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Spatial heterogeneity of aggregate stability and soil carbon in semi-arid rangeland

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"Capsule": *The authors argue that multi-scale soil heterogeneity must be considered when measuring and managing carbon sequestration.*

Abstract

To measure and manage for C sequestration in heterogeneous rangeland systems, we need to more fully understand spatial patterns of soil resources. Spatial distributions of aggregate stability and soil carbon were investigated in a semiarid rangeland in New Mexico, USA. Soil was analyzed from plant interspaces, black grama (*Bouteloua eriopoda* (Torr.) Torr.), and mesquite (*Prosopis glandulosa* Torr.) in a landscape-replicated study. Aggregate stability at the 250 μm scale, carbonate C, organic C and N, C:N ratio, and glomalin, were all highest under mesquite. Soil C:N ratio was the best predictor of aggregate stability. Estimates of metric tons of C per hectare in the top 10 cm were highly variable at patch and landscape scales, varying from 4.2 to 10.5 under mesquite and from 3.0 to 7.0 in interspaces. High variability of aggregate stability and soil C has important implications for C sequestration. We argue that this multi-scale soil heterogeneity must be considered when measuring and managing for C sequestration.

Keywords: Soil structure; Soil organic matter; Carbon sequestration; Spatial heterogeneity; Chihuahuan desert

1. Introduction

1.1. Rangelands and carbon sequestration

The potential of US rangeland soils to sequester carbon as a means of offsetting increasing levels of atmospheric carbon dioxide and other greenhouse gases is much lower per unit area than in some other ecosystems, such as forests and cropland (Waltman and Bliss, 1997). However, the relatively large land cover percentage of North American rangelands means that the cumulative carbon sequestration in these systems has the potential to be significant at regional and national scales (Kimble et al., 2001).

One of the challenges to both increasing and monitoring carbon sequestration in rangeland soils is the inherently patchy spatial and temporal distribution of resources in many rangeland systems. This heterogeneity is particularly strong in semiarid and arid regions where plant production often varies by an order of magnitude or more at scales ranging from sub meter to thousands of hectares. Spatial and temporal patchiness of vegetation and soil resources in these systems therefore makes monitoring changes in C storage difficult (Christensen, 1996).

1.2. Heterogeneity of rangelands

Vegetation distribution is visibly more heterogeneous in rangelands than in many other ecosystems, such as croplands (Cornelius et al., 1991). Spatial distribution of soil organic carbon (SOC) in rangelands tends to be highly correlated with vegetation patterns and plant community dynamics (Schlesinger et al., 1990, 1996; Smith et al., 1994; Schlesinger and Pilmanis, 1998). However, our understanding of how soil carbon is

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distributed at different spatial scales in semiarid and arid rangelands is limited. The ability to predict soil carbon distributions in these systems is further complicated by dramatic changes in plant community composition in western US rangelands. Vegetation shifts frequently result in SOC being out of equilibrium with new plant communities, as illustrated by ^{13}C studies (e.g. Connin et al., 1997). Such changes are the result of various combinations of the elimination of fire, invasion of native and exotic species, overgrazing, and climate change (Schlesinger et al., 1990).

In southwestern US semiarid rangelands, degradation is associated with a shift from a grass- to a shrub-dominated vegetation community, which in turn is associated with a shift to a more patchy distribution of soil resources and vegetation (Schlesinger et al., 1990; Gallardo and Schlesinger, 1992). Carbon sequestration and soil quality may not always be positively correlated in these systems where shrubs may sequester more SOC, but the landscape as a whole is frequently associated with higher rates of soil erosion (Gibbens et al., 1983; Schuman et al., 2000).

1.3. Soil organic matter, soil aggregation, and carbon sequestration

To be able to cost-effectively monitor and manage for carbon sequestration in these ecosystems, we need to know (1) the spatial distribution of soil carbon at different spatial scales, and (2) how soil structure interacts with SOC and its different fractions. We need to understand spatial variability in order to design sampling protocols to accurately quantify soil carbon at the landscape scale with the lowest sampling effort possible. Defining or characterizing SOC-soil structure interactions is key to understanding the complex feedbacks between SOC, spatial variability in infiltration and soil water-holding capacity, and plant community dynamics (Coffin and Herrick, 1999).

Soil organic matter (SOM) affects soil aggregation and the stability of aggregates, and conversely, aggregation affects SOM dynamics and carbon storage (Herrick and Wander, 1998). The process of aggregation and aggregate stabilization is complex, operates at a variety of spatial and temporal scales, and is not fully understood (Golchin et al., 1995; Puget et al., 1995). It has been proposed that there is a direct link between soil aggregation and carbon cycling (Golchin et al., 1994, 1995) and that aggregation is an indicator of soil quality directly relevant to carbon sequestration (Lal et al., 1998). Soil aggregation affects the formation, destruction, and stabilization of SOM, can protect soil organic matter from microbial breakdown, and affects decomposer microenvironmental conditions (Jastrow and Miller, 1991; Carter, 1996; Christensen, 1996). Aggregates smaller than 250 μm in diameter are often more stable than larger aggregates and have the potential to protect soil carbon within them, thus affecting the relatively long-term soil carbon pool (Elliot, 1986; Carter, 1996; Tisdall, 1996; Lal et al., 1998).

Concentration of glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi, has been found to be related to aggregate stability in cropped soils from Maryland (Wright et al., 1999), Colorado (Wright and Anderson, 2000), and Arizona (Rillig et al., 2001). The relationship between aggregate stability and glomalin in semi-arid rangeland systems has not yet been tested, however, and may be an important factor affecting soil stability in these systems.

1.4. Objectives

Our primary research objective was to characterize the spatial distribution of aggregate stability, total organic and inorganic carbon, and different carbon fractions in the top 10 cm of soil in an area of black grama (*Bouteloua eriopoda* (Torr.) Torr.) grassland in early stages of transition to mesquite (*Prosopis glandulosa* Torr.) shrubland. Based on the resource island hypothesis proposed by Schlesinger et al. (1990) and related literature (Wright and Honea, 1986; Schlesinger et al., 1996), we expected that spatial variability of soil carbon and aggregate stability at the plant-interspace scale would be high due to the high patchiness of vegetation in this ecosystem. We further expected that carbon content and related properties would be reduced in interspaces and in surface soils under mesquite.

2. Materials and methods

2.1. Study location and plots

The study was conducted on the USDA-ARS Jornada Experimental Range and the New Mexico State University Chihuahuan Desert Rangeland Research Center. The two research stations are located in the Jornada del Muerto basin at the northern end of the Chihuahuan Desert in south-central New Mexico, USA (Fig. 1). Mean annual rainfall is 247 mm, approximately 50% of which falls between 1 July and 30 September (Gile et al., 1998). Summer precipitation occurs primarily as short, high intensity, localized convective storms and there are three distinct seasons: a hot, wet summer (from July to October), a cool, dry winter (from November to March), and a hot, dry spring (from April to June; Virginia et al., 1992). Mean annual temperature is 15.6 °C, the hottest month is July with a mean temperature of 26 °C, and the coolest month is January with a mean temperature of 6 °C (Gile et al., 1998). Maximum summer temperatures reach 40 °C (Buffington and Herbel, 1965). Mean elevation is approximately 1250 m.

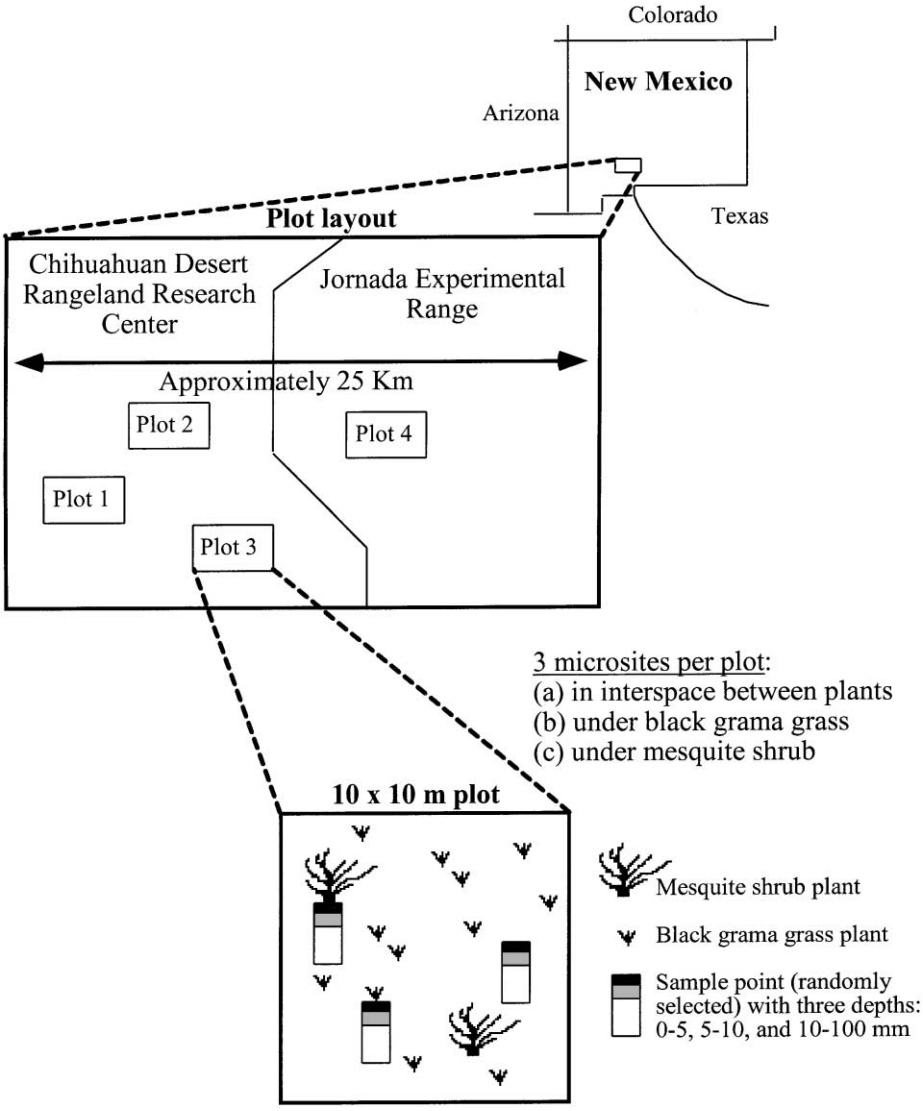

Fig. 1. Location of study plots and sample points in south-central New Mexico, USA.

Study plots were situated in a vegetation community transition zone between black grama grassland and mesquite-dominated shrubland. Four 0.5-ha plots were chosen within a 25-km radius to provide landscape-level replication. All four plots were located on a sandy loam underlain by a petrocalcic horizon at a depth of 0.6–1.5 m. Soil surface texture and bulk density (0–10 cm) data are summarized in Table 1. Across plots, black grama represented 30–54% of the total perennial plant cover. A single 10×10 m sub plot was randomly selected within each plot. To ensure that different plots had comparable black grama cover, and similar levels of cattle disturbance, it was necessary to locate them in two different ways. Two of the plots were placed within 25-year-old cattle exclosures. The other two plots were located in areas minimally disturbed by cattle due to distance from water.

2.2. Soil sampling

Three sample points were randomly selected in each of the four plots: one each from under a black grama grass plant, under a mesquite plant, and in a plant interspace (Fig. 2). Soil samples were removed from 0–5 mm depth using a modified masonry trowel, and from 5–20 and 20–100 mm depths using a 5-cm diameter soil core (Fig. 1). Litter was included in the surface samples. We chose to intensively sample shallow depths because we are ultimately interested in the interactions between soil organic matter cycling, plant community dynamics, infiltration and erosion at the soil surface. Soil was sampled at three depths because earlier observations indicated that soil organic matter accumulation is highly stratified in the top 10 cm. Soil was collected under plant canopies as close to the center of the plant as

Table 1
Study plot soil characteristics

		Bulk density[a]	Surface texture[b]			Soil series[c]
			% Sand (>50 μm)	% Silt (2–50 μm)	% Clay (<2 μm)	
Plot 1	Average		79.3	13.1	7.6	Wink–Harrisburg[d]
	Interspace	1.37				
	Black grama	1.27				
	Mesquite	1.46				
Plot 2	Average		78.8	14.6	6.6	Wink–Harrisburg
	Interspace	1.16				
	Black grama	1.08				
	Mesquite	1.03				
Plot 3	Average		78.6	13.7	7.8	Onite–Pajarito[e]
	Interspace	1.16				
	Black grama	1.06				
	Mesquite	1.04				
Plot 4	Average		81.5	12.5	6.0	Onite–Pajarito
	Interspace	1.30				
	Black grama	1.12				
	Mesquite	1.21				

[a] Values are means weighted by soil depth, $n=3$.
[b] Based on the hydrometer test of Gee and Bauder (1986) performed on a composite of nine 100-mm deep random samples removed from each 10×10 m sub plot.
[c] From Bulloch and Neher (1980).
[d] Complex of coarse-loamy, mixed, thermic Typic Calciorthid and coarse-loamy, mixed, thermic Typic Paleorthid.
[e] Complex of coarse-loamy, mixed, thermic Typic Haplargid and coarse-loamy, mixed, thermic Typic Camborthid.

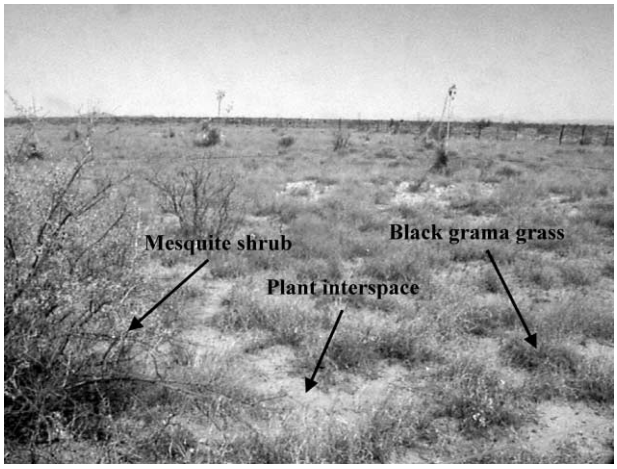

Fig. 2. Example of a study plot showing sample microsites.

possible and at the approximate center of interspaces. Sampling was completed between 1 and 6 September, 1999. The soil was dry to a depth of greater than 10 cm throughout the sampling period.

Samples were transported from the field to a laboratory in paper bags and left to air dry for a minimum of 3 days. Each soil sample was split into 20-g subsamples for use in different analyses. Soil was gently pressed through a 2-mm sieve and coarse organic matter larger than 1 mm diameter or 5 mm long removed. A 2-mm sieve was used because there were very few aggregates larger than 2 mm in this soil, and this sieve size allowed us to more precisely separate the coarse organic matter.

2.3. Wet aggregate stability

Between 3.5 and 4.5 g of homogenized bulk soil from each sample were placed onto 250-μm sieves. Each sample was immersed in deionized water and immediately sieved for 5 min on a motorized platform (as described by Kemper and Rosenau, 1986) which generated 1.5 cm of vertical movement at a rate of one cycle every 2 s and kept samples immersed throughout the 5-min period. Residual fine (<250 μm) and coarse (>250 μm) material oven-dry weights were recorded following sieving. Gravimetric moisture content was calculated for each sample from a 5- to 10-g subsample. Both total and sand-free aggregate stability were calculated. Sand-free aggregate stability was calculated by subtracting the coarse sand (>250 μm) from the weight of both the stable aggregates and the original oven-dry soil weight.

2.4. Bulk density

Soil bulk density was calculated from a second set of known-volume samples taken with a soil corer adjacent

to the locations from which aggregate stability samples were removed (Blake and Hartge, 1986).

2.5. Carbonate carbon

Calcium carbonate equivalent was measured manometrically on 5-g subsamples of soil treated with 1 N phosphoric acid with a method described by Nelson (1986). Calcium carbonate content was determined from a standard curve. Dry weight of carbon (expressed as g of C per kg of soil) was calculated by a molecular weight conversion of these values.

2.6. Organic carbon and nitrogen

Twenty grams of each soil sample were treated with 1 N phosphoric acid to remove carbonates, oven-dried, ground in a Shatterbox® soil grinder for 45 s, and then oven-dried again. For each sample, 0.025–0.030 g of treated soil was packed in an aluminum foil capsule and analyzed for total carbon and total nitrogen using the Micro-Dumas combustion method and an IR detector (Kirsten, 1983). The percentage of organic C per soil weight, the percentage of organic N per soil weight, and carbon:nitrogen ratios were calculated.

Percent organic carbon by weight was converted into g of C per kg of soil and metric tons of C per hectare (MTC/ha) using plot-specific bulk density values and soil depths for each microsite (interspace, black grama, and mesquite). The calculated MTC/ha values for black grama and mesquite are best regarded as maximum estimates for each plot because soil samples were taken as close to the center of a plant as possible.

2.7. Glomalin

Fractions of glomalin were extracted from 1-g samples. The easily-extracted glomalin (Wright and Upadhyaya, 1996) was extracted with 8 ml of 20 mM citrate, pH 7.0 at 121 °C for 30 min. Supernatant containing solubilized glomalin was separated by centrifugation at $5000\times g$ for 10 min and decanted. A 1-ml aliquot of easily-extractable glomalin was set aside for protein and immunoreactive protein assays. The remaining material was subjected to two more 1-h extraction cycles to remove total glomalin with 8 ml of 50 mM citrate, pH 8.0, at 121 °C. The remainder of easily extractable glomalin was pooled with supernatants from the two 50 mM citrate extractions and a 1-ml aliquot was removed. The 1-ml aliquots for easily extractable and total glomalin were centrifuged at $10{,}000\times g$. Material remaining after centrifugation and removal of solublilized glomalin was passed through a 250-μm sieve. Coarse material remaining on the sieve was washed with deionized water, dried at 103 °C, and weighed. For a more detailed explanation of extraction procedures, please see Wright and Upadhyaya (1996).

Protein and immunoreactive protein in the easily extractable (EEG) and total glomalin (TG) fractions was measured by the Bradford assay (Wright and Upadhyaya, 1996, 1998). Immunoreactive protein in these fractions (IREEG and IRTG) is based on an enzyme-linked immunosorbent assay described by Wright and Upadhyaya (1998). Assay values were extrapolated to mg/g of soil using the total volume of liquid containing solubilized easily extractable or total glomalin and a correction of the original weight for coarse material.

2.8. Statistical analysis

All statistical analyses were performed using Statview® computer software (Abacus Concepts, 1996). Means and standard errors were calculated by microsite and soil depth for total and sand-free aggregate stability. Means weighted by soil depth, and means for individual depths, were calculated for organic C, organic N, C:N ratio, and all glomalin fractions.

Pearson correlation coefficients were calculated for all possible variable pairs to generate a correlation matrix. For each pairwise comparison, Fisher's r to z transformation was used to test the null hypothesis that the correlation was equal to zero. Simple bivariate scatter plots and linear regressions were performed to compare all C, N, and glomalin fractions with sand-free aggregate stability. In addition, stepwise multiple regression using all C, N, and glomalin variables was used to investigate the influence of different independent variable combinations on sand-free aggregate stability. Those multi-variate regression models that had the highest coefficient of determination (r-square) were noted. To avoid problems with colinearity,% organic C and % organic N were not used in combination with C:N ratio in any analysis. Linearity assumptions were tested with residual versus fitted plots for these best-fit regressions.

3. Results

3.1. Aggregate stability

Mean 250 μm aggregate stability was consistently greater than 40% in all microsites and at all soil depths (Fig. 3). Aggregate stability tended to decrease with soil depth and was highest under mesquite and lowest in plant interspaces. Within-patch variability of aggregate stability between interspaces, black grama, and mesquite was higher at upper soil depths. Trends in aggregate stability were similar in all plots.

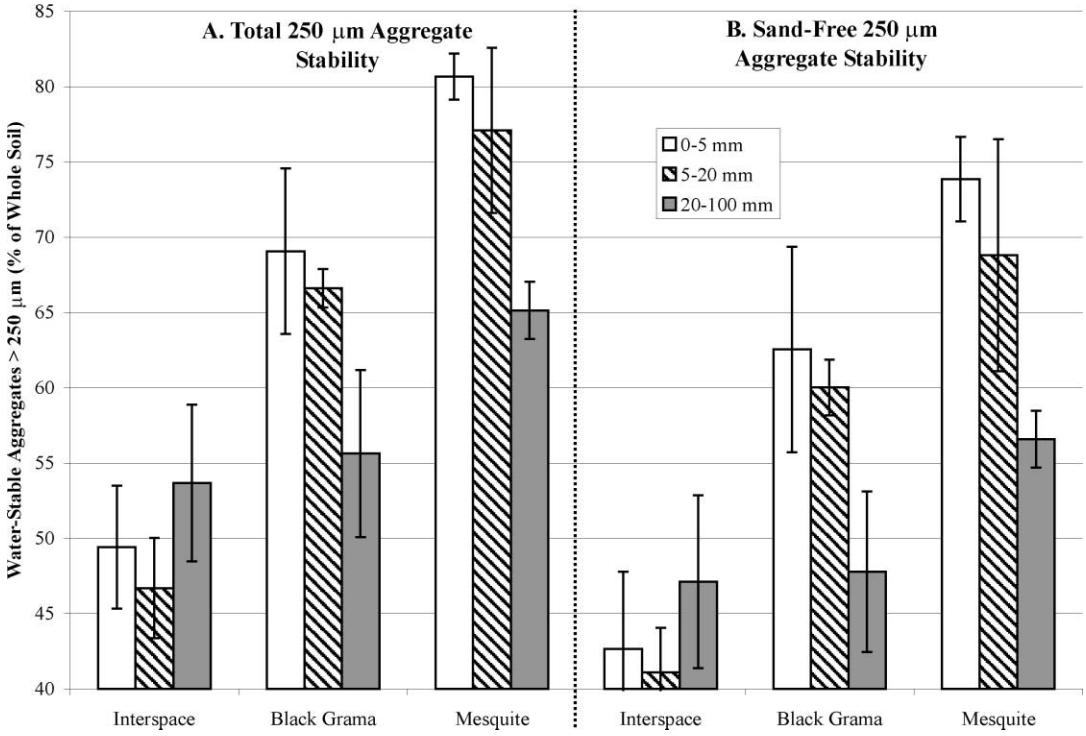

Fig. 3. Mean percentage of 250 μm wet aggregate stability split by microsite and soil depth for (A) total and (B) sand-free aggregate stability. Error bars represent standard errors, $n=4$.

3.2. Carbonate carbon

Carbonate C values were low overall, but like aggregate stability, values were highest under mesquite and lowest in interspaces (Table 2). Variability was high between plots at all soil depths. Carbonate C was slightly higher in the top 5 mm under black grama and mesquite than at lower depths, whereas the 5–20 mm depth had highest carbonate C in interspaces (Table 2).

3.3. Organic carbon, organic nitrogen, and glomalin

Organic C, organic N, C:N ratio, and all measures of glomalin (EEG, TG, IREEG, and IRTG) were highest under mesquite (Tables 2 and 3). There was little difference in C and N between black grama and plant interspaces, and organic C and organic N were higher at the soil surface than at lower depths (Table 2). Glomalin showed a sequential increase from interspace to black grama to mesquite (Table 3). Glomalin is approximately 30% carbon by weight. Based on this estimate, the proportion of total organic carbon in the top 10 cm represented by glomalin ranged from 7% in the interspaces to 10% under black grama and 12% under mesquite (cf. Tables 2 and 3). Maximum potential MTC/ha was highest under mesquite (Tables 2 and 4) and demonstrated high variability between the four study plots (Table 4).

Nearly all pairwise correlations between aggregate stability and soil carbon fractions were significantly positive (Table 5). Soil C:N ratio had the highest correlation with aggregate stability of all the SOM-related values measured. Organic C, organic N, and carbonate C were all strongly correlated with glomalin and protein. Simple linear regression suggested that C:N ratio and easily-extractable glomalin had the strongest positive relationships with sand-free aggregate stability (Figs. 4 and 5). The best-fit multiple regressions suggested that C:N ratio and carbonate C were the best predictors of sand-free aggregate stability (Table 6). A maximum of 62% of the variability in sand-free aggregate stability was explained with these regression models.

4. Discussion

4.1. Aggregate stability

Aggregate stability percentages were surprisingly high overall given the fact that these soils are "weakly structured" at the pedon scale (Bulloch and Naher, 1980). The differences in aggregate stability between interspaces, black grama, and mesquite clearly demonstrated the heterogeneity at the patch scale within this ecosystem. Litter inputs are higher under plant canopies. Hence, it follows that higher aggregate stability was observed at upper soil depths, given the potential for microbial activity and shallow plant roots to positively affect stability in this zone (Miller and Jastrow, 1990;

Table 2
Carbon and nitrogen by microsite and soil depth

	Carbonate C (mg/g soil)	Organic C (mg/g soil)	Organic N (mg/g soil)	C:N ratio	MTC/ha[a]
Interspace: depth weighted mean[b]	0.029 (0.013)	3.54 (0.80)	0.38 (0.08)	9.29 (0.42)	2.92 (0.59)
0–5 mm[c]	0.023 (0.011)	5.32 (1.67)	0.62 (0.19)	8.56 (0.28)	0.28 (0.07)
5–20 mm	0.074 (0.010)	2.98 (0.47)	0.34 (0.04)	8.52 (0.41)	2.11 (0.23)
20–100 mm	0.032 (0.014)	3.53 (0.82)	0.37 (0.08)	9.48 (0.43)	3.50 (0.72)
Black grama: depth weighted mean	0.045 (0.019)	3.82 (0.57)	0.42 (0.05)	9.02 (0.29)	2.75 (0.49)
0–5 mm	0.050 (0.021)	6.94 (0.74)	0.67 (0.08)	10.46 (0.56)	0.40 (0.04)
5–20 mm	0.036 (0.015)	4.45 (0.74)	0.47 (0.07)	9.35 (0.28)	0.98 (0.17)
20–100 mm	0.046 (0.020)	3.51 (0.54)	0.39 (0.05)	8.86 (0.31)	3.23 (0.58)
Mesquite: depth weighted mean	0.057 (0.023)	6.60 (1.19)	0.65 (0.11)	9.86 (0.31)	4.60 (0.89)
0–5 mm	0.074 (0.031)	14.31 (2.73)	1.28 (0.24)	11.19 (0.09)	0.76 (0.17)
5–20 mm	0.062 (0.026)	8.88 (0.93)	0.84 (0.10)	10.62 (0.18)	2.11 (0.23)
20–100 mm	0.055 (0.024)	5.69 (1.20)	0.58 (0.10)	9.63 (0.40)	5.31 (1.07)

[a] Represents metric tons of C per hectare for each microsite weighted by bulk density and soil depth.
[b] Depth weighted means with standard errors in parentheses from four plots, $n=4$.
[c] Depth means with standard errors in parentheses from four plots, $n=4$.

Table 3
Glomalin and total protein by microsite

	Easily extractable glomalin mg/g soil	Total glomalin mg/g soil	Immunoreactive easily extractable glomalin mg/g soil	Immunoreactive total glomalin mg/g soil
Interspace	0.08 (0.02)[a]	0.25 (0.06)	0.0001 (0.0001)	0.0015 (0.0003)
Black grama	0.14 (0.02)	0.37 (0.06)	0.0006 (0.0001)	0.0031 (0.0009)
Mesquite	0.25 (0.01)	0.55 (0.07)	0.0014 (0.0003)	0.0046 (0.0014)

[a] Values are means weighted by soil depth with standard errors in parentheses from four plots, $n=12$.

Table 4
Landscape variability of organic carbon in the top 10 cm of soil for each microsite

	Plot 1	Plot 2	Plot 3	Plot 4
		MTC/ha[a]		
Interspace	3.05	6.96	3.83	4.08
Black grama	6.14	5.62	3.71	2.96
Mesquite	10.49	9.38	8.50	4.22
		g C/kg soil[b]		
Interspace	2.14	5.83	3.16	3.01
Black grama	4.56	4.95	3.27	2.51
Mesquite	6.96	8.57	7.70	3.15

[a] Values are metric tons of C per hectare for each microsite weighted by bulk density and soil depth.
[b] Values are grams of C per kilogram of soil for each microsite weighted by soil depth.

Dorioz et al., 1993). Likewise, it is not surprising that shrub, grass, and interspaces differed in aggregate stability. Plant canopies protect the soil surface from disturbance and soil beneath canopies receives higher organic matter inputs and generally has higher moisture content. SOM and rainfall water accumulation therefore enhances aggregation (Harris et al., 1966). Mesquite shrubs have a more extensive canopy and root system than black grama grass plants, and therefore have the potential to increase aggregate stability to a greater degree.

4.2. Carbonate carbon

Carbonate C values were surprisingly low, given the presence of a petrocalcic horizon at a depth of 0.6–1.5 m. Carbonate C variability between microsites was similar to that observed in aggregate stability and probably reflects higher rates of respiration under the mesquite and grass that results in higher concentrations of bicarbonate (Goudie, 1996).

4.3. Carbon, nitrogen, and glomalin

Aggregate stability of the 1–2 mm size range from cropped soils in Maryland (Wright et al., 1999), Colorado (Wright and Anderson, 2000), and Arizona (Rillig et al., 2001) were found to be related to at least one fraction of glomalin. The range in mean concentration of total glomalin in these soils (Table 3) is comparable to that found in the top 30 cm of non-irrigated soils cropped to sorghum in Arizona (Rillig et al., 2001).

Table 5
Correlation matrix for aggregate stability and all carbon, nitrogen, and glomalin fractions

	Total 250 μm agg. stab.	Sand-free 250 μm agg. stab.	CO_3 C	% Organic C	% Organic N	C:N ratio	EEG	TG	IREEG
Sand-free 250 μm aggregate stability	0.98[a]*								
Carbonate (CO_3) C	0.24	0.14							
% Organic C	0.55*	0.45*	0.59*						
% Organic N	0.49*	0.37	0.56*	0.99*					
C:N ratio	0.81*	0.74*	0.50*	0.70*	0.62*				
Easily extractable glomalin (EEG)	0.65*	0.55*	0.43*	0.84*	0.82*	0.71*			
Total glomalin (TG)	0.54*	0.44*	0.72*	0.86*	0.86*	0.66*	0.87*		
Immunoreactive easily extractable glomalin (IREEG)	0.45*	0.35*	0.56*	0.75*	0.76*	0.56*	0.79*	0.81*	
Immunoreactive total glomalin (IRTG)	0.33	0.19	0.82*	0.79*	0.80*	0.50*	0.69*	0.87*	0.77*

[a] All values are the Pearson correlation coefficient (varies 0–1), $n = 36$. * Indicates a correlation coefficient significantly different from 0 at the $P < 0.01$ level following a Fisher's r–z transformation and significance test.

Higher levels of organic C, organic N, and glomalin were found under mesquite shrubs. These trends support the results of other studies where soil resource accumulation has been reported under shrubs in degrading Chihuahuan desert rangeland (e.g. Schlesinger et al., 1996) and under mesquite in the Sonoran Desert (Virginia and Jarrell, 1983). C and N differed little between black grama and interspaces, while all measures of glomalin were higher under black grama than in interspaces. Glomalin therefore followed similar trends to aggregate stability. This suggests a qualitative difference in SOM between grass and interspaces. Both black grama and mesquite are hosts for mycorrhizal fungi. Mesquite canopies accumulate litter to a greater extent than do black grama canopies and therefore, may reduce evaporation from under shrub canopies. Hence, the protection afforded by more litter under mesquite could create more favorable conditions for fine root and mycorrhizal growth, explaining the higher levels of glomalin observed under mesquite. Fungal biomass is generally higher under plants, particularly in ecosystems in which litter is concentrated under plant canopies (Gallardo and Schlesinger, 1992; Kieft et al., 1994), while cyanobacteria is more prevalent on bare soil than under plants (J. Belnap, unpublished data). A natural extension of this study, therefore, would be to analyze soil for microbial biomass and diversity to further explain the plant-interspace differences observed here.

Despite the relatively weak relationships between organic C and N, and aggregate stability, regression analysis showed C:N ratio to be a significant factor related to aggregate stability. Higher soil C:N ratios are associated with younger, more labile SOM (Wander and Traina, 1996; Jastrow and Miller, 1998). Given the strongly positive relationship between C:N ratio and aggregate stability, plus the higher levels of both under mesquite, our data suggest that higher organic matter inputs from plant litter and root exudates under shrub canopies may be driving faster labile SOM accumulation, which in turn increases aggregate stability.

4.4. Total carbon per hectare

Converting percentage organic C values to MTC/ha for each microsite clearly demonstrated higher amounts of C under mesquite shrubs than under black grama and in plant interspaces. Between-plot variability of MTC/ha was high, showing that heterogeneity exists at the landscape scale. Not only was total C different in different plots, but the within-plot variability also varied across plots. Plot 1 varied from 3.05 in interspaces to 10.49 MTC/ha under mesquite (Table 4). Plot 4 varied from 2.96 under black grama to 4.22 MTC/ha under mesquite. Due to the small sample size within each plot, these values probably represent a high estimate of the variability across the landscape. However, given this between-plot variability, our data still suggests that landscape position affects the distribution of soil C at the patch scale, with much higher landscape-level variability under mesquite than under black grama or in interspaces. Additional studies replicated across different plant communities and ecosystems are needed to test these observations.

4.5. Carbon sequestration management and measurement

Our data clearly show higher soil C and aggregate stability under mesquite compared to black grama and plant interspaces. Despite the potential for maintaining higher C levels under mesquite, it must be remembered that the spatial redistribution of vegetation and soil resources (from fine scale heterogeneity in black grama-dominated systems to coarse scale heterogeneity in mesquite-dominated systems) that results from mesquite invasion does not necessarily mean higher total C across

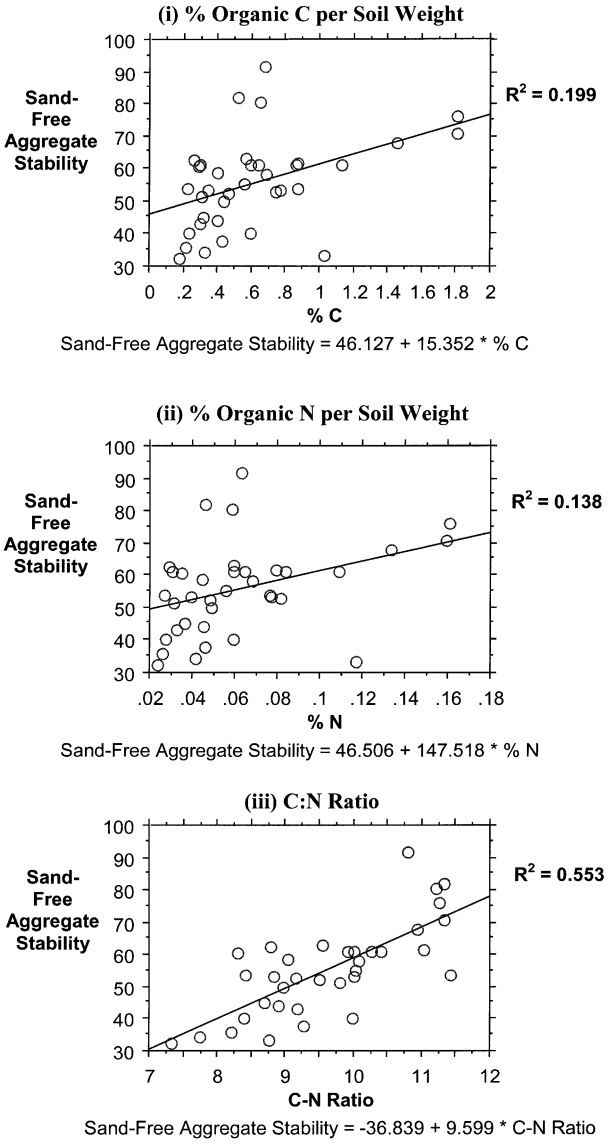

Fig. 4. Bivariate scatter plots and simple linear regressions for sand-free aggregate stability versus (i) % organic C, (ii) % organic N, and (iii) C:N ratios.

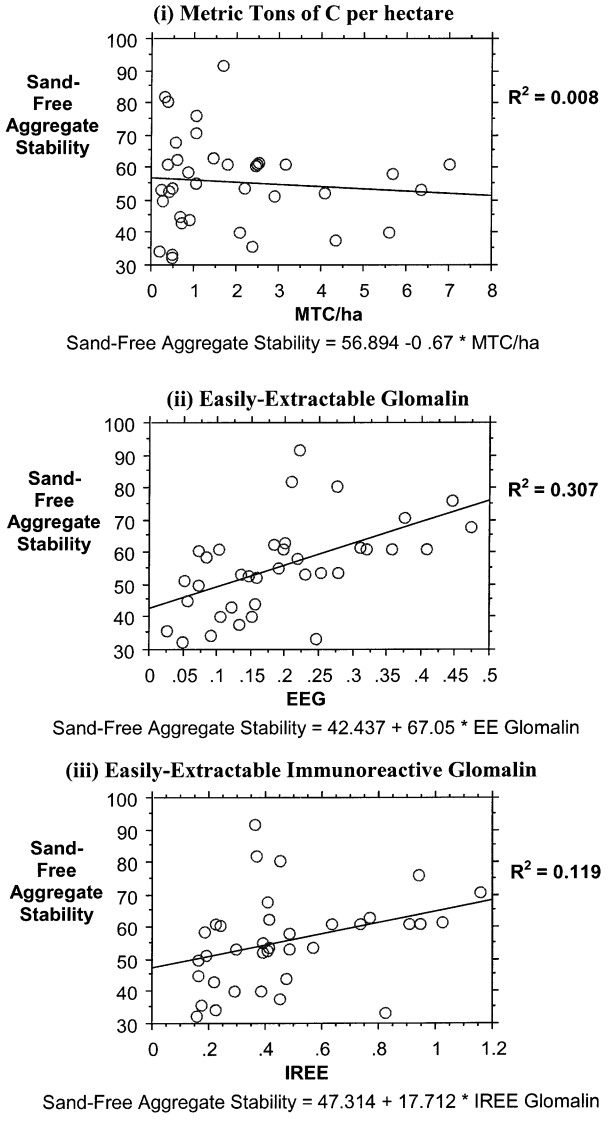

Fig. 5. Bivariate scatter plots and simple linear regressions for sand-free aggregate stability versus (i) metric tons of C per hectare (MTC/ha), (ii) easily extractable glomalin (EEG) protein, and (iii) easily extractable immunoreactive glomalin (IREEG).

the ecosystem and landscape (Gibbens et al., 1983). One logical progression of this research would be to compare aggregate stability and soil C distribution across different levels of degradation to investigate how patch scale distribution of total C changes with vegetation shifts.

Our data show heterogeneity of C distribution at both patch and landscape scales. To reliably measure total soil C across these semiarid landscapes therefore, one must use caution when extrapolating C values generated from soil samples to broader land areas. How representative of a particular area those samples are, given the high heterogeneity of C distribution, must always be questioned. A successful sampling regime demands careful design and implementation to avoid risks of erroneous estimates of total soil C. The multi-scale variability of aggregate stability and soil C we report here also has implications for C sequestration management (Bird et al., 2000). For example, different landscape areas will respond very differently to organic inputs based on vegetation, soil structure and stability, SOM, and the spatial and temporal dynamics of each. Being able to identify areas of the landscape that potentially respond more effectively to such inputs has both ecological and economic benefits.

5. Conclusions

Aggregate stability, carbonate C, organic C and N, C:N ratios, and glomalin were all higher under mesquite plants than under black grama plants or in plant interspaces. Aggregate stability and glomalin were higher

Table 6
Selected multiple linear regression models describing the dependence of sand-free aggregate stability on C, N, and glomalin soil fractions

				Regression ANOVA	
	Independent variables	Regression coefficient	R^2	F	P
MODEL I[a]			0.6212	17.49	<0.0001
	Intercept	−50.84			
	Carbonate C	−100073.18			
	C:N ratio	11.57			
	Immunoreactive total glomalin	−164.01			
MODEL II			0.6209	27.03	<0.0001
	Intercept	−50.62			
	Carbonate C	−50.62			
	C:N ratio	11.53			
MODEL III			0.5597	9.85	<0.0001
	Intercept	58.05			
	Carbonate C	−9537.93			
	% Organic C	140.51			
	% Organic N	−1510.78			
	Easily extractable glomalin	41.83			

[a] All regression models were generated using stepwise independent variable selection procedure based on a partial F-ratio with an F-to-remove value of 3.996 and an F-to-enter of 4.000. Residual vs. fitted plots for each model suggested the dependant variable met assumptions of linearity.

under black grama grass than in plant interspaces. Soil C:N ratios, carbonate C, and easily extractable glomalin were the best predictors of aggregate stability. MTC/ha varied between plants and interspaces at the patch scale, and between plots at the landscape scale. Given the importance of aggregate stability and soil C distribution to C sequestration, this heterogeneity needs to be taken into consideration when developing strategies for measurement of SOC and management to enhance C storage in these semiarid rangeland soils.

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