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Density fractionation and ^{13}C reveal changes in soil carbon following woody encroachment in a desert ecosystem

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Abstract Woody encroachment has dramatically changed land cover patterns in arid and semiarid systems (drylands) worldwide over the past 150 years. This change is known to influence bulk soil carbon (C) pools, but the implications for dynamics and stability of these pools are not well understood. Working in a Chihuahuan Desert C_4 grassland encroached by C_3 creosote bush (*Larrea tridentata*), we used two density fractionation techniques (2 and 7 pool density fractionations) and isotopic analysis to quantify changes in C pools and dynamics among vegetation microsites typical of an encroachment scenario (remnant intact grassland, shrub subcanopies, and in shrub intercanopy spaces within a shrub-encroached area). The C concentration of bulk soils varied with microsite, with almost twice the C in shrub subcanopies as in intercanopy spaces or remnant grasslands. Estimated SOC accumulation rates from *Larrea* encroachment (4.79 g C m^{-2} $year^{-1}$ under canopies and 1.75 g C m^{-2} $year^{-1}$ when intercanopy losses were taken into account) were lower than reported for higher productivity *Prosopis* systems, but still represent a potentially large regional C sink. The composition of soil C varied among microsites, with the shrub subcanopy C composed of proportionally more light fraction C (<1.85 g cm^{-3}) and C that was soluble in sodium polytungstate. Grassland soils contained very little carbonate C compared to shrub subcanopies or shrub intercanopy spaces. Stable isotope analyses indicate that inputs from C_3 shrubs were incorporated into all density fractions, even in heavy fractions in which shrub inputs did not change overall C concentration. The seven density fractionation yielded unexpected $\delta^{13}C$ patterns, where the two heaviest fractions were strongly depleted in ^{13}C, indicating strong fractionation following organic matter inputs. These results suggest that the utility of isotope mixing models for determining input sources may be limited in systems with similar fractionation patterns. We propose a five pool model for dryland soil C that includes a relatively dynamic light fraction, aggregate and heavy fractions that are stable in size but that reflect dynamic inputs and outputs, a potentially large and seasonally dynamic pool of soluble C, and a large pool of carbonate C. Combined, these results suggest that dryland soil C pools may be more dynamic than previously recognized.

Keywords Larrea · Bouteloua · Soil organic matter · Dryland · Carbonates · Soil carbon stabilization · Woody encroachment

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Introduction

Soil organic carbon (SOC) is a major component of the global carbon (C) cycle, accounting for more C than the terrestrial biomass and atmospheric pools combined (Amundson 2001). The annual CO_2 flux from soils to the atmosphere is > 10 times that from fossil fuel combustion (Schlesinger 1997), so small changes in SOC pools have the potential to greatly influence the atmospheric CO_2 concentration and subsequently affect Earth's climate. Arid and semi-arid ecosystems (hereafter 'drylands') cover 40 % of the terrestrial land surface and account for 30–35 % of terrestrial net primary productivity (Bailey 1996; Field et al. 1998), making them a major component of the global C cycle. While SOC *concentrations* in dryland soils are typically low, extensive land cover change and human disturbances in these areas alter the *fluxes* between atmospheric and SOC pools. Integrated over the large geographical extent of drylands, these flux changes may represent a significant source or sink of atmospheric C (Lal 2004). Woody encroachment, an increase in woody plant cover in formerly grass-dominated ecosystems, may currently be dramatically altering the sink strength of dryland soils. Modeling and field-based inventories suggest that geographically extensive woody proliferation in drylands accounts for a potentially large, although highly uncertain, portion of the North American C sink. For example, Pacala et al. (2001) estimate that woody encroachment in drylands accounts for 18–40 % of the C sink in the continental United States. Understanding the current and future dynamics of this terrestrial sink requires understanding both how vegetation change affects SOC pools and controls over the stability of these pools.

Woody encroachment has fundamentally changed many of the world's drylands over the past 150 years (Archer 1994). While the causes of this land cover change are subject to considerable debate, changes in land management practices (particularly increased grazing pressure and decreased fire frequency) appear to be major factors (Archer et al. 2001). Climate change, exotic species, N deposition, and atmospheric CO_2 enrichment may also play a role (Archer 1994, 1995; Van Auken 2000). Several recent syntheses suggest that aboveground C typically increases with woody encroachment. The magnitude of this change is positively related to mean annual precipitation, with net losses in aboveground C possible in very dry sites or with increased fire frequency (Barger et al. 2011; Eldridge et al. 2011; Knapp et al. 2008). A synthetic understanding of belowground C responses to woody encroachment has proven more elusive; the magnitude, and even direction (positive, negative, or neutral) of belowground C change in response to woody encroachment remains difficult to generalize (reviewed in Wessman et al. 2004; Barger et al. 2011). The prevailing dogma for dryland woody encroachment has been that woody plants create "islands of fertility" where SOC and soil nutrients accumulate due to changes in litter input quality and quantity (e.g., Garcia-Moya and McKell 1970; Schlesinger et al. 1990). Woody plants may also promote nutrient accumulation in subcanopy zones by translocating nutrients from intercanopy areas, enhancing deposition from aeolian, fluvial or animal transport processes (Belsky et al. 1989; Okin and Gillette 2001; Weltz et al. 1998; Lajtha and Schlesinger 1986) or slowing organic matter losses through depressed subcanopy decomposition (Throop and Archer 2007). The distribution of inputs may also shift, with greater root biomass in shrub subcanopy patches than intact grasslands (Hibbard et al. 2001), and a deeper distribution of woody roots than herbaceous roots (Jackson et al. 1996). Improving generalizations about the consequence of woody encroachment to SOC pools and dynamics is crucial to reducing uncertainty about ecosystem C storage responses to woody encroachment.

One challenge to understanding and generalizing woody encroachment impacts on SOC is that the majority of SOC analyses in drylands to date has focused on *bulk* SOC pools. SOC exists in various states of chemical, physical, or biological stabilization. As such, SOC consists of pools that vary in turnover rates, from highly labile pools (e.g., surface detritus that often persists for <1 year) to those that persist for decades to millennia (e.g., C in highly stabilized organo-mineral complexes; Trumbore 2000). The controls over the formation and destabilization of organo-mineral complexes are still not well understood, particularly in the context of soil disturbance or changing vegetation or climate (e.g., Diochon and Kellman 2009; Kane et al. 2005). Data on bulk (whole soil) SOC provide a short-term snapshot of C pools, but provide limited insight into long-term C dynamics (Trumbore 2000; Trumbore et al. 1995). In drylands, SOC may accumulate for many decades to centuries

following initial woody encroachment (Liao et al. 2006b; Throop and Archer 2008; Wheeler et al. 2007) and SOC may persist following woody plant removal for >4 decades (McClaran et al. 2008). Understanding controls over SOC stability is crucial for understanding under what conditions SOC will persist, and whether changes in bulk pools are likely to translate into long-term storage. Furthermore, understanding controls over SOC stabilization is crucial for developing and parameterizing models that can accurately predict SOC dynamics under future climate, vegetation, and land management scenarios (e.g., Hatton et al. 2012; Parton et al. 1993, 1988).

A variety of physical, chemical, and biological fractionation techniques have been used to separate out meaningful fractions of SOC that differ in relative stability (Christensen 2002; Crow et al. 2007; McLauchlan and Hobbie 2004). While no single universally accepted method exists, separation of soils into two or more density fractions via floatation provides functionally-relevant information on both associations between organic material and mineral particles and their stability (Baisden et al. 2002; Crow et al. 2007; Sollins et al. 2006). The density of soil particles varies as a function of organic matter concentration, mineral particle density, and particle porosity (Sollins et al. 2009). Previous work in mesic systems suggests that sequential density fractionation (SDF) divides soil into fractions that differ in both mineralogy and organic matter composition (Sollins et al. 2009, 2006). Organic matter concentration typically decreases with increasing particle density, and C:N ratios, $\delta^{13}C$, and other biochemical indices suggest that organic matter associated with denser particles has undergone greater microbial processing than that associated with less dense particles. Furthermore, radiocarbon dating indicates that C associated with denser particles typically has a greater mean residence time (Sollins et al. 2009). To date, SDF has been performed in relatively mesic systems, and it is unclear whether the patterns observed in those systems would hold under the different climate and soil composition of drylands. However, SDF procedures are expensive and time intensive, and thus are typically performed on unreplicated soil samples (e.g., Sollins et al. 2009), limiting their relevance for understanding ecological patterns that differ in time and space. However, SDF procedures could be combined with other less time intensive and expensive measurements (e.g., two pool density fractionation or incubation techniques), thus allowing inferences from SDF to be extended through time or space.

We coupled density fraction techniques and stable isotope analyses to explore changes in SOC composition and input sources following woody encroachment by creosote bush, *Larrea tridentata,* in a former grassland in the northern Chihuahuan Desert in New Mexico, USA. *Larrea* is one of the prominent woody encroachers on shallow soils in lowland deserts throughout the southwestern United States. In contrast to mesquite (*Prosopis* spp.), which has encroached into deeper soils, *Larrea* is not capable of symbiotic N_2 fixation. We performed a two pool density separation on a replicated suite of soils from three microsite types typical of an encroachment scenario (remnant intact grassland, shrub subcanopies, and in shrub intercanopy spaces within a shrub-encroached area; $n = 3$ microsites $\times$ 10 replicates $= 30$), separating soils into commonly-used light fraction ("LF"; particle density <1.85 g cm^{-3}) and heavy fraction ("HF"; >1.85 g cm^{-3}) pools. Soils were sampled to 10 cm depth under the entire subcanopy area (or 1 $\times$ 1 m patches for shrub intercanopy spaces and grassland), thus providing an integrated representation of the subcanopy area and embracing expected patterns of sub-canopy spatial variability (Throop and Archer 2008). To further explore how C was distributed with mineral particle density, we fractionated soils from two of the vegetation microsites (intact grassland and shrub subcanopy) into seven different density fractions, ranging in particle density from <1.65 to >2.65 g cm^{-3} (Sollins et al. 2009). The two density fractionation allowed us to conduct a replicated study quantifying differences in C distribution among microsites, while the more costly and labor intensive seven density fractionation provided more detail about C distribution among fractions differing in particle density. For both fractionation techniques, we used stable isotope analyses to assess the contribution of C_3 and C_4 pathways to soil C pools. Our goal was to explore C pools and potential stabilization processes following land cover change in a desert grassland ecosystem.

Methods

Study location

Soil samples were collected from the Chihuahuan Desert Rangeland Research Center in the northern

Chihuahuan Desert (Doña Ana County, New Mexico, USA; 32°30′N, 106°47′W), where shrub establishment into former grassland has occurred over the past 150 years (Gibbens et al. 2005). The study site forms part of the National Science Foundation's Jornada Basin Long Term Ecological Research site. The climate is arid (MAP = 245 mm, MAT = 14.7 °C), with the majority (>60 %) of precipitation occurring as monsoonal thunderstorms between 1 June and 1 October (Wainwright 2006). Soils were collected from the upper bajada of Mt. Summerford, where the historically dominant C_4 perennial bunchgrasss (black grama, *Bouteloua eriopoda*) has been largely replaced by the evergreen C_3 shrub creosote bush (*Larrea tridentata*) during the past century. Remnant patches of intact black grama grasslands selected for sampling were located slightly upslope, but in close proximity to, areas encroached by creosote bush (*Larrea tridentata*) that were selected for sampling. In areas dominated by creosote bush, shrub interspaces are largely devoid of perennial plants, with the exception of patches of the invasive African grass *Eragrostis lehmanniana*. Areas invaded by *E. lehmanniana* were avoided in the sampling campaigns. Soils at all sites selected for sampling are igneous-derived coarse-loamy alluvium in the Onite-Pajarito association (coarse-loamy mixed superactive thermic Typic Calciargids and Typic Haplocambids). Although historical livestock grazing at the site has been attributed as a primary cause of the grassland to shrubland transition, grazing has been absent from the site since 1982 (Havstad and Schlesinger 2006). Soil sampling focused on surface soils (0–10 and 0–15 cm) as these depths account for a large fraction of soil profile C in deserts (Jobbagy and Jackson 2000). Furthermore, surface soils (<10 cm depth) typically exhibit the most dynamic change in SOC as a response to woody plant establishment or removal in drylands and reported woody encroachment impacts on SOC appear to be typically restricted to <20 cm depths (Barth and Klemmedson 1978; Boutton et al. 2009; McClaran et al. 2008; Tiedemann and Klemmedson 1986).

Density fractionation

A sampling campaign was conducted in November 2010 to characterize the SOC pool difference in response to *Larrea* encroachment. We selected 10 replicates for each of three vegetation microsites ($n = 30$). *Larrea* subcanopy (hereafter 'subcanopy') samples were collected under individual *Larrea* shrubs that were representative of the shrubs present at the site: approximately 2.0 m canopy diameter, at least one canopy diameter from the nearest neighboring *Larrea* or other woody plants, and no evidence of recent surface erosion. Shrub subcanopy soils may have strong bole to dripline gradients in SOC (Throop and Archer 2008). To integrate these spatial patterns in SOC across the entire subcanopy area, we collected all the subcanopy soil to 10 cm depth, homogenized it, and retained a 250 g subsample. For the *Larrea* intercanopy (hereafter 'intercanopy') and intact black grama grassland (hereafter 'grassland') microsites, we obtained all the soil from a 1 m × 1 m patch, homogenized it, and retained a 250 g subsample. Selected microsite patches were at least one canopy diameter from neighboring *Larrea* canopies and had no evidence of recent surface erosional processes or small mammal activity. Prior to bulk sample collection at each microsite replicate, a volumetric soil core to 10 cm depth was obtained for bulk density calculation. Soils were oven dried at 60 °C, passed through a 2 mm sieve, and stored dry until density fractionation. Bulk density was calculated as the mass of the fine earth (<2 mm) fraction divided by the volume of the entire core, thus accounting for volume displaced by >2 mm fragments (Throop et al. 2012).

Soils were separated into two density fractions using sodium polytungstate (SPT) following the procedures of Sollins et al. (2006), using an initial mass of 40 g soil for each microsite sample. Samples were gently shaken in 250 ml centrifuge tubes for 3 h and spun at 1,285 rpm for 25 min. The floating material and supernatant (hereafter 'LF' for light fraction) were aspirated off. Both LF and the remaining heavy fraction (HF) were rinsed multiple times with deionized water and collected on glass fiber filters (Whatman GF/F). An SPT density of 1.85 g cm^{-3} was used because results from the seven density fractionation (below) suggested that this density provided a clear separation between free organic matter and that bound to mineral particles. We refer to this density separation as the "two density fractionation".

To explore the density distribution of C in more detail, two soil samples from contrasting microsites (grassland and shrub subcanopy, $n = 1$ sample/microsite) were subjected to a more detailed SDF procedure that yielded seven density fractions. The

shrub subcanopy soil was collected from the edge of a *Larrea* canopy. Approximately 1 kg of soil was collected with a trowel from the top 15 cm of soil profile at each sampling location. An initial mass of 180 g soil for each sample was shaken (1–3 h) with SPT in a 1 L tube, centrifuged at 3,000 rpm, and the floating material and supernatant was aspirated off and rinsed. This procedure was repeated with sequentially increasing SPT target densities of 1.65, 1.85, 2.00, 2.20, 2.45, and 2.65 g cm^{-3} (actual values ± 0.03 g cm^{-3} of target densities); for expediency we refer to the resulting density fractions by the maximum particle density (e.g. 1.65, 1.85 g cm^{-3}). We refer to this sequential density separation as the "seven density fractionation".

Analytical Methods

For both density fractionation procedures, samples were dried at 60 °C, weighed, and ground using a ball mill. Subsamples of each density fraction and the bulk soil were analyzed in triplicate for C and N concentration on an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) at New Mexico State University. A second set of replicate subsamples were acid fumigated prior to CN analysis to remove any carbonates (Harris et al. 2001); carbonate concentration of the soils was calculated from the difference in C concentration between fumigated and non-fumigated samples. Analysis of internal standards indicated an analytical error of <3 % for C. In addition to mass-based concentration of C and N of individual fractions (e.g., mg C g^{-1} of a fraction), C and N concentration of individual fractions relative to bulk soil were calculated from fraction C or N concentration and total fraction mass data (e.g., mg C g^{-1} bulk soil). Samples were analyzed for $\delta^{13}C$ with a coupled continuous-flow elemental analyzer-isotope ratio mass spectrometer (EA-IRMS) system with a Carlo-Erba model 1108 EA interfaced to a Thermo-Finnigan Delta Plus XP IRMS at the Light Stable Isotope Facility of the University of California, Santa Cruz. ^{13}C data are reported relative to the Pee Dee Belemnite (PDB) standard. Precision of in-house standards, which had been calibrated using international standards, was typically better that 0.2 per mil for $\delta^{13}C$. One standard was run for every ten unknowns, and two blanks and conditioning and calibration standards were included at the beginning and end of each run. Samples were run in duplicate and were always within the range of the standards.

Statistical analyses on the two density fractionation samples were performed in JMP 7.0.1 (SAS Institute, Cary, NC). One-way ANOVA procedures were used to test for among-vegetation microsite differences in response variables. LF, HF, and bulk pools were analyzed separately. Significance of differences among means were assessed with a post hoc Student–Newman–Kuels test. No statistical analyses were performed on the seven density fractionation samples due to lack of replication.

Results

Carbon and nitrogen pools

Organic C concentrations in the bulk soil samples differed among vegetation microsites, with shrub subcanopy soils averaging nearly twice that of grassland soils and nearly three times that of shrub intercanopy soils (Fig. 1; $F_{2,27} = 10.40$, $P = 0.0004$). Bulk soils also differed in concentration of inorganic C as $CaCO_3$ ($F_{2,27} = 9.08$, $P = 0.001$), with essentially no carbonates in grasslands and on average nearly twice as much carbonate C in intercanopy soils as in subcanopy soils (1.58 ± 0.412 and 0.84 ± 0.240 mg $CaCO_3$-C g^{-1} bulk soil, respectively; mean ± SE). Consequently, total C (organic + inorganic) concentration was

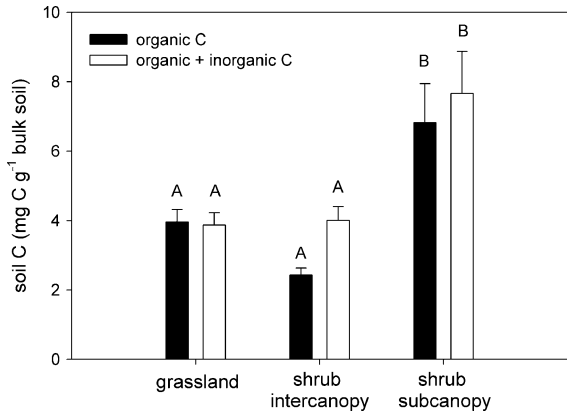

Fig. 1 Soil organic C and total (inorganic and organic) soil C in three vegetation microsites at the Jornada Basin LTER. *Error bars* are standard error for microsite replicates ($n = 10$ replicates microsite^{-1}). Within each of the two C groupings (organic C and organic + inorganic C), different letters indicate a significant difference among vegetation microsites

significantly greater in the shrub subcanopy than the two other microsites (Fig. 1; $F_{2,27} = 8.00$, $P = 0.0019$). Bulk density was significantly greater in the two shrub microsites (subcanopy: 0.98 ± 0.031, intercanopy: 0.99 ± 0.026 g cm^{-3}) than the grassland (0.83 ± 0.035 g cm^{-3}; $F_{2,27} = 8.76$, $P = 0.001$), magnifying the difference in C among microsites when total C was expressed on an areal basis (326 ± 28.9, 236 ± 14.5, and 662 ± 113.8 g C m^{-2} to 10 cm depth for grassland, intercanopy, and subcanopy, respectively; $F_{2,27} = 10.76$, $P = 0.0004$).

Patterns of C in the two density fractionation study were strongly affected by vegetation microsite. There was proportionally less LF dry mass in the shrub intercanopy microsite than the other two microsites ($F_{2,27} = 6.42$, $P = 0.005$), although there was no difference in organic C concentration of the LF among microsites ($F_{2,27} = 0.41$, $P = 0.67$). Consequently, the concentration of LF organic C in the bulk soil (mg LF C g^{-1} bulk soil) was significantly greater in the subcanopy than the intercanopy microsite (Fig. 2; $F_{2,27} = 7.00$, $P = 0.004$). For the HF, proportional dry mass was greater in the intercanopy than subcanopy ($F_{2,27} = 3.43$, $P = 0.047$) and organic C concentration of the HF was lower in the intercanopy than the other two microsites ($F_{2,27} = 5.93$, $P = 0.007$). Consequently, the concentration of HF organic C in the bulk soil (mg HF C g^{-1} bulk soil) was significantly lower in the intercanopy than the other two microsites (Fig. 2; $F_{2,27} = 5.96$, $P = 0.007$). More soluble organic C was mobilized by SPT in shrub subcanopy soils than in the other two soils (Fig. 2; $F_{2,27} = 9.43$, $P = 0.0008$), and this was roughly equal in magnitude to HF C in shrub subcanopy soils. Pedogenic carbonates were found in significant quantities in the two shrub microsite soils but not in the grassland soils ($F_{2,27} = 3.67$, $P = 0.039$), with means trending higher in intercanopy soils than in shrub subcanopy soils. Trends in soil N concentration followed those of soil organic C (Fig. 3a; LF: $F_{2,27} = 7.59$, $P = 0.002$; HF: $F_{2,27} = 4.83$, $P = 0.016$). Organic C:N of LF grassland soils was significantly greater than organic C:N of either subcanopy or intercanopy shrub LF soils (Fig. 3b; $F_{2,27} = 19.51$, $P < 0.0001$), while organic C:N decreased from grassland to subcanopy to intercanopy (Fig. 3b; $F_{2,27} = 14.93$, $P = 0.001$).

Results from the seven density fractionation provide further insight into differences in C distribution and stabilization between the grassland and

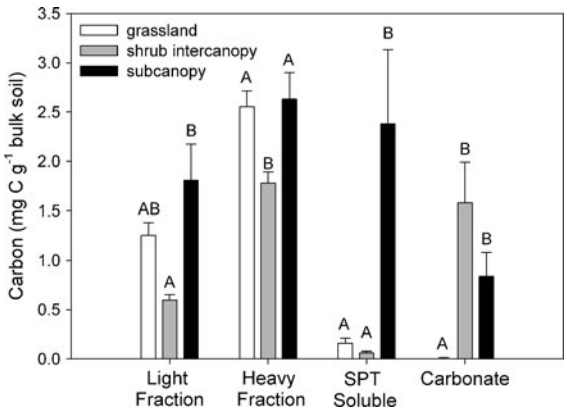

Fig. 2 Soil carbon in light, heavy, soluble, and carbonate fractions in the three vegetation microsites at the Jornada Basin LTER. Results are from the two density fractionation. *Error bars* are standard error for microsite replicates ($n = 10$ replicates microsite^{-1}). Within a fraction, *different letters* indicate a significant difference among vegetation microsites

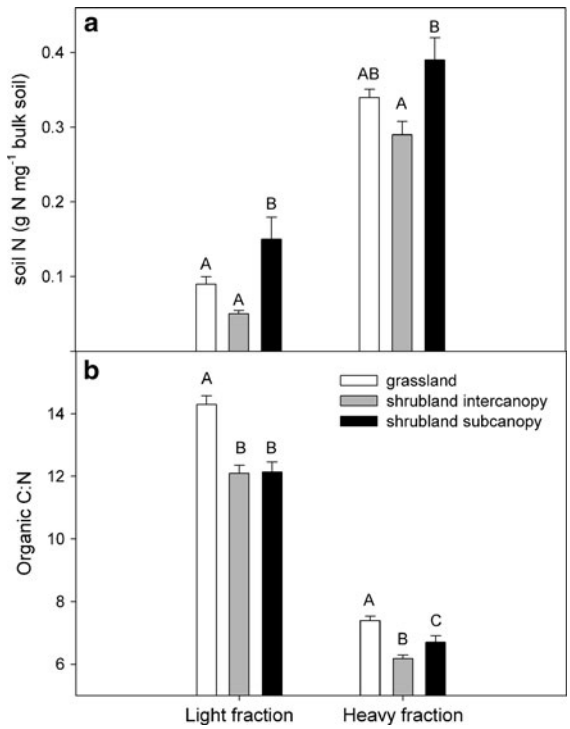

Fig. 3 Patterns of **a** soil organic N and **b** soil C:N in the three vegetation microsites at the Jornada Basin LTER. Results are from the two density fractionation. *Error bars* are standard error for microsite replicates ($n = 10$ replicates microsite^{-1}). Within a fraction, *different letters* indicate a significant difference among vegetation microsites

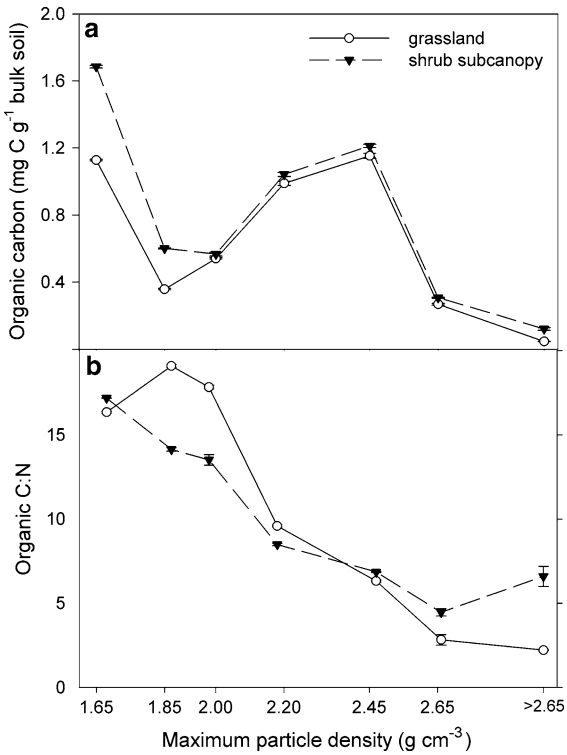

Fig. 4 Patterns of **a** soil organic carbon and **b** soil organic C:N for the seven density fractionation from shrub subcanopy and grass microsites at the Jornada Basin LTER. Error bars are standard error for analytical replicates of each sample (n = 3 replicates sample^{-1})

shrub subcanopy. For the two lightest fractions (1.65 and 1.85 g cm^{-3}), organic C concentration (mg C g^{-1} bulk soil) was greater in the shrub subcanopy soil than in grassland soil (Fig. 4a). For all heavier density fractions, organic C was similar between the two microsites (Fig. 4a). However, C:N patterns of density fractions were more complex (Fig. 4b). In the two density fractionation, LF C:N of grassland soils was greater than that of the shrub subcanopy soils (Fig. 3b). The seven density fractionation illustrated that C:N in the LF was driven by the 1.85 g cm^{-3} fraction rather than the 1.65 g cm^{-3} fraction (Fig. 4b). Similarly, while C:N of HFs in the two density fractionation were similar between grass and shrub subcanopy sites, C:N of specific heavy density fractions in the seven density fractionation differed.

Stable isotopes

The bulk shrub subcanopy soil was depleted in δ^{13}C relative to the bulk grassland soil (−20.54 ‰ and

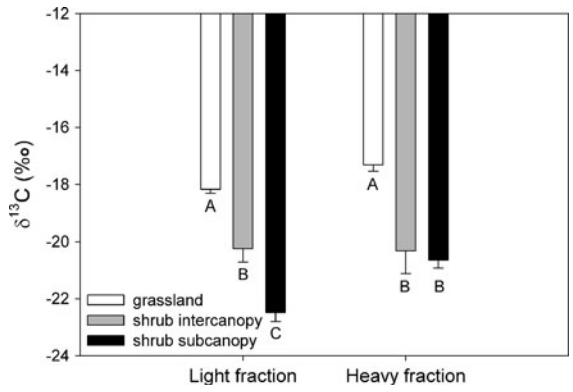

Fig. 5 δ^{13}C in light (<1.85 g cm^{-3}) and heavy (>1.85 g cm^{-3}) soil fractions in the three vegetation microsites at the Jornada Basin LTER. *Error bars* are standard error for microsite replicates (n = 10 replicates microsite^{-1}). Within a fraction, *different letters* indicate a significant difference among vegetation microsites

−18.17 ‰, respectively). In the two density fractionation, both LF and HF were depleted of δ^{13}C in shrub subcanopy microsites relative to grassland microsites (Fig. 5; LF: $F_{2,27} = 40.75$, $P < 0.0001$; HF: $F_{2,27} = 13.24$, $P < 0.0001$). LF of intercanopy soils was intermediate between grassland and shrub subcanopy values, while HF values of intercanopy soils did not differ significantly from shrub subcanopy soils. Data from the seven density fractionation showed that all density fractions of the shrub subcanopy soil were ^{13}C depleted compared to the grassland soil (Fig. 6). For the lightest fraction, the subcanopy soil was depleted in δ^{13}C relative to the grassland soil by 4.9 ‰. For all other fractions, the subcanopy soil was depleted relative to the grassland by approximately 1 ‰. Both

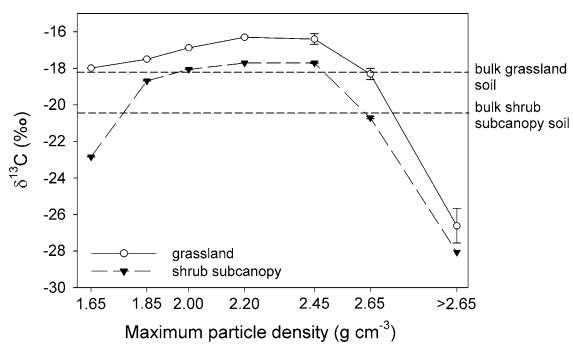

Fig. 6 δ^{13}C for the seven density fractionation from shrub subcanopy and grass microsites at the Jornada Basin LTER. Error bars are standard error for analytical replicates of each sample (n = 2 replicates sample^{-1})

soils exhibited a general increase in $\delta^{13}C$ with increasing fraction density until the 2.45 g cm^{-3} fraction, followed by substantial declines in $\delta^{13}C$ in the two densest fractions, such that the densest fraction was more depleted in $\delta^{13}C$ than C_3 *Larrea* leaves and leaf litter (−24.6 ‰ and −24.8 ‰ for leaves and litter, respectively; Rasmussen and White 2010).

Discussion

Grass and shrub contributions to C pools

Increases in SOC under shrubs at our study site are congruent with the well-described island of fertility effect (Garcia-Moya and McKell 1970) that sometimes includes losses of C from intercanopy soils following shrub encroachment (Schlesinger et al. 1990). While we report our results primarily on a per mass basis, greater bulk density in the shrub microsites magnify the positive impact of shrubs on areally-based C estimates. Both density fractionation techniques suggest that increases in C under shrubs are driven by light fractions composed of plant debris and entrained mineral material. In contrast, C in the heavy fractions remained essentially unchanged between the subcanopy and grassland vegetation microsites. Although *P. glandulosa* encroachment led to increases in particulate organic matter C within a few decades of encroachment in south Texas, accumulation of C in more stabilized macroaggregates increased dramatically, but only in stands <80 years old (Liao et al. 2006b). Incorporation of C into heavy fractions may likewise occur in the future following continued growth and organic inputs from *Larrea.* Our stable isotope data suggest that while the heavy fraction C concentration remains quite static relative to vegetation change, the isotopic composition of all fractions, including the heavy ones, show shifts in isotopic signature consistent with C_3 inputs into these pools. Thus, even the heavy fractions, which are thought to be most stabilized (Sollins et al. 2009), appear to have dynamic inputs and outputs of recently-derived organic material.

Although the concentration of C in our dryland study system is quite low, the magnitude and rate of change in SOC in response to woody encroachment were quite high. Shrub subcanopy microsites averaged 335 g C m^{-2} more than grassland sites, while shrub intercanopy sites averaged 90 g C m^{-2} less than grassland sites. Assuming that encroachment at this site occurred in the last 70 years (Gibbens et al. 2005) and linear C accumulation under shrubs through time, we estimate a subcanopy accumulation rate of 4.8 g C m^{-2} $year^{-1}$ (to 10 cm depth). If *Larrea* canopies account for 50 % of the land area (Rango et al. 2005), landscape-level accumulation (subtracting out losses in intercanopy areas) would be 1.75 g C m^{-2} $year^{-1}$. These values are much lower than values reported for N-fixing *Prosopis glandulosa* in south Texas (10–30 g C m^{-2} $year^{-1}$ to 15 cm depth; Liao et al. 2006b) or *P. velutina* in the Sonoran Desert (12 g m^{-2} $year^{-1}$ to 20 cm depth; Wheeler et al. 2007). However, Throop and Archer (2008) point out that single-point sampling under shrub canopies can drastically overestimate rates of C accumulation, and suggest that C accumulates under *P. velutina* in the Sonoran Desert at only 2.6 g C m^{-2} $year^{-1}$ to 20 cm depth when spatial patterns are taken into account. Our method of sampling all the subcanopy soil integrates across the entire canopy area, and thus is most equivalent to the Throop and Archer (2008) estimate. This would translate into a substantial flux of C if similar patterns are found in the >19 million ha of southwestern North America where *Larrea* is the dominant shrub (Van Auken 2000).

Stable isotope analyses can be used to characterize the contribution of plants with C_3 and C_4 photosynthetic pathways to soil C pools, and woody expansion in southwestern US drylands have been particularly amenable to these analyses due to C_3 shrub encroachment into former C_4 grasslands (Boutton et al. 1998). Woody encroachment at our study site leads to an approximate −2 ‰ shift in $\delta^{13}C$ for bulk soils, similar to that caused by small *Prosopis velutina* shrubs encroaching into Sonoran Desert grasslands (Wheeler et al. 2007) but smaller than the −3 ‰ to −6 ‰ shift following *P. glandulosa* encroachment in Texas (Liao et al. 2006a). However, although our soil collection locations in the remnant C_4 grasslands were devoid of C_3 shrubs in close proximity, $\delta^{13}C$ of bulk grassland soils (−18.2 ‰) was depleted in ^{13}C relative to C_4 grass inputs (−14.2 ‰). This ^{13}C depletion can not be explained by isotopic fractionation during SOM formation, as SOM is typically ^{13}C enriched due to preferential respiration of light ^{12}C (Ehleringer et al. 2000). Scattered C_3 shrubs, annual C_3 forbs present in high favorable precipitation years, or erosional inputs

from C_3 shrubs found upslope (e.g., *Juniperous* and *Quercus*) may account for this. Alternatively, low $^{13}\delta$C values may reflect disproportionate retention of organic compounds such as lignin that are typically depleted in ^{13}C (Benner et al. 1987).

Increases in δ^{13}C with increasing density fraction (up to the 2.45 g cm^{-3} fraction) are consistent with previous observations that have been interpreted as fractionation during microbial processing, although the dramatic drop in δ^{13}C in the two heaviest fractions has not been reported in other studies (Dijkstra et al. 2006; Sollins et al. 2009). Residual $CaCO_3$ following acid fumigation is not an explanation, as the isotopic signature of $CaCO_3$ is relatively enriched in ^{13}C (Monger et al. 2009). The low δ^{13}C could reflect a disproportionate retention of material with low δ^{13}C or an unknown fractionation source that preferentially removed ^{13}C. With respect to the first possibility, the two heaviest pools may be enriched in lignin, which is generally depleted in ^{13}C relative to bulk litter (Benner et al. 1987). However, while lignin is relatively resistant to decay in surface litters (e.g., Meentemeyer 1978), recent studies suggest that it is not preferentially preserved in soils and exerts little influence on the stability of mineral-associated soil fractions (reviewed in Thevenot et al. 2010). Furthermore, C stabilized onto mineral fractions generally has an isotopic signature more similar to microbially processed organic matter than to plant compounds (Grandy and Neff 2008; Kiem and Kögel-Knabner 2003).

Isotope mixing models are used on bulk soils and, increasingly, following physical or density separation techniques, to assess the relative contribution of C_3 and C_4 sources to SOC pools, but our results reveal some difficulties in model interpretation posed by fractionation during SOM formation. Ideally we would have a pure C_4 grassland soil and a C_3 shrub soil with no previous C_4 history to serve as mixing model end-members. Such pure end-members can be obtained in controlled cropping systems, yet are rare in natural systems, and thus plant isotopic signatures are generally used as at least one, if not both, end-members in mixing models. However, SOM is generally 2–5 ‰ δ^{13}C isotopically heavier than plant inputs due to fractionation during decomposition (Krull et al. 2002; Stevenson et al. 2005); isotopic differences among our seven density fractions suggest such fractionation. To estimate the C_3 and C_4 contribution to SOC, we used the lightest fraction material from the grassland and shrub subcanopy. This end-member mixing model suggests that roughly 50 % shrub subcanopy C is derived from C_3 inputs. Calculating contributions to stable heavier fraction C is more complex. The large clay-rich fraction (2.45 g cm^{-3}) in the grassland was enriched by 1.6 ‰ compared to the lightest fraction. Assuming that the same fractionation would occur for a pure shrub signal, we calculated that heavy fraction C in the shrub subcanopy reflects a 70 % contribution of residual C_4-C. These rough calculations suggest input of C_3 material into both labile and more stable C pools.

Comparison with soils from more mesic environments

To gain insight into differences between processes in drylands and better studied mesic systems, we compared our seven density fractionation results with a broader survey of soils from more mesic environments reported in Sollins et al. (2009). As expected, organic C in our desert soils was low compared to more mesic and forested ecosystems (Fig. 7a). Jornada shrub subcanopy soils had a higher percent of total C in the lightest fraction (41 %) than the other soils, and the Jornada grassland had as high a percent of C in the lightest fraction material (33 %) as the highest forests measured. While mineralogy and clay content may drive some of these differences (Torn et al. 1997), climate controls on litter vs. SOM decomposition processes may also play a role. The tropical dry forest shows a relatively small proportion of C in the lightest fraction; this suggests that the desert soils have conditions more favorable for SOM degradation or else that a greater proportion of desert litter decomposes efficiently to CO_2 and is not stabilized in soil heavy fractions. The low root biomass and seasonally low root activity likely lead to lower aggregate stabilization in drylands, and indeed, the dryland soils were unique in not having spikes in C in the 1.85–2.4 g cm^{-3} fractions, which are typically dominated by aggregates (Hatton et al. 2012). The isotopic composition of our dryland soils differed strikingly from previously studied mesic and forested ecosystems, suggesting differences both in input source and SOM stabilization processes. Except for the heaviest fraction, the dryland

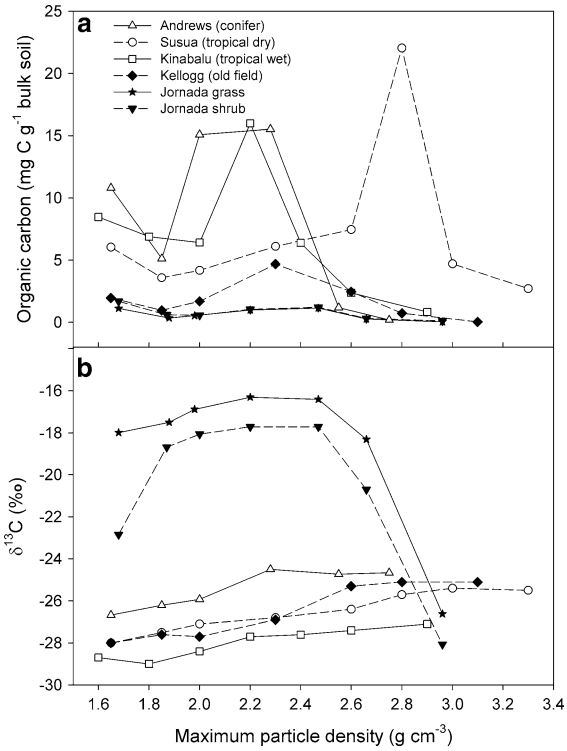

Fig. 7 Patterns of **a** soil organic carbon and **b** $\delta^{13}C$ in soil sequential density fractions from shrub and grass microsites at the Jornada Basin LTER plotted in comparison with data from soils studied by Sollins et al. (2009). Grassland and shrub sites are plotted with *closed symbols*, forests with *open symbols*

soils were considerably enriched in ^{13}C relative to the other soils due to significant C_4 plant inputs (Fig. 7b). While all soils follow the pattern of ^{13}C enrichment with increasing density in the lighter fractions, the dramatic ^{13}C depletion of the two heaviest fractions is particularly striking given that this pattern occurred only in the dryland soils.

Dryland soluble C pools

Many density fraction studies using SPT have noted losses of particulate or soluble C during the fractionation procedure. Kramer et al. (2009) reported losses of under 8 % for several soils during an overnight soaking experiment in SPT, perhaps due to particulate loss during the fractionation procedure. Indeed, Crow et al. (2007) reported larger losses of C (mean = 20 %) from the same Pacific Northwest coniferous soils after a larger-scale density fractionation, perhaps due to the greater number of steps involved during that experiment. However, patterns of C loss in our two density fractionation with SPT appear to be too great to be attributable to laboratory particulate losses during a single density separation, and the microsite pattern of soluble C loss suggests an alternate, more ecologically meaningful explanation. Because the largest soluble C losses occurred in shrub subcanopy soils (35 % of total C on a per mass basis versus 2–4 % in grass or intercanopy soils), we hypothesize that microbial activity and root exudation during periods where soils are drying, but still wet enough for biotic activity, lead to the build-up of soluble organic acids in surface soils. With the onset of rain, these products are likely mobilized or respired. Results of the Crow et al. (2007) study might also reflect stores of soluble C, as these soils were collected during the prolonged summer dry season in the Pacific Northwest. An alternative explanation, that C losses were composed of residual $CaCO_3$, is unlikely due to both isotopic results (reported $\delta^{13}C$ of CaCO3 is −12 to +2 ‰ at our study site; Monger et al. 2009) and the disparity between the distribution of $CaCO_3$ and SPT soluble C among vegetation microsites. Support for our hypothesis of a soluble, perhaps seasonal, C pool comes from studies of streamwater chemistry in ecosystems with marked seasonality of precipitation where increased DOC flushes occur during rains following dry periods (Brooks et al. 2007; van Verseveld et al. 2009; Vanderbilt et al. 2003), also likely due to a build up of small organic molecules as soils are drying. The existence of a pool of potentially mobilized SOC in drylands has significant implications for our understanding of mechanisms of SOC stabilization.

Dryland carbonate C pools

Carbonates are a significant C pool both locally and globally, with soil carbonates accounting for the third largest pool in the global C cycle (Schlesinger 1997). Results from this study of surface soils indicate microsite differences in carbonates, with shrub intercanopy soils having greater carbonate concentration than grasslands or shrub subcanopies. Given the same parent material for all soils, we hypothesize that greater carbonates in intercanopy soils is related to erosion of surface horizons (Wilcox et al. 1996) rather than to microsite differences in carbonate formation. Our estimates of bulk SOC changes suggest that accumulation rates under *Larrea* canopies (4.79 g

C m^{-2} $year^{-1}$) are greater than carbonate accumulation rates (0.012–1.3 g C m^{-2} $year^{-1}$; Monger and Martinez-Rios 2000), and SOC accumulation rates are likely greater than carbonates even when intercanopy SOC losses are accounted for (1.75 g C m^{-2} $year^{-1}$).

Conceptual model of dryland soil carbon

Models of SOM dynamics have used different numbers of pools, defined in different ways, to represent fractions of organic matter that are chemically or biophysically distinct and have different turnover rates, even when it is generally acknowledged that turnover times and pools are likely continuous, not discrete. For example, the CENTURY model has been widely used to represent soil C pools based on three compartments for SOM (active, slow and passive) with different potential decomposition rates defined on a theoretical basis rather than experimentally (Parton et al. 1993, 1988). Hatton et al. (2012) built on this conceptual framework, proposing a similar model for forest SOM based on density fractions. Their model contains a light fraction composed of plant fragments not associated with minerals (equivalent to our LF), aggregates or organic matter associated with light clays (1.85–2.4 g cm^{-3}), and primary mineral particles coated with pedogenic oxides and patches of organic matter (>2.4 g cm^{-3}). This model provides a testable and simple framework for understanding soil C pools and their dynamics.

Results from our study suggest that two other pools should be added to this conceptual model in dryland ecosystems: the seasonally soluble pool and carbonates (Fig. 8). We expect all five pools to vary considerably among dryland ecosystems that differ in climate and vegetative regimes, and also we expect that local spatial heterogeneity will generally increase dramatically in these pools with conversion of grassland to shrubland, as we found in this study. In this model, light fraction and root exudate material can decompose into a soluble, but not mobilized pool, in soil or can contribute to aggregate or mineral-associated C. Aggregate and organo-mineral complexes together comprise a heavy fraction (>1.85 g cm^{-3}) pool, and it may be difficult to draw clear distinctions between these pools.

In our study, the soluble pool and the light fraction pools both increased with woody encroachment,

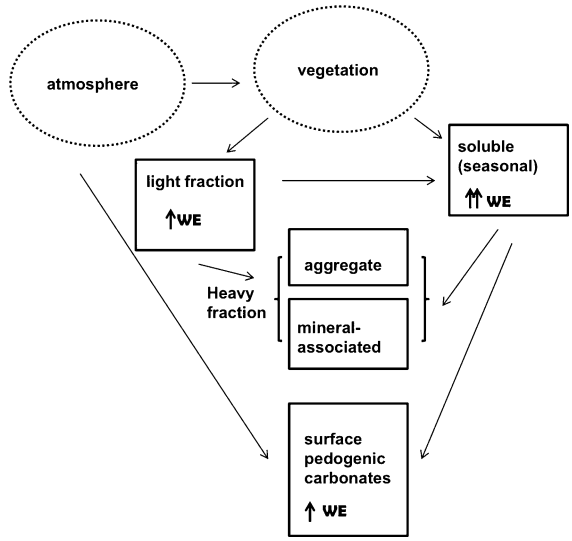

Fig. 8 The proposed 5-pool model of dryland surface soil carbon. In this model, carbonate dust, CO_2 from the atmosphere, and plant root and litter decomposition activity can influence the formation of pedogenic carbonates. Light fraction (<1.85 g cm^{-3}) material can decompose into a soluble but not mobilized pool in soil or can contribute to aggregate or mineral-associated C via microbial activity and transport. Aggregate and organo-mineral complexes together comprise the heavy fraction (>1.85 g cm^{-3}) pool. With woody encroachment (WE), the soluble pool and, at least initially, the light fraction pools increase. Surface carbonate C may increase with WE due to surface soil erosion, exposing lower horizon carbonates

suggesting that woody encroachment at in this system has significant impacts on short-term C dynamics. Increases in carbonate-C with woody encroachment may reflect increased erosion of surface soils with the loss of grasses, while changes in the isotopic composition of the heavy fraction indicate that this fraction reflects dynamic inputs and outputs. Understanding the processes and rates of C stabilization in drylands are crucial for estimating the current and future dynamics of C pools in globally extensive drylands, particularly in light of dramatic land cover changes due to woody encroachment and the current uncertainty of the role of this land cover change as a terrestrial C sink.

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References

Amundson R (2001) The carbon budget in soils. Annu Rev Earth Pl Sc 29:535–562

Archer S (1994) Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Vavra M, Laycock WA, Pieper RD (eds) Ecological implications of livestock herbivory in the West. Soc Range Manag, Denver, CO, pp 13–68

Archer S (1995) Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: Reconstructing the past and predicting the future. Ecoscience 2:83–99

Archer S, Boutton T, Hibbard K (2001) Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schultz E, Harrison S, Heiman M et al (eds) Global biogeochemical cycles in the climate system. Academic Press, San Diego, pp 115–137

Bailey RG (1996) Ecosystem geography. Springer, New York

Baisden WT, Amundson R, Cook AC, Brenner DL (2002) Turnover and storage of C and N in five density fractions from California annual grassland surface soils. Global Biogeochem Cy 16:1117. doi:10.1029/2001GB001822

Barger NN, Archer SR, Campbell JL, Huang CH, Morton JA, Knapp AK (2011) Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. J Geophys Res Biogeo. doi:10.1029/2010JG001506

Barth RC, Klemmedson JO (1978) Shrub-induced spatial patterns of dry matter, nitrogen, and organic carbon. Soil Sci Soc Am J 42:804–809

Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM (1989) The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. J Appl Ecol 26:1005–1024

Benner R, Fogel ML, Sprague EK, Hodson RE (1987) Depletion of ^{13}C in lignin and its implications for stable carbon isotope studies. Nature 329:708–710

Boutton TW, Archer SR, Midwood AJ, Zitzer SF, Bol R (1998) $\delta^{13}C$ values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. Geoderma 82:5–41

Boutton TW, Liao JD, Filley TR, Archer SR (2009) Belowground carbon storage and dynamics accompanying woody plant encroachment in a subtropical savanna. In: Lal R, Follett R (eds) Soil carbon sequestration and the greenhouse effect. 2nd edn. Soil Science Society of America, Madison, pp 181–205

Brooks PD, Haas PA, Huth AK (2007) Seasonal variability in the concentration and flux of organic matter and inorganic nitrogen in a semiarid catchment, San Pedro River, Arizona. J Geophys Res 112:G03S04. doi:10.1029/2006jg000275

Christensen BT (2002) Physical fractionation of soil and structural and functional complexity in organic matter turnover. Eur J Soil Sci 52:345–353

Crow SE, Swanston C, Lajtha K, Brooks JR, Keirstead H (2007) Density fractionation of forest soils: Methodological questions and interpretation of incubation results and turnover time in an ecosystem context. Biogeochemistry 85:69–90

Dijkstra P, Ishizu A, Doucett R, Hart S, Schwartz E, Menyailo O, Hungate B (2006) ^{13}C and ^{15}N natural abundance of the soil microbial biomass. Soil Biol Biochem 38:3257–3266. doi:10.1016/j.soilbio.2006.04.005

Diochon AC, Kellman L (2009) Physical fractionation of soil organic matter: Destabilization of deep soil carbon following harvesting of a temperate coniferous forest. J Geophys Res 114:G01016

Ehleringer JR, Buchmann N, Flanagan LB (2000) Carbon isotope ratios in belowground carbon cycle processes. Ecol Appl 10:412–422

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol Lett 14:709–722. doi:10.1111/j.1461-0248.2011.01630.x

Field C, Behrenfeld M, Randerson J, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281:237–240

Garcia-Moya E, McKell CM (1970) Contributions of shrubs to the nitrogen economy of a desert wash plant community. Ecology 51:81–88

Gibbens RP, McNeely RP, Havstad KM, Beck RF, Nolen B (2005) Vegetation changes in the Jornada Basin from 1858 to 1998. J Arid Environ 61:651–668

Grandy AS, Neff JC (2008) Molecular C dynamics downstream: The biochemical decomposition sequence and its impact on soil organic matter structure and function. Sci Total Environ 404:297–307. doi:10.1016.j.scitotenv.2007.11.013

Harris D, Horwath WR, van Kessel C (2001) Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. Soil Sci Soc Am J 65:1853–1856

Hatton P-J, Kleber M, Zeller B, Moni C, Plante AF, Townsend K, Gelhaye L, Lajtha K, Derrien D (2012) Transfer of litter-derived N to soil mineral–organic associations: evidence from decadal ^{15}N tracer experiments. Org Geochem 42:1489–1501. doi:10.1016/j.orggeochem.2011.05.002

Havstad KM, Schlesinger WH (2006) Introduction. In: Havstad KM, Huenneke LF, Schlesinger WH (eds) Structure and function of a Chihuahuan Desert ecosystem: the Jornada Basin long-term ecological research site. Oxford University Press, New York, pp 3–14

Hibbard KA, Archer S, Schimel DS, Valentine DW (2001) Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82:1999–2011

Jackson R, Canadell J, Ehleringer J, Mooney H, Sala O, Schulze E (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411

Jobbagy E, Jackson R (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10:423–436

Kane ES, Valentine DW, Schuur EAG, Dutta K (2005) Soil carbon stabilization along climate and stand productivity gradients in black spruce forests of interior Alaska. Can J For Res 35:2118–2129

Kiem R, Kögel-Knabner I (2003) Contribution of lignin and polysaccharides to the refractory carbon pool in C-depleted arable soils. Soil Biol Biochem 35:101–118

Knapp AK, Briggs JM, Collins SL, Archer SR, Bret-Harte MS, Ewers BE, Peters DP, Young DR, Shaver GR, Pendall E, Cleary MB (2008) Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Glob Change Biol 14:615–623. doi:10.1111/j.1365-2486.2007.01512.x

Kramer MG, Lajtha K, Thomas G, Sollins P (2009) Contamination effects on soil density fractions from high N or C content sodium polytungstate. Biogeochemistry 92:177–181

Krull ES, Bestland EA, Gates WP (2002) Soil organic matter decomposition and turnover in a tropical ultisol: evidence from $\delta^{13}C$, $\delta^{15}N$ and geochemistry. Radiocarbon 44: 93–112

Lajtha K, Schlesinger WH (1986) Plant response to variations in nitrogen availability in a desert shrubland community. Biogeochemistry 2:29–37

Lal R (2004) Carbon sequestration in dryland ecosystems. Environ Manag 33:528–544

Liao JD, Boutton TW, Jastrow JD (2006a) Organic matter turnover in soil physical fractions following woody plant invasion of grassland: Evidence from natural ^{13}C and ^{15}N. Soil Biol Biochem 38:3197–3210

Liao JD, Boutton TW, Jastrow JD (2006b) Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland. Soil Biol Biochem 38:3184–3196

McClaran MP, Moore-Kucera J, Martens DA, van Haren J, Marsh SE (2008) Soil carbon and nitrogen in relation to shrub size and death in a semi-arid grassland. Geoderma 148:60–68

McLauchlan KK, Hobbie SE (2004) Comparison of labile soil organic matter fractionation techniques. Soil Sci Soc Am J 68:1616–1625

Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472

Monger HC, Martinez-Rios JJ (2000) Inorganic carbon sequestration in grazing lands. In: Kimble JM, Lal R (eds) Follett RF. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Lewis Publishers, Boca Raton, pp 87–118

Monger HC, Cole DR, Buck BJ, Gallegos RA (2009) Scale and the isotopic record of C4 plants in pedogenic carbonate: from the biome to the rhizosphere. Ecology 90:1498–1511. doi:10.1890/08-0670.1

Okin GS, Gillette DA (2001) Distribution of vegetation in wind-dominated landscapes: implications for wind erosion modeling and landscape processes. J Geophys Res 106(D9):9673–9684

Pacala SW, Hurtt GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath L, Sundquist ET, Stallard RF, Ciais P, Moorcroft P, Caspersen JP, Shevliakova E, Moore B, Kohlmaier G, Holland E, Gloor M, Harmon ME, Fan S-M, Sarmiento JL, Goodale CL, Schimel D, Field CB (2001) Consistent land- and atmosphere-based U.S. carbon sink estimates. Science 292:2316–2320

Parton WJ, Stewart JWB, Cole CV (1988) Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5:109–131

Parton WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut J-C, Seastedt T, Gardia Moya E, Kamnalrut A, Kinymario JI (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochem Cy 7:785–809

Rango A, Huenneke L, Buonopane M, Herrick JE, Havstad KM (2005) Using historic data to assess effectiveness of shrub removal in southern New Mexico. J Arid Environ 62:75–91

Rasmussen C, White DA II (2010) Vegetation effects on soil organic carbon quality in an arid hyperthermic ecosystem. Soil Sci 175:438–446

Schlesinger WH (1997) Biogeochemistry: an analysis of global change, 2nd edn. Academic Press, San Diego

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. Science 247:1043–1048

Sollins P, Swanston C, Kleber M, Filley T, Kramer M, Crow S, Caldwell BA, Lajtha K, Bowden R (2006) Organic C and N stabilization in a forest soil: Evidence from sequential density fractionation. Soil Biol Biochem 38:3313–3324

Sollins P, Kramer MG, Swanston C, Lajtha K, Filley T, Aufdenkampe AK, Wagai R, Bowden R (2009) Sequential density fractionation across soils of contrasting mineralogy: evidence for both microbial- and mineral-controlled soil organic matter stabilization. Biogeochemistry 96:209–231

Stevenson BA, Kelly EF, McDonald EV, Busacca AJ (2005) The stable carbon isotope composition of soil organic carbon and pedogenic carbonates along a bioclimatic gradient in the Palouse region, Washington State, USA. Geoderma 124:37–47

Thevenot M, Dignac M-F, Rumpel C (2010) Fate of lignins in soils: a review. Soil Biol Biochem 42:1200–1211

Throop HL, Archer SR (2007) Interrelationships among shrub encroachment, land management, and leaf litter decomposition in a semi-desert grassland. Ecol Appl 17:1809–1823

Throop HL, Archer SR (2008) Shrub (*Prosopis velutina*) encroachment in a semi-desert grassland: spatial-temporal changes in soil organic carbon and nitrogen pools. Glob Change Biol 14:2420–2431

Throop HL, Archer SR, Monger HC, Waltman SW (2012) When bulk density methods matter: implications for estimating soil organic carbon pools in coarse soils. J Arid Environ 77:66–71. doi:10.1016/j.jaridenv.2011.08.020

Tiedemann AR, Klemmedson J (1986) Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. Soil Sci Soc Am J 50:472–475

Torn MS, Trumbore SE, Chadwick OA, Vitousek PM, Hendricks DM (1997) Mineral control of soil organic carbon storage and turnover. Nature 389:170–173

Trumbore S (2000) Age of soil organic matter and soil respiration: radiocarbon constraints on belowground dynamics. Ecol Appl 10:399–411. doi:10.1890/1051-0761(2000)010[0399:AOSOMA]2.0.CO;2

Trumbore SE, Davidson EA, Camargo PB, Nepstad DC, Martinelli LA (1995) Belowground cycling of carbon in forests and pastures of eastern Amazonia. Global Biogeochem Cy 9:515–528

Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. Annu Rev Ecol Syst 31:197–215

van Verseveld WJ, McDonnell JJ, Lajtha K (2009) The role of hillslope hydrology in controlling nutrient loss. J Hydrol 367:177–187

Vanderbilt KL, Lajtha K, Swanson F (2003) Biogeochemistry of unpolluted forested watersheds in the Oregon Cascades:

temporal patterns of precipitation and stream nitrogen fluxes. Biogeochemistry 62:87–117

Wainwright J (2006) Climate and climatological variations in the Jornada Basin. In: Havstad KM, Huenneke LF, Schlesinger WH (eds) Structure and function of a Chihuahuan desert ecosystem. Oxford University Press, Oxford, pp 44–80

Weltz MA, Kidwell MR, Fox HD (1998) Influence of abiotic and biotic factors in measuring and modeling soil erosion on rangelands: state of knowledge. J Range Manag 51:482–495

Wessman C, Archer S, Johnson L, Asner G (2004) Woodland expansion in US grasslands: assessing land-cover change and biogeochemical impacts. In: Gutman G, Janetos AC, Justice CO et al (eds) Land change science: observing, monitoring and understanding trajectories of change on the Earth's surface. Kluwer Academic Publishers, Dordrecht, pp 185–208

Wheeler CW, Archer SR, Asner GP, McMurtry CR (2007) Climate and edaphic controls on soil carbon-nitrogen responses to woody plant encroachment in desert grassland. Ecol Appl 17:1911–1928

Wilcox BP, Pitlick J, Allen CD, Davenport DW (1996) Runoff and erosion from a rapidly eroding pinyon-juniper hillslope, vol 1. In: Anderson MG, Brooks SM (eds) Advances in hillslope processes. Wiley, New York, pp 61–77