

# Soil Organic Carbon Stability Across a Mediterranean Oak Agroecosystem<sup>1</sup>

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## Abstract

Rangelands are estimated to cover 30 to 50 percent of the world's land surface and have significant belowground carbon (C) storage potential. Given their geographical extent, many have suggested that even modest changes in C storage via management practices could alter the global C cycle, creating climate change mitigation opportunities. Our objective was to investigate soil organic carbon (SOC) stability across a managed annual grassland, savanna, and oak woodland landscape. We sampled A and AB horizons from 20 soil profiles to assess long-term SOC stabilization pathways using combined physical and chemical SOC laboratory fractionation techniques. We found that although total SOC was positively correlated with woody plant cover, the SOC stabilization mechanisms differed only slightly across this gradient of woody cover (0 to 100 percent)—for all practical purposes, the relative proportions of physically protected C, biochemically protected C, and unprotected C were largely non-responsive to woody cover. Therefore, we found woodland and savanna soil carbon stores were not more resilient to disturbances than grassland carbon stores, and so can be quickly degraded and lost upon removal of woody cover.

*Key words:* carbon sequestration, hardwood rangeland, soil organic carbon stabilization

## Introduction

Soil organic matter (SOM) is the largest carbon (C) reservoir in the terrestrial biosphere (~1,550 Gt C), and contains over two-fold the C found in the atmospheric pool (~750 Gt C) (Schlesinger 1997). Over the last decade, there has been substantial concern regarding the impacts of land management practices and associated land-use changes on terrestrial C stocks (Follett and Reed 2010). Land-use and land-cover influence SOM pools, and thus exert strong controls over the mean residence time of soil organic C (SOC) (Houghton and others 1999, Schimel 1995). Understanding the relationship between land management practices and SOC stability is critical. Land management potentially impacts SOC stability via impacts to dynamic soil properties such as soil structure and aggregate stability, which determine soil's capacity to retain C (Six and others 2000a). Management practices can also alter dominant vegetation classes, which control both organic C inputs and inherent biochemical resistance to decomposition (Guo and Gifford 2002, Post and Kwon 2000).

Rangelands span diverse land resources—including uncultivated grasslands, shrublands, and forested lands—and are estimated to cover approximately 30 to 50 percent of the world's terrestrial surface and store 10 to 30 percent of the world's SOC (Conant and others 2001, Derner and Schuman 2007, Ojima and others 1993,

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Schlesinger 1997, Watson and others 2000). Current global estimates for rangelands put SOC sequestration rates as high as 0.3–0.5 Pg C/yr (Lal 2004, Schlesinger 1997, Scurlock and Hall 1998), positioning rangelands as a major terrestrial C reservoir. Given the large geographical extent of rangelands, many have suggested that even modest increases in C storage via management practices could alter the global C cycle—providing opportunities for climate change mitigation (Dahlgren and others 2003, Derner and Schuman 2007, Laca and others 2010).

Previous research on rangeland ecosystems has largely focused on total SOC pools, with limited attention to the principal drivers affecting SOC dynamics and C sequestration. Total SOC alone is not a sensitive measure of SOC dynamics and may not accurately predict SOC stabilization over longer time scales in response to land management practices or environmental conditions. Previous efforts in more intensive cropping systems have utilized physical and chemical fractionation techniques to isolate functional SOC fractions, which are defined by stabilization mechanisms and can therefore be related to SOC stability (Denef and others 2004, Jagadamma and Lal 2010, Six and others 2000a). The two major pathways of SOC stabilization are 1) physical protection of SOC in soil microaggregates, and 2) biochemical protection of SOC via inherent recalcitrance (Six and others 2000a). Together, these pathways create a complex protection stratum that potentially grades SOC stability on a spectrum of labile to stable SOC pools.

Oak woodland-savanna-grassland rangelands in Mediterranean regions around the world cover approximately 7 million hectares, and receive substantial management and removal of oak and other woody species to enhance forage and livestock production goals (Roche and others 2012). In California's oak rangelands, loss of relatively high total SOC levels has been documented within two decades of woody species removal (Dahlgren and others 1997). The objective of this study was to investigate pathways of SOC stability across a landscape mosaic spanning open savanna to oak forest in an attempt to identify underlying mechanisms for SOC loss.

## Methods

### **Study area**

This study was conducted at the University of California Sierra Foothill Research and Extension Center (SFREC) in Yuba County, CA (39°14'22"N, 121°17'46"W). Located in the northern Sierra Nevada foothills, SFREC has a Mediterranean climate with hot, dry summers and cool, wet winters—mean annual precipitation is 740 mm and mean annual air temperature is 15 °C. Soils were formed on basic metavolcanic (greenstone) bedrock and are classified as Typic or Mollic Haploxeralfs. The clay mineralogy consists of vermiculite-chlorite, vermiculite, chlorite, kaolinite, and some smectite (Dahlgren and others 2003).

The landscape is a mosaic of open grassland and oak canopy, producing patches of open grassland, savanna, woodland, and forest. This hardwood rangeland is dominated by *Quercus douglasii* (blue oak), a deciduous oak, with *Q. wislizenii* (live oak) and *Pinus sabiniana* (foothill pine) also present. Understory vegetation is dominated by annual grasses such as *Avena fatua* (wild oats) and *Bromus* spp. Common forbs include *Erodium* spp. (filaree) and *Trifolium* spp. (annual clovers).

## Field sampling and bulk soil analysis

We excavated 20 soil profiles across a woody plant canopy cover gradient from open savanna to closed forest. Soil profiles were excavated at one to two subplots prior to onset of the rainfall season. Soils were sampled from A and AB horizons as intact clods. At each soil profile sampling site, we used a modified convex spherical densitometer to calculate percent canopy cover (Mulvey and others 1992). Sampling sites were classified as open savanna (<25 percent), oak woodland (25 to 80 percent), or oak forest (>80 percent).

Total C/N analysis using a dry combustion elemental analyzer (ECS 4010, Costech Analytical Technologies Inc., Valencia, CA) and standard chemical and physical soil analyses were performed on bulk soil samples (fig. 1). Bulk density was determined using the 3D scanner method (NextEngine DeskTop 3D Scanner Model 2020i, NextEngine, Inc., Santa Monica, CA) (Rossi and others 2008). Soil texture and pH were analyzed using the pipette method (Jackson 2005) and a 1:1 soil to water ratio (Soil Survey Staff 2004), respectively.

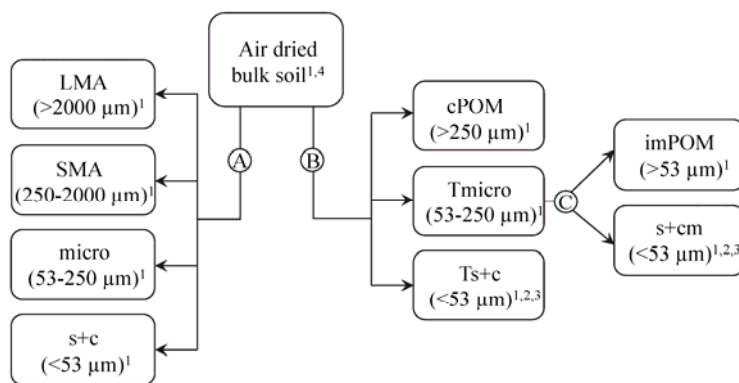


Figure 1—Soil analysis scheme. Letters indicate the soil separation procedure: A) aggregate size class separation, B) microaggregate separation, C) intra-microaggregate particulate organic matter separation. Superscript numbers denote treatments and analyses: 1) total C/N, 2) hot water carbon extraction, and 3) wet oxidation treatment, and 4) selective dissolution of Fe. LMA = large macroaggregates, SMA = small macroaggregates, micro = free microaggregates, s+c = free silt plus clay. cPOM = coarse particulate organic matter, Tmicro = total microaggregates, Ts+c = total silt plus clay not occluded in microaggregates, imPOM= particulate organic matter inside total microaggregate, s+cm = silt plus clay inside total microaggregates.

Selective dissolution of extractable Fe was also performed to assess potential effects of soil mineralogy on SOC stability (O'Geen and others 2010). We acquired quantitative mineralogical properties by performing selective dissolution of extractable Fe on bulk soil samples adapted from standard methods (Soil Survey Staff 2004). Selective dissolution procedures were conducted to yield three forms of extractable Fe, which were measured via atomic adsorption (AAAnalyst 200, PerkinElmer Instruments, Shelton, CT) 1) dithionite-citrate extractable Fe ( $Fe_{dc}$ ), considered as total extractable Fe; 2) sodium pyrophosphate extractable Fe ( $Fe_{pyro}$ ), considered as total organo-metal complexed Fe; and 3) ammonium oxalate extractable Fe ( $Fe_{ox}$ ).

### ***Physical and chemical SOC fractionation***

SOC fractions were acquired in order of microbial accessibility by first physically fractionating bulk soil into aggregate size classes, followed by sequential hot water extractions and wet oxidation treatments (fig. 1).

### ***Aggregate size class separation and microaggregate isolation***

To assess soil aggregate stability, four aggregate size classes were first isolated via wet sieving of bulk soil (Benchfly 2013b) (fig. 1, procedure A). Each aggregate size class was then forced-air dried at 60 °C and prepared for total C/N analysis.

An additional 20 g soil subsample separated into three additional fractions (Benchfly 2013a, Gentile and others 2011, Six and others 2000b): particulate organic matter plus sand (cPOM, >250 µm), total microaggregates (free microaggregates and microaggregates protected within macroaggregates; Tmicro, 53 to 250 µm), and total silt plus clay outside of Tmicros (Ts+c, <53 µm) (fig. 1, procedure B). Fine POM occluded in Tmicros (imPOM, >53 µm) were separated from silt plus clay inside total microaggregates (s+cm, <53 µm) (fig. 1, procedure C) according to Zotarelli and others (2005). All fractions were forced-air dried at 60 °C and stored at room temperature for subsequent analyses, including total C/N analysis.

### ***Hot-water extraction and wet chemical oxidation treatments***

Hot water extractable SOC (HWC) was obtained from Ts+c (HWC-Ts+c) and s+cm (HWC-s+cm) size classes with methods modified from Haynes and Francis (Haynes and Francis 1993) (fig. 1, procedure 2). Total dissolved organic C in water extracts were analyzed with a Shimadzu TOC Analyzer (Model TOC-VCSH, Japan).

Following hot water extraction, Ts+c and s+cm subsamples underwent wet chemical oxidation treatments according to Siregar and others (2005) (fig. 1, treatment 3), and then prepared for total C/N analysis.

### ***Physical and biochemical SOC protection pathways***

Using results from physical and chemical fractionation techniques, we integrated the measured fractions into three functional SOC pools:

$$\text{Unprotected SOC} = \text{cPOM} + \text{HWC-Ts+c} + \text{NaOCl-Ts+cXB}^5$$

$$\text{Physically Protected SOC} = \text{imPOM} + \text{HWC-s+cm} + \text{NaOCl-s+cmXB}^5$$

$$\text{Biochemically Protected SOC} = \text{NaOCl-Ts+c} + \text{NaOCl-s+cm}$$

We standardized functional SOC values by total SOC (cPOM + Tmicro + Ts+c) to produce relative values for each pool.

### ***Statistical analysis***

Given that the samples sites were located across a hardwood gradient, we first examined potential relationships between woody plant canopy cover and total SOC. For this initial analysis only, we combined A and AB horizon data and constructed multiple linear mixed effects (LME) regression models (Pinheiro and Bates 2000, Rabe-Hesketh and Skrondal 2008) to test effects of woody plant canopy cover

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<sup>5</sup> XB represents SOC oxidized during NaOCl treatment.

(continuous, fixed effect) on total soil organic carbon (response variables). To account for hierarchical nesting of multiple soil profiles within a single vegetation plot, plot ID was designated as a grouping variable (random effect).

To investigate pathways of SOC stability across woody plant canopy cover classes, we examined differences in 1) aggregate size class distributions, 2) SOC fractions, and 3) the three functional SOC pools (unprotected, physically protected, and biochemically protected C pools) for the A and AB soil horizons. To account for hierarchical nesting of multiple soil profiles within a single vegetation plot, we designated plot ID as a grouping variable (random effect).

We also examined biochemically labile and stable SOC fractions. We constructed separate LME regression models for each woody plant canopy cover class and soil horizon combination to compare mean SOC concentrations between 1) HWC-Ts+c and HWC-s+cm, and 2) NaOCl-Ts+c and NaOCl-s+cm. For these models, vegetation plot identity remained the grouping variable (random effect), and the HWC and NaOCl treatment IDs were fixed effects (in other words HWC-Ts+c/HWC-s+cm and NaOCl-Ts+c/NaOCl-s+cm). Standard diagnostic analyses were utilized, and all models were estimated in Stata/SE 13.0 (StataCorp 2013).

## **Results and discussion**

### ***Soil characteristics and total SOC patterns***

Tables 1 and 2 summarize general study site soil characteristics across the woody plant canopy cover classes. Mean total SOC and total N concentrations were consistently greater in A horizons than AB horizons for all woody plant canopy cover classes (table 2). O horizons were most prevalent in oak forest soil profile sites—O horizons were observed in five of six oak forest sites, two of six oak woodland sites, and no O horizons were observed at open savanna sites.

Preliminary analyses of Total SOC contents showed significant ( $P = 0.037$ ) increases in SOC along a gradient (0 to 100 percent) of woody plant canopy cover. This pattern of increasing total SOC with woody cover is consistent with previous research demonstrating enhanced soil fertility under tree canopy relative to adjacent open grassland (Dahlgren and others 2003, Dahlgren and others 1997, Kay 1987).

The high concentration of Fe in these soils (table 2) potentially facilitates the formation of stable organo-mineral complexes and Fe hydr(oxides) that enhance resilience of aggregates, where organic C can be physically protected from microbial attack (Barthes and others 2008, Panayiotopoulos and others 2004). The high mineral surface area of poorly crystalline Fe-(hydr)oxides likely further enhances SOC stability through greater aggregation (Six and others 2000b) and adsorption sites for polyvalent organic materials (Duiker and others 2003).

**Table 1—Mean bulk soil properties ( $\pm 1$  SE) of the fine earth fraction in A and AB soil horizons for each woody plant canopy cover class**

	Thickness (cm)	Texture			Bulk density (g cm <sup>-3</sup> )	pH
		sand (%)	silt (%)	clay (%)		
<u>A Horizon</u>						
Open savanna	5.3 $\pm$ 0.5	40.9 $\pm$ 1.9	41.0 $\pm$ 1.3	18.1 $\pm$ 1.3	1.25 $\pm$ 0.06	5.9 $\pm$ 0.1
Oak woodland	5.8 $\pm$ 0.7	35.1 $\pm$ 1.8	44.4 $\pm$ 1.0	20.5 $\pm$ 0.9	1.30 $\pm$ 0.06	6.3 $\pm$ 0.1
Oak forest	6.2 $\pm$ 0.7	37.7 $\pm$ 1.0	44.5 $\pm$ 0.6	17.8 $\pm$ 1.1	1.22 $\pm$ 0.07	6.4 $\pm$ 0.1
<u>AB Horizon</u>						
Open savanna	17.0 $\pm$ 1.3	39.0 $\pm$ 2.3	41.2 $\pm$ 1.1	19.8 $\pm$ 1.9	1.54 $\pm$ 0.06	6.3 $\pm$ 0.1
Oak woodland	14.5 $\pm$ 1.6	33.6 $\pm$ 2.5	45.0 $\pm$ 1.2	21.4 $\pm$ 1.4	1.58 $\pm$ 0.08	6.7 $\pm$ 0.1
Oak forest	14.0 $\pm$ 2.0	35.1 $\pm$ 1.1	44.5 $\pm$ 1.1	20.4 $\pm$ 1.2	1.49 $\pm$ 0.05	5.8 $\pm$ 0.2

**Table 2—Mean concentrations (g C/kg soil) ( $\pm 1$  SE) of total SOC<sup>1</sup>, total N, Fe<sub>dc</sub> (total extractable Fe), Fe<sub>ox</sub> (poorly crystalline + organo-metal complexed Fe), and Fe<sub>pyro</sub> (organo-metal complexed Fe) and mean C/N of A and AB soil horizons for each woody plant canopy cover class**

	Total SOC <sup>a</sup> (g/kg soil)	Total N (g/kg soil)	C:N	Fe <sub>dc</sub> (g/kg soil)	Fe <sub>ox</sub> (g/kg soil)	Fe <sub>pyro</sub> (g/kg soil)
<u>A Horizon</u>						
Open savanna	30.5 $\pm$ 2.6	2.9 $\pm$ 0.4	11.7 $\pm$ 1.7	20.2 $\pm$ 1.0	2.7 $\pm$ 0.21	2.2 $\pm$ 0.13
Oak woodland	42.0 $\pm$ 8.3	3.1 $\pm$ 0.6	13.8 $\pm$ 1.3	32.0 $\pm$ 5.4	2.6 $\pm$ 0.34	2.4 $\pm$ 0.17
Oak forest	36.0 $\pm$ 4.1	3.8 $\pm$ 1.0	12.1 $\pm$ 2.0	25.8 $\pm$ 3.4	3.2 $\pm$ 0.39	2.1 $\pm$ 0.32
<u>AB Horizon</u>						
Open savanna	12.6 $\pm$ 1.9	0.9 $\pm$ 0.1	14.6 $\pm$ 2.2	21.8 $\pm$ 1.2	2.2 $\pm$ 0.11	2.7 $\pm$ 0.30
Oak woodland	13.0 $\pm$ 2.4	0.7 $\pm$ 0.04	17.8 $\pm$ 3.3	31.6 $\pm$ 7.2	2.3 $\pm$ 0.14	3.1 $\pm$ 0.14
Oak forest	15.4 $\pm$ 1.9	1.0 $\pm$ 0.1	16.4 $\pm$ 2.3	28.9 $\pm$ 3.2	3.1 $\pm$ 0.27	3.2 $\pm$ 0.31

<sup>a</sup>. Total SOC calculated as cPOM + Tmicro + Ts+c

### **Aggregate stability and SOC fractions**

Proportions of large and small macroaggregate (LMA and SMA) size classes were not significantly different among vegetation classes (fig. 2), which suggests soil stability and resistance to disturbances is similar for open savanna, oak woodland, and oak forest soils. Size class distributions were generally skewed toward larger classes in A soil horizons, while the LMA, SMA, and microaggregate size classes were more evenly distributed in AB soil horizons (fig. 2). It is well known that more stable C pools are found with increasing soil depth (Rumpel and Kogel-Knabner

2011), and so the increase in proportion of microaggregates with depth is not surprising. Microaggregates are more stable than the larger macroaggregate size classes (LMA and SMA), and therefore represent a longer term pool for soil carbon storage (Six and others 2000a).

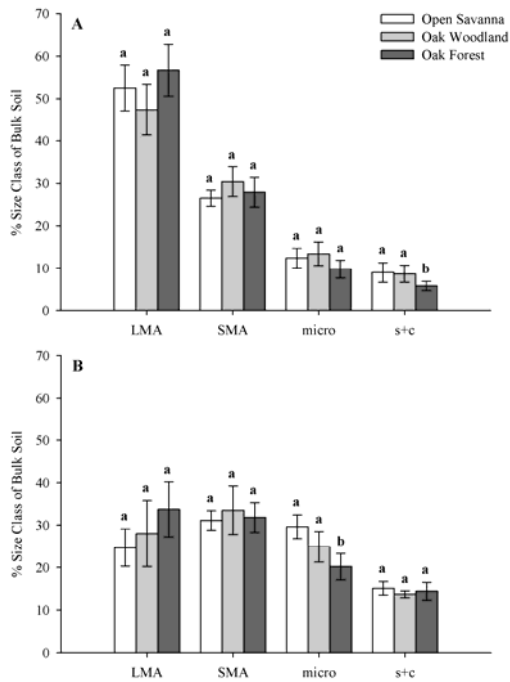


Figure 2—Mean ( $\pm 1$  SE) weight distribution (percent size class of bulk soil) of aggregate size classes across woody plant canopy cover classes for A (A) and AB (B) horizons. LMA=large macroaggregates ( $> 2000 \mu\text{m}$ ), SMA=small macroaggregates ( $2000\text{-}250 \mu\text{m}$ ), micro=microaggregates ( $25\text{-}53 \mu\text{m}$ ), and s+c=silt plus clay ( $<53 \mu\text{m}$ ). For each size class, different successive letters indicate significant differences ( $p < 0.05$ ).

Overall, the larger aggregate size classes appeared to store more SOC than smaller aggregate size classes, and SOC concentrations in macroaggregates (LMA and SMA) and microaggregates (micro) generally decreased with depth (fig. 3). For the cPOM, T<sub>micro</sub>, T<sub>s+c</sub>, s+c<sub>m</sub>, and imPOM fractions, SOC concentrations also generally decreased with depth. There were no significant differences in SOC between vegetation classes for the T<sub>s+c</sub>, s+c<sub>m</sub>, or imPOM fractions (table 3); however, T<sub>micro</sub>-SOC significantly increased with woody plant cover for A horizons, and cPOM-SOC significantly increased with woody plant cover for AB horizons.

For hot-water extraction and wet chemical oxidation treatments, only HWC-s+c<sub>m</sub> (considered biochemically labile) significantly differed between vegetation classes (table 4). The concentration of HWC characterizes the relative availability of “active” SOC, which is energetically preferred for microbial assimilation (Ghani and others 2003, Haynes and Francis 1993). The overall apparent accumulation of HWC T<sub>s+c</sub> and s+c<sub>m</sub> with greater canopy cover may be attributed to inputs of fresh residue-C from degradation of organic materials in overlying O horizons observed at oak forest and woodland sites.

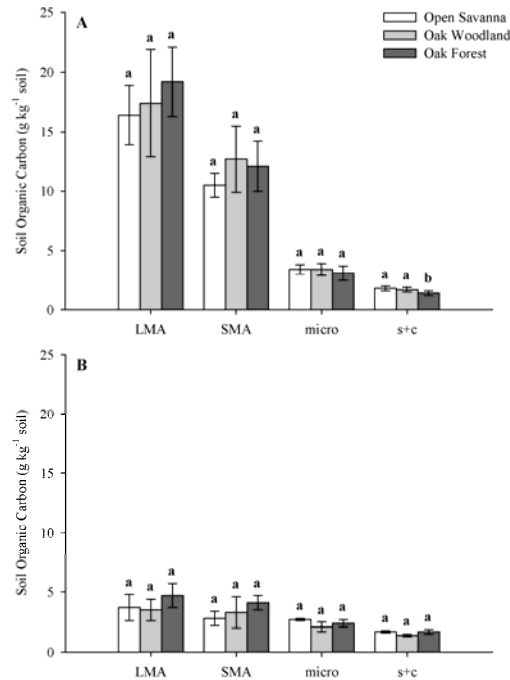


Figure 3—Mean ( $\pm 1$  SE) SOC concentrations (g C/kg soil) of aggregate size classes across woody plant canopy cover classes for A (A) and AB (B) horizons.

**Table 3—Mean ( $\pm 1$  SE) concentration (g C/kg soil) of SOC fractions across woody plant canopy cover classes for A and AB horizons. For each size class within a horizon, means with different letters are significantly different ( $P < 0.05$ )**

	cPOM (g/kg soil)	Tmicro (g/kg soil)	Ts+c (g/kg soil)	s+cm (g/kg soil)	imPOM (g/kg soil)
<b>A Horizon</b>					
Open savanna	7.9 $\pm$ 0.6	12.6 $\pm$ 1.6 <b>a</b>	10.0 $\pm$ 0.9	5.2 $\pm$ 0.5	7.6 $\pm$ 1.3
Oak woodland	10.3 $\pm$ 3.4	18.8 $\pm$ 3.9 <b>b</b>	12.8 $\pm$ 1.7	6.9 $\pm$ 1.4	10.0 $\pm$ 2.3
Oak forest	8.4 $\pm$ 1.7	16.3 $\pm$ 1.8 <b>b</b>	11.2 $\pm$ 1.2	8.1 $\pm$ 0.9	8.8 $\pm$ 1.6
<b>AB Horizon</b>					
Open savanna	1.1 $\pm$ 0.3 <b>a</b>	5.3 $\pm$ 0.9	6.2 $\pm$ 0.9	3.2 $\pm$ 0.4	1.5 $\pm$ 0.4
Oak woodland	1.3 $\pm$ 0.2 <b>a</b>	5.8 $\pm$ 1.6	5.8 $\pm$ 0.7	3.7 $\pm$ 1.0	1.8 $\pm$ 0.6
Oak forest	2.4 $\pm$ 0.5 <b>b</b>	6.6 $\pm$ 1.1	6.4 $\pm$ 0.5	3.9 $\pm$ 0.4	2.5 $\pm$ 0.8

For the A soil horizon, mean HWC concentrations were significantly ( $P < 0.05$ ) lower in the s+cm than in the Ts+c fractions across all vegetation classes; for the AB soil horizon, mean HWC concentrations were significantly ( $P < 0.05$ ) lower in the s+cm than in the Ts+c fractions for the oak savanna and oak woodland classes (table 4, statistical test results not shown in table). This suggests a strong microbial influence on the Ts+c fraction, where mucilages produced during SOM decomposition become binding agents for macroaggregation.



**Table 4—Mean ( $\pm 1$  SE) concentration (g C/kg soil) of hot water extractable C (HWC-) and sodium hypochlorite resistant C (NaOCl-) associated with total silt plus clay outside (Ts+c < 53) and inside (s+cm) microaggregate size classes in the A and AB horizons for each woody plant canopy cover class. For each size class within a horizon, means with different letters are significantly different ( $P < 0.05$ )**

	HWC-Ts+c (g/kg soil)	HWC-s+cm (g/kg soil)	NaOCl-Ts+c (g/kg soil)	NaOCl- s+cm (g/kg soil)
A Horizon				
Open savanna	0.52 $\pm$ 0.06	0.25 $\pm$ 0.01 a	2.5 $\pm$ 0.3	2.0 $\pm$ 0.3
Oak woodland	0.49 $\pm$ 0.09	0.29 $\pm$ 0.03 ab	3.9 $\pm$ 0.8	2.2 $\pm$ 0.8
Oak forest	0.63 $\pm$ 0.12	0.36 $\pm$ 0.05 b	3.0 $\pm$ 0.6	2.3 $\pm$ 0.3
AB Horizon				
Open savanna	0.19 $\pm$ 0.02	0.15 $\pm$ 0.03	1.3 $\pm$ 0.2	1.0 $\pm$ 0.2
Oak woodland	0.26 $\pm$ 0.06	0.13 $\pm$ 0.01	1.2 $\pm$ 0.2	1.0 $\pm$ 0.2
Oak forest	0.21 $\pm$ 0.02	0.15 $\pm$ 0.04	1.5 $\pm$ 0.4	1.1 $\pm$ 0.1

SOC remaining after a NaOCl treatment represents C that is biochemically protected via complex organic assemblages inherent in plant tissues (Siregar and others 2005). NaOCl-resistant SOC in s+cm represents SOC that is further protected by physical occlusion in microaggregates. NaOCl-resistant SOC concentrations were significantly lower in the s+cm than in the Ts+c fractions for open savanna and oak woodland A horizons (table 4, statistical results not shown)—suggesting a stronger biotic control. In contrast, NaOCl-resistant SOC concentrations found in the AB horizon were relatively similar across Ts+c and s+cm, suggesting a stronger abiotic control. The observed high concentrations of poorly crystalline Fe (hydr)oxides in these soils (table 1) potentially enhances SOC stability (Kleber and others 2005, Mikutta and others 2006).

### **Pathways of SOC stabilization**

Canopy cover had limited influence on the proportions of unprotected, physically protected, and biochemically protected SOC pools. The percent unprotected and percent physically protected C were significantly ( $P < 0.05$ ) different between vegetation classes for A soil horizons; however the difference in mean responses between the open savanna and oak forest classes was only 6 to 7 percent (fig. 4). Additionally, the percent biochemically protected C pool was not significantly ( $P > 0.10$ ) related to woody plant canopy cover.

An unexpected and important finding was that the unprotected carbon pool was > 44 percent for all vegetation classes. That is, the dominant fraction of the total carbon pool is determined by abiotic and biotic controls (for example, moisture, temperature, intrinsic biodegradability of inputs, and N availability) on microbial activity (Six and others 2002). Although there is considerable potential for carbon sequestration with woodland conservation and restoration, these carbon stores are not more resilient to disturbances than grassland carbon pools and can be quickly degraded and lost upon oak removal. These findings provide evidence for the underlying mechanisms driving

documented losses of total SOC levels with oak removal on hardwood rangelands (Dahlgren and others 1997).

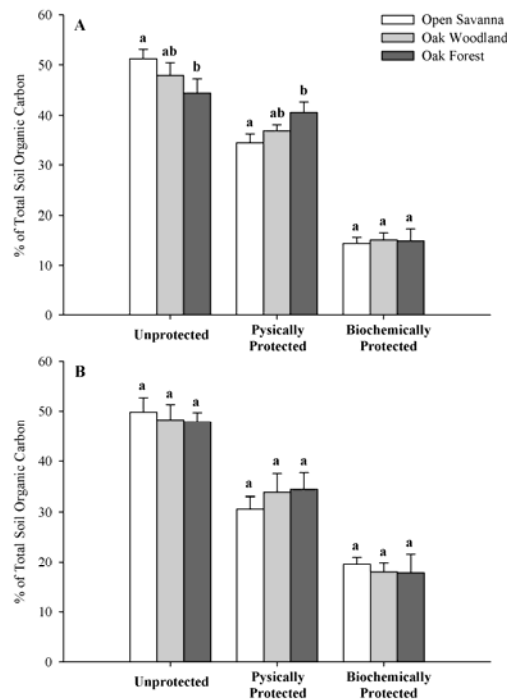


Figure 4—Carbon pool values (fraction of total carbon  $\pm$  1 SE) for the three functional SOC pools for A (A) and AB (B) horizons for each woody plant canopy cover class. For each functional SOC pool, different successive letters indicate significant differences ( $p < 0.05$ ).

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