Selective Transport and Stabilization of Microbial C in California Forest Soils

*William R. Horwath and Heather M. Throckmorton

Project Objectives

O1: To determine the importance of microbial cell type and specific biochemistry in governing its stability in soil.

O2: To determine relative protection of diverse microbial group isolates in soil via interaction with, and protection by, the mineral matrix (physical and chemical associations).

O3: To examine the effect of parent material and climate in controlling specific organo-mineral interactions by depth.

Approach and Procedures

The overarching goal of this study is to elucidate factors and mechanisms controlling the concentration and stability of C in California forest soils. Variables of interest include: microbial community inputs and biochemistry; organo-mineral interactions; climate and soil development; parent material and mineralogy; and depth.

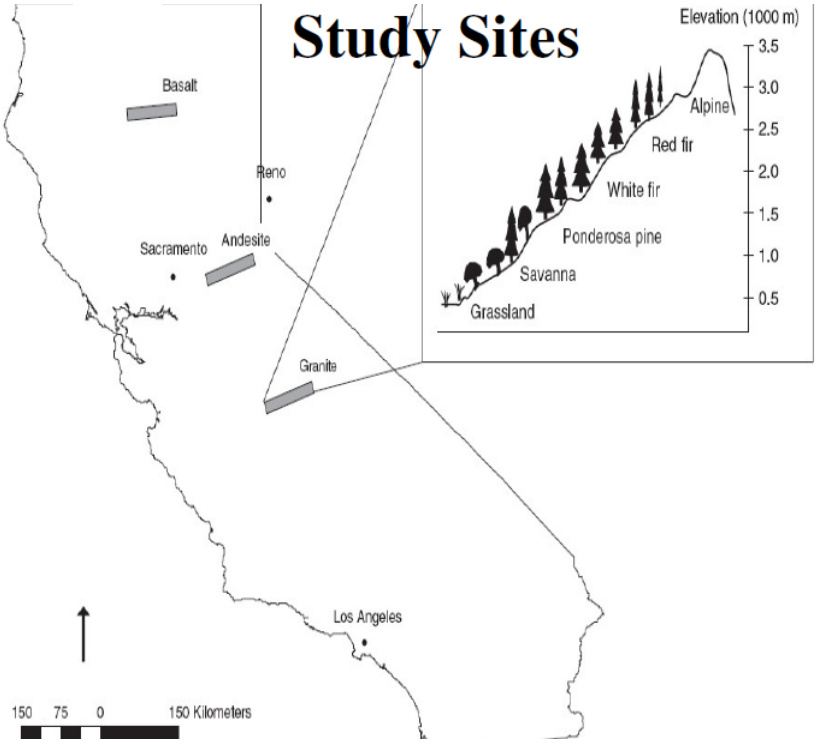
In order to test O1, microorganisms were cultured in the laboratory with ^{13}C media to obtain ^{13}C labeled microbial biomass (~99 atom %). 3-4 species for each of the following microbial groups were composited for final isolate mixtures: fungi, actinomycetes, Gm (+) bacteria, and Gm (-) bacteria (isolated from California and Puerto Rican soils to obtain temperate and tropical isolates for each group). Microbial isolates were analyzed for biochemical composition with pyrolysis-gas chromatography mass spectrometry (Py-GC-MS). Selected ^{13}C microbial isolates were lypholyzed and autoclaved, and residues were added to soils in Blodgett Experimental forest in Georgetown, CA. Treated soil replicates were collected at 5 time points and analyzed over a 3 year period. ^{13}C recoveries for microbial isolates in soils were determined. Compound-specific recovery for microbial residues in whole soils is being determined with Py-GC-MS-isotope ratio mass spectrometry (Py-GC-MS-IRMS).

In order to test O2, soils were fractioned using a density fractionation approach into: i) light fraction (LF; unassociated with the mineral matrix); ii) aggregate-occluded fraction (OF; physically occluded in aggregates); and iii) and mineral-associated fraction (MF; strongly associated with mineral surfaces). Fractions were characterized using Py-GC-MS; and ^{13}C recoveries for microbial isolates in fractions were determined. Compound-specific recovery for microbial residues in soil fractions is being determined with Py-GC-MS-IRMS.

In order to test O3, soils were collected from 9 forest sites, along 3 elevation gradients formed from different parent materials (granite, andesite, basalt), in the Sierra Nevada and Cascade Mountain Ranges of CA. Elevation gradients corresponded with unique climate regimes

Department of Land, Air and Water Resources, University of California, Davis
*Principal Investigator
For more information contact Dr. William Horwath (wrhorwath@ucdavis.edu)

and stage of soil development, and dominant overstory being ponderosa pine, white fir, and red fir. Site variables were a 3 x 3 factorial of parent material and biome. Three replicate pits were examined for each site. Soil horizons were designated in the field, and profiles were characterized. Total C, N, DOC, and microbial biomass were measured for all horizons. Surface and subsurface soils were fractioned into LF, OF, and MF. Particle size, selective dissolution for Al and Fe humus complexes is being determined for all horizons.



Results

3.1. Microbial isolate composition

Microbial group isolates contained unique biochemical fingerprints. Notable differences occurred for temperate and tropical fungi and tropical gram (-) compared with other microbial isolates: these isolates were characterized by a relatively low abundance of phenol, benzene, and N-compounds (Table 1).

Table 1. *Relative abundance of compound classes for all compounds. Abbreviations: lipid (Lp); phenol (Ph); benzene (B); polysaccharides (Ps); nitrogen-compounds (N); lignin (Lg).*

		Lp	Ph	B	Ps	N
Microbes: temperate	Actinos	14.5	13.9	13.0	11.2	45.1

	Fungi	20.5	6.9	7.7	34.8	27.4
	Gram+	4.6	11.9	12.7	20.0	49.4
	Gram-	15.0	18.0	17.9	14.8	33.0
Microbes: tropical	Actinos	0.8	13.0	15.7	21.3	46.6
	Fungi	34.4	6.7	7.7	24.2	24.1
	Gram+	21.0	17.0	17.1	9.6	33.9
	Gram-	56.5	10.0	11.1	8.9	13.0

3.2. Microbial ^{13}C turnover in soils

There were no differences in ^{13}C recoveries among the 8 microbial treatment isolates. However, there was a significant group effect (microbial origin removed as a variable from the model), whereby Gram (+) bacteria group isolates mineralized more slowly initially (through 163 d), while fungal isolates mineralized more slowly in later stages of decay (763 d) (Figure 1; Group*Time, $P = 0.046$).

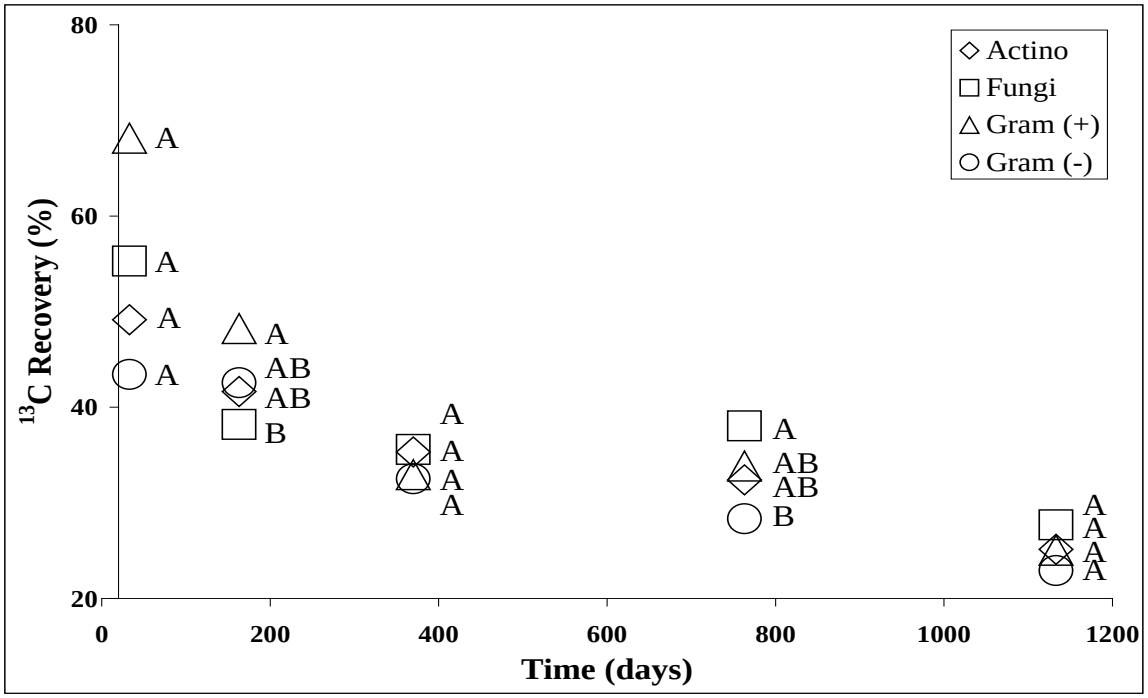


Figure 1. Recovery of microbial groups ^{13}C-excess (% of applied) in soil mesocosms (0-15 cm depth) at Blodgett Experimental Forest. Means for microbial groups shown (n = 3). LSD letter groups for ^{13}C recovery at indicated time. Groups with shared letters are not significantly different within time.

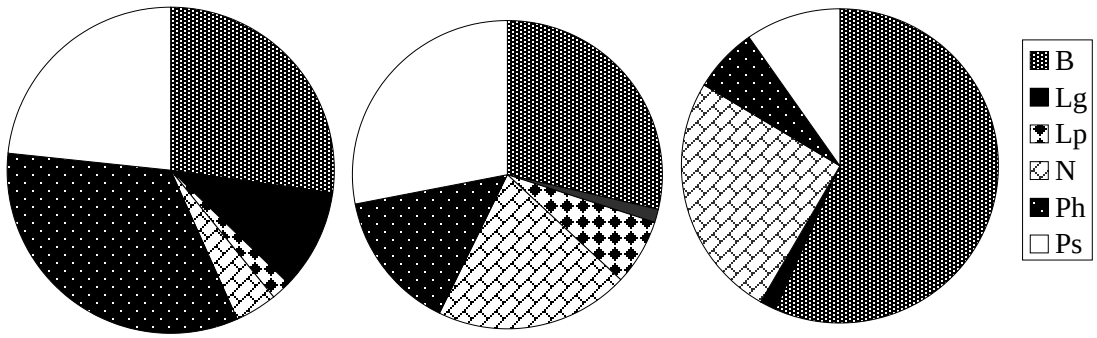
3.3 Soil fraction properties and chemical characterization

Over 70% of total soil mass in Blodgett soils was contained within the MF; however, due to differences in C concentrations among fractions, the MF contained only around 1/3 of total C; and over 50% of soil C was contained within the LF (Table 2). The OF was highly concentrated with C; however, due to the low total OF yield, the OF comprised only ~16% of total soil C.

Compound class analyses revealed compositional differences among fractions. Benzene and N-compounds were most concentrated in the MF; lignin and phenol compounds were most concentrated in the LF; and lipids and polysaccharides were most concentrated in the OF.

Table 2. *Fraction characterization for Blodgett Experimental forest soils. Produced from fractioning 20 g whole soil sample. Averaged across all sampling time points. Means and standard errors (N= 135).*

	Blodgett Forest					
	LF		**OF**		**MF**	
Total weight (g^{-1})*	4.12	(0.19)	0.92	(0.03)	14.90	(0.23)
C (%)	31.15	(0.33)	41.09	(0.52)	5.26	(0.10)
N (%)	1.04	(0.02)	1.32	(0.02)	0.34	(0.01)
C/N ratio (elemental)	35.55	(0.61)	36.71	(0.46)	17.98	(0.11)
Portion of whole soils (%wt.)	20.19	(0.90)	4.49	(0.14)	73.02	(1.10)
Portion of whole soils (%C)	50.21	(1.25)	16.10	(0.53)	33.70	(0.96)



A **B** **C**

Figure 2. Compound class distribution for Blodgett Experimental forest: LF (A); OF (B); MF (C). Compound class abbreviations: benzene (B); lignin (Lg); lipid (Lp); N-containing compound (N); phenol (Ph); polysaccharide (Ps).

3.4. Microbial ^{13}C recovery in fractions

Microbial ^{13}C treatment recoveries differed significantly within the LF and OF, but did not differ within the MF (Table 3; group*origin*fraction, P = 0.035); an effect that was independent of time (group*origin*fraction*time, P = 0.949). For relative ^{13}C recoveries among treatments, the relative recoveries of ^{13}C microbial isolates in the OF and LF in Blodgett Experimental forest soils seemed to reflect that of whole soils (Figure 3); whereas the MF was not as strongly related (Figure 3).

Table 3. *Means and LSD letter groups for microbial treatment ^{13}C recovery. Microbial treatments with a shared letter for indicated fraction do not significantly differ. Fractions analyzed separately (n = 3).*

		LF		OF		MF	
Temperate	Actino	AB	14.03	BC	1.19	A	15.15
	Fungi	BC	9.40	ABC	1.68	A	15.83
	Gram (+)	A	15.63	A	2.47	A	15.67
	Gram (-)	AB	11.84	ABC	1.36	A	14.61
Tropical	Actino	C	7.48	D	0.85	A	12.65
	Fungi	AB	12.71	AB	1.79	A	16.14
	Gram (+)	BC	9.66	BC	1.06	A	14.97
	Gram (-)	ABC	10.76	AB	2.13	A	11.90

origin*group*fraction (P = 0.035)

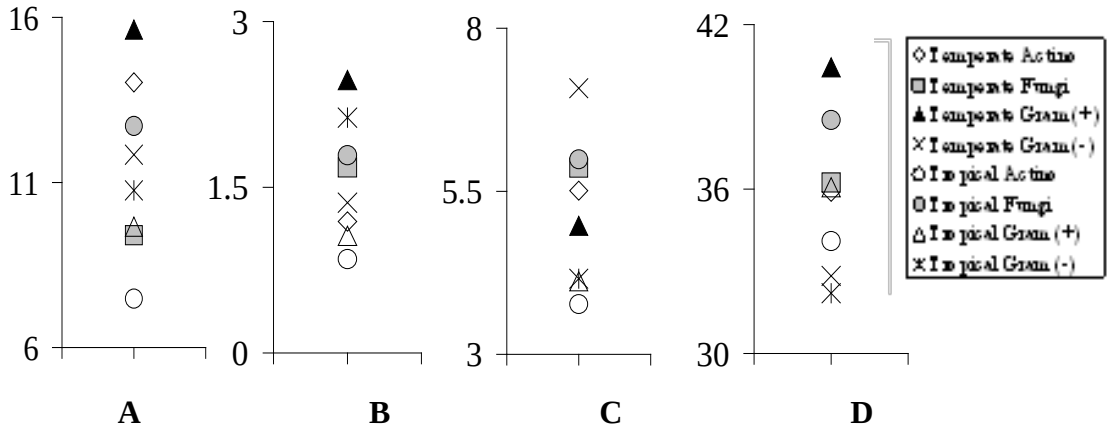


Figure 3. Means for microbial treatment ^{13}C recoveries in A) LF; B) OF; C) MF; D) whole soils at Blodgett Experimental Forest.

The dynamics of input ^{13}C label within fractions differed significantly over time (Table 4, Fraction*Time, P <0.0001). Based on typical cell densities (Bakken and Olsen, 1983), microbial ^{13}C inputs were assumed to be primarily associated with the LF immediately upon additions (day 0; Figure 4). However, by the first sampling event, a significant amount of input ^{13}C had moved into the OF, and even more so in the MF. The partitioning of microbial ^{13}C within the OF and the MF became more prominent throughout the course of the study compared with the LF, which exhibited a more rapid loss of ^{13}C over time. Total ^{13}C recoveries in the OF increased over time, despite the fact that ^{13}C recoveries in whole soils decreased over time (Table 4, Figure 4).

By the first sampling point, total microbial ^{13}C was similarly distributed between the LF (22.3%) and the MF (20.7%) (Table 4); however, the MF was more concentrated with input ^{13}C than the LF (Figure 5). The OF was initially the least concentrated fraction, but by the final sampling date, the OF and the LF were similarly concentrated with new C, while the MF remained consistently more concentrated in input ^{13}C throughout the course of the study (Figure 5).

Table 4. *Microbial ^{13}C recovery (% relative to input). Means and standard errors. (n = 24). Fractions sharing a letter are not significantly different at indicated time point.*

	Time (days)											
	33			***163***			***370***			***763***			***1133***		
Light Fraction	22.3	(1.3)	A	15.7	(0.7)	A	14.0	(0.4)	A	9.3	(0.6)	B	7.4	(0.3)	B
Occluded Fraction	1.9	(0.1)	B	2.0	(0.2)	B	2.7	(0.2)	B	1.2	(0.1)	C	3.2	(0.2)	C
Mineral Fraction	20.7	(0.8)	A	18.6	(0.9)	A	13.8	(0.4)	A	15.9	(0.3)	A	12.6	(0.4)	A
Whole Soils	***54.0***	***(3.9)***		***42.7***	***(1.8)***		***34.1***	***(0.8)***		***33.2***	***(1.4)***		***24.3***	***(1.0)***	

*Microbial treatments composited

3.5. Compound-specific ^{13}C recovery in whole soils and fractions

Preliminary compound-specific ^{13}C recoveries of temperate fungal residues suggest differential enrichment and label dynamics for biomarkers associated with different compound classes (protein; polysaccharides, and lipids): with relatively high enrichment of protein biomarkers, which increased throughout the course of the study; a lesser enrichment of polysaccharide biomarkers, which showed a decreasing trend by the 2nd sampling point; and the lowest enrichment of lipid compounds that remained relatively constant throughout the course of the study (Figure 6). Continued and future analysis examines additional microbial isolates and fractions for compound-specific recovery.

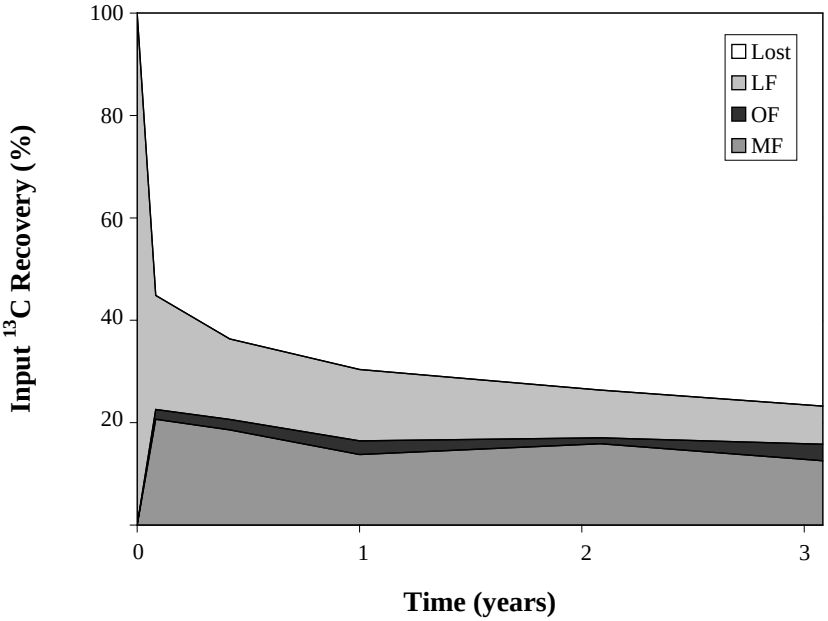


Figure 4. Microbial ^{13}C distribution in fractions (% relative to input). ^{13}C recovery assumed to be 100% in LF at zero-days. Means shown. (n = 24).

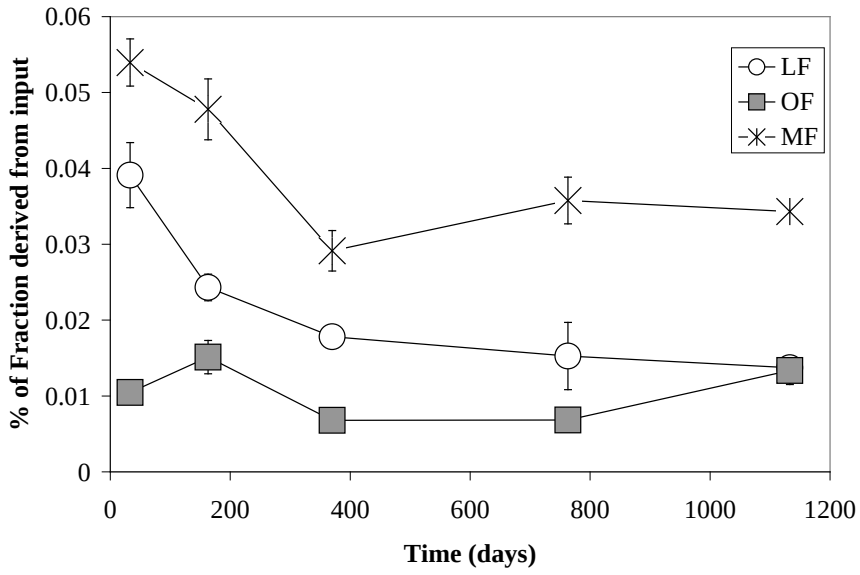


Figure 5. Fraction enrichment: percent of fraction derived from input ^{13}C.

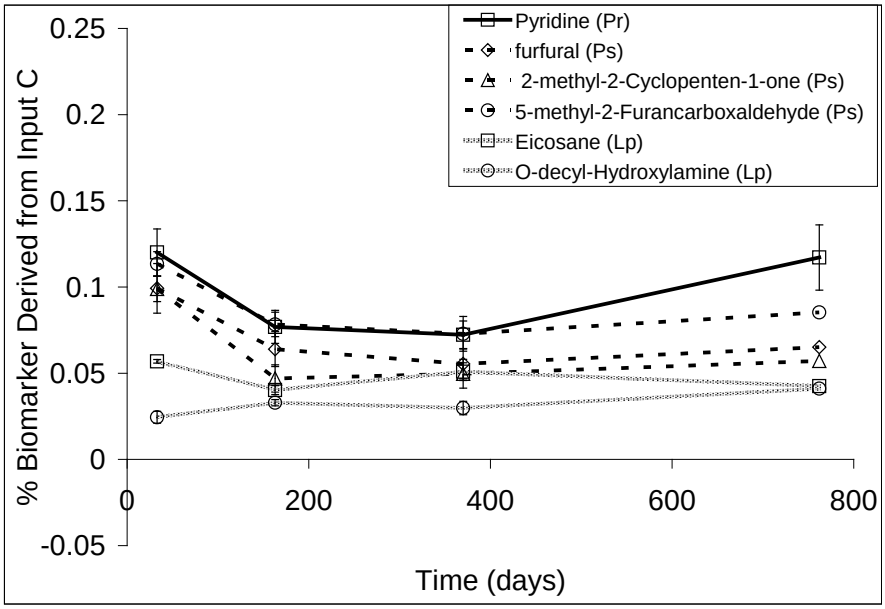
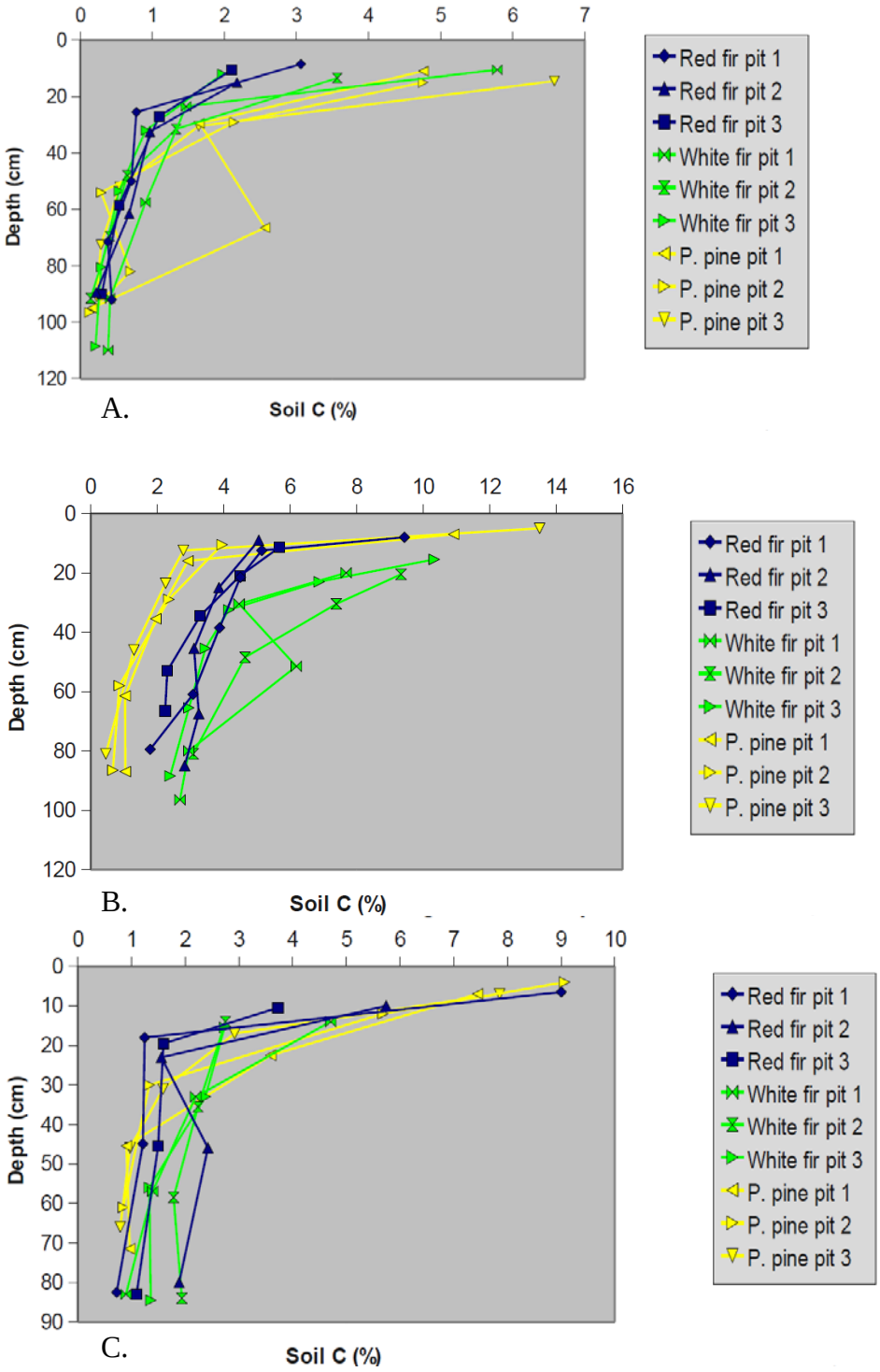


Figure 6. Percent of compound derived from input microbial C (temperate fungal isolates) over time in the field. Compounds are associated with specific compound classes (Pr = protein, Ps = polysaccharide, Lp = lipid), N=3.

3.6. Parent material and climate effects in California forest soils

Total C content along the 3 California transects generally exhibited a decreasing trend with depth. The decreasing trend of C with depth was less uniform in the andesite transect than the basalt or granite transects, in particular for the white fir site. C content in the andesite transect was generally higher than the basalt and granite transects throughout the soil profile (Figures 7a, 7b, 7c).

Fractionation data for representative pits (for the LF, OF, and MF) surface and subsurface soils suggest differences in the partitioning of total mass and C among fractions with depth for different parent materials (e.g. red fir biome results: Table 5). The C/N ratios for fractions were highly variable, and varied with depth among sites (Table 6).



Figures. 7. Soil C by depth for replicate pits along transects for parent materials: a) granite; b) andesite; c) basalt

Table 5*. Sample dataset for fraction properties (LF, OF, MF) for red fir biome (RF). Surface and subsurface soils: horizon designation included in sample ID. Parent materials corresponding to sample ID: BS (basalt); AN (andesite); GR (granite). Total fraction weight produced from original sample weight as indicated. % wt. is mass recovery relative to whole soils.*

Sample ID	Fraction	Sample wt. (g)	Fraction wt. (g)	% wt.	Final total wt. (g)	% recovery
BS-RF-1 A	Whole	20.291			20.162	99.36%
	LF		2.076	10.23%		
	OF		0.132	0.65%		
	MF		17.954	88.48%		
BS-RF-1 2Bw1	Whole	20.744			20.466	98.66%
	LF		0.302	1.46%		
	OF		0.028	0.13%		
	MF		20.136	97.07%		
AN-RF-1 A1	Whole	20.34			20.002	98.34%
	LF		7.352	36.15%		
	OF		0.264	1.30%		
	MF		12.386	60.89%		
AN-RF-1 Bw1	Whole	20.179			19.993	99.08%
	LF		1.530	7.58%		
	OF		0.197	0.98%		
	MF		18.266	90.52%		
GR-RF-1 A	Whole	20.219			18.589	91.94%
	LF		sample lost	0.00%		
	OF		0.120	0.59%		
	MF		18.469	91.34%		
GR-RF-1 Bw	Whole	20.124			19.994	99.35%
	LF		0.329	1.63%		
	OF		0.027	0.13%		
	MF		19.638	97.58%		

***Table 6**. Sample dataset for elemental analyses for fractions (LF, OF, MF) for red fir biome (RF). Surface and subsurface soils: horizon designation included in ID. Parent materials corresponding to sample ID: BS (basalt); AN (andesite); GR (granite).*

Sample ID	Fraction	Sample wt. (mg)	N wt. (mg)	%N	C wt. (mg)	% C	C/N
BS-RF-1 A	LF	8.151	0.115	1.411	2.584	31.703	22.470
	OF	6.515	0.117	1.803	2.385	36.615	20.385
	MF	46.031	0.021	0.047	0.298	0.647	14.190
BS-RF-1 2Bw1	LF	8.526	0.039	0.457	1.377	16.151	35.308
	OF	sample too small to analyze					
	MF	79.197	0.051	0.064	0.782	0.988	15.333
AN-RF-1 A1	LF	8.802	0.054	0.616	1.898	21.56	35.148
	OF	6.939	0.058	0.843	2.517	36.268	43.397
	MF	86.113	0.067	0.078	1.241	1.441	18.522
AN-RF-1 Bw1	LF	8.19	0.051	0.618	1.912	23.351	37.490
	OF	6.329	0.047	0.745	2.332	36.849	49.617
	MF	95.474	0.096	0.101	1.546	1.619	16.104
GR-RF-1 A	LF	8.651	0.052	0.605	2.538	29.336	48.808
	OF	6.337	0.068	1.065	2.619	41.333	38.515
	MF	Analysis not yet complete					
GR-RF-1 Bw	LF	8.429	0.031	0.369	2.23	26.454	71.935
	OF	3.837	0.022	0.569	1.943	50.629	88.318
	MF	Analysis not yet complete					

Discussion

4.1. Microbial residue quality and turnover (O1)

Microbial biochemistry differed across groups and origins, illustrating the potential for variation among different microorganisms in the quality of microbial inputs to SOM. Fungal isolates notably differed from other microbes, containing a higher C/N ratio and lipid content, and a lower abundance of benzene, phenol, and N-compounds. High C/N ratio of fungi relative to bacteria is well supported in existing literature (Paul and Clark, 1996, Wallander et al., 2003). The high lipid content in the fungal isolates is supported by 2-D NMR analysis (Fan et al., 2009). High fungal polysaccharide content likely reflects differences in cell wall chemistry, and the large content of unique sugar containing compounds like n-acetylglucosamine associated with fungal chitin (Madigan et al., 2002). In addition to differences across microbial group- isolates, there were differences between microbial isolates of the same phenetic classification from different origins. In particular, the tropical Gm (-) bacteria isolates differed dramatically from temperate Gm (-), more closely resembling fungal isolates: with notably high C/N ratio and lipid content, and low abundance of N-compounds.

Despite observed biochemical differences among microbial isolates, overall, our results do not support the hypothesis that diverse microbial groups decompose at different rates, and do not

suggest that C mineralization rates are strongly linked to the source and quality of microbial necromass. Our results showed slightly greater stability of Gm (+) bacteria in early stages of decay (through day 163), and slightly greater long-term stability of fungal isolates (through 763 d). However, no significant differences occurred on the last sampling date, and MRTs were similar for microbial groups (data not shown).

A widely maintained view among soil microbiologists and biogeochemists is that a community dominated by fungi will stabilize more C than a community dominated by bacteria (Moore et al., 2005; Six et al., 2006; Jastro et al., 2007; Strickland and Rousk, 2010): a view that has evolved from a handful of laboratory incubation studies that either: i) directly compared the decay of fungal and bacterial cellular products (Nakas and Klein, 1979), or ii) provided a basis for indirect comparison by reporting on mineralization of one microbial group or microbial product (Martin and Haider, 1979; Bailey et al., 2002; Li and Brune, 2005a, 2005b). Such existing studies have provided only limited information to extrapolate and broadly predict the turnover of fungal and bacterial necromass and products. The present study sheds new light on relative stability of microbial biomass as a source of C to soil. Results do not support preferential stabilization of fungal biomass compared with bacteria, and suggests only minor effects by the source and quality of microbial C as a factor in microbial C turnover.

Compound-specific turnover analyses indicate some differences in the relative stability and dynamics of unique microbial compounds in soil; however, the influence of specific compound chemistry and microbial makeup on microbial ^{13}C turnover is still being determined.

4.2. Compositional differences and microbial ^{13}C recoveries in soil physical fractions in Blodgett Experimental Forest (O2)

The density fractionation approach used in this study is based on the theory that isolated fractions differ in their relative associations with, and protection by, the mineral matrix: the free LF is primarily unassociated with the mineral matrix; the OF is physically occluded within aggregates; and the MF is intimately associated with mineral surfaces (Golchin et al., 1994a;1994b). Differences in elemental composition and compound class abundance demonstrate unique chemical properties among fractions, and likely reflect differences in the decomposition stage and associated source material (i.e., plant vs. microbial) (Wagai et al., 2008; Swanson et al., 2005).

The LF is commonly described as residual and mostly unaltered plant litter (Wagai et al., 2009), which is consistent with the observed abundance of lignin biomarkers, and the high phenol and polysaccharide content likely attributed to fresh plant materials. The origin and composition of the OF is less established than the LF (Wagai, 2009). However, it is generally accepted that the OF is protected via physical occlusion by aggregates (Golchin, 1994a). The OF has been found to exhibit some characteristic properties (Wagai, 2008) consistent with our findings: the OF typically has a higher C and N concentration than the LF (Swanston et al., 2005); a higher C/N ratio (Wagai); and high abundance of lipids (Golchin et al. 1997b; Kölbl and Kögel-Knabner 2004; Marin-Spiotta et al. 2008; Sohi et al., 2001; Poirier et al., 2005; Wagai et al. 2008). High lipid content likely promotes aggregate stability by repelling water; thus increasing SOM stability by prolonging its occlusion and separation from grazers and enzymes. The low C and N content in the MF occurs due to high mineral content and soil particles, which interact with SOM through chemical complexation, resulting in increased SOM stability (Gaudinski et al., 2000; Swanston et al., 2005; Kogel-Knabner et al., 2008; Rasmussen et al.,

2005). The observed low C/N ratio and abundance of N-compounds associated with the MF is consistent with other studies, and likely reflects concentration of N-rich microbial biomass adhered to mineral surfaces (Swanston et al., 2005; Sollins et al., 2009), and the association of negatively charged N-groups (Kleber et al., 2007; Wagai et al., 2009).

In addition to observed compositional differences among fractions, relative stabilities of microbial ^{13}C also differed among fractions. Results generally supported the theory that association of organic matter with the mineral matrix increases its stability (Golchin et al., 1994a; 1994b; Wagai et al. 2008). Recovery of microbial ^{13}C within the LF decreased more rapidly than that of the OF and MF over time, regardless of microbial isolate type (Table 4, Figure 4). These findings serve as evidence for increased stability of microbial ^{13}C via chemical (MF) and physical (OF) organo-mineral interactions.

There were some differences among microbial isolates in ^{13}C recovery in the LF and OF, which related to relative ^{13}C recoveries in whole soils (Figure 3). In the MF, microbial ^{13}C recoveries did not significantly differ, and in generally lower variability among treatments was observed. Overall, results support increased protection of microbial ^{13}C via association with the MF; however, differential sorption of various microbial cell types over others was not observed. Differences among ^{13}C microbial isolates recoveries were more pronounced in the OF and LF, suggesting that inherent properties of microbial residues may be more important to determining its stability when it is i) unassociated with the mineral matrix (LF); or ii) physically occluded within aggregates; compared with that intimately associated with mineral surfaces (MF).

4.3. Parent material and climate as factors in controlling mechanisms for C protection and storage in CA forest soils (O3)

Results illustrate the importance of climate and parent material as important determinants of mechanisms controlling C stabilization and concentration, and profile changes with depth. Statistical analyses are being conducted to highlight significant differences in C partitioning among fractions- with parent material, climate, and depth as variables. Additional mechanisms for organo-mineral associations will be determined through: selective dissolution analyses to determine soil organic matter association with Fe and Al; particle-size analyses to elucidate the effects of clay; and XRD to characterize soil mineralogy.

4.4 Summary

This research addresses the 2006-2011 Kearney Foundation of Soil Science mission: "Understanding and managing soil-ecosystem functions across spatial and temporal scales" by emphasizing factors, mechanisms, and processes influencing soil C at multiple scales. Results range from the micro-scale (molecular), to the meso-scale (aggregate protection; pedon profile) and macro- scale (regional- mineralogy and climate) in California forest soils. There is a strong soil-ecosystem link that examines microbial residues as a source of soil C, and specific organo-mineral interactions influencing the turnover of microbial residues. Although some additional analyses are underway, all field work is complete, as well as a large majority of the laboratory work and analyses. The California transect component of this research has yielded an extensive dataset that requires multivariate statistical analyses for comprehensive interpretation of results. The integration of organo-mineral interactions via physical (OF) and chemical (MF) associations, with and Al and Fe humic interactions and soil properties, promises to elucidate important

predictions for C concentration at a regional scale in California forest soils, and how these effects may vary in surface and subsurface soils.

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This research was funded by the Kearney Foundation of Soil Science: Understanding and Managing Soil-Ecosystem Functions Across Spatial and Temporal Scales, 2006-2011 Mission (http://kearney.ucdavis.edu). The Kearney Foundation is an endowed research program created to encourage and support research in the fields of soil, plant nutrition, and water science within the Division of Agriculture and Natural Resources of the University of California.