Shrub (*Prosopis velutina*) encroachment in a semidesert grassland: spatial–temporal changes in soil organic carbon and nitrogen pools

H E A T H E R L . T H R O O P * and S T E V E N R . A R C H E R †
*Department of Biology, New Mexico State University, MSC 3AF, Las Cruces, NM 88003, USA, †School of Natural Resources, University of Arizona, Tucson, AZ 85721-0043, USA

Abstract

Recent trends of increasing woody vegetation in arid and semiarid ecosystems may contribute substantially to the North American C sink. There is considerable uncertainty, however, in the extent to which woody encroachment alters dryland soil organic carbon (SOC) and total nitrogen (TN) pools. To date, studies assessing SOC and TN response to woody plant proliferation have not explicitly assessed the variability caused by shrub age or size and subcanopy spatial gradients. These factors were quantified via spatially intensive soil sampling around *Prosopis velutina* shrubs in a semidesert grassland, using shrub size as a proxy for age. We found that bulk density increased with distance from the bole ($P < 0.005$) and decreased with increasing shrub size ($P = 0.056$), while both SOC and TN increased with shrub size and decreased with distance from the bole ($P < 0.001$ for both). Significant (and predictable) spatial variation in bulk density suggests that use of generic values would generate unreliable estimates of SOC and TN mass, and subcanopy SOC pools could be overestimated by nearly 30% if intercanopy bulk density values were applied to subcanopy sites. Predictive models based on field-documented spatial patterns were used to generate integrated estimates of under-shrub SOC and TN pools, and these were compared with results obtained by typical area-weighting protocols based on point samples obtained next to the bole or at a specified distance from the bole. Values obtained using traditional area-weighting approaches generally overestimated SOC pools relative to those obtained using the spatially integrated approach, the discrepancy increasing with increasing shrub size and proximity of the point sample to the bole. These discrepancies were observed at the individual plant scale and for landscapes populated by various shrub size classes. Results suggest that sampling aimed at quantifying shrub encroachment impacts on SOC and TN pools will require area-weighting algorithms that simultaneously account for shrub size (age) and subcanopy spatial patterns.

Keywords: carbon sequestration, land cover change, *Prosopis*, Santa Rita Experimental Range, semidesert grassland, shrub encroachment, soil nitrogen, soil organic carbon

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Introduction

Arid and semiarid systems (hereafter 'drylands') play an integral role in the global carbon (C) cycle. Although dryland net primary production (NPP) tends to be low, these systems account for approximately 40% of the terrestrial land surface and 30% of the terrestrial NPP

(e.g. Bailey, 1996; Field *et al.*, 1998). Increasing woody plant biomass has been a prevailing global pattern in dryland systems over the past century, leading to transitions of grasslands to savannas and savannas to woodlands (Archer, 1994). While the causes of woody encroachment remain an active debate, grazing and fire suppression appear to be important factors (Archer *et al.*, 1995; van Auken, 2000). Woody encroachment impacts livestock production and wildlife habitat and has therefore historically sparked active research in

Correspondence: Heather L. Throop, tel. + 1 575 646 5970, fax + 1 575 646 5665, e-mail: throop@nmsu.edu

these topic areas. Less well studied are the biogeo-chemical consequences of this global-scale change in physiognomy. Understanding the role of woody encroachment in the global C cycle is crucial, particularly as land managers and policy makers grapple with developing and evaluating C sequestration initiatives in terrestrial ecosystems.

Several recent C budget analyses suggest that woody encroachment and 'thickening' of woody vegetation in dryland and montane ecosystems represent a potentially large, but highly uncertain, portion of the North American C sink (Schimel et al., 2000; Pacala et al., 2001; Houghton, 2003a, b). Understanding the influence of woody plant proliferation on belowground C pools is critical to decreasing the uncertainty of estimates of dryland sink strength, as belowground pools typically dwarf aboveground pools in dryland systems (Scholes & Hall, 1996; Hughes et al., 2006). The prevailing dogma for woody encroachment has been that woody plants create 'islands of fertility' where soil organic carbon (SOC) and soil nutrients accumulate as a result of increased above- and belowground litter inputs, translocation of nutrients from intercanopy areas to zones beneath shrub canopies via extensive lateral root systems occur, or decomposition of lignin-rich woody litter is slower (Virginia, 1986; Schlesinger & Pilmanis, 1998; Hibbard et al., 2001). Woody plants may also promote nutrient accumulation in subcanopy zones by enhancing deposition from aeolian, fluvial or animal transport processes (Belsky et al., 1989; Weltz et al., 1998; Okin & Gillette, 2001). However, a review of literature indicates that changes in SOC in response to woody encroachment vary widely, ranging from net SOC accumulation, to no change, to declines (Wessman et al., 2004). Further characterization of both the direction and magnitude of SOC response to woody encroachment is crucial for making robust predictions about changes in large-scale terrestrial C budgets associated with changes in vegetation and for devising effective local and regional terrestrial C management or sequestration strategies.

Decreasing uncertainty in the role of woody encroachment in the global C cycle requires improvements in (1) estimating current C pools in dryland systems, (2) estimating historical pool sizes, and (3) generating accurate predictions of future pool sizes under current and novel management strategies and environmental conditions. While aboveground changes in C storage can be assessed at local to regional levels using remote sensing (Asner et al., 2003), current remote sensing technologies cannot penetrate into soil pools (Johnston et al., 2004). Our understanding of woody plant influences on SOC is therefore driven by analyses of soil cores, for which replication in time and space is typically very limited due to the labor required for core acquisition, proces-

sing, and analysis. Scaling up from very localized data available from cores of soils associated with individual plants to the landscape level necessitates making predictions based on simplified spatial patterns. Our ability to scale up from core studies is limited by an incomplete understanding of spatial and temporal patterns of soil response to vegetation change.

To date, studies assessing SOC response to woody plant encroachment have provided very limited information on within- and among-shrub variability. Geostatistical approaches have been used to demonstrate that patterns of soil properties tend to occur at the scale of shrub canopies (Jackson & Caldwell, 1993; Schlesinger et al., 1996), but to our knowledge, the implications of these patterns have not been explicitly used to generate landscape-scale estimates of SOC pools. Shrub size or age has been shown to strongly influence soil nutrient pools (e.g. Barth, 1980; Archer et al., 2004; Ludwig et al., 2004; Wheeler et al., 2007). This implies that potentially strong within-canopy spatial gradients may exist, because soils nearest to the bole are influenced by shrubs for the longest time and soils at the canopy perimeter are affected for the shortest period of time. However, field studies are not typically designed to quantify these spatial gradients. Instead, estimates of shrub impacts on soils are typically based on cores taken at constant distances from woody plant boles (e.g. Tiedemann & Klemmedson, 1973; Hibbard et al., 2001) or at a set position relative to canopy size (e.g. Connin et al., 1997; Gill & Burke, 1999). In many cases, sampling position relative to the bole or canopy size is not reported (e.g. Jackson et al., 2002; Hughes et al., 2006). Furthermore, woody plant size or age is seldom explicitly considered or reported. Extrapolating these subcanopy results to a larger spatial scale using area-weighting algorithms assumes a uniform spatial distribution of SOC in the subcanopy zones, and ignores factors such as shrub age that may affect SOC mass estimates. In doing so, SOC pools could be substantially over- or underestimated, depending on the size and age structure of the shrub population on a given landscape.

We assessed spatial patterns in SOC and total nitrogen (TN) in a semidesert grassland, in which encroachment by the shrub Prosopis velutina (Woot., Fabaceae) is known to have has occurred over the past 100 years (McClaran, 2003; Wheeler et al., 2007). We hypothesized that (1) Prosopis-induced changes in SOC and TN would be positively correlated with the shrub size; (2) SOC and TN would be greatest near the bole and decrease with increasing distance from the bole; and (3) measurable shrub influences on these variables would extend beyond the canopy dripline owing to the presence of extensive, shallow, lateral shrub root systems (e.g. Cable, 1977). By using shrub size as a proxy for age, we

quantified how spatial patterns of SOC and TN change with time since *Prosopis* encroachment. We then used the relationships between shrub size and undercanopy gradients of SOC and TN to generate predictions for subcanopy SOC and TN pools for a range of shrub sizes, and explored how these predictions differed from estimates based on less spatially extensive measurements.

Methods

Study site

Soil samples were collected in Pasture 2S (110°53′4.32″W, 31°47′36.07″N; 1100 m a.s.l.) of the Santa Rita Experimental Range (SRER), a 21 513 ha semidesert grassland research site ca. 80 km south of Tucson in Pima County, Arizona (http://ag.arizona.edu/SRER/). Vegetation and climate of the site have been described in detail by McClaran (2003). Mean annual precipitation (370 mm) is divided roughly equally between winter rains and late summer monsoons. The dominant ground cover is Lehmann lovegrass (*Eragrostis lehmanniana* Nees), a C_4 grass native to southern Africa and introduced into the SRER in the 1930s. Lehmann lovegrass has displaced native perennial grasses and is now the dominant grass species in many parts of southern Arizona and western New Mexico (Schussman *et al.*, 2006). Other common perennial species include the native grasses Arizona cottontop (*Digitaria californica*) and bush muhly (*Muhlenbergia porteri*); burroweed (*Isocoma tenuisecta*), a small, suffruticose shrub; and cholla cactus (*Opuntia* spp.). Site records have documented increases in woody plant cover, primarily *P. velutina* (velvet mesquite), since the early 1900s (McClaran, 2003). Current land cover at the study site is ~55% herbaceous, ~30% woody plant, and ~15% bare ground (Browning *et al.*, 2008). Pasture 2S has been rotationally grazed since 1957 (3 years of continuous livestock grazing followed by 2 consecutive years of March through October rest; Ruyle, 2003). Cattle were present at the time of the study. Although experimental brush management treatments (cutting and aerial herbicide applications) have occurred in Pasture 2S, no such treatments were documented in the areas from which we collected our data, and there is no visual evidence of herbicide wind drift. Soils at the site are Holocene-derived coarse-loamy alluvial material in the Combate–Diaspar complex, classified as thermic Ustic Haplargids (Breckenfeld & Robinett, 2003).

Soil collection and analyses

We selected 17 focal shrubs for soil sampling. The focal shrubs (basal diameter range, 2–102 cm; mean ± SE,

29 ± 7.5 cm) evenly and completely spanned the size range of shrubs present at the field site. Canopies of selected shrubs were separated from those of their nearest neighbor by at least 2 m. Basal stem diameter and canopy radius, both strongly correlated with each other and with aboveground shrub biomass ($r^2 > 0.80$ and $P < 0.01$ for all; S. R. Archer *et al.*, in preparation), were recorded for each shrub.

Five to ten soil cores (2.3 cm diameter; 20 cm depth) were extracted with a slide hammer around each focal shrub for SOC and TN analyses. Cores were taken at varying 'canopy positions' beginning at the bole and radiating beyond the canopy dripline. Canopy position 1 was immediately adjacent to the bole, canopy position 6 was at the dripline, and canopy positions 2–5 were arrayed at equally spaced intervals between the bole and dripline. Canopy positions 7–10 were arrayed at equally spaced intervals extending from the dripline to a distance beyond the dripline equivalent to 25% of the canopy radius. For the six smallest shrubs (basal diameter, <7 cm), cores were taken at every other canopy position due to the small size of canopies. Bearings were generated randomly for each sampling point on each shrub and were adjusted if necessary to avoid coring in areas with evidence of recent rodent activity or underneath *I. tenuisecta* plants. Surface litter, if present, was brushed away before coring. An additional four cores (20 cm depth, 4.76 cm diameter) were collected with a slide hammer at each shrub for bulk density (BD) analysis (two cores for the six shrubs with basal diameters <7 cm). These cores were excavated by hand to prevent any loss of core volume. Sampling locations for the BD cores were spaced equally from the bole to one-eighth of a canopy radius beyond the dripline. Subcanopy BD cores corresponded with SOC canopy positions 1, 3, and 5. For small shrubs with only two BD cores, cores were taken at either the first and third or second and fourth BD sampling locations. Soils were collected on April 4–5 and October 29, 2005; and the properties of interest (SOC, TN, and BD) are known to be highly stable over this short time-frame (Amundson, 2001; Conen *et al.*, 2003; Smith, 2004).

Cores were dried at 60 °C immediately after collection. BD cores were processed and analyzed as described by Blake & Hartge (1986). BD was calculated as the mass of soil (<2 mm fraction) for entire core volume (including the >2 mm fraction). Although standard methodology excludes the volume of the >2 mm fraction from BD calculation, we included this volume in order to correct SOC and TN values on an areal basis for the considerable rock volume present in this system. Cores used for SOC and TN analyses were passed through a 2 mm sieve, litter and fine root material were removed by hand from subsamples, and subsamples

were pulverized in electric coffee grinders. Although calcium carbonate accumulation is negligible at this site to the depth cored for this study (H. Throop, personal observation), soils were acid fumigated to remove any carbonates present (Harris *et al.*, 2001). Samples were analyzed in triplicate for C and N content on an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA, USA).

Plant-scale C estimates

A predictive model for BD based on *Prosopis* basal diameter and canopy position was developed using a mixed model with Proc Mixed (SAS Institute, Cary, NC, USA). Both canopy position and the square of canopy position were included in the model, thus allowing a linear analysis of a quadratic model. Because multiple samples were taken from individual shrubs, shrub was included in the model as a random effect. This predictive model was then used to generate predicted BD values at each canopy position cored for SOC and TN. Predicted BD values were used to convert %C and %N values to $g\,m^{-2}$ for each SOC and TN soil core.

Proc Mixed was used to generate predictive models for SOC and TN ($g\,m^{-2}$) based on *Prosopis* basal diameter and canopy position. We employed a mixed-model analysis using continuous variables rather than a categorical approach (e.g. ANOVA) in order to develop a predictive model that would show the SOC response patterns, as we expected these patterns to occur in a continuous rather than discrete manner. Canopy position and basal diameter were natural log-transformed before inclusion in the model, thus allowing analysis as a linear model. Shrub was included in the model as a random effect. Relationships between SOC and TN were assessed using stepwise linear regression, in which SOC, canopy position, and basal diameter were assessed as predictors of TN.

Predictive models for SOC and TN were used to generate total subcanopy pools for seven hypothetical shrubs with a range of basal diameters (2–100 cm). Canopy positions in the predictive models were converted to distance from bole (m) using relationships between basal diameter (cm) and canopy diameter (m) [ln(1 + canopy diameter) = 0.2516 + 0.4761 ln(basal diameter), $R^2 = 0.90$, $P < 0.0001$; S. R. Archer *et al.*, in preparation] in order to express the subcanopy pools on an areal basis. Total subcanopy SOC and TN pools were determined using the shell method for solids of rotation (Stewart, 2002). SOC and TN predictive models were rotated around the boles, and the resulting functions were integrated to determine total subcanopy pools. The functions were solved for each hypothetical shrub for the distance (m) between the bole and canopy edge

(canopy position 6) using Maple 10 (Maplesoft, Waterloo, Canada). Total subcanopy area and background SOC and TN (calculated as the average value of all cores beyond the dripline) were used to express enhancement of subcanopy SOC and TN relative to background values.

Estimates of subcanopy SOC obtained from the integration method were then compared with results that would be obtained using spatially less-intensive sampling procedures. Using the SOC predictive model, we generated SOC values from canopy positions that mimic each of three commonly used single-point sampling procedures (next to the bole, 1 m from the bole, and approximately mid-way between the bole and dripline at canopy position 3). For each of these sampling protocols, we used linear regression to generate predictive equations of SOC and TN based on shrub basal diameter. We used these equations to predict SOC and TN for each of the hypothetical shrubs and multiplied this value by subcanopy area to obtain an area-weighted estimate of shrub impacts on SOC and TN pools.

Landscape-scale SOC estimates

The plant-scale models described earlier were used to explore the implications of including shrub size and SOC spatial distribution information on landscape-scale SOC estimates. We calculated total subcanopy and intercanopy SOC for a hypothetical 1 ha landscape that had 30% shrub canopy cover (average cover for SRER; Browning *et al.*, 2008). We estimated subcanopy SOC under three different shrub size scenarios, in which all shrubs were either 5, 25, or 75 cm basal diameter. A regression equation relating basal diameter to canopy diameter [ln(1 + canopy diameter) = 0.2516 + 0.4761 ln (basal diameter), $r^2 = 0.90$, $P < 0.0001$; S. R. Archer *et al.*, in preparation] was used to calculate the canopy area and number of shrubs present on a landscape with 30% shrub cover. For each shrub size, we estimated subcanopy SOC using our integration method and the three spatially less-intensive methods described in the preceding paragraph. Landscape-scale estimates were obtained by summing area-weighted subcanopy and background (= values from cores beyond canopy driplines: $896 \pm 27\,g\,C\,m^{-2}$; $n = 45$) SOC values. In addition, we generated one landscape-level SOC estimate based on the actual size-class distribution of shrubs present at our study site as determined from 16 (4 m × 15 m) belt transects from field surveys conducted in 2004. Landscape-scale SOC estimates were then standardized by scaling up to a 1 ha landscape with 30% canopy cover.

Results

Plant-scale estimates

BD increased with distance from bole and decreased with increasing shrub basal diameter (Fig. 1). Parameter estimates were significant at $P = 0.056$ for basal diameter and at $P < 0.005$ for canopy position and canopy position squared. Simple linear regressions in which BD was regressed against *P. velutina* basal diameter for each canopy position revealed no significant relationship at any given canopy position (Table 1).

Both SOC and TN were positively correlated with shrub basal diameter and negatively correlated with distance from the bole (Fig. 2). Basal diameter and canopy position were significant parameters in the models ($P < 0.001$ for both). The modeled response surface had the poorest fit to the data for soil cores close to the bole of large shrubs (e.g. > 80 cm basal diameter), where the model tended to underestimate both SOC and TN. The interaction between basal diameter and canopy position effects on SOC and TN was stronger under large shrubs than under small shrubs (Fig. 3). Simple linear regressions in which SOC and TN were regressed against log-transformed *P. velutina* basal diameters for each canopy position indicated significant relationships for cores in positions 1–3 and no relationship for cores in positions 4–6 (Table 1). Beyond the
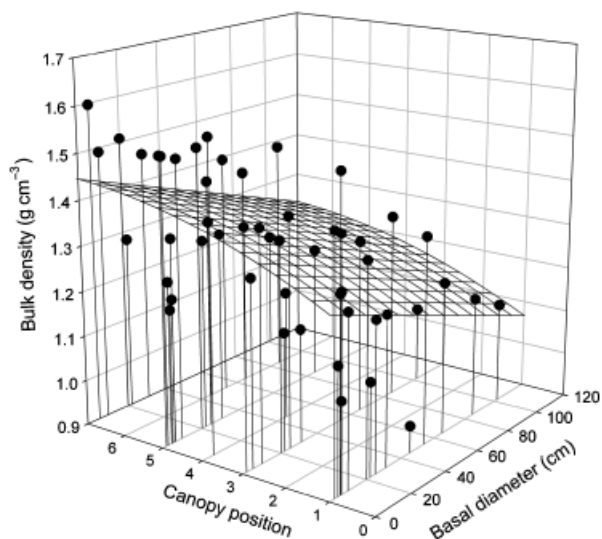

Fig. 1 Measured bulk density values (points) overlaid upon the predictive model ($z = 1.230 + 0.056x - 0.004x^2 - 0.002y$, where z is the bulk density, x is the canopy position, and y is the basal diameter). Canopy position refers to the relative distance between the bole and dripline, with canopy position 1 immediately adjacent to the bole, canopy position 6 at the dripline, and canopy positions 2–5 arrayed at equally spaced intervals between the bole and dripline.

dripline (canopy positions 6 and beyond), there was no significant influence of basal diameter or canopy position on either SOC or TN ($P > 0.3$ for all parameters). The pooled mean ($\pm$ SE) of the cores beyond the shrub canopy driplines, 8957 ($\pm$ 267) kg C ha^{-1}, was therefore used as the background value from which to evaluate area-weighted changes in SOC pool sizes induced by shrubs in the following sections.

Stepwise linear regression indicated a strong linear relationship between TN and SOC [TN = 11.5705 + 0.0844(SOC), $r^2 = 0.939$, TN and SOC in g m^{-2}]. Including basal diameter in the model only slightly enhanced model fit, and basal diameter had a slight negative influence on TN relative to SOC [TN = 12.3032 + 0.0858(SOC) − 0.0624(basal diameter), $r^2 = 0.945$, TN and SOC in g m^{-2} and basal diameter in cm], but including canopy position did not enhance the model fit. Due to the strong relationship between TN and SOC, subsequent results will focus on SOC for expediency.

Single-point sampling generally overestimated SOC pools weighted by shrub canopy area relative to integrated sampling along bole-to-canopy gradients, and the discrepancy increased with increasing shrub size and proximity of the point sample to the bole (Fig. 4). Canopy area-weighted SOC estimates based on sampling adjacent to the bole produced the highest values (131% of the integration value for a 50-cm basal diameter shrub) and sampling 1 m from the bole produced the next highest estimates. Estimates based on mid-canopy sampling yielded the closest response to the integration method (110% of the integration value for a 50-cm basal diameter shrub).

Landscape-scale estimates

Estimates of the extent to which woody plants influenced landscape-scale SOC differed depending on both

Table 1 Coefficients of determination from simple linear regressions, in which soil variables were regressed against natural log-transformed basal diameter

	Canopy position					
	1	2	3	4	5	6
Bulk density	0.149	–	0.270	–	0.151	–
SOC	**0.313***	**0.432****	**0.433***	0.153	0.001	0.0001
TN	**0.308***	**0.436****	**0.482***	0.168	0.135	0.012

*$P < 0.05$.
**$P < 0.01$.
Significant responses are indicated in bold. Regressions for cores beyond the canopy edge (cores 7–10) were not significant and are not shown. Note that bulk density cores were taken at a subset of canopy positions.
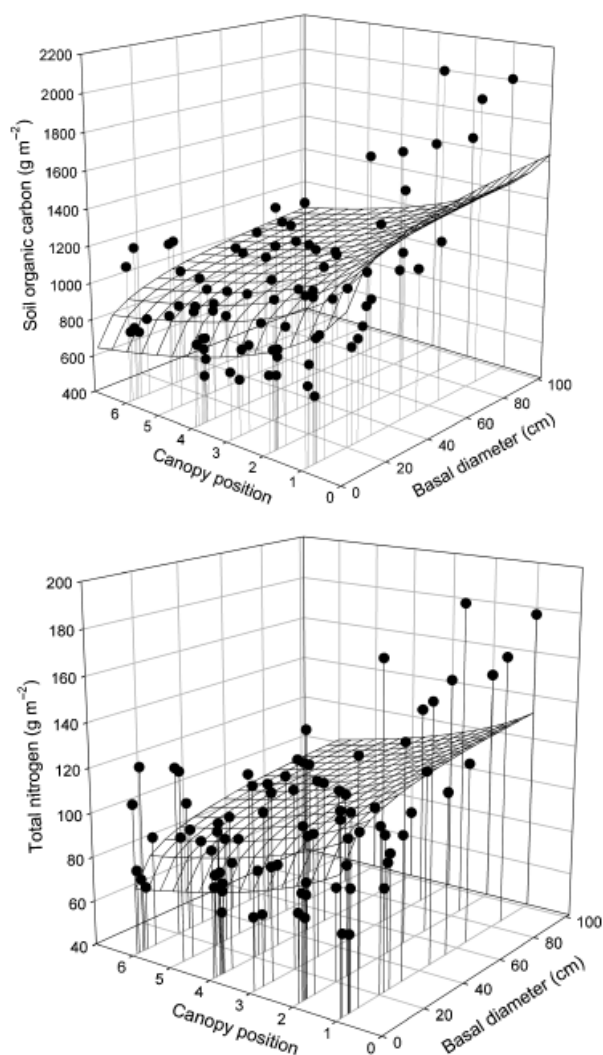
Fig. 2 Comparison of measured SOC and TN values (points) with the predictive models based on canopy position and shrub basal diameter. See Fig. 1 legend for canopy position scale codes. (a) SOC field data and model [$z = 1159.61 - 287.11 \ln(x+1) + 102.96 \ln(y)$, where z is SOC, x is the canopy position, and y is the basal diameter]. (b) TN field data and model [$z = 111.13 - 24.22 \ln(x+1) + 8.11 \ln(y)$, where z is SOC, x is the canopy position, and y is the basal diameter].

the shrub size scenario and subcanopy sampling protocol. Estimates for total SOC in the hypothetical 1 ha landscape varied from 8908 (5 cm basal diameter shrubs, integration method) to 11 209 kg C (75 cm basal diameter shrubs, bole sampling; Fig. 5). Using an estimate of 8957 kg C ha^{-1} for background SOC (mean from cores beyond canopy driplines) on a landscape with no woody plant encroachment, estimates of SOC sequestration following woody encroachment ranged from essentially zero (-48 kg C ha^{-1}) to an increase of 2252 kg C ha^{-1}. This represents a -0.005% decrease to

25.1% increase in SOC, with net C sequestration for 25 and 75 cm basal diameter shrubs averaging across all methods. Total SOC estimates for a 1 ha landscape based on actual shrub size-class distribution were slightly higher than estimates for 25 cm basal diameter shrubs, ranging from 9403 kg C for the integration method to 10 169 kg C for sampling next to the bole (Fig. 5).

Discussion

Shrub influence on bulk density

BD was strongly affected by shrub size and canopy position. Declines in BD toward the bole and with increasing shrub size suggest that modification of soil density occurs with time, where factors such as stem flow, modification of microclimate, and inputs of organic matter have had the longest time of influence and greatest cumulative mass input. Other factors that can influence subcanopy soil BD, such as bioturbation by burrowing animals, compaction by large grazers, and altered raindrop impact energy, may differ along the bole-to-dripline gradient as well.

The inverse relationship between shrub size and BD illustrates a potential pitfall associated with scaling up from spatially limited BD sampling. The range of BD values predicted by our field-based model, 1.1–1.5 g cm^{-3}, has considerable implications for predicting SOC on a unit area basis. Subcanopy SOC pools could be overestimated by nearly 30% if intercanopy BD values were applied to subcanopy sites. Furthermore, we caution that the frequently employed methodology of removing the volume of >2 mm rock fragments from density calculations will overestimate SOC pools in soils with a large percentage of coarse fragments. These rock fragments accounted for ca. 9% of the soil volume in our samples; excluding this volume as soil in BD calculations would increase SOC estimates accordingly at all canopy positions (e.g. mean background SOC was 895 g m^{-2} with our method and would be 991 g m^{-2} if rock volume were excluded from BD calculations, and mean SOC next to the bole of a 100 cm basal diameter shrub would be 1434 g m^{-2} vs. 1593 g m^{-2}, respectively).

Shrub influence on SOC and TN accumulation

Prosopis encroachment at this dryland site leads to increased subcanopy SOC and TN, but this change is a function of shrub size and location along the bole-to-dripline gradient. This positive response of SOC to woody encroachment mirrors patterns found at many other sites (e.g. Archer *et al.*, 2001; Hibbard *et al.*, 2001) and may originate from increased organic matter input,

depressed loss rates, or a combination of these factors. Shrub–grass relationships of relative biomass exhibit high among-site variability (Scholes & Archer, 1997),
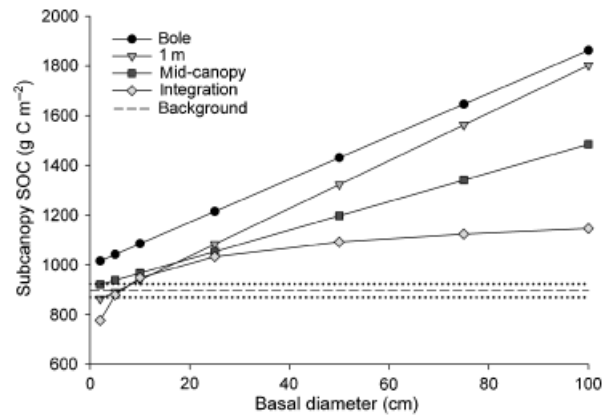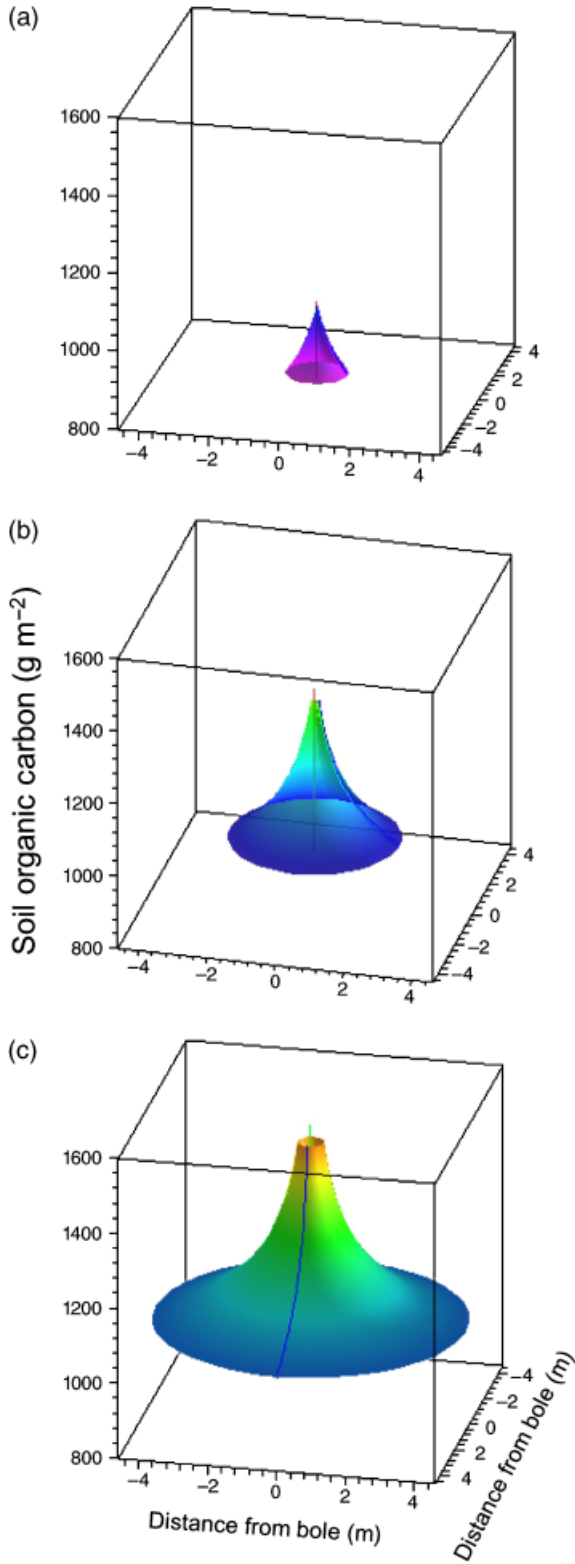

Fig. 4 Comparison of average subcanopy SOC values using different sampling protocols for a range of tree sizes. Estimates of SOC pools obtained from the integration method (Figs 2a and 3) are compared against those that would be obtained from area weighting based on single-point sampling protocols where the single points were at the bole, 1 m from the bole, or mid-way between the bole and dripline. The 'background' value ($896 \pm 27 \, g \, C \, m^{-2}$) represents the mean ($\pm$ SE; depicted as dotted lines around the mean) of 45 samples collected from intercanopy zones at the study site.

and subcanopy SOC patterns at our study site may reflect enhanced subcanopy herbaceous biomass relative to intercanopy spaces found previously at this study site (Tiedemann & Klemmedson, 1977). This facilitative relationship may enhance subcanopy litter inputs due to herbaceous biomass production, enhance accumulation of organic material that is transported by aeolian and fluvial processes, and lead to depressed subcanopy decomposition due to limited subcanopy soil–litter mixing and depressed UV photodegradation (Austin & Vivanco, 2006; Throop & Archer, 2007).

Fig. 3 Representative influence of small, medium, and large *Prosopis velutina* shrubs on SOC pools. Functions for SOC response to distance from bole (m) were obtained for hypothetical tree sizes from the SOC response surface (Fig. 2a). Total SOC was calculated through integration using the shell method for solids of rotation. The volume of the solid represents SOC above background (intercanopy) levels. The gap in the middle (visible in panel c) represents the bole and the shapes extend out on the horizontal axis to the canopy edge. Colors represent a continuum of SOC concentrations, with highest values depicted as orange and lowest values as purple. See Fig. 1 legend for canopy position scale codes. (a) SOC under a 5 cm basal diameter tree, where total SOC pool is 2156 g C. (b) SOC under a 25 cm basal diameter shrub, where total SOC pool is 19 872 g C. (c) SOC under a 75 cm basal diameter shrub, where total SOC pool is 71 743 g C.
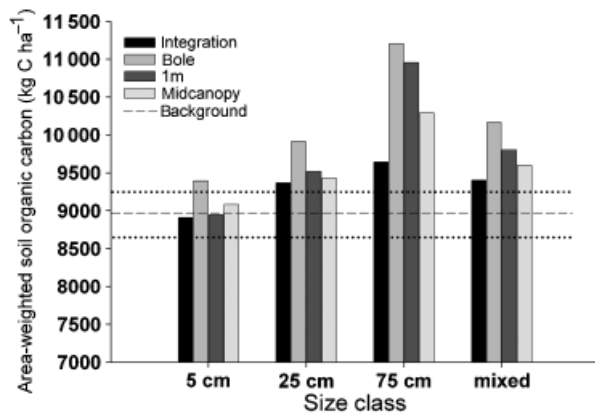
Fig. 5 Landscape-scale SOC estimates of semidesert grassland invaded by *Prosopis velutina* shrubs. Values are calculated SOC for a hypothetical 1 ha landscape, assuming 30% canopy cover. Estimates depict 'even-age' cases where all plants in the stand have the same basal diameter (5, 25, 75 cm size classes) or, in the 'mixed' case, values reflect an actual size-class distribution obtained in a survey of 16 belt transects at the study site. The area not covered by shrub canopies is assumed to have a constant SOC value of 8957 ± 270 kg C ha^{-1} (denoted as 'background'). The 'background' value represents the mean ($\pm$ SE; depicted as dotted lines around the mean) of 45 samples collected from intercanopy zones at the study site.

Given the potential N$_2$-fixing capacity of *P. velutina* (Johnson & Mayeux, 1990; Zitzer *et al.*, 1996), the lack of shrub influence on relationships between SOC and TN was surprising. If N$_2$-fixation promoted the observed accumulation in soil TN with time, we would expect an increase in TN relative to SOC with increasing basal diameter and decreasing distance from the bole. Similar to our findings, Wheeler *et al.* (2007) noted a linear relationship between SOC and TN across a range of shrub sizes and soil surfaces. These results suggest that N$_2$-fixation by *P. velutina* may not be a significant source of N in this system, but explicit tests of N$_2$-fixation activity or stable isotope analysis would be needed to confirm this inference.

Temporal patterns of SOC and TN

Strong changes in SOC and TN with increasing shrub size suggest that subcanopy soil properties change as a function of *P. velutina* age. In the absence of annual ring data, we cannot explicitly explore the relationship between SOC and TN accumulation and tree age. However, field estimates of *P. velutina* growth rates provide a basis for estimating short- and long-term SOC accumulation dynamics. Repeat field measurements of plants in long-term plots at the SRER study site indicate that shrubs take ca. 16 years to reach ca. 4 m^2 canopy area and 7 cm basal diameter (Browning *et al.*, 2008). Mod-

eled SOC values in soils associated with shrubs of this size (911 g m^{-2}, using the integration method) are only slightly (and nonsignificantly) above background values (895.7 g m^{-2}). Woody encroachment at the SRER site has occurred over the past 100 years (McClaran, 2003). The observed SOC accumulation must therefore occur beneath trees between 16 and 100 years of age. Coupled tree ring and SOC analyses in Texas indicated a linear relationship between *P. glandulosa* age and SOC pools (Archer *et al.*, 2004). Assuming linear SOC accumulation for 100 years at our semidesert site, values adjacent to the bole suggest an increase of 9.7 g SOC m^{-2} yr^{-1} to 20 cm depth for a 100 cm basal diameter shrub (calculated as 1862 g SOC m^{-2} at the bole of a 100 cm shrub minus 895.7 g SOC m^{-2} background value divided by 100 years). This is just slightly slower than accumulation estimates in the proximity of the bole at other locations on the SRER (10–12 g m^{-2} yr^{-1} to 20 cm depth; Wheeler *et al.*, 2007), and lower than accumulation rates below *P. glandulosa* canopies in more mesic Texas grasslands invaded by *P. glandulosa* (11–21 g C m^{-2} yr^{-1} to 20 cm depth, Archer *et al.*, 2004; 10–30 g C m^{-2} yr^{-1} to 15 cm depth, Liao *et al.*, 2006). However, all of these estimates are based on single-location sampling beneath shrub canopies. Using our subcanopy integration approach, area-weighted rates of SOC accumulation at the SRER site decline to 2.6 g C m^{-2} yr^{-1}. Thus, single-point canopy area-weighting functions appear to overestimate integrated canopy area assessments of SOC accumulation rates ca. 3.7-fold.

SOC (and by extension TN, owing to their strong correlation) pool dynamics is a function of long-term patterns of *P. velutina* growth and mortality, as well as SOC stabilization capability of the soil. We therefore expect SOC pools to follow a three-phase model subsequent to shrub establishment: an accumulation phase, a stabilization phase, and a loss phase. In the accumulation phase, SOC and TN initially accrue in various particle size-fractions and in stable soil macroaggregates with shrub growth (e.g. Liao *et al.*, 2006). In the stabilization phase, SOC concentrations plateau, either as a result of saturation in plant production or in SOC protection via biochemical, silt and clay, and microaggregate mechanisms (Six *et al.*, 2002). We saw no evidence for SOC saturation in our study (Figs 2 and 3), although total subcanopy SOC accumulated much more slowly with increasing shrub size for the integration method than for the less spatially intensive (single-point) sampling protocols (Fig. 4). This lower accumulation rate is presumably the result of a proportional increase in area toward the dripline that effectively dilutes the strong near-bole shrub influences on SOC.

How long after woody plant encroachment does it take to reach the stabilization phase? Ecosystem carbon

cycling models suggest that C saturation would occur beyond the 100-year window of encroachment at our study site. For example, modeled *P. glandulosa* encroachment in southern Great Plains grasslands leads to plant C stabilization ca. 200 years after woody encroachment, with SOC stabilization lagging behind and not occurring until ca. 400 years after woody plant establishment (Hibbard *et al.*, 2003). However, another more spatially extensive study at our site suggests that SOC may be nearing a plateau on some soil types at some elevations (Wheeler *et al.*, 2007).

An SOC and TN loss phase is expected to occur when woody plants die, and this phase may be initiated before the saturation phase is reached. While age-dependent mortality is not yet apparent at the SRER for even the oldest age classes of shrubs present, subcanopy *P. velutina* SOC pools are known to decline in the decades following experimental removal (Klemmedson & Tiedemann, 1986). We therefore expect an SOC decline phase in response to shrub mortality, such as occurs under *Acacia* in Australia (Facelli & Brock, 2000).

Spatial patterns of SOC and TN

Where shrubs are known to have invaded grassland, bole-to-dripline spatial gradients represent a temporal gradient that reflects the length of time that soil developing under grasses has been impacted by shrubs. Based on long-term vegetation records of grassland–shrubland conversion (McClaran, 2003), we know the maximum age of *P. velutina* shrubs in our study would be ca. 100 years. Thus, for the largest *P. velutina* plants on our site, soils near the boles would likely have experienced ca. 100 years of shrub-induced change, whereas soils near the driplines would have experienced only a few months or years of canopy influence. Furthermore, input, accumulation, and physical effects of shrub canopies, such as modification of microclimate and water and nutrient accumulation via stemflow (Martinez-Meza & Whitford, 1996), are likely to decrease toward the dripline. In addition to direct canopy effects on SOC, canopy influences on spatial patterns of TN and water availability may drive changes in subcanopy species composition that in turn affect SOC (Ludwig *et al.*, 2004).

Contrary to our hypothesis, we did not find measurable shrub influences on SOC and TN beyond the canopy dripline, suggesting that shallow lateral roots extending beyond shrub canopies are not causing substantial net effects on soils beyond the canopy. Shallow lateral roots beyond the dripline could be expected to 'mine' nutrients, alter nutrient fluxes via soil moisture redistribution (Hultine *et al.*, 2003), or to enhance SOC and TN via inputs from root turnover and exudates. It is possible each of these mechanisms is in operation but that inputs and outputs are in a net balance.

Implications for SOC estimates

Understanding spatial and temporal changes in SOC distribution relative to vegetation development is critical for accurate assessments of current and future patterns of C sequestration in areas where woody plants are proliferating. Our analyses suggest that traditional methods that fail to account for these temporal and spatial patterns have potentially serious limitations for assessing woody encroachment impacts on SOC pools in drylands. Furthermore, a lack of standardized spatial sampling methodology and failure to explicitly account for shrub size can lead to dramatic differences in subcanopy SOC estimates. For example, depending on the spatial sampling protocol used, our data suggest anywhere from a 14% decline (2 cm basal diameter shrubs, integration method) to 208% increase (100 cm basal diameter shrubs, sampling at bole) in SOC for individual shrub-scale estimates. In contrast, the landscape-scale assessments range from a 4% decline (a population of 2 cm basal diameter shrubs, integration method) to 132% increase (a population of 100 cm basal diameter shrubs, sampling at bole) in SOC.

Methods for landscape-scale SOC inventories that are to be widely adopted require a balance between accuracy and expediency. Remote sensing approaches have made considerable progress in estimating aboveground C stores (Foody, 2002; Asner *et al.*, 2003; Lu, 2006), and linking aboveground canopy cover to SOC pools would provide important information on woody plant impacts on C sequestration. Results of our study illustrate, however, that simple estimates of SOC stores based on area-weighted woody plant cover alone will not provide accurate estimates of SOC stores. As pointed out by Hurtt *et al.* (2002), knowledge of stand age-structure is critical for forecasting ecosystem C sequestration potential. Along these lines, our data suggest that remote sensing approaches that derive shrub canopy size-class distributions in drylands could be coupled with algorithms that relate spatial patterns of SOC to shrub canopy area (e.g. by assuming the center of a shrub canopy to be the 'bole' location, then applying a bole-to-dripline SOC function) to estimate ecosystem C (aboveground woody plant + SOC) pools over large areas. A library of SOC-canopy area algorithms would be needed to account for specific differences likely to occur for soils, land forms, woody species or functional groups, land management scenarios, and climate regimes (e.g. Hughes *et al.*, 2006; Wheeler *et al.*, 2007).

Recent state, federal, and international initiatives aimed at C flux regulation suggest that C emission reduction credits may soon be a reality. We suggest that landscape-scale SOC estimates in drylands based on woody plant presence or absence alone will be inaccurate unless additional information on shrub size and SOC distribution is included. Current C accounting tools (e.g. Comet-VR, a USDA-NRCS voluntary reporting C management tool; http://www.cometvr.colostate.edu/) provide crude estimates of changes in SOC in response to management based on information such as soil type. These coarse-scale tools are currently limited, however, by lack of inclusion of spatial and temporal data on the structure of vegetation cover and land management history (Foster *et al.*, 2003). Development of algorithms that can represent or account for these factors will be needed to advance our ability to conduct large-scale C accounting programs.

Acknowledgements

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