Spatial scaling of ecosystem C and N in a subtropical savanna landscape

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Abstract

Widely occurred woody encroachment in grass-dominated ecosystems has the potential to influence soil organic carbon (SOC) and total nitrogen (TN) pools at local, regional, and global scales. Evaluation of this potential requires assessment of both pool sizes and their spatial patterns. We quantified SOC and TN, their relationships with soil and vegetation attributes, and their spatial scaling along a catena (hill-slope) gradient in the southern Great Plains, USA where woody cover has increased substantially over the past 100 years. Quadrat variance analysis revealed spatial variation in SOC and TN at two scales. The larger scale variation (40–45 m) was approximately the distance between centers of woody plant communities and their adjoining herbaceous patches. The smaller scale variation (10 m) appeared to reflect the local influence of shrubs on SOC and TN. Litter, root biomass, shrub, and tree basal area (a proxy for plant age) exhibited not only similar spatial scales, but also strong correlations with SOC and TN, suggesting invasive woody plants alter both the storage and spatial scaling of SOC and TN through ecological processes related primarily to root turnover and, to a lesser extent litter production, as mediated by time of occupancy. Forb and grass biomass were not significantly correlated with SOC and TN suggesting that changes in herbaceous vegetation have not been the driving force for the observed changes in SOC and TN. Because SOC and TN varied at two scales, it would be inappropriate to estimate SOC and TN pools at broad scales by extrapolating from point sampling at fine scales. Sampling designs that capture variation at multiple scales are required to estimate SOC and TN pools at broader scales. Knowledge of spatial scaling and correlations will be necessary to design field sampling protocols to quantify the biogeochemical consequences of woody plant encroachment at broad scales.

Keywords: carbon sequestration, modified *t*-test for correlation, *Prosopis glandulosa*, quadrat variance methods, savanna parkland, scale, soil organic carbon, woody encroachment

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Introduction

Increased woody plant abundance in grassland and savanna ecosystems has been reported worldwide. Drivers of this change potentially include livestock grazing, fire suppression, climate change, and atmospheric CO_2 enrichment (Archer, 1995; Van Auken, 2000). Subsequent to their establishment, woody plants can markedly alter ecosystem biodiversity, production, trophic structure, land surface-atmosphere interactions and water and nutrient cycles (Hughes *et al.* 2006; Archer, 2009). Modification of soil nutrient pools, fluxes, and microclimate are particularly noteworthy (e.g., the creation of 'fertile islands', Virginia, 1986; Jackson & Cald-

well, 1993; Schlesinger *et al.*, 1996; Scholes & Archer, 1997). Since grasslands and savannas cover a large portion of the world's land surface, these vegetation-induced changes in soil organic carbon (SOC) and total nitrogen (TN) status could have potential significance at local, regional, and global scales. The great majority of C and N in arid and semiarid systems reside below ground; and robust generalizations regarding the impact of vegetation change on these pools have yet to emerge. Improved understanding of correlations among soil C, N, and environmental variables and their spatial patterns is necessary for estimating soil C and N storage at different scales and for elucidating the ecological processes that control soil C and N pools.

Although recent estimates of the C budget in the US regard shifts from grass- to woody plant-domination as a major C sink (CCSP, 2007), there is a high degree of

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uncertainty as to whether woody plant proliferation has a positive, neutral or negative effect on soil C storage (Jackson *et al.*, 2002; Wessman *et al.*, 2004; Knapp *et al.* 2008). In addition to potentially altering SOC pool size, woody plant encroachment in grasslands and savannas also increases its spatial heterogeneity (Schlesinger *et al.*, 1996; Bekele & Hudnall, 2006; Okin *et al.*, 2009), thus presenting additional challenges for inventorying, monitoring, and predicting. To evaluate the impact of woody invasion on C and N cycles at regional and global scales, it will be necessary to understand their effects on spatial patterns of SOC and TN at landscape scales.

Factors controlling SOC and TN storage include climate (Burke *et al.*, 1989; Amundson, 2001), topography (Powers & Schlesinger, 2002), soil moisture (Wang *et al.*, 2002), plant species (Hobbie, 1992; Lovett *et al.*, 2004), herbivory (Asner & Archer, 2009), time (Schlesinger *et al.*, 1990) and their interactions (Jenny, 1980; Wheeler *et al.*, 2007; McClaran *et al.*, 2008). However, these factors are not equally important in determining the concentration and spatial pattern of SOC and TN; and their relative importance is likely to change with spatial scale.

Ecological patterns and processes differ across spatial and temporal scales (Allen & Starr, 1982; O'Neill *et al.*, 1986; Wiens, 1989). Spatial heterogeneity of ecological phenomena typically has a multiple-scale structure because the processes that affect patterns at one scale may differ from those predominating at other scales (Levin, 1992). One of the major issues in the science of ecology is the development of methods that will allow extrapolation and extension of results obtained at one scale to other spatial and/or temporal scales (Ehleringer & Field, 1993; Miller *et al.*, 2004). Predicting changes in SOC and TN storage that might accompany changes in woody plant abundance through time in drylands and extrapolating this across heterogeneous landscapes will require an improved understanding of pattern–process relationships and how they might change across space and time.

Scaling is the extrapolation of known results or the transformation of information from one scale to another. Changes in the type and intensity of ecological processes across scales influence pattern–process relationships. Therefore, one important step in scaling is to determine domains of scale and to elucidate the driving ecological processes characteristic of a given domain (Woodmansee & Adamsen, 1983; Ludwig *et al.*, 2000; Schneider, 2001). Numerous statistical methods, including geostatistics (Rossi *et al.*, 1992; Gustafson, 1998), quadrat variance methods (Dale, 1999), lacunarity (Plotnick *et al.*, 1996; Wu *et al.*, 2000), fractals (Sugihara & May, 1990), and wavelet analysis (Dale & Mah, 1998),

have been used to address multiscale questions. However, few studies have simultaneously characterized scales and their relationships for both vegetation and soil.

The purpose of this study was to quantify spatial patterns and scaling of SOC and TN in relation to vegetation and soil properties that may be controlling these parameters. We addressed this pattern-scaling issue along an upland-to-lowland catena (hill-slope) gradient where the abundance of woody plants is known to have increased dramatically in recent history (Archer, 1995) and to have substantively impacted pools and fluxes of C and N (Archer *et al.*, 2001; Boutton *et al.*, 2009). Specific objectives were to (1) quantify correlations between soil (SOC, TN, texture, bulk density) and plant (root biomass; shrub and tree basal area; grass, forb, and litter biomass) variables across the catena gradient; and (2) identify the spatial scale(s) of SOC and TN variation and their relationship to other variables at the landscape scale. We hypothesized that (a) spatial patterns of SOC and TN pools across the catena gradient would be dictated more by spatial patterns of invasive woody plants than by spatial variation in other soil attributes or herbaceous vegetation; and as a result (b) SOC and TN would vary at a scale(s) similar to that of encroaching woody plants.

Materials and methods

Study site

This study was conducted at the Texas AgriLife La Copita Research Area (LCRA, 27°40′N, 98°12′W; elevation 75–90 m a.s.l.) 65 km west of Corpus Christi, TX, USA. The site has been grazed by livestock continuously from the late 1800s before its designation as a research area in early 1980s. Landscapes at the LCRA consist of gentle slopes (≤ 3%) grading from well-drained uplands into intermittent drainages and small, closed-basin playas (lakebeds). The climate is subtropical with warm, moist winters and hot, dry summers (mean annual temperature 22.4 °C; growing season is 289 days). Average annual precipitation is 680 mm with bimodal peaks in May and September. Upland soils are Typic and Pachic Argiustolls with a laterally extensive but discontinuous clay-rich, argillic horizon at 40–60 cm. The lower-lying drainages are clay loams (Pachic Argiustolls).

Woody plant encroachment in southern Texas over the past century has been well-documented (Archer, 1995). Historical aerial photos, tree rings, C isotopes and simulation models have all shown that woody plant invasion occurred in this area over the past 100 years (Boutton *et al.*, 1998; Archer *et al.*, 2001). Honey

mesquite (*Prosopis glandulosa*), a N_2-fixing tree legume, is typically the first woody plant established in the grassland, where it appears to serve as a nurse plant to facilitate the establishment and development of numerous other woody species beneath its canopy (Archer, 1995).

Uplands at our study site are characterized by savanna parkland vegetation consisting of discrete woody patches distributed within a continuous C_4 grassland matrix (e.g., Whittaker *et al.*, 1979). Woody patches are comprised of smaller shrub clusters (usually one mesquite in the center with other shrub species beneath its canopy) or larger groves. At this site, shrub cluster and grassland communities occur where the argillic horizon is well-developed, whereas groves represent tree/shrub clusters that have expanded and fused together on soils where the argillic horizon is lacking (Archer, 1995; Bai *et al.*, 2009). Understory shrub species in both clusters and groves include *Zanthoxylum fagara*, *Celtis pallida*, *Condalia hookeri*, *Diospyros texana*, *Schaefferia cunefolia*, *Ziziphus obtusifolia*, and *Berberis trifoliolata*. The herbaceous grassland matrix is dominated by C_4 grasses including *Paspalum setaceum*, *Setaria geniculata*, *Bouteloua rigidiseta*, and *Chloris cucullata*, but also has a significant forb component (Archer, 1990).

Continuous-canopy thorn woodlands are distributed in the lower-lying intermittent drainages. Species composition of woodlands is similar to that of upland woody patches, with mesquite dominating the overstory canopy. Playas are oval shaped basins occupying the lowest portion of the landscape, and may have standing water following high rainfall periods. The vegetation composition of playas ranges from relatively open grassland with widely scattered mesquite trees to dense woodland with little grass cover (Farley *et al.*, 2010). Additional details on climate, vegetation and soil can be found in Archer *et al.* (1988) and Boutton *et al.* (1998).

Field sampling

A 309 m transect, which included five plant communities (grassland, shrub cluster, grove, drainage woodland, and playa) was established in 2004. We opted to use a transect rather than random plots as the former more readily represents gradations of vegetation and soil change along a hillslope gradient. Transect data would also enable us to more readily detect spatial scales of soil and vegetation variables. The transect extended from the crown of the convex upland downslope through a drainage woodland and across a concave playa basin (Fig. 1). Transect coordinates were determined at 5 m intervals using a global positioning system (Pathfinder Pro XRS, Trimble Navigation Ltd., Sunnyvale, CA, USA). Elevation (Fig. 2) was obtained by a topographic field survey conducted in October 2004 with elevation of base points determined using a USGS 7.5-min topographic map. Soil cores (0–15 cm) were collected along the transect (1 m intervals) in spring 2004. The resulting 309 sample points were distributed as follows: grassland = 66, cluster = 18, grove = 59, woodland = 125, and playa = 41. Three cores (15 cm deep; 2.24 cm diameter) were collected at each sample point: one for bulk density and texture
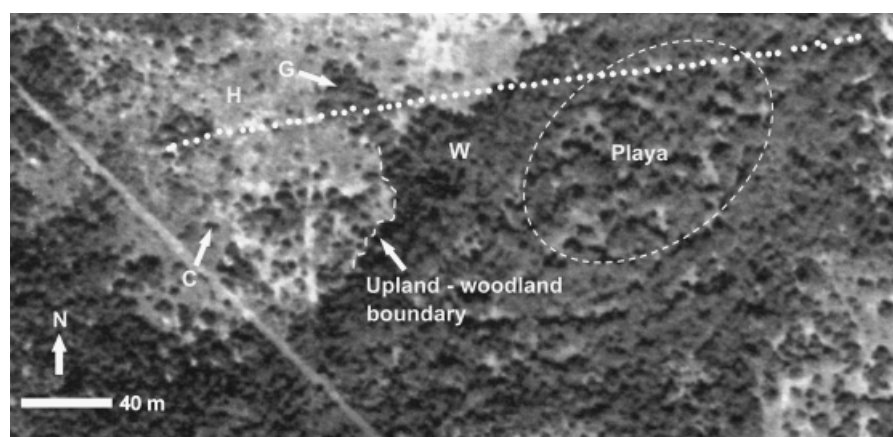

Fig. 1 Aerial view of the 309 m transect (white dots at 5 m intervals) showing herbaceous grassland (H), clusters (C), groves (G) within savanna parkland uplands; and woodlands of intermittent drainages (W) and closed-basin playas (Playa) in low-lying portions of the landscape (see Fig. 2 for topographic details). Dark areas represent woody plant canopies; light and dark gray areas indicate herbaceous cover. Savanna parkland uplands are characterized by discrete woody plant communities (shrub clusters and groves) embedded within an herbaceous matrix, whereas woodlands and playas have nearly continuous cover of woody plants. In uplands, shrub clusters and grassland occur where an argillic horizon is laterally extensive and well-developed; groves of *Prosopis* have developed where nonargillic inclusions occur (see Archer, 1995 for detailed description of these landscape elements).
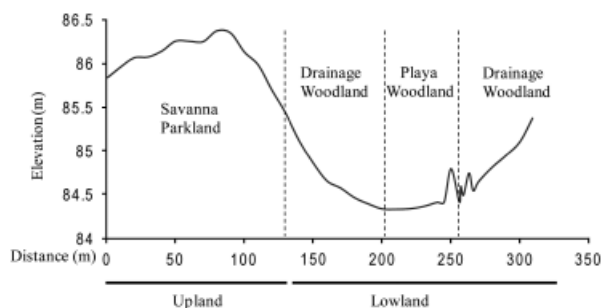
Fig. 2 Elevation (m, a.s.l.) and landscape elements along the 309 m transect depicted in Fig. 1. Approximate boundaries between upland savanna parkland (with grassland, shrub cluster, and grove patches), woodlands of intermittent drainages and closed-basin playa woodland landscape elements are indicated with dashed lines.

(particle size distribution), one for SOC, TN and δ^{13}C, and one for root biomass. All soil cores were stored at 4 °C until processed.

All woody plants with stem basal diameters (BD) > 5 cm (hereafter, 'trees'; primarily *P. glandulosa*) were measured (BD, *x–y* location) within a 12 m wide strip centered on the transect line with 6 m on each side. *Prosopis* plants were typically single-stemmed at ground level and their architecture did not vary noticeably along the gradient. All smaller woody plants (BD < 5 cm; hereafter 'shrubs') within a 2 m wide belt centered on the transect with 1 m on each side were sampled for species and BD. Grass green biomass, forb green biomass, and litter mass (standing dead + surface) were collected separately from a 0.5×0.5 m plot ($n = 309$ total) centered on each soil sample point in August 2003, at peak live biomass. The plant materials were oven-dried for at least 72 h at 60 °C to determine dry weight.

Lab analyses

Soil bulk density was determined using the core method (Soil Survey Staff, 2009). Soil cores obtained for C and N determination were dried at 60 °C for at least 48 h. Coarse roots and gravel were removed by passing the soil through a 2 mm screen. Soils were then pulverized to a fine powder in a centrifugal mill (Angstrom Inc., Belleville, MI, USA). Samples were weighed into silver capsules (5×7 mm), incubated with HCl vapor in a desiccator to remove carbonates (Harris *et al.*, 2001), dried, and sealed in the capsules. SOC, TN, and δ^{13}C of SOC were measured with an elemental analyzer (Carlo Erba EA-1108, CE Elantech, Lakewood, NJ, USA) interfaced with a Delta Plus isotope ratio mass spectrometer (ThermoFinnigan, San Jose, CA, USA). Root biomass

was determined by washing soil cores through a hydro-pneumatic elutriation system (Gillison's Variety Fabrication Inc., Benzonia, MI, USA) (Smucker *et al.*, 1982) equipped with 410 µm filters. The collected roots were dried for at least 72 h at 60 °C to determine dry weight, and then ashed at 400 °C in a muffle furnace to obtain ash-free root biomass (root biomass hereafter). Soil particle size distribution was determined by the pipette method (Soil Survey Staff, 2009).

Statistical analyses

One-way ANOVA was used to compare soil and plant variables in different plant communities using SAS version 9.2 (SAS Institute Inc., Cary, NC, USA). We first ran ANOVA models for each variable with all transect samples and checked for spatial autocorrelation in the residuals. When spatial autocorrelation occurred, it was modeled with semivariograms. We then used a generalized mixed model to perform an ANOVA that accounted for spatial autocorrelation (including a spatial covariance component for adjustment in the MIXED procedure in SAS, Littell *et al.*, 2006). *Post hoc* comparisons of these variables in different plant communities were also conducted using the mixed models with Tukey's correction. A cutoff value of $P = 0.05$ was used to indicate significant differences. Mantel and cross-Mantel tests (Fortin & Gurevitch, 1993) were used to test spatial autocorrelation and spatial cross-correlations between variables using PASSaGE (Rosenberg, 2001).

Pearson's correlation coefficients between SOC, TN and environmental and vegetation variables were calculated using SPSS version 12.2 (SPSS Inc., Chicago, IL, USA). Mantel tests indicated that SOC and TN were spatially autocorrelated, so the significance levels of these correlation coefficients was assessed with a modified *t*-test for correlation (Clifford *et al.*, 1989), which adjusts the degrees of freedom based on the extent of spatial autocorrelation in the data.

Quadrat variance methods that calculate the variance of differences among blocks of different sizes (Hill, 1973; Ludwig & Goodall, 1978; Dale, 1999) were used to detect scales for all plant and soil variables. The resulting pattern of variances was then used to determine the scale of pattern. We assessed spatial scales for plant and soil variables using sample variograms and two quadrat variance methods – Two Term Local Quadrat Variance (TTLQV) and Three Term Local Quadrat Variance (3TLQV). All methods showed similar scale results (Liu, 2007). Here, we present results from the 3TLQV method, as it is less sensitive to trends in the data and has less peak drift (the difference between the scale that is detected and the true scale; Dale, 1999)

than the TTLQV method. Results were not compared against null models because randomization destroys the spatial structure of the data and thus tests only the hypothesis that there is no pattern (Fortin & Dale, 2005); and we know from previous studies at this site that strong patterns do occur.

Results

Patterns of SOC and TN along the catena

Comparison of soil and plant variables among contrasting plant communities indicated differences across the catena gradient (Table 1). Soils in patches dominated by woody vegetation had higher SOC, TN, litter, root biomass, silt, and clay content and lower bulk density than that of patches dominated by herbaceous plants. Soil bulk density was the highest in grassland ($1.40 \, g \, cm^{-3}$) and comparable in shrub cluster, grove, woodland, and playa communities ($1.17–1.29 \, g \, cm^{-3}$). Soil pH was lowest in the playa community (6.15) and statistically comparable in the other plant communities (7.09–7.21). SOC $\delta^{13}C$ was comparable in grassland (−19.3‰) and playa communities (−18.8‰), but lower in shrub cluster, grove, and woodland communities (−20.4‰, −21.5‰, −21.9‰, respectively). Soil texture showed a strong pattern of decreasing sand and increasing silt and clay with decreasing elevation (Table 1, Fig. 2). The playa had the highest tree basal area of all plant communities, but less shrub basal area than that in woodlands. Aboveground grass biomass varied in the rank order playa > grassland > grove ~ woodland (Table 1) with clusters not significantly different from either grasslands or groves. Forb biomass varied in the rank order cluster ~ grassland > grove > playa, with woodlands not statically different from either groves or playas (Table 1).

SOC differed significantly among plant communities, in the rank order playa ~ woodland > grove ~ cluster ~ grassland (Fig. 3). TN varied in the rank order woodland > grove ~ cluster ~ grassland with playas not statistically significant from either woodlands or groves. Soil C:N ratios were comparable in grassland, cluster, grove, and drainage woodland soils and lower than that in the playa (Fig. 3). Root biomass was significantly different among plant communities, in the rank order woodland > cluster ~ grassland with playas and groves in between. Litter also varied significantly different among plant communities, in the rank order woodland > cluster ~ playa ~ grassland with groves in between (Fig. 3).

Correlation among variables

Mantel and cross-Mantel tests indicated SOC and TN were spatially autocorrelated. Cross-Mantel tests indicated significant ($P < 0.05$) spatial correlations between SOC and TN with litter, root biomass, shrub basal area, tree basal area, soil bulk density, and soil texture (sand, silt, and clay percentages) (Table 2). Neither forb nor grass biomass was spatially correlated with either SOC or TN.

The modified t-test for correlation indicated SOC was strongly correlated with TN ($r = 0.96$; Table 3). Among the plant and soil variables examined, litter had the highest correlation with both SOC ($r = 0.54$) and TN

Table 1 Mean and standard error (SE) of plant and soil variables with ANOVA results in contrasting plant communities along a catena gradient in a subtropical savanna parkland

| | Grassland | | Cluster | | Grove | | Woodland | | Playa | | ANOVA |
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	F
Forb biomass ($g \, m^{-2}$)	76[a]	6.7	101.55[a]	12.85	42.61[b]	7.1	21.7[bc]	4.87	0.71[c]	8.51	<0.0001
Grass biomass ($g \, m^{-2}$)	89.83[a]	16.21	32.43[ab]	26.99	21.19[b]	17.71	14.5[b]	12.46	236.11[c]	21.38	<0.0001
Shrub basal area ($cm^2 \, m^{-2}$)	0.48[a]	13.33	15.46[a]	25.54	35.22[ac]	14.11	64.14[b]	9.69	9.8[ac]	16.92	0.0012
Tree basal area ($cm^2 \, m^{-2}$)	0.54[a]	6.13	18.32[ad]	11.74	45.55[bd]	6.48	57.4[b]	4.45	79.25[c]	7.78	<0.0001
Soil bulk density ($g \, cm^{-3}$)	1.4[a]	0.022	1.29[ab]	0.039	1.2[b]	0.024	1.18[b]	0.016	1.17[b]	0.029	<0.0001
Soil PH	7.09[a]	0.15	7.09[a]	0.19	7.21[a]	0.17	7.15[a]	0.13	6.15[b]	0.2	<0.0001
Soil organic $\delta^{13}C$ (‰)	−19.3[a]	0.33	−20.4[ab]	0.52	−21.51[b]	0.37	−21.96[b]	0.26	−18.81[a]	0.44	<0.0001
Sand (%)	77.38[a]	0.98	78.05[a]	1.44	78.26[a]	1.1	69.21[b]	0.8	52.36[c]	1.33	<0.0001
Silt (%)	9.66[a]	0.37	9.37[a]	0.58	9.2[a]	0.41	13.16[b]	0.3	18.87[c]	0.5	<0.0001
Clay (%)	12.85[a]	0.76	12.63[a]	1.08	12.51[a]	0.85	17.76[b]	0.62	28.49[c]	1.04	<0.0001

'Tree' denotes woody plants (primarily *Prosopis glandulosa*) with basal diameter >5 cm; 'shrub' includes all woody plants <5 cm basal diameter. Forb and grass values are for aboveground green biomass for plots clipped in August 2003. Significant difference between means in plant communities are indicated with different superscript letters. Number of samples: grassland = 66, cluster = 18, grove = 59, woodland = 125, and playa = 41.
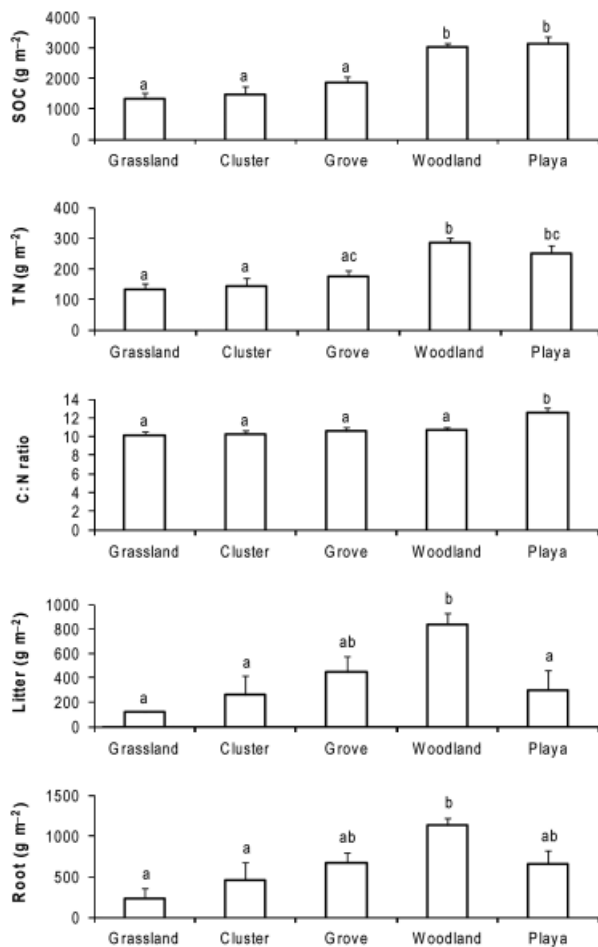
Fig. 3 Mean and standard error (SE) of soil organic carbon (SOC), total nitrogen (TN), C: N ratio, litter, and root biomass (ash free) in different plant communities (grassland, shrub cluster, grove, woodland, and playa). Different letters above bars indicate significant ($P < 0.05$) differences between means. Root and litter mass data were collected in August 2004. Mass values for SOC, TN and roots are to 15 cm depth.

($r = 0.61$), followed by root biomass (SOC: $r = 0.51$; TN: $r = 0.52$). Soil bulk density was negatively correlated with both SOC ($r = -0.48$) and TN ($r = -0.46$). Tree and shrub basal area were also significantly correlated with SOC and TN, but their correlations were weaker than those with other variables (Table 3). Forb and grass biomass had no significant correlation with either SOC or TN. Soil particle size distributions were not correlated with either SOC or TN.

Spatial scales

Quadrat variance methods revealed a scale of 43–45 m for litter and root biomass, shrub and tree basal area, SOC and TN (Table 4, Fig. 4). It also indicated scales in the variation of grass biomass (40 m), forb biomass

Table 2 Mantel and cross-Mantel results for spatial correlations between various plant and soil attributes with either soil organic carbon (SOC) or soil total nitrogen (TN) [P = significance level; ns = not significant ($P > 0.05$)]

	SOC		TN	
	Mantel's r	P	Mantel's r	P
Autocorrelation				
SOC	0.239	0.001		
TN			0.168	0.001
Cross correlation				
Forb biomass (g m^{-2})	0.005	ns	−0.035	ns
Grass biomass (g m^{-2})	−0.047	ns	−0.070	ns
Litter (g m^{-2})	0.306	0.001	0.396	0.001
Root biomass (g m^{-2})	0.331	0.001	0.345	0.001
Shrub basal area (cm^2 m^{-2})	0.188	0.004	0.223	0.001
Tree basal area (cm^2 m^{-2})	0.229	0.001	0.200	0.001
Soil bulk density (g cm^{-3})	0.225	0.001	0.206	0.001
Sand (%)	0.217	0.001	0.104	0.006
Silt (%)	0.231	0.001	0.122	0.001
Clay (%)	0.182	0.001	0.071	0.041

'Tree' denotes woody plants (primarily *Prosopois glandulosa*) with basal diameters >5 cm; 'shrub' includes all woody plants <5 cm basal diameter.

Table 3 Pearson correlation coefficients (r) for the relationship between SOC, TN and other plant and soil variables

	SOC		TN	
	r	P	r	P
Forb biomass (g m^{-2})	−0.36	ns	−0.31	ns
Grass biomass (g m^{-2})	−0.08	ns	−0.17	ns
Litter (g m^{-2})	0.54	0.01	0.61	0.01
Root biomass (g m^{-2})	0.51	0.01	0.52	0.01
Shrub basal area (cm^2 m^{-2})	0.29	0.01	0.32	0.01
Tree basal area (cm^2 m^{-2})	0.47	0.02	0.42	0.02
Soil bulk density (g cm^{-3})	−0.48	0.01	−0.46	0.01
Sand (%)	−0.49	ns	−0.35	ns
Silt (%)	0.53	ns	0.41	ns
Clay (%)	0.45	ns	0.30	ns

Significance (P) was calculated using modified t-test for correlation; ns = non-significant ($P < 0.05$). 'Tree' denotes woody plants (primarily *Prosopois glandulosa*) with basal diameters >5 cm; 'shrub' includes all woody plants <5 cm basal diameter. SOC and TN had a correlation coefficient of 0.96. Number of samples: grassland = 66, cluster = 18, grove = 59, woodland = 125, and playa = 41.

(47 m), and soil bulk density (37 m), respectively. A smaller scale of variation in shrub basal area (5 m), root biomass, SOC, TN, soil sand, and silt (9–10 m); and forb biomass (19 m) was also detected (Table 4). Soil sand and silt percentages had scales of about 10 and 40 m, respectively, while clay had a scale of 49 m.

Table 4 Spatial scales (m) of plant and soil variables derived from the three term local quadrat variance method (3TLQV)

	Scale, m
Forb biomass	19, 47
Grass biomass	40
Litter	44
Root biomass	9, 44
Shrub basal area	5, 44
Tree basal area	43
Bulk density	37
SOC	9, 44
TN	9, 45
Sand	10, 39
Silt	9, 40
Clay	49

When variables exhibited two scales, values are separated by a comma. 'Tree' denotes woody plants (primarily *Prosopois glandulosa*) with basal diameters >5 cm; 'shrub' includes all woody plants <5 cm basal diameter.

Discussion

SOC and TN along the topoedaphic gradient

Encroachment of woody plants into grasslands alters ecosystem structure and function by altering species and functional group composition, primary production, and microclimate. It also affects nutrient cycling processes and SOC storage by altering rooting depth, root turnover, litter quantity and quality, and soil biological communities. The alterations of grassland ecosystems by encroaching woody plants have been well-studied in the southern Great Plains (Archer et al., 2001; Boutton et al., 2009 and references therein). Patterns of SOC and TN at the landscape–scale at La Copita therefore reflect the recent (past 100 + years) impacts of woody plants on grassland soils as mediated by pre-existing variation in soil physical properties (e.g. texture, depth, parent material) along the catena gradient.

We observed significant increases in SOC and TN under recently developed woody communities compared with remnant grasslands (Fig. 3). This is consistent with previous studies showing soils under woody vegetation had higher SOC, TN, litter, and root mass than grassland soils (Boutton et al., 2009). In addition, SOC and TN were significantly higher in the drainage woodlands and playa compared with all other landscape elements. These higher SOC and TN values probably reflect a combination of (i) higher rates of primary production enabled by favorable soil moist-

ure/nutrient status in this low-lying portion of the landscape, and (ii) a higher silt and clay content that enables these fine-textured soils to accumulate and retain more SOC and TN than the more coarsely textured upland soils (Liao et al., 2006 and references therein). However, while the more finely textured playas and drainage woodlands had significantly higher SOC and TN than the coarse-textured upland landscape elements, particle size distributions were not significantly correlated with SOC and TN content. This suggests other factors, such as length of the time since encroachment (e.g., Wheeler et al., 2007; Boutton et al., 2009) or the quantity and quality of woody plant litter and root biomass inputs, may be more important than soil physical characteristics in determining SOC and TN in this subtropical landscape.

Stable carbon isotopes have been used to identify SOC derived from C_4-dominated grasslands and C_3-dominated woodlands (Boutton et al., 1998). This technique is based on the fact that plants with C_3 photosynthesis have $\delta^{13}C$ values ranging from –32‰ to –22‰ (mean ca. –27‰), while C_4 plants have $\delta^{13}C$ values ranging from –17‰ to –9‰ (mean ca. –13‰) (Bai et al., 2008). The natural differences in $\delta^{13}C$ between these two photosynthetic pathways can therefore be traced into soil organic matter when there is a shift from C_4 grasses to C_3 shrubs. The lower soil $\delta^{13}C$ values in cluster, grove and woodland indicate that a significant proportion of SOC in those plant communities has been derived from C_3 woody tissues (Table 1) (Boutton et al., 1998; Bai et al., 2008). In contrast, higher soil $\delta^{13}C$ values in playa and grassland communities indicate the majority of SOC in those areas has been derived from C_4 grasses. The higher $\delta^{13}C$ values in playa soils compared with that of the other woody communities developing on grasslands along the catena gradient may reflect (i) more recent establishment of C_3 woody plants in the playa topoedaphic settings; (ii) the substantially higher C_4 grass primary production in this setting; (iii) a slower turnover of SOC in fine-textured playa soils; or (iv) some combination of i–iii. To what extent has woody plant proliferation in playas altered SOC and TN pools in this topoedaphic setting? To address this question would require comparisons with playa communities that have not undergone woody plant encroachment. This was not possible at our site.

Relationship between SOC and TN and other soil and vegetation variables

Although correlations between variables are not necessarily an indication of cause–effect relationships, they can be used in conjunction with other lines of evidence to provide clues as to the underlying ecological

processes that govern their behavior. The strong correlations between SOC, TN and litter and root biomass are consistent with the notion that litter and root production have strong influences on SOC and TN (Rasse *et al.*, 2005). Both litter and root biomass were higher in woody communities (drainage woodlands > groves > clusters) than in grassland, which indicated that woody plant proliferation is accompanied by increased inputs of organic matter to soil. In addition, litter and root tissues are more enriched in recalcitrant biochemical compounds (e.g., cutin, suberin, and resistant lignin subunits) in wooded areas vs. grasslands at this site (Filley *et al.*, 2008). This is likely another mechanism favoring SOC and TN accrual subsequent to woody plant establishment in grasslands.

It is widely assumed that shifts from grass to woody plant dominance in drylands are accompanied by reductions in root biomass (and hence C and N inputs) in near-surface soils as grasses, with their dense, fibrous, shallow root systems give way to shrubs with sparse, coarse, deep root systems. However, soils associated with woody communities at our site had comparable or substantially higher root biomass than remnant grasslands (Fig. 3), despite having substantially lower aboveground grass biomass (Table 1). Thus, generalizations regarding impacts of woody plant encroachment on

root biomass and its contribution to SOC and TN pools should be made with caution. Furthermore, the negative correlation between soil bulk density and SOC and TN ostensibly reflects the functional consequences of woody plant encroachment in modifying soil bulk density, perhaps by intercepting wind-borne soil particles, increasing soil porosity and improving soil structure by root exudation. This, in turn, would have consequences for SOC turnover and sequestration potential and the nature and extent of spatial variation of soil properties in shrub- vs. grass-dominated communities (e.g., Liu *et al.*, 2009).

Spatial scales of SOC and TN patterns

Variation in SOC, TN, litter, root biomass, tree basal area, and shrub basal area all scaled at about 40–45 m, which was about the average distance from the centroid of woody patches to the centroid of adjoining neighboring grassland communities (Fig. 4, Table 3). This scale therefore reflects the influence of different types of woody patches on soil properties along the catena gradient. Similar scales for this group of variables suggested that both trees (primarily *P. glandulosa*) and shrubs (numerous species) interact to influence the spatial pattern of SOC and TN through their influences
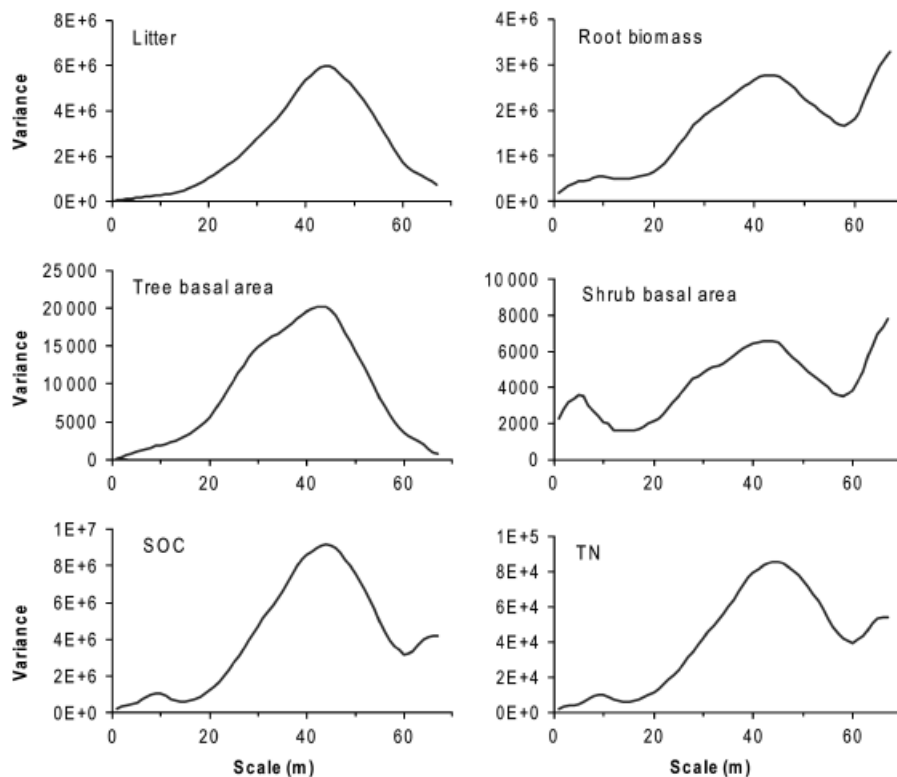

Fig. 4 Three term local quadrat variance (3TLQV) results for litter, ash-free root biomass, tree basal area, shrub basal area, soil organic carbon (SOC) and total nitrogen (TN). Peaks of variance indicate spatial scales (m). Values for peaks are given in Table 4.

on root and litter inputs. These influences are super-imposed against the backdrop of geomorphic properties (e.g., texture, depth to argillic horizon) that vary along the catena gradient.

Invasion of woody plants is known to alter the spatial pattern of herbaceous species distribution and abundance (Ludwig *et al.*, 2004; McClaran & Angell, 2007) and their productivity (Knapp *et al.* 2008; Simmons *et al.*, 2008). These changes in the ground layer could potentially influence the magnitude and patterns of SOC and TN. However, while forb and grass biomass exhibited spatial scales approaching that of woody vegetation (38–47 vs. 40–45 m), they were not significantly correlated with SOC and TN (Table 2). This consistent with our earlier arguments that increases in woody plants are driving changes in SOC and TN, not decreases in herbaceous vegetation. Scales detected for soil texture were also different from those of SOC and TN. Although establishment of shrubs in grassland can markedly alter patterns of wind and water transport of soils in arid regions (Okin & Gillette, 2001; Ravi *et al.*, 2007), but we saw little evidence of soil redistribution in the uplands of this semi-arid system (see texture values in Table 1). Instead, soil texture appeared to be primarily a function of geomorphic processes operating along the catena (hill-slope) gradient.

Ecological patterns and processes occur across multiple scales, and their relationships are often scale-dependent (O'Neill *et al.*, 1986; Wiens, 1989; Levin, 1992). Scaling properties of soil variables are known to differ among the grass- and shrub-dominated plant communities at our site (Liu *et al.*, 2009). In this study, we also see how the spatial patterns of soil and vegetation variables vary across a catena (hill slope) gradient. SOC, TN, and root biomass showed a small spatial scale of about 10 m, which we suggest is a reflection of the variation of these variables within woody patches. The spatial pattern of root biomass in shrub clusters at this site is known to approximate the extent of cluster canopy margins (Watts, 1993); and studies on other arid and semiarid ecosystems have found that the impact of woody plants on soil properties extended over a distance approximately equal to the size of their canopies (Jackson & Caldwell, 1993; Schlesinger *et al.*, 1996; Throop & Archer, 2008). We therefore hypothesize that this small-scale variation reflects the collective influence of individual trees (primarily *Prosopis*) and associated understory shrub species on spatial patterns of root biomass. Although spatial variation in litter biomass was also closely related to spatial variation in SOC and TN, it did not share this small spatial scale. This likely reflects the fact that spatial patterns of litter within woody patches are influenced by other factors besides woody plant distribution. These would include

seasonality, wind and water translocation, and animal disturbance. The difference in scales for root and litter biomass supports the notion that within woody communities in this savanna parkland/woodland system, roots exert greater control over SOC and TN pool than does litter. This is consistent with a recent review showing that most SOC is derived from roots (Rasse *et al.*, 2005), and with an experimental study in temperate forest showing that aboveground litter inputs have little impact on SOC over decadal time scales (Garten, 2009).

Summary

The widespread occurrence of woody invasion into grasslands has the potential to influence C and N cycles at regional and perhaps global scales (Schlesinger *et al.*, 1990; Houghton *et al.*, 1999; CCSP, 2007). Accurate assessments of changes in SOC and TN pools following woody invasion are essential in order to determine the potential impacts of this phenomenon on the biogeochemistry of C and N. However, the estimation of SOC and TN storage over large areas is logistically challenging. In this study, we found that SOC and TN varied at two spatial scales, one reflecting the distribution of woody patches and the other the within-patch impacts of woody plants. Given that spatial variation was significant at two scales it would therefore not be appropriate to simply extrapolate estimates of SOC and TN from local point samples collected at small scales to larger scales. Instead, accurate estimates SOC and TN at large spatial scales will require the use of algorithms developed from nested sampling designs that capture variation at multiple scales. Woody cover data obtained from readily available and relatively inexpensive remote sensing imagery could potentially be used in conjunction with spatially explicit soil sampling to improve the estimation of SOC and TN storage in landscapes where woody plant encroachment has occurred. Owing to the variety of grass-dominated ecosystems undergoing woody plant invasion, spatial patterns of SOC and TN and their relationships with other environmental variables may well differ from what we observed here. Spatial patterns of SOC and TN and their relationship to invasive woody plants should therefore be examined carefully rather than assumed.

Acknowledgements

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