil Biol Biochem* 32:1079–1090
- Cox P, Wilkinson SP, Anderson JM (2001) Effects of fungal inocula on the decomposition of lignin and structural polysaccharides in *Pinus sylvestris* litter. *Biol Fertil Soils* 33:246–251
- Crawford DL, Crawford RL, Pometto AL III (1977) Preparation of specifically labeled ¹⁴C-(lignin)- and ¹⁴C-(cellulose)-lignocelluloses and their decomposition by the microflora of soil. *Appl Environ Microbiol* 33:1247–1251
- Franzluebbers AJ, Arshad MA (1997) Particulate organic carbon content and potential mineralization as affected by tillage and texture. *Soil Sci Soc Am J* 61:1382–1386
- Girisha GK, Condron LM, Clinton PW, Davis MR (2003) Decomposition and nutrient dynamics of green and freshly fallen radiata pine (*Pinus radiata*) needles. *For Ecol Manag* 179:169–181
- Gregorich EG, Voroney RP, Kachanoski RG (1991) Turnover of carbon through the microbial biomass in soils with different texture. *Soil Biol Biochem* 23:799–805
- Hook PB, Burke IC (2000) Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate. *Ecology* 81:2686–2703
- Jandl R, Kopeszki H, Bruckner A, Hager H (2003) Forest soil chemistry and mesofauna 20 years after an amelioration fertilization. *Restor Ecol* 11:239–246
- Jastrow JD (1996) Soil aggregate formation and the accrual of particulate and mineral-associated organic matter. *Soil Biol Biochem* 28:665–676
- Jenkinson DS (1966) The priming action. In: The use of isotopes in soil organic matter studies. FAO/IAEA technical meeting. Pergamon Press, Oxford, pp 199–208
- Ladd JN, Monrozier LJ, Amato M (1992) Carbon turnover and nitrogen transformations in an Alfisol and Vertisol amended with [U-¹⁴C] glucose and [¹⁵N] ammonium sulfate. *Soil Biol Biochem* 24:359–371
- Ladd JN, Foster RC, Nannipieri P, Oades JM (1996) Soil structure and biological activity. In: Stotzky G, Bollag JM (eds) Soil biochemistry, vol. 9. Marcel Dekker, New York, pp 23–78
- Lang E, Nerud F, Zadrazil F (1998) Production of ligninolytic enzymes by *Pleurotus* sp. and *Dichomitus squalens* in soil and lignocellulose substrate as influenced by soil microorganisms. *FEMS Microbiol Lett* 167:239–244
- Lang E, Kleeberg I, Zadrazil F (2000) Extractable organic carbon and counts of bacteria near the lignocellulose–soil interface during the interaction of soil microbiota and white rot fungi. *Bioresour Technol* 75:57–65
- Link SO, Smith JL, Halvorson JJ, Bolton H (2003) A reciprocal transplant experiment within a climatic gradient in a semiarid shrub-steppe ecosystem: effects on bunchgrass growth and reproduction, soil carbon, and soil nitrogen. *Glob Chang Biol* 9:1097–1105
- Paul EA, Collins HP, Paustian K, Elliott ET, Frey S, Juma N, Janzen H, Campbell CA, Zentner RP, Lafond GP, Moulin AP (2004) Management effects on the dynamics and storage rates of organic matter in long-term crop rotations. *Can J Soil Sci* 84:49–61
- Saber N, Mrabet R (2002) Impact of no tillage and crop sequence on selected soil quality attributes of a vertic calcixeroll soil in Morocco. *Agronomie* 22:451–459
- Saggar S, Parshotam A, Sparling GP, Feltham CW, Hart PBS (1996) ¹⁴C-labelled ryegrass turnover and residence times in soils varying in clay content and mineralogy. *Soil Biol Biochem* 28:1677–1686
- Sauerbeck D (1966) A critical evaluation of incubation experiments on the priming effect of green manure. In: The use of isotopes in soil organic matter studies. FAO/IAEA technical meeting. Pergamon Press, Oxford, pp 209–222

- Six J, Elliott ET, Paustian K, Doran JW (1998) Aggregation and soil organic matter accumulation in cultivated and native grassland soils. *Soil Sci Soc Am J* 62:1367–1377
- Smith JL (1994) Cycling of nitrogen through microbial activity. In: Hatfield JL, Stewart BA (eds) *Soil biology: effects on soil quality*. CRC Press, Boca Raton, FL, pp 91–120
- Smith JL, Halvorson JJ, Bolton H (2002) Soil properties and microbial activity across a 500 m elevation gradient in a semi-arid environment. *Soil Biol Biochem* 34:1749–1757
- Sorensen H (1963) Studies on the decomposition of C14-labeled barley straw in soil. *Soil Sci* 95:45–51
- Sorensen P, Ladd JN, Amato M (1996) Microbial assimilation of 14C of ground and unground plant materials decomposing in loamy sand and a clay soil. *Soil Biol Biochem* 28:1425–1434
- Stott DE, Kassim G, Jarrell WM, Martin JP, Haider K (1983) Stabilization and incorporation into biomass of specific plant carbons during biodegradation in soil. *Plant Soil* 70:15–26
- Tuomela M, Oivanen P, Hatakka A (2002) Degradation of synthetic C-14-lignin by various white-rot fungi in soil. *Soil Biol Biochem* 34:1613–1620
- Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass C. *Soil Biol Biochem* 19:703–707
- Voroney RP, Winter JP, Beyaert RP (1993) Soil microbial biomass C and N. In: Carter MR (ed) *Soil sampling and methods of analysis*. Lewis Publishers, Boca Raton, pp 277–286
- Yang XM, Kay BD (2001) Impacts of tillage practices on total, loose- and occluded-particulate, and humified organic carbon fractions in soils within a field in southern Ontario. *Can J Soil Sci* 81:149–156
- Zibilske LM (1994) Carbon mineralization. In: Weaver RW, Angle JS, Bottomley PS (eds) *Methods of soil analysis. Part 2. Microbiological and biochemical properties*. Soil Science Society of America Book Series 5, Madison, WI, USA