

CLIMATIC/EDAPHIC CONTROLS ON SOIL CARBON/NITROGEN RESPONSE TO SHRUB ENCROACHMENT IN DESERT GRASSLAND

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Abstract. The proliferation of woody plants in grasslands over the past 100+ years can alter carbon, nitrogen, and water cycles and influence land surface–atmosphere interactions. Although the majority of organic carbon in these ecosystems resides belowground, there is no consensus on how this change in land cover has affected soil organic carbon (SOC) and total nitrogen (TN) pools. The degree to which duration of woody plant occupation, climate, and edaphic conditions have mediated SOC and TN responses to changes in life-form composition are poorly understood. We addressed these issues at a desert grassland site in Arizona, USA, where the leguminous shrub velvet mesquite (*Prosopis velutina*) has proliferated along an elevation/precipitation/temperature gradient and on contrasting soil morphologic surfaces.

On sandy loam complexes of mid-Holocene origin, mean SOC and TN of soils in the grassland matrix increased ~68% and ~45%, respectively, with increasing elevation. Soil organic carbon pools were comparable and TN pools were ~23% higher in Pleistocene-aged clay loam complexes co-occurring with Holocene-aged soils at the upper elevation/climatic zone. Across the site, belowground resources associated with large *Prosopis* plants were 21–154% (SOC) and 18–127% (TN) higher than those in the grassy matrix.

The variance in SOC and TN pools accounted for by *Prosopis* stem size (a rough surrogate for time of site occupation) was highest at the low- and mid-elevation sites (69–74%) and lowest at the upper elevation site (32–38%). Soil $\delta^{15}\text{N}$ values ranged from 5.5‰ to 6.7‰ across the soil/elevation zones but were comparable in herbaceous and shrub-impacted soils and exhibited a weak relationship with *Prosopis* basal stem diameter ($r^2 < 0.1$) and TN ($r^2 < 0.08$). The SOC $\delta^{13}\text{C}$ values decreased linearly with increasing *Prosopis* basal diameter, suggesting that size and isotopic composition of the SOC pool is a function of time of *Prosopis* site occupation. Isotopic mixture models indicate that encroachment of C_3 woody plants has also promoted SOC additions from C_4 plant sources, indicative of long-term herbaceous facilitation. Grassy sites in contrasting soil/elevation combinations, initially highly distinctive in their SOC pool size and $\delta^{13}\text{C}$, appear to be converging on similar values following ~100 years of woody plant proliferation.

Key words: carbon cycle; carbon isotopes; carbon sequestration; mesquite; *Prosopis velutina*; Santa Rita Experimental Range, Arizona, USA; soil nitrogen; soil organic carbon; Sonoran Desert; ^{13}C ; woody plant encroachment.

INTRODUCTION

Land cover records reveal that many grassland and savanna ecosystems in North and South America, Australia, Africa, and Southeast Asia have experienced increases in the biomass, density, and stature of trees and shrubs over the past century (Archer et al. 2001). Livestock grazing and fire suppression are most often cited as the dominant causes of woody plant proliferation, but changes in climate, increased atmospheric CO_2 concentrations, and nitrogen deposition have also been implicated (e.g., Archer 1994, 1995, Scholes and Archer 1997, van Auken 2000). The proliferation of

woody plants in drylands has the potential to influence regional and global net CO_2 sequestration, especially if there are long-term cumulative responses in the soil pool, where the majority of organic carbon typically resides (Schlesinger 1997). Woody plant encroachment has been recognized as an important component of Australia's greenhouse gas inventory (Gifford and Howden 2001, Williams et al. 2005) and as a potential contributor to a U.S. carbon sink (Houghton et al. 1999, Schimel et al. 2000). Recent estimates of this phenomenon in the U.S. carbon budget (0.12–0.13 Pg C/yr; Pacala et al. 2001, Houghton 2003) acknowledge major uncertainties in the magnitude and direction of net CO_2 sequestration stemming from a poor understanding of how soil organic carbon (SOC) pools change following woody encroachment. Accordingly, the lack of a quantitative understanding of carbon storage and dynamics in SOC and long-lived woody tissue within

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drylands of the southwestern United States has emerged as a limitation to assessing the health and services of U.S. ecosystems (Heinz Center 2002).

Although the woody encroachment phenomenon has been widely observed, ecosystem responses are less certain and the subject of debate. In particular, it is unclear how SOC stocks respond to changes in woody vegetation cover and how climatic or edaphic conditions mediate SOC responses to woody encroachment. Soil organic carbon mass reflects the balance between organic matter inputs from plants and losses from the decay of organic matter (Chapin et al. 2002). Changes in plant composition or diversity can influence the quantity and quality of litter inputs (e.g., Enriquez et al. 1993, Scott and Binkley 1997, Spehn et al. 2000, Knops et al. 2001). In the context of woody plant proliferation, SOC could increase if woody plants are more productive than herbaceous vegetation and/or if woody plant tissues decay more slowly than herbaceous plant inputs. Alternatively, SOC pools could decrease if woody plants are less productive and allocate less biomass to roots than grasses or if decomposition rates increase with increased litter quality or improvement of microclimate (e.g., Scott et al. 1999, Jackson et al. 2002). Precipitation and temperature mediate plant life-form trade-offs by exerting control over the quantity and quality of plant inputs and the rates of decomposition outputs (e.g., Hobbie 1996, Binkley and Giardina 1998, Moorhead et al. 1999, Throop and Archer 2007). Bioclimatic controls are, in turn, influenced by soil properties such as depth, texture, and mineralogy (e.g., Schimel et al. 1994, Hassink 1997, Baldock and Skjemstad. 2000, Krull et al. 2002). The relative importance of climatic and edaphic factors as drivers of or constraints to SOC accumulation during woody encroachment is not well understood.

Woody plant effects on SOC pools range from positive to neutral to negative (Asner and Martin 2004, Wessman et al. 2004). Soil and microclimate modification by woody plants is well-documented (e.g., "islands of fertility," whereby nutrients are concentrated in soils below shrub canopies; Schlesinger et al. 1990). However, rates of shrub-induced changes to soil properties are largely unknown. Correlations between plant size and soil nutrients suggest the nature and extent of woody plant modification of soils may change with time (Barth 1980, Bernhard-Reversat 1982, Ludwig et al. 2004). Limited field data indicate organic carbon and total nitrogen (TN) pools in soils beneath shrub canopies increase linearly with time since shrub establishment (Archer et al. 2004). Thus, the answer to the question "How do shrubs establishing in grassland affect SOC/TN pools?" may well depend on which shrubs on the landscape are sampled and the age class distribution of plants in the sampled stands. As a result, it is difficult to predict how SOC pools might change with the development of woody plant communities in grasslands. Data spanning a regional precipitation

gradient in the southwestern United States suggest a negative linear relationship between mean annual precipitation and SOC pool size after woody encroachment, with net accumulation occurring at arid sites and net losses at wetter (>460 mm/yr) sites (Jackson et al. 2002). However, a broader survey of the literature suggests this correlation may be spurious in that woody plant encroachment has resulted in substantial increases in SOC pools in a variety of high-rainfall sites (e.g., temperate forests [Tilman et al. 2000], subtropical woodlands [Boutton et al. 1998, Geesing et al. 2000], tropical savannas [Mordelet et al. 1993, San Jose et al. 1998]).

There is a need to improve our understanding of the manner in which vegetation-induced changes of SOC stocks are constrained or promoted by climatic and edaphic conditions. Generalizations emerging from cross-site/cross-study comparisons should be viewed with caution, as they typically do not explicitly account for differences in woody plant growth forms, disturbance/land use history, soil physical/chemical properties, sampling protocol, and analytical methodologies that may confound or mask relationships. In this study, we evaluated how intrinsic soil and climatic conditions mediate decadal-scale responses of SOC and soil N stocks to shrub (*Prosopis velutina*) encroachment in a semiarid grassland. To provide empirical constraints for landscape- and regional-scale carbon modeling efforts (e.g., Potter et al. 1993, Sellers et al. 1996, Parton et al. 1998, White et al. 2000, Dai et al. 2003), we (1) determined how SOC/TN stocks vary with shrub size (a coarse surrogate for time of woody plant occupation) across a climatic gradient (holding soils constant) and between contrasting soil morphologic surfaces (holding climate constant), (2) assessed changes in the relative contribution of C₄ (grass) and C₃ (shrub) sources to SOC stocks using stable carbon isotopes ($\delta^{13}\text{C}$); and (3) quantified soil C/N and $\delta^{15}\text{N}$ to ascertain whether *Prosopis* plants might be altering decomposition processes subsequent to their establishment (e.g., Liao et al. 2006b). We hypothesized that (1) SOC and TN pools would be larger in soils associated with *Prosopis* canopies than in soils in the surrounding grassland matrix (island of fertility effect; e.g., Virginia 1986), with the magnitude of difference being (2) positively correlated with *Prosopis* size and (3) greater on fine- than on coarse-textured soils. We further predicted that (4) SOC $\delta^{13}\text{C}$ values would be inversely related to *Prosopis* size, but that the rate of change in SOC $\delta^{13}\text{C}$ with *Prosopis* size would (5) change with elevation and, at a given elevation, (6) be greatest on coarser textured soils compared to finer textured soils (owing to higher rates of SOC turnover on the coarse-texture soil). We further hypothesized that (7) soil $\delta^{15}\text{N}$ would increase with time of *Prosopis* occupation, a reflection of the progression of humification (e.g., Nadelhoffer et al. 1996, Koba et al. 1998). Regarding (5) we had two competing hypotheses. On the one hand, higher mean annual temperatures at

lower elevations would promote decomposition and SOC turnover, thus making the SOC $\delta^{13}\text{C}$ more responsive to changes in C_3 vs. C_4 vegetation inputs. On the other hand, greater annual rainfall at higher elevations could promote greater C_4 grass production and hence C_4 inputs. This could cause the SOC $\delta^{13}\text{C}$ to be less responsive to inputs from encroaching C_3 shrubs, especially if rates of SOC turnover are reduced by lower mean annual temperatures.

MATERIALS AND METHODS

Study site

Our study was conducted on the 215-km² Santa Rita Experimental Range (SRER; 31.9° N, 110.8° W) ~35 km south of Tucson, Arizona, within the Upper Sonoran Desert (Fig. 1; see Plate 1). Located on the western flank of the Santa Rita Mountains, elevation at the SRER ranges from 900 to 1450 m. Mean annual precipitation increases from 275 to 450 mm/yr along the elevation gradient; and Sonoran desert-scrub, semidesert grassland, and Madrean evergreen woodland biotic communities (Brown 1994) appear in ascending order (see McClaran [2003] for additional details on rainfall and vegetation). Our study encompassed the semidesert grassland–*Prosopis* shrubland complex situated between *Larrea tridentata* shrublands (lower elevations) and *Quercus* spp. woodlands (higher elevations). Soil surfaces on the SRER have evolved from alluvial sediments deposited from the Santa Rita Mountains (McAuliffe 1995). Our studies focused on two contrasting morphologies: (1) loamy sand–sandy loam complexes of mid-Holocene origin and (2) sandy loam–clay loam complexes of Pleistocene origin with well-developed argillic horizons (Fig. 1; Breckenfeld and Robinette 1997, Batchily et al. 2003).

Established in 1902 by the U.S. Department of Agriculture to develop approaches for rangeland restoration and livestock grazing management (Sayre 2003), the SRER has accrued extensive historical and ecological databases, including soil and geological surveys, livestock grazing, fire, and precipitation records, and vegetation histories based on repeated ground photos, aerial photography, and permanent vegetation transects. The SRER records document the spread and proliferation of *Prosopis velutina* Woot. (velvet mesquite) from drainage arroyos into upland grasslands since 1903 (Glendening 1952, McClaran 2003). Soil maps, along with precipitation, grazing management, and fire records, enabled us to make minimally confounded determinations of how SOC and soil N stocks changed subsequent to *Prosopis* encroachment into these grasslands across a climate gradient and between contrasting morphologic surfaces.

Climatic gradient

In southern Arizona, mean annual precipitation increases and temperature decreases with elevation due to orographic processes and adiabatic cooling (Michaud

et al. 1995, Sheppard et al. 1999). To objectively distinguish climatic zones across the SRER for comparative analyses, mean annual precipitation (MAP) was computed for rain-years (October–September) from 1974 to 2003, utilizing data from a distributed network of 22–30 rain gauges (McClaran et al. 2002). The spatial continuity of MAP was modeled with a spherical variogram for each year (Deutsch and Journel 1997), because the number and location of active rain gauges varied through time. A 10-m resolution digital elevation model (DEM) of the SRER was then linearly transformed into a precipitation surface based on the empirical linear relationship between annual precipitation and rain gauge elevation (Daly et al. 1994). Simple kriging with varying local means (SKLM) was used to produce an unbiased interpolation of the irregularly distributed rain gauge data for each year. This approach incorporated observation data, variogram-modeled continuity, and observed secondary precipitation–elevation relationships derived from a precipitation-transformed DEM (Deutsch and Journel 1997, Goovaerts 1999). A MAP surface was calculated by averaging the 1974–2003 SKLM output surfaces.

Temperature has not been regularly monitored across the SRER. However, analysis of data from nearby NOAA National Climate Data Center stations (Cooperative Stations numbers 20080, 20287, 22807, 24675, 26132, 26513, 27593, 27619, 28795, 28820, and 28865) yielded strong linear relationships between monthly mean temperature and elevation ($r = 0.89\text{--}0.93$). This relationship was then used with the SRER DEM to compute a spatial coverage and generate sample-specific estimates of mean monthly and mean annual temperatures (MAT) from 1974–2003 data weighted by the number of days.

Modeled spatial (Table 1) and temporal (data not shown) distributions of precipitation and temperature for the SRER were consistent with observed climatic patterns found throughout southern Arizona (i.e., bimodal annual distribution of precipitation having a maximum associated with the summer North American monsoon and a lesser peak in winter associated with cyclonic storms and troughing of westward storm tracks [Sheppard et al. 1999]). The models also showed the expected midsummer maxima/midwinter minima temperature distributions and strong correlations between elevation and precipitation and temperature.

Experimental design

Using a geographic information system (GIS), we identified sampling locations along contours corresponding to the lower, middle, and upper MAP portions of the mesquite-grassland vegetation zone (330, 380, and 430 mm/yr, respectively). The Holocene soil morphologic surfaces spanned the entire climate gradient. Pleistocene surfaces were confined to the highest elevations and thus the highest precipitation, lowest temperature zone. Two 100-m transects were established

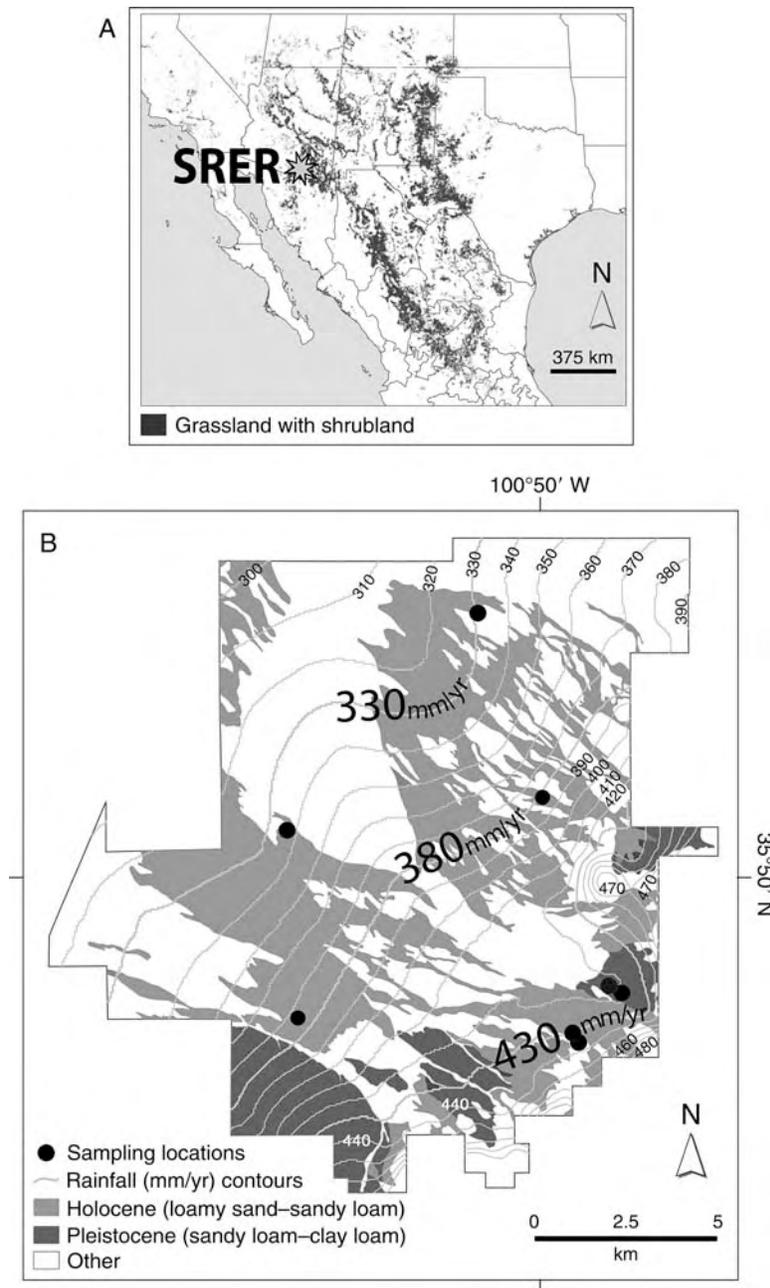


FIG. 1. (A) The location of the Santa Rita Experimental Range (SRER) within southwestern U.S. and Mexico grasslands with shrubland cover (demarcated in dark gray; Loveland et al. 2000). (B) The location of sampling transects on the SRER in relation to soil types and modeled annual precipitation.

at each MAP contour in the Holocene-aged surfaces and at the 430 mm/yr MAP contour on a Pleistocene-aged surface (Fig. 1). Transect locations were determined in a directed random fashion, such that the following criteria were met: slope inclination $<5^\circ$, ~ 1 km from the closest livestock watering point, low- to moderate-intensity livestock grazing regime, and no known brush management or fire. These constraints were imposed to minimize factors that might otherwise confound inter-

pretation of *Prosopis* effects on SOC and TN pools. Within areas matching these constraints, transect starting point coordinates and directions were generated randomly. Given that all sampling was restricted to nearly level uplands, slope aspect was not explicitly considered. Overall, our sampling occurred across a large alluvial fan representing a northwest-facing bajada. Logistical constraints prevented us from accounting for factors such as site-specific differences in

soil clay mineralogy, elemental composition, and aggregate structure that are known to influence SOC accumulation and turnover (e.g., Hassink 1997, Baldock and Skjemstad 2000, Liao et al. 2006a, b).

In January 2004, soil cores (20 cm depth) were collected from the following patch types: (1) the inter-canopy grassland matrix (herbaceous and bare areas >5 m from shrub canopies), (2) the sub-canopy zone of small (6–15 cm basal diameter of largest stem on the plant) *Prosopis velutina* plants, and (3) the sub-canopy zone of large (>15 cm basal stem diameter) *P. velutina* plants. Vegetation end members thus corresponded to units of a woody encroachment transitional sequence (grassland → small, “younger” *Prosopis* → large, “older” *Prosopis*) within each comparative climatic/edaphic zone. Representative patches closest to points located at 20-m intervals along each transect were targeted for sampling. Each transect thus generated samples from five interspace, small *Prosopis* and large *Prosopis* patches. *Prosopis*-associated soil samples and surface litter were collected 0.5 m from the largest live stem on the plant, and the basal diameter of that stem was measured. This sampling protocol was designed to obtain a good representation of the SOC and TN pools associated with relatively small and large plants and to ascertain the size at which *Prosopis* plants have a measurable effect on SOC and TN pools. Sampling locations were geographically registered with a high-resolution global positioning system and assessed on aerial photographs from February 1936, May 1966, and June 1996 to verify that the sampled herbaceous patches had been devoid of shrubs and that all *Prosopis* individuals in the large size class had been present over this 67-year period (Fig. 2).

Previous studies examining the loamy sand–sandy loam soil morphology of mid-Holocene origin at a MAP = 380 mm site revealed that differences in SOC stocks in soils associated with grassland and *Prosopis* patches were confined to the upper 20 cm and that there were no significant differences in SOC pools in soils with and without herbaceous cover at time of sampling in the grassland matrix. Thus, a 0–20 cm mineral soil sampling depth was used for this study, and we did not stratify sampling with respect to bare vs. vegetated soil surfaces. Furthermore, the 0–20 cm soil depth is commonly used in inter-study comparisons (Boone et al. 1999) and biogeochemical modeling (e.g., Hibbard et al. 2003).

Laboratory analysis

Soil cores and *Prosopis* litter samples were dried at 60°C for 72 h. Dried soils were weighed and sieved to remove coarse organic fragments and rocks ≥ 2 mm. Bulk density was calculated on the <2-mm size fraction of all cores as the mass of the core sample minus the >2-mm fraction divided by the core volume minus the volume of the >2-mm fraction (Elliott et al. 1999). Soil texture (percentages of sand, silt, clay) was determined via the hydrometer method (Elliott et al. 1999).

Subsequently, each soil core sample was subsampled, cleaned of identifiable root fragments (but not other particulate organic matter [POM]) with forceps, homogenized and pulverized with a coffee grinder, and progressively acidified with 6% sulfurous acid to remove carbonate phases (Verardo et al. 1990, Sollins et al. 1999). Thus, our soil samples consisted of unaggregated (free) sand, silt and clay particles, soil aggregates, POM and POM-soil aggregates. Logistical constraints prevented us from separating POM C from soil SOC and the SOC associated with various aggregate or particle size fractions (e.g., Boutton et al. 1998, Gill and Burke 1999, Liao et al. 2006a) and thus estimating the relative contribution of these constituents to SOC across our soil surface age/elevation gradients and with *Prosopis* encroachment. *Prosopis* leaves and roots were isolated respectively from random subsets of the *Prosopis* surface litter and >2-mm soil fractions and milled to ≤ 0.5 mm (Sollins et al. 1999). All subsamples were combusted and analyzed for C and N concentrations, as well as stable isotope ratios of C and N ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in an elemental analyzer (Carlo Erba NA1500 series II; Carlo Erba, Milan, Italy) coupled to an isotope ratio mass spectrometer (Finnigan MAT Delta Plus, Finnigan MAT, Waltham, Massachusetts, USA) at the Stanford University Stable Isotope Laboratory. Duplicate or triplicate runs were performed every 15–20 samples to ensure repeatability of analyses. By convention, each sample's isotopic values are expressed as ratios on a parts per thousand basis (‰), relative to the Pee Dee Belemnite (PDB) limestone standard for C and an air standard for N, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were computed as per Boutton (1996). Based on acetanilide and U.S. Geological Survey (USGS)-24 graphite chemical standards for $\delta^{13}\text{C}$ and acetanilide and the International Atomic Energy Agency (IAEA)-N1 ammonium sulfate standards for $\delta^{15}\text{N}$, precision was within 0.15‰. Carbon and nitrogen density (as grams per square meter) for the <2-mm soil fraction was computed as the product of C and N concentration (as a percentage), bulk density (as grams per cubic centimeter), and depth (20 cm).

Statistical analysis

Statistical analyses were conducted with SPSS 12.0 (SPSS, Chicago, Illinois, USA). Shapiro-Wilk's tests and Levene's tests were employed to examine data normality and homogeneity of variances, respectively (Levene 1960, Shapiro and Wilk 1965). Analysis of variance (ANOVA) and post-hoc Tukey tests were used to quantify differences in soil properties by cover type and climate/soil zones. Data not fitting parametric assumptions were assessed using Kruskal-Wallis and Mann-Whitney rank analyses (Zar 1996). Stepwise multiple linear regression analyses were performed to determine the extent to which variation in elevation, MAT, MAP, soil physical properties (fractions of sand, silt, and clay; bulk density), and *Prosopis* basal diameter

TABLE 1. Characteristics (mean with SE in parentheses) of the climatic/edaphic zones on the Santa Rita Experimental Range, Arizona, USA, according to surface age, texture class, and precipitation zone.

Characteristic	Holocene			Pleistocene
	Loamy sand–sandy loam			Sandy loam–clay loam
	330 mm/yr	380 mm/yr	430 mm/yr	430 mm/yr
Elevation (m)	978 ^a (0.2)	1075 ^b (3.8)	1288 ^{c,A} (1.8)	1293 ^B (1.5)
Precipitation (mm/yr)	335 ^a (0.4)	378 ^b (0.6)	435 ^{c,A} (0.6)	419 ^B (0.2)
Temperature (°C)	18.9 ^a (0.00)	18.3 ^b (0.04)	17.2 ^{c,A} (0.01)	17.2 ^B (0.01)
Soil properties				
Sand (%)	75.5 ^a (1.1)	78.2 ^a (0.8)	82.9 ^{b,A} (0.6)	73.7 ^B (1.0)
Silt (%)	14.8 ^a (0.7)	13.2 ^a (0.6)	9.7 ^{b,A} (0.5)	13.0 ^B (0.5)
Clay (%)	10.0 ^a (0.6)	8.5 ^{a,b} (0.4)	7.4 ^{b,A} (0.3)	13.3 ^B (0.8)
Bulk density (mg/cm ³)	1.38 ^a (0.04)	1.31 ^b (0.15)	1.34 ^{a,b,A} (0.02)	1.29 ^B (0.02)

Notes: Bulk density and soil particle size fractions classes were statistically comparable ($P > 0.05$) for vegetation cover types, so data were pooled across grassland matrix; small *Prosopis* and large *Prosopis* patches are presented. Significant differences ($P < 0.05$) between values within a row are indicated by differing superscripted letters (lowercase letters for precipitation comparison; uppercase letters for soil type comparison).

might explain variation in SOC, TN, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values. For simple regressions, differences in slope and intercept were tested as described in Kleinbaum and Kupper (1978).

Isotope mixing model

The $\delta^{13}\text{C}$ of SOC reflects the relative contributions of C_3 and C_4 plants to primary production (Boutton 1996, Balesdent et al. 1998). The relative proportions of SOC derived from C_4 and C_3 photosynthetic pathway sources were estimated with mass balance equations:

$$F_{\text{C}_4} = (\delta^{13}\text{C}_{\text{SAM}} - \delta^{13}\text{C}_{\text{C}_3}) / (\delta^{13}\text{C}_{\text{C}_4} - \delta^{13}\text{C}_{\text{C}_3}) \quad (1)$$

$$F_{\text{C}_3} = 1 - F_{\text{C}_4} \quad (2)$$

where F_{C_4} is the mean carbon fraction derived from C_4 sources, $\delta^{13}\text{C}_{\text{SAM}}$ is the measured $\delta^{13}\text{C}$ of the soil sample, $\delta^{13}\text{C}_{\text{C}_3}$ is the mean $\delta^{13}\text{C}$ of C_3 sources, $\delta^{13}\text{C}_{\text{C}_4}$ is the mean $\delta^{13}\text{C}$ of C_4 sources, and F_{C_3} is the mean fraction carbon derived from C_3 inputs (Balesdent and Mariotti 1996). Standard errors (SE) were calculated for mean values using the methods and formulas presented by Phillips and Gregg (2001) that account for the observed variability in $\delta^{13}\text{C}$ signatures of the sources as well as the mixture.

Prosopis root and leaf litter values were the basis for $\delta^{13}\text{C}_{\text{C}_3}$ values. Three different source scenarios were used to define $\delta^{13}\text{C}_{\text{C}_4}$, because the specific grass species contributing to the SOC pool may be transitory in nature. For a given climate/soil complex sample, $\delta^{13}\text{C}_{\text{C}_4}$ for scenario A was defined as the mean $\delta^{13}\text{C}$ of SOC in samples from areas devoid of woody cover (e.g., grass patches >5 m from a woody plant). Lower and upper bounds of $\delta^{13}\text{C}_{\text{C}_4}$ values were represented in scenarios B and C by using the most negative and most positive C_4 species $\delta^{13}\text{C}$ values known for the site (based on fresh aboveground tissues collected in the 380-mm/yr precipitation zone on loamy sand–sandy loam soils of mid-Holocene origin; D. Martens and M. McClaran,

unpublished data). Our estimates of the C_4 grass contribution to SOC pools were based on the $\delta^{13}\text{C}$ of aboveground biomass and do not account for the fact that the $\delta^{13}\text{C}$ of roots tend to run $\sim 1\text{--}3\%$ higher than leaves and other plant tissues (von Fischer and Tieszen 1995, Boutton 1996).

RESULTS

Soil physical properties

Neither texture (percentages of sand, silt, and clay) nor bulk density differed significantly between the three vegetation cover types within any of the climate/soil combinations. Thus, Table 1 represents means of data pooled across samples from the herbaceous grassland and small *Prosopis* and large *Prosopis* patches. Significant differences in texture class distribution were observed along the elevation gradient spanning the Holocene complex, with soils in the upper elevation zone having higher sand, lower silt, and lower clay content than those at middle and lower elevations (Table 1). Within the 430-mm/yr precipitation zone, soils in the Pleistocene complex had higher clay, lower silt, lower sand, and slightly lower bulk density than soils in the Holocene complex.

Soil organic carbon, TN, and isotope chemistry in the herbaceous matrix

Among grassland matrix patches within the Holocene complex, SOC and TN pools were lower in the low-to-mid-elevation zones than in the upper elevation zone (Table 2). Stepwise multiple regression analyses evaluating the climate and soil variables listed in Table 1 generated single-factor models that accounted for 65–70% of the variance in SOC pools and 51–54% of the variance in the soil TN pool (Table 3). In the upper elevation zone, SOC and TN pools were $\sim 13\%$ ($P = 0.055$) and 23% ($P = 0.009$) greater on Pleistocene than on Holocene surfaces (Table 2). Within the Holocene complex, C:N ratios in soils increased from 10.6 ± 0.2 and 11.3 ± 0.5 (mean \pm SE) at low- and mid-elevation

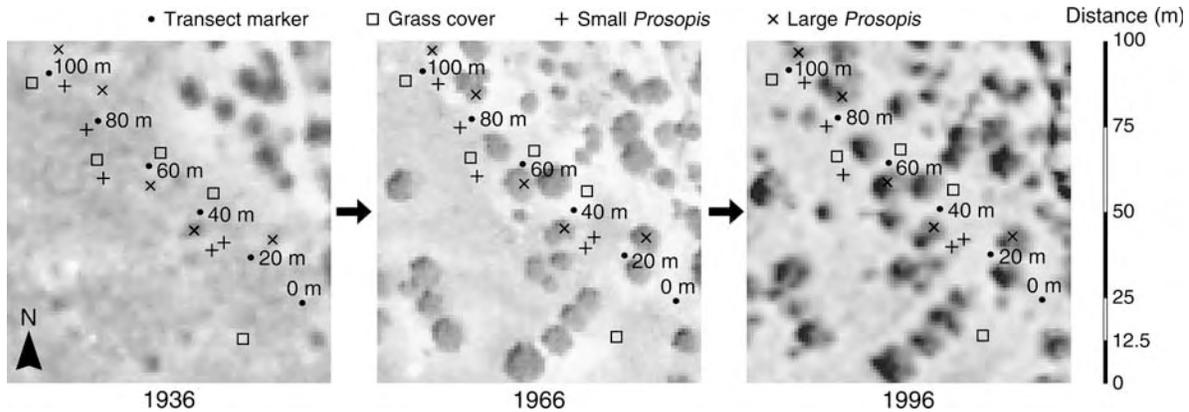


FIG. 2. Aerial photo time series (February 1936, May 1966, and June 1996) showing sampling locations on a typical transect in relation to vegetation cover (note right-hand scale). Time series aerial photographs were used to verify that all large *Prosopis velutina* (velvet mesquite) canopies were at least 67 years old and that all grass areas sampled have been devoid of shrubs since 1936.

zones to 12.3 ± 0.1 in the upper elevation zone. Soil C:N ratios in upper elevation Holocene soils were slightly higher than those in co-occurring Pleistocene soils (11.3 ± 0.2).

The herbaceous flora of the SRER is dominated by C₄ grasses (McClaran 1995) with species-specific grass shoot $\delta^{13}\text{C}$ values ranging from -13.3‰ to -14.9‰ (M. McClaran and D. Martens, unpublished data). The $\delta^{13}\text{C}$ signatures of SOC in the grassland patches reflected this, but with some small, statistically significant variation (Table 2). Stepwise multiple regression analyses yielded significant single-factor models for the relationship between $\delta^{13}\text{C}$ and elevation ($r^2 = 0.42$), MAT ($r^2 = 0.48$), MAP ($r^2 = 0.46$), and percentage of sand ($r^2 = 0.41$; data not shown). The $\delta^{15}\text{N}$ values in soils at the upper elevation zone (6.1‰) were slightly but significantly lower than those in mid- to lower elevation zones (6.7‰).

Prosopis influences on SOC, TN, and isotope chemistry

The mean basal stem diameter (BSD) of *Prosopis* plants defined a priori as the “small” category was statistically comparable across zones in the Holocene complex (10.8–11.2 cm; Table 2). The BSD of “large” *Prosopis* in the upper Holocene zone (36.4 cm) was greater than that of plants in the low- and mid-elevation zones (18.4 and 24.0 cm, respectively) and was 77% higher than that of large plants on the Pleistocene surface (20.5 cm). Soils associated with *Prosopis* plants had significantly larger SOC and TN pools than inter-canopy grassland patches ($P < 0.001$; Table 2). On average, carbon pools of soils associated with small *Prosopis* plants (6–15 cm BSD) were larger than those in inter-canopy grassland patches; however, differences between small and large (>15 cm BSD) *Prosopis* plants were generally not significant. Patterns for TN were generally similar, but more variable.

Prosopis BSD explained more variance in SOC and TN stocks in low-to-mid-elevation zones ($r^2 = 0.69$ – 0.74) than it did in the upper elevation Holocene ($r^2 = 0.32$ –

0.36) and Pleistocene soils ($r^2 = 0.36$ and 0.38 ; Table 3). When grassland patch end members (BSD = 0 cm) were excluded from the regression analyses, there was no significant relationship between *Prosopis* BSD and SOC or TN in the upper elevation sites, and r^2 values declined slightly, but remained significant, at mid- and low-elevation sites. Within the Holocene complex, slopes of the SOC and TN vs. BSD regression lines varied in the rank order lower elevation \sim mid-elevation $>$ upper elevation; and slopes of these regressions were statistically comparable for Pleistocene and Holocene soils at the upper elevation. Inclusion of elevation, MAT, or MAP explained only 5–7% more of the variance in SOC and only 3% more of the variance in TN. Overall, TN and SOC of soils associated with inter-canopy grassland and *Prosopis* patches were strongly and linearly correlated ($\text{TN} = 0.054 + 0.09[\text{SOC}]$, where TN and SOC are in milligrams per cubic centimeter; $r^2 = 0.96$).

The $\delta^{13}\text{C}$ values for *Prosopis* leaf litter ($-25.76\text{‰} \pm 0.12\text{‰}$) and root samples ($-25.31\text{‰} \pm 0.28\text{‰}$) were statistically comparable (mean of pooled samples: $-25.6\text{‰} \pm 0.13\text{‰}$). Additionally, mean $\delta^{13}\text{C}$ *Prosopis* values were comparable among elevation, soil type, and plant size comparisons (Table 2). The $\delta^{13}\text{C}$ values of soils associated with shrub patches were significantly depleted (1–3‰, $P < 0.001$) relative to grassland patches. The $\delta^{13}\text{C}$ values of SOC associated with *Prosopis* plants were inversely related to *Prosopis* size, with *Prosopis* BSD explaining 63–84% of its variance (Fig. 3). Slopes of these regression lines were statistically comparable for all elevation zones within the Holocene complex, while intercepts for lower and mid-elevation zones were comparable but significantly lower than that for the upper zone. Slopes and intercepts for the SOC $\delta^{13}\text{C}$ –*Prosopis* BSD relationship on Pleistocene soils differed significantly from those on Holocene soils within the 430-mm/yr zone. A simple regression of *Prosopis* BSD against $\delta^{13}\text{C}$ using data from all sites yielded an $r^2 = 0.53$; adding MAT, MAP, or elevation to

TABLE 2. Characteristics (mean with SE in parentheses) of the vegetation patches in various climatic/edaphic combinations.

Precipitation zone and cover	BSD (cm) mean (SE)	SOC (g C/m ²) mean (SE)	SOC increase relative to grass (%)	δ ¹³ C (‰) mean (SE)	TN (gN/m ²) mean (SE)
Holocene					
330 mm/yr					
Grass		640 ^{a,1} (31)		-18.6 ^{a,1} (0.4)	71 ^{a,1} (4)
Small <i>Prosopis</i>	11.2 ^{d,2} (1.0)	1072 ^{d,2} (103)	45-93	-19.7 ^{d,1} (0.3)	113 ^{d,1} (9)
Large <i>Prosopis</i>	18.4 ^{g,3} (0.4)	1403 ^{g,2} (144)	88-154	-20.6 ^{g,2} (0.2)	140 ^{g,2} (12)
380 mm/yr					
Grass		715 ^{a,1} (44)		-17.5 ^{a,1} (0.2)	74 ^{a,1} (4)
Small <i>Prosopis</i>	10.7 ^{d,2} (1.1)	1040 ^{d,2} (80)	27-67	-18.6 ^{d,e,2} (0.2)	104 ^{d,2} (6)
Large <i>Prosopis</i>	24.0 ^{g,h,3} (3.0)	1400 ^{g,3} (161)	63-133	-20.0 ^{g,3} (0.2)	141 ^{g,3} (13)
430 mm/yr					
Grass		1081 ^{b,A,1} (57)		-17.0 ^{b,A,1} (0.1)	102 ^{b,A,1} (5)
Small <i>Prosopis</i>	10.8 ^{d,D,2} (1.0)	1574 ^{e,D,2} (103)	29-64	-18.4 ^{e,D,2} (0.2)	148 ^{e,D,2} (10)
Large <i>Prosopis</i>	36.4 ^{h,G,3} (4.7)	1680 ^{g,G,2} (175)	32-81	-20.2 ^{g,G,3} (0.4)	156 ^{g,G,2} (15)
Pleistocene					
430 mm/yr					
Grass		1217 ^{A,1} (57)		-16.5 ^{B,1} (0.1)	125 ^{B,1} (5)
Small <i>Prosopis</i>	10.6 ^{D,2} (0.8)	1662 ^{D,2} (67)	26-49	-18.2 ^{D,2} (0.3)	163 ^{D,1,2} (7)
Large <i>Prosopis</i>	20.5 ^{H,3} (1.4)	1640 ^{G,2} (93)	21-49	-19.1 ^{H,3} (0.1)	164 ^{G,2} (9)

Notes: "Grass" refers to the inter-canopy grassland patches; BSD refers to *Prosopis* basal stem diameter. Within a column, significant differences ($P < 0.05$) between equivalent cover types of different climatic/edaphic zones are indicated by differing superscripts (lowercase letters for precipitation comparison; uppercase letters for soil type comparison); significant differences between cover types within a climatic/edaphic zone are indicated by differing superscripted numbers. The range of observed increases (%) in soil organic carbon (SOC) and total nitrogen (TN) in shrub patches relative to grass patches is also shown.

TABLE 3. Relationships between soil organic carbon (SOC) and total nitrogen (TN) pools, *Prosopis velutina* basal stem diameter (BSD; cm), and climatic/edaphic variables (Table 1).

Soil and precipitation zone	Soil organic carbon (g C/m ²)	r ²	Soil nitrogen (g N/m ²)	r ²
Grassland matrix				
Holocene/all	= 1.56 × elevation - 930.41	0.70	= 0.111 × elevation - 42.01	0.54
	= -287.088 × MAT + 6010.76	0.69	= -19.877 × MAT + 442.35	0.51
	= 4.895 × MAP - 1069.43	0.65	= 0.353 × MAP - 53.411	0.51
<i>Prosopis</i> shrub patches†				
Holocene, 330 mm/yr	= 42.805 ^a × BSD + 615.26	0.69	= 3.873 ^a × BSD + 69.63	0.71
Holocene, 380 mm/yr	= 30.493 ^a × BSD + 700.15	0.70	= 2.809 ^a × BSD + 74.02	0.74
Holocene, 430 mm/yr	= 15.906 ^{b,A} × BSD + 1187.56	0.36‡	= 1.347 ^{b,A} × BSD + 113.64	0.32‡
Pleistocene, 430 mm/yr	= 20.006 ^A × BSD + 1302.69	0.36‡	= 1.962 ^A × BSD + 130.49	0.38‡
Holocene, all	= 24.183 × BSD + 887.19	0.47	= 2.099 × BSD + 90.907	0.47
	= 22.385 × BSD + 1.09	0.56	...	
	× elevation - 320.64			
	= 22.358 × BSD - 202.087	0.57	= 1.991 × BSD - 11.989	0.51
	× MAT + 4557.95		× MAT + 308.68	
	= 22.601 × BSD + 3.225	0.55	...	
	× MAP - 343.66			
Both, 430 mm/yr	= 16.099 × BSD + 1264.73	0.32	= 1.378 × BSD + 124.98	0.27
	= 18.176 × BSD - 25.057	0.45	= 1.64 × BSD - 3.158 × sand + 370	0.51
	× sand + 3208.77			

Notes: For the Holocene surface, "all" refers to pooled low, middle, and upper elevation zones; MAT and MAP represent mean annual temperature and precipitation, respectively. Superscripts associated with slope values denote significant differences between elevation zones within the Holocene complex (lowercase) and differences between the Holocene and Pleistocene complex at the upper elevation (uppercase). Blank entries in the soil N column indicate that no variables in Table 1 significantly improved r² over stem basal diameter. Units for variables are: BSD, cm; elevation, m; MAP, mm; MAT, °C; sand, %.

† Reported r² values and equations using grassland end members for *Prosopis* stem = 0 cm.

‡ When regressions were run without grassland end members for *Prosopis* stem = 0 cm, r² values decreased, but regressions were still significant, except in these instances.

TABLE 2. Extended.

TN increase relative to grass (%)	$\delta^{15}\text{N}$ (‰) mean (SE)	C:N ratio mean (SE)
39–82	6.7 ^{a,1} (0.1)	10.6 ^{a,1} (0.5)
72–127	6.4 ^{d,1} (0.1)	11.0 ^{d,1} (0.2)
	6.1 ^{g,1} (0.3)	11.6 ^{g,1} (0.5)
25–58	6.7 ^{a,b,1} (0.2)	11.3 ^{a,b,1} (0.5)
62–120	6.1 ^{d,e,1} (0.3)	11.5 ^{d,1} (0.3)
	5.9 ^{g,1} (0.3)	11.4 ^{g,1} (0.3)
29–63	6.1 ^{b,A,1} (0.1)	12.3 ^{b,A,1} (0.1)
32–75	5.7 ^{e,D,1,2} (0.1)	12.4 ^{e,D,1} (0.2)
	5.5 ^{g,G,2} (0.2)	12.4 ^{h,G,1} (0.2)
20–41	6.1 ^{A,1} (0.1)	11.3 ^{B,1} (0.2)
18–44	5.4 ^{D,2} (0.1)	11.9 ^{D,1} (0.1)
	5.6 ^{G,2} (0.2)	11.7 ^{H,1} (0.1)

the equation explained an additional 16–17% of the measured variance (data not shown). Soil particle size class and bulk density variables did not emerge as significant predictors. The relationship between SOC mass and SOC $\delta^{13}\text{C}$ was strong and linear at the low- and mid-elevation Holocene sites but was distinctly nonlinear at both high-elevation sites (Fig. 4). The nonlinearity in the latter setting reflects the fact that differences in SOC mass between small and large *Prosopis* size classes were small in comparison to changes that occurred in SOC $\delta^{13}\text{C}$.

Soil $\delta^{15}\text{N}$ values ranged from 5.5‰ to 6.7‰ across the soil/elevation zones (Table 2). In contrast to soil $\delta^{13}\text{C}$

values, soil $\delta^{15}\text{N}$ values exhibited very weak relationships with *Prosopis* BSD ($r^2 < 0.1$) and TN ($r^2 < 0.08$; data not shown). The C:N ratios in soils associated with small and large *Prosopis* plants were comparable to one another (range of paired differences = 0.0–0.6) and to that in soils of herbaceous patches (≤ 1 unit difference; range = 10.6–12.4; Table 2).

Carbon source fractions

Isotopic mixing model estimates of the proportion of SOC in each soil/climate setting revealed the expected pattern of progressively increasing C_3 contributions with development of C_3 *Prosopis* plants (Fig. 5). Mixture model sensitivity to the $\delta^{13}\text{C}$ of C_4 end members was tested by varying the $\delta^{13}\text{C}_{\text{C}_4}$ in Eq. 1. Applying mixing model fractions to end member SOC stocks allowed us to approximate the lower and upper limits of C_3 and C_4 source contributions to SOC pools during the course of woody plant encroachment (Fig. 6). Although stock quantities differed, the direction and pattern of change for C_3 and/or C_4 stocks were consistent among scenarios. The C_4 plant contributions to the SOC pool were typically maintained or enhanced subsequent to the establishment of the C_3 *Prosopis*.

DISCUSSION

The SOC and TN pools in the herbaceous matrix

To understand SOC and TN responses to woody plant encroachment, it is first important to understand the background variability in soil carbon in areas without *Prosopis* cover (e.g., grassland end members). The SOC $\delta^{13}\text{C}$ values in the grassland matrix were not “pure” C_4 ; and the strength of the C_4 signal diminished slightly (but significantly) with decreasing elevation and clay content. The principal factors contributing to ^{13}C

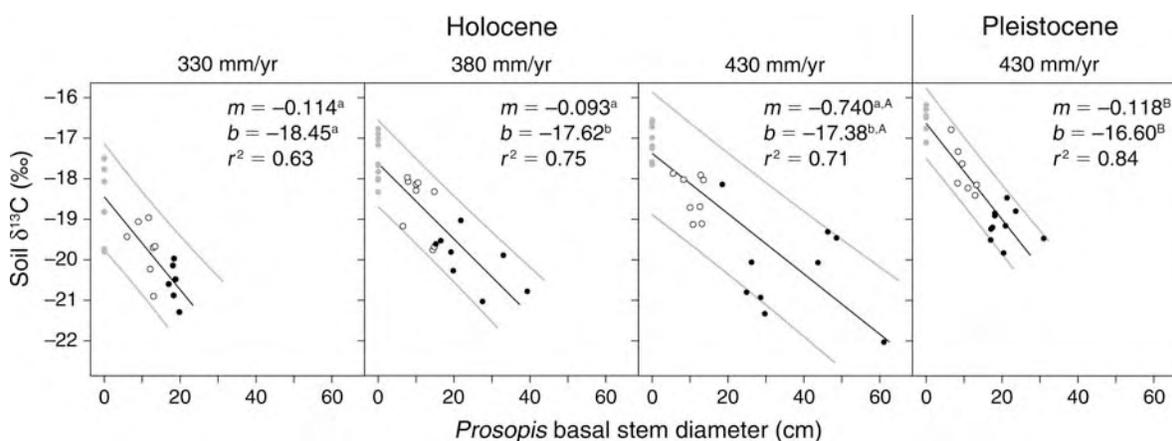


FIG. 3. Relationship between the basal stem diameter of the largest living *Prosopis velutina* stem and the organic carbon $\delta^{13}\text{C}$ of soils (0–20 cm) under and away from its canopy in each of four climatic/edaphic zones (first three panels, Holocene origin; last panel, Pleistocene). Gray circles represent inter-canopy grassland patches (*Prosopis* stem diameter = 0); open circles represent small *Prosopis* plants (stem diameter = 6–15 cm); black circles represent large *Prosopis* plants (stem diameter > 15 cm). Black lines denote least-square linear regressions; gray lines indicate 95% confidence limits. Comparing slope (m) and intercept (b) values, differing superscripts denote significant differences ($P < 0.05$) between mean annual precipitation zones (lowercase letters) and between soil types (uppercase letters).

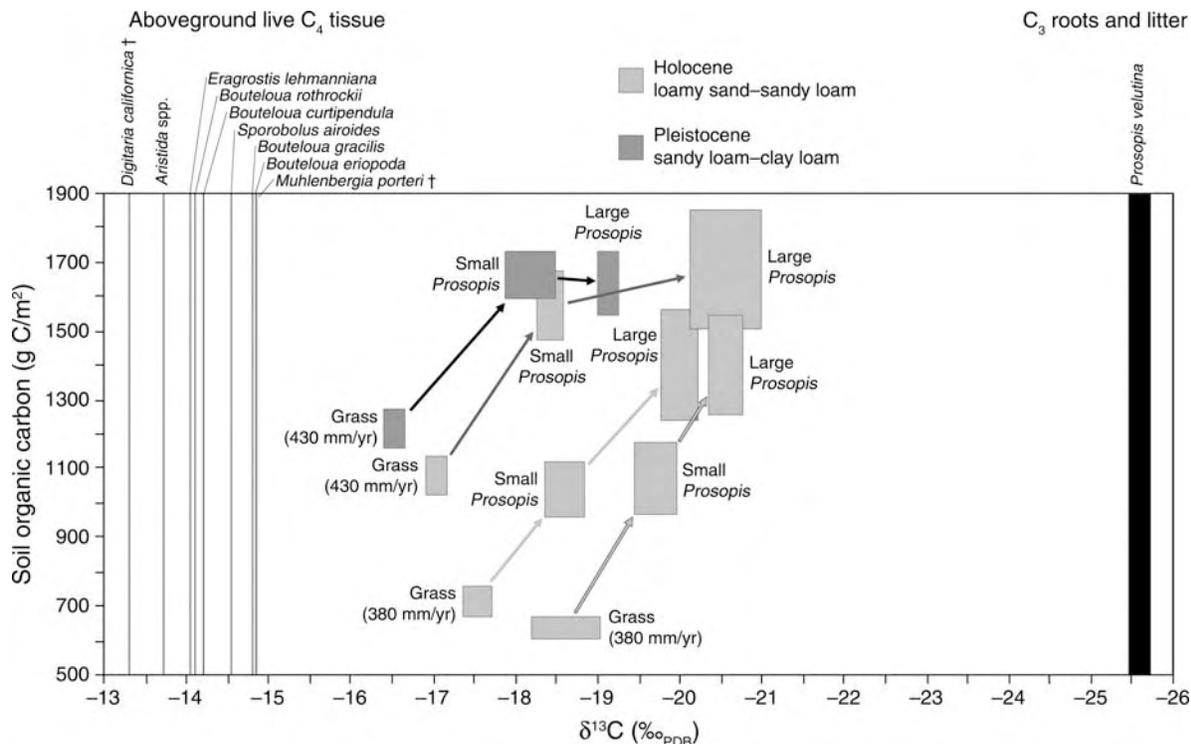


FIG. 4. Relationship between soil organic carbon (SOC) pools (at 0–20 cm depth) and their $\delta^{13}\text{C}$ values (relative to the Pee Dee Belemnite [PDB] limestone standard for C). Tracking the development of woody plant (*Prosopis velutina*) patches in a desert grassland, cover types within the same climate zone (mean annual precipitation [MAP] and mean annual temperature [MAT]) and soil type are linked with arrows. Boxes demarcate mean \pm SE values. Vertical lines denote mean $\delta^{13}\text{C}$ values for common C_3 and C_4 plants on the site that would influence the $\delta^{13}\text{C}$ of SOC pools via litter inputs (values for C_4 grasses courtesy of M. McClaran and D. Martens, unpublished data). Daggert symbols denote $\delta^{13}\text{C}$ values used to represent C_4 end members in isotopic modeling scenarios presented in Figs. 5 and 6.

depletion likely include organic matter contributions from C_3 plants and, to a lesser extent, biochemical modification of tissues during decomposition (e.g., Ehleringer 1989, Ehleringer et al. 2000). The slight attenuation of the C_4 signal observed in the herbaceous matrix may reflect elevation-related differences in inputs by C_3 annuals and ephemeral herbaceous dicots, by small, suffrutescent C_3 shrubs whose populations turn over at decadal timescales (e.g., *Isocoma tenuisecta*; McClaran [2003]) and by shallow lateral roots of C_3 *Prosopis* shrubs that are known to extend >15 m beyond canopy drip lines (Clark 1947).

When elevation, MAP, and MAT were held constant, the SOC and TN stocks in Pleistocene soils (12.5% clay) exceeded that of Holocene soils (7.5% clay) by 10% and 20%, respectively, conforming to the expectation of a positive relationship between clay content and soil carbon and nitrogen pools (Schimel et al. 1994, Burke et al. 1995, Hook and Burke 2000). The extent to which these differences reflects slower decomposition or higher herbaceous production is not known, but herbaceous production has been reported to be ~ 1.6 times greater on clay-rich loamy soils at the Santa Rita site (Subirge 1983).

In the Holocene soils, SOC and TN pools varied with elevation. The occurrence of higher sand content at upper elevations and higher clay and silt content at lower elevations is consistent with geomorphic sorting along bajada gradients (Graf 1988, Wysocki et al. 2000). Although local studies of grassland soils typically show a positive relationship between clay content and SOC stocks, we observed an inverse soil texture–pool size relationship across our 310-m elevation gradient, suggesting that higher MAP and lower MAT may be compensating for the lower clay content of soils at upper elevations to promote greater SOC and TN accumulation in these locales. This interpretation is supported by our regression analyses wherein climatic, but not soil texture variables, emerged to explain a significant fraction of the variation in SOC and TN stocks within the grassland matrix found on Holocene soils (Table 3). Our data from the grassland patches along the elevation gradient mirror regional trends whereby grassland SOC stocks are positively related to mean annual precipitation and inversely related to temperatures (Burke et al. 1989). This relationship is thought to reflect the greater responsiveness of production to precipitation relative to decomposition in arid grasslands (Austin 2002). Consistent with this explanation, several studies at the Santa

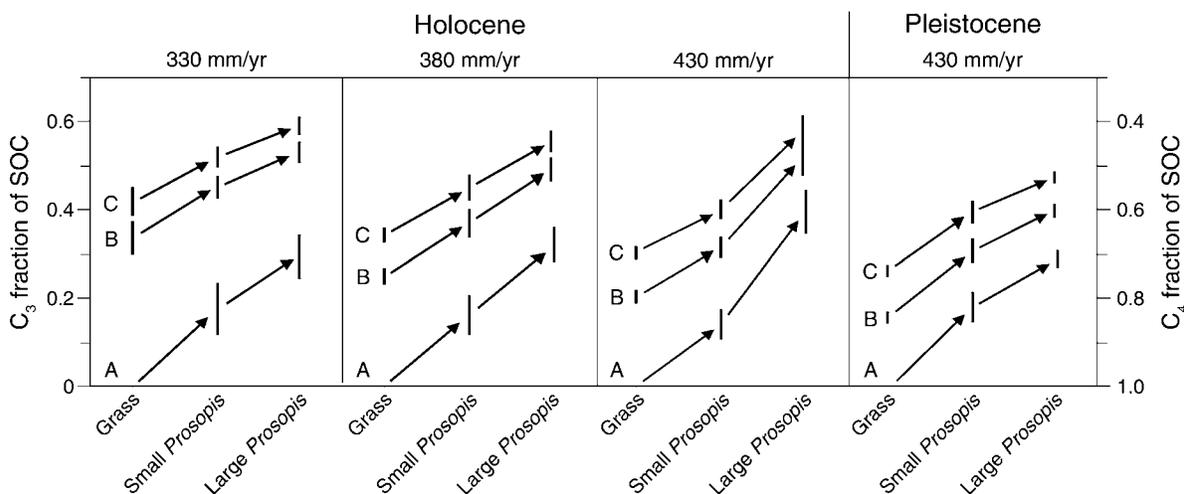


FIG. 5. Fraction of soil organic carbon (at 0–20 cm; mean \pm SE) derived from C_3 and C_4 sources in contrasting climatic/edaphic zones. Three modeling scenarios are presented that vary in the $\delta^{13}C_{C_4}$ values used in Eq. 1: (A) the $\delta^{13}C$ (mean \pm SE) of soils devoid of woody cover for each climate/edaphic zone (Table 2); (B) the $\delta^{13}C$ of *Muhlenbergia porteri* (-14.9‰); and (C) the $\delta^{13}C$ of *Digitalita californica* (-13.3‰).

Rita site have demonstrated that herbaceous production is positively related to elevation and precipitation (Cable 1975, 1976, Ruyle 2003).

The extent to which current SOC and TN pools differ from those that might have been historically present on the site is not known. Concerns over unlimited open livestock grazing and widespread signs of soil erosion in the Southwest led to the formation of the Santa Rita Experimental Range in 1902; and on this basis, it is tempting to assume that SOC and TN pools may have been substantially depleted by this time. However, the effects of grazing on SOC and TN pools are highly variable (Milchunas and Lauenroth 1993, Reeder and Shuman 2002, Derner et al. 2006). If nutrient stocks had been depleted by the early 1900s on the Santa Rita, the exclusion of livestock grazing from 1903 to 1916 and subsequent reductions in stocking rates when grazing was resumed (Ruyle 2003) may have reversed some of the C and N depletion. The soil pools evident today thus have a complex and potentially dynamic history.

Woody plant effects on soil $\delta^{13}C$

The SOC pools increased and their $\delta^{13}C$ decreased with increasing *Prosopis* BSD in each climatic/edaphic zone, presumably reflecting changes in carbon inputs and mineralization related to time of site occupation by C_3 *Prosopis* plants. The linear nature of these correlations is consistent with a simple two-source mixing relationship (Balesdent et al. 1988). However, interpretation of the relationship between SOC $\delta^{13}C$ and *Prosopis* BSD is complicated because slope values can vary as an ambiguous function of production inputs, decomposition rates, existing pool $C_3:C_4$ ratios, and tree growth rates. *Prosopis* BSD explained 63–84% of the variance in SOC $\delta^{13}C$ in a given elevation zone/soil type.

As mentioned in the Introduction, we envisioned scenarios wherein the slopes of these lines might either increase or decrease with increasing elevation. The fact that the slopes did not change significantly with elevation suggests (1) differences in C_3/C_4 inputs and rates of SOC turnover either do not change with *Prosopis* encroachment over the elevations in this study or (2) differences in C_3/C_4 inputs at some elevations were offset by changes in SOC turnover rates at other elevations.

Significant differences in slope of the *Prosopis* BSD–SOC $\delta^{13}C$ relationship on the contrasting upper elevation soils suggest that SOC $\delta^{13}C$ was more responsive to *Prosopis* encroachment on the finer-textured Pleistocene site than on the coarser-textured Holocene site. This was contrary to expectations. Compared to the Holocene site, *Prosopis* plants on the Pleistocene site are smaller (Table 2, Fig. 3), subject to more challenging growth conditions (Fravolini et al. 2005), occur at much lower densities, and have been slower to invade (Medina 1996). Thus, if anything, we would expect C_3 inputs from *Prosopis* at the Pleistocene site to be lower than those at the Holocene site. Given these edaphic constraints on *Prosopis* growth, it is likely that plants of a given size on the Pleistocene site have been present longer than similar-sized plants on the Holocene site. A longer time of occupation could thus be offsetting lower levels of C_3 inputs to effect greater changes in SOC $\delta^{13}C$. Differences in size–age relationships may also be at play to influence the manner in which SOC $\delta^{13}C$ values change with *Prosopis* BSD along the elevation gradient within soils of the Holocene complex.

Woody plants encroaching in grasslands can also affect SOC pools and isotopic composition by altering

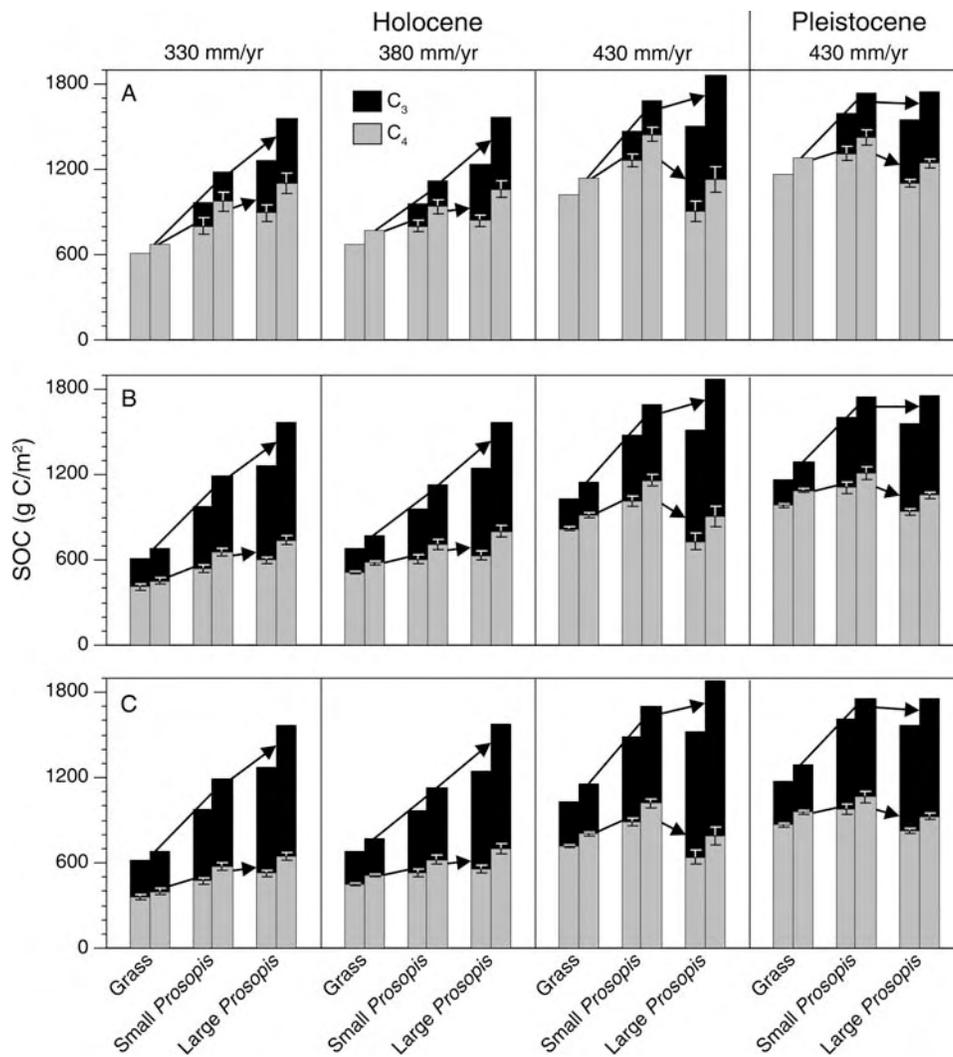


FIG. 6. The contribution of C₃ (i.e., *Prosopis velutina*) and C₄ (grass) sources to the soil organic carbon (SOC) pool (at 0–20 cm) in four soil/climate (precipitation) zones on the Santa Rita Experimental Range. For each climatic/edaphic zone, SOC stocks are presented in relation to cover type: the left bar in each pair illustrates modeling results applied to SOC stock means minus SE values, and the right bar denotes SOC stock mean plus SE values. Error bars indicate \pm SE of the mean C₃ and C₄ modeled fractions. Arrows track mean stocks in the cover transition from grassland matrix to small *P. velutina* plants and to large *P. velutina* plants. Panels (A), (B), and (C) correspond to scenarios A, B, and C described in Fig. 5.

herbaceous inputs in the soils beneath their canopies. The effects of woody plants on grass composition and production varies from negative to positive, often changing as a function of woody plant density and climatic/edaphic conditions (reviewed by Scholes and Archer 1997, Ludwig et al. 2004). In the southern Great Plains of the United States, development of C₃ shrub communities in grasslands substantially reduced herbaceous production and, hence, C₄ inputs to SOC (Archer 1995, Boutton et al. 1999). In contrast, *Prosopis* encroachment into desert grasslands at the Santa Rita appears to have promoted gains in both C₃ and C₄ SOC stocks relative to the grassland matrix, particularly during the early stages of *Prosopis* encroachment (Fig. 6). Thus, it appears that the net long-term shrub-on-

grass relationship in areas beneath *Prosopis* canopies is one of facilitation and coexistence rather than asymmetric competitive exclusion, an interpretation consistent with short-term field inventories on this site (McClaran and Angell 2006) and others in the region (e.g., Yavitt and Smith 1983, Schade et al. 2003). Indeed, Tiedemann and Klemmedson (1973a) found perennial herbaceous production under *P. velutina* canopies to be up to five times that occurring in the inter-canopy, grassland matrix. This suggests ecosystem (woody and herbaceous) aboveground net primary production in desert grasslands may increase subsequent to woody plant encroachment (e.g., Hughes et al. 2006) and helps explain the observed increases in SOC and TN documented in this study.

*Soil organic carbon and nitrogen stocks
following woody plant encroachment*

The SOC and TN pools in grasslands experiencing woody plant encroachment may increase, decrease, or show no net change (Asner and Martin 2004, Wessman et al. 2004). Throughout our study area, these pools were consistently higher in soils associated with *Prosopis* plants in comparison with soils in the grassland matrix, consistent with observations on other desert grassland sites in the area (Tiedemann and Klemmedson 1973a, b, Biggs et al. 2002, Biedenbender et al. 2004; M. P. McClaran, D. Martens, and S. Marsh, *unpublished manuscript*). Our data document how shrub impacts on SOC and TN pools change with time of woody plant site occupation along elevation gradients and on contrasting soil types. However, the extent to which differences in soil C and N stocks associated with under-shrubs vs. inter-shrub zones reflects accumulations associated with *Prosopis* biomass inputs, alteration of microclimate (e.g., soil temperature attenuation), and stimulation of herbaceous production (Tiedemann and Klemmedson 1973b) vs. lower production and SOC losses associated with higher soil temperatures and erosion in the grassland matrix (e.g., Schlesinger et al. 1999, 2000) is unclear. While *Prosopis* plants have the potential for symbiotic N₂ fixation (e.g., Virginia et al. 1984, Zitzer et al. 1996), we saw no $\delta^{15}\text{N}$ evidence suggesting N₂ fixation has contributed to TN accretion in shrub-impacted soils. However, simple $\delta^{15}\text{N}$ -based assessments of N₂ fixation are not definitive (Högberg 1997). Globally, soil $\delta^{15}\text{N}$ values are positively correlated with mean annual temperature and negatively correlated with mean annual precipitation (Amundson et al. 2003). However, we saw no systematic changes over the MAP and MAT ranges encompassed in this study. Although $\delta^{15}\text{N}$ in bulk soil can be related to degree of organic matter humification, increasing with higher degree of decomposition (Nadelhoffer et al. 1996, Koba et al. 1998), we saw no evidence for systematic changes in soil $\delta^{15}\text{N}$ across our *Prosopis* time series. The SOC and TN values were highly correlated. Surprisingly, C:N ratios changed little with woody plant encroachment, despite the fact that lignified shrub litter inputs and inputs of foliar tannins and other secondary compounds that are not present in herbaceous grassland litter (e.g., Horner et al. 1988, Sharma et al. 1995, Kraus et al. 2003) would be expected to elevate C:N values. However, the observed lack of responsiveness of grassland C:N to *Prosopis* encroachment at our desert grassland site is mirrored in uplands invaded by *Prosopis* in the temperate (Hughes et al. 2006) and subtropical (McCulley et al. 2004) southern Great Plains grasslands; and the C:N values for each of these three disparate sites were in the 10–12 range.

The SOC $\delta^{13}\text{C}$ values suggest that the recorded increases in SOC were due to increases in C₃ plant inputs and the maintenance or an increase in C₄ plant inputs (Fig. 6). This interpretation is supported by the



PLATE 1. Desert grassland being invaded by the native leguminous shrub *Prosopis velutina*. Shrub encroachment at the Santa Rita Experimental Range in southeastern Arizona (USA) has been well documented, but little is known of the biogeochemical impacts of this vegetation change. In this study we quantified how *Prosopis* shrubs modify grassland soils following establishment by comparing soil organic carbon and total nitrogen pools in shrub-free, grass-dominated patches (upper panel) to that of soils associated with small (young) and large (old) *Prosopis* shrubs (middle and lower panels, respectively). Photo credits: C. W. Wheeler.

fact that among the variables taken into account, the BSD of C_3 *Prosopis* plants emerged as the single most important factor explaining the variance in SOC pool sizes (Table 3). The MAP and MAT co-varied across the elevation gradient. As a result, it was not possible to tease apart or evaluate their relative effects on SOC/TN pools. Even so, MAP, MAT, and elevation added separately to BSD regressions explained only an additional 3–7% of the total variance in SOC/TN pool sizes.

Our results suggest that time of site occupation by *Prosopis* shrubs has a substantial influence on SOC and TN. Landscape-scale inventories of these variables should thus take into account size or age class distributions of woody plants. The variance explained by *Prosopis* BSD in this study was similar to that of *Prosopis* communities developing in grasslands on contrasting soils in the southern Great Plains ($r^2 = 0.21$ – 0.57 for SOC, 0.44 – 0.68 for TN; Archer et al. 2004). It is interesting to note that the variance in SOC and TN explained by *Prosopis* BSD was greatest in low and mid-elevation zones on Holocene soils ($r^2 = 0.61$ – 0.68), dropping to 0.39 – 0.42 on upper elevation Holocene soils and to 0.25 on upper elevation Pleistocene soils. This decline may reflect differences in the linearity of SOC/TN temporal responses to *P. velutina* influences. The fact that correlations between SOC or TN and *Prosopis* BSD went from significant to nonsignificant at the two upper elevation sites when grassland end members (*Prosopis* BSD = 0) were excluded from the regression analyses indicates that SOC and TN pools differed between grasslands and small *Prosopis* plants, but not between small and large *Prosopis* plants. This suggests SOC levels may be reaching a stable upper asymptote by the time *Prosopis* plants reach a BSD of ~ 15 cm at upper elevation sites. By contrast, excluding grassland end members did not alter the significance of the regression relationships at the two lower elevation sites, suggesting that SOC/TN pools associated with *Prosopis* plants in these areas are still on a positive trajectory. This interpretation is substantiated in Fig. 4, in which SOC at the two upper elevation sites appears to be stabilizing with respect to pool size in small vs. large *Prosopis* plants, while still changing with respect to its $\delta^{13}C$. Conversely, both SOC pools and their $\delta^{13}C$ appear to be on a linear trajectory for the two lower elevation sites. It remains to be seen whether SOC will continue to accumulate in the two lower elevation sites or if these sites are on the brink of stabilizing at a new equilibrium. If the latter turns out to be the case, then future accumulations of SOC and TN on these landscapes would be contingent on the maturation of existing small *Prosopis* plants and the recruitment and growth of new *Prosopis* plants. The net result to this point, based on a space-for-time perspective, is that grass-dominated patches in the four climatic/edaphic zones, which are distinctly different from each other in terms of the size and $\delta^{13}C$ of the SOC pool, appear to converge on a

higher and relatively comparable SOC pool size and $\delta^{13}C$ subsequent to *Prosopis* establishment.

Caution should be taken in assuming *Prosopis* BSD is a direct surrogate for time, because this species is highly tolerant of disturbance and regenerates vegetatively when stems are damaged or killed. Thus, a relatively small stem may represent a young plant or a much older plant vegetatively regenerating after its original stem(s) were killed by fire, drought, or other disturbance. This may explain why some relatively small *Prosopis* plants had $\delta^{13}C$ values and SOC/TN pools comparable to that of larger *Prosopis* plants. Thus, it is possible that the differences in the variance in soil properties accounted for by stem size along the elevation gradient and on the contrasting soil types (Table 3) may reflect differences in stem mortality experienced by individual *Prosopis* plants.

Having stated the challenges associated with ascribing a timeline to quantifying woody plant encroachment effects on SOC/TN pools, the fact that shrub encroachment into desert grasslands on the Santa Rita has been well documented afforded a unique opportunity to quantify grassland soils change subsequent to shrub establishment. This opportunity was enhanced by the fact we were able to control for potentially confounding effects associated with livestock grazing history, climate, soils, and fire history. Small (< 1 m tall) *Prosopis velutina* plants were observed in Santa Rita grasslands in 1902 and an increase in their stature and abundance was qualitatively noted by 1915 (Wooten 1916). We thus have confidence that the largest/oldest plants on our sites are up to ~ 100 years of age. However, between 1934 and 1954, there was a 33% increase in the land area where densities exceeded 198 plants/ha and shrub cover on permanent transects increased from $\sim 6\%$ in 1960 to $\sim 20\%$ in 1990 (McClaran 2003). Based on this chronology, we have some confidence that the differences in *Prosopis* plant sizes within a given elevation zone/soil type accurately represent passage of time. If we assume that the oldest shrubs in our sampling were 100 years of age and that differences in SOC and TN pools between grass- and shrub-dominated patches represent shrub-induced accumulations, then we get rough SOC accrual rates of ~ 10 – 12 and 6 $g\cdot m^{-2}\cdot yr^{-1}$ on Holocene and Pleistocene surfaces, respectively, and TN accrual rates of ~ 0.8 – 1.3 (Holocene) and 0.6 (Pleistocene) $g\cdot m^{-2}\cdot yr^{-1}$. These compare favorably to estimated rates in southern Great Plains grasslands (MAP 720 mm/yr) undergoing shrub encroachment (8 – 30 $g\ C\cdot m^{-2}\cdot yr^{-1}$ and 0.9 – 3 $g\ N\cdot m^{-2}\cdot yr^{-1}$ depending on soil type; Hibbard et al. 2001, Liao et al. 2006a).

As mentioned in the previous section, it is likely that *Prosopis* growth rates vary across the elevation gradient within the Holocene complex and between plants found on the Pleistocene and Holocene soils. This makes it difficult to establish a timeline for rates of change in soil properties among our sites. Our study points to the need for basic monitoring that includes site-specific measure-

ments of woody plant growth rates. With such information, one could model *Prosopis* growth rates and more reliably infer time of woody plant occupation from size and, by extension, estimate rates of SOC and TN accumulation in soils.

Our results provide a bulk soil perspective on SOC, TN, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ in grassland soils experiencing shrub encroachment across a precipitation gradient. However, the constituents of bulk soils include various particulate organic matter classes and organic carbon and nitrogen associated with various aggregate or particle size fractions that differ in their C and N accumulation and turnover rates and residence times (e.g., Boutton et al. 1998, Gill and Burke 1999, Liao et al. 2006a). In addition, SOC and TN change with depth at this site (Tiedemann and Klemmedson 1973a), and our pooling of soil across the upper 20 cm prevented us from determining more precisely where the changes in SOC and TN pools were occurring and which constituent fractions were contributing the most to the changes. Thus, a refined depth/constituent partitioning sampling scheme would be instructive next steps.

Current approaches for inventorying landscape-scale SOC and TN pools typically take average values for bulk soils under shrubs and weight these by the total areal cover of shrubs. Our data suggest the accuracy of such inventories could be improved by computing the fractional contribution of shrub size classes to total shrub cover on a landscape, assigning size (or age, when possible) class-specific values of SOC and TN, then summing these. Furthermore, there may also be strong horizontal spatial gradients of C and N in soils associated with shrubs establishing in grasslands, whereby concentrations and pools are elevated and highest near the shrub bole (the point of longest occupation) and comparable to the herbaceous matrix at the shrub canopy perimeter (the point of shortest time of shrub occupation; Wu et al. 2006). Thus, accurate landscape assessments of shrub encroachment influences on grassland soils should simultaneously consider the extent of cover of shrub age states and horizontal/vertical gradients beneath shrub canopies.

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