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Does vegetation structure regulate the spatial structure of soil respiration within a sagebrush steppe ecosystem?

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ABSTRACT

Patchy distribution of sagebrush (*Artemisia tridentata*), also known as 'islands of fertility' strongly modulates the biogeochemical dynamics of the sagebrush-steppe ecosystem. We tested the hypothesis that islands of fertility influence the spatial structure of soil respiration. We employed a spatial sampling design, which consisted of 0.5 m diameter plots placed in a repeating pattern within a grid of 12 m × 12 m. At each sample point, we measured soil respiration rates, aboveground vegetation cover, root biomass to 10 cm depth and distance and dimensions of the nearest shrub in four quadrants. Total aboveground leaf biomass was estimated from allometric relationships. We found that soil respiration was spatially autocorrelated with a range of 2.5–8.82 m in June and July in 2009. While soil temperature modulated the spatial pattern of soil respiration, the influence of islands of fertility was not as strong as expected. Spatial autocorrelation also highlights the importance of proper sampling design of point measurements of soil respiration and provides strong justification for including additional factors such as vegetation cover and aboveground leaf biomass in future mechanistic models of soil respiration.

1. Introduction

Considered to be the "Rosetta Stone of ecology" (Keitt and Urban, 2005), analysis of spatial patterns to gain insight to the underlying mechanism has been one of the key themes of ecological research (Legendre and Fortin, 1989). Spatial patterns exist in nature at all levels: in soils (Schlesinger et al., 1996), plants (Robertson, 1987) and in mountains (Bishop et al., 2003). Analysis of spatial pattern in soil respiration has been primarily motivated by our attempt to identify additional covariate/covariates (beside soil moisture &temperature) for incorporation in process-based models of soil respiration as well as establish a mechanistic theory to scale up point measurement of soil respiration to large landscape level (Xu and Qi, 2001). Many recent ecological studies have stressed the importance of analyzing ecological processes across different spatio-temporal scales (Jarvis, 1995). For example, spatial structure of tree transpiration has been found to be regulated by the temporal drivers of transpiration (Loranty et al., 2008). Such study helps the scientific community to mechanistically scale up spatiotemporal processes.

In case of soil respiration, the environmental drivers that regulate the temporal variation of soil respiration: soil moisture and soil temperature are used to scale up chamber measurements of soil respiration to eddy covariance tower footprint as well as landscape level. A primary reason for the failure to move beyond moisture and temperature can be attributed to the limitation of our ability to observe the complex biogeochemical processes that govern carbon flux beneath the soil (Vargas et al., 2011). Recent reviews have highlighted the lack of understanding of the scientific community vis-a-vis dynamics of carbon cycle and respiratory processes in dryland ecosystems (Scholes et al., 2009). Respiration from the rhizosphere, root and organic matter decomposition have been documented to have different response functions to environmental drivers and are strongly regulated by substrate flow (Pendall et al., 2004). Tree girdling (Hogberg et al., 2001) and clipping and shading experiments (Wan and Luo, 2003) have conclusively shown that beside moisture and temperature, substrates from aboveground plant organs play a critical role in modulating the dynamics of soil respiration.

The landscape in the semiarid sagebrush steppe ecosystem is characterized by patchy distribution of vegetation with

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intermittent bare soil (Ewers and Pendall, 2008). These patchy distribution of shrubs, characteristic of desert ecosystem in Southwest USA are known as islands of fertility (Schlesinger and Pilmanis, 1998). Lateral transport of nutrients from interspaced bare soil to shrubs modulated primarily by roots and soil moisture have been documented to be the primary mechanism that regulate the formation of islands of fertility (Housman et al., 2007). Nutrients like nitrogen (N), phosphorus (P) and microbial biomass are found in greater concentration beneath canopies compared to the interspaced bare soil (Housman et al., 2007). Geostatistical analysis in the semiarid ecosystem found that some of the biotic factors that influence soil respiration (N, soil microbes and net aboveground primary production) interact to create the island of fertility (Schlesinger et al., 1996). Jackson and Caldwell (1993) found soil organic matter to be spatially autocorrelated (range <1 m) around sagebrush vegetation. This evidence leads to the hypothesis that spatial patterns of soil respiration are a function of vegetation structure in semiarid shrublands.

Other biotic factors that influence the spatial pattern of soil respiration in general include vegetation cover (Law et al., 2001), root density (Fang et al., 1998), microbial biomass (Xu and Qi, 2001), soil organic matter (Rayment and Jarvis, 2000) and distance from woody plants or litter (Fang et al., 1998).Abiotic factors that have been documented to control the spatial dynamics of soil respiration include soil moisture, soil temperature, litter moisture content (Keith et al., 1997), precipitation events (Sotta et al., 2004) and topography (Hanson et al., 1993).

Our primary challenge was therefore to test the linkages between the spatial heterogeneity of soil respiration with the conventional temporal drivers of soil respiration (soil moisture, soil temperature) as well as its various biotic drivers. Given the above issues, we addressed the following four questions within a sagebrush ecosystem:

Question 1: Is aboveground vegetation, root biomass and vegetation cover spatially heterogeneous?
Question 2: Does soil moisture and temperature have a spatial structure?
Question 3: Is soil respiration spatially auto correlated?
Question 4: Is the spatial structure of soil respiration regulated by aboveground vegetation, vegetation cover, root biomass as well as soil moisture and soil temperature?

We show through spatial analysis that both abiotic and biotic factors significantly affect the spatial heterogeneity of soil respiration and hence the scalability of soil respiration models developed for sagebrush steppe systems.

2. Methods

2.1. Study site

The study site was a sagebrush shrubland located near Saratoga, Wyoming (N 41.454474, W 106.808413, 2173 m asl). The site possessed near-level topography (<1%) with deep sandy loam soils. The mean annual temperature and precipitation at Saratoga are 6.3 °C and 255 mm respectively. Small precipitation events of size 2 mm or less accounted for 60% of precipitation events over a two-year period. Snow accumulation and melt recharged the soil profile in some years (Kwon et al., 2008). Vegetation cover consisted primarily of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), perennial grasses (e.g., *Festuca idahoensis* and *Poa secunda*, *Koeleria macrantha*) and forbs (e.g., *Stenotus acaulis*, *Eriogonum umbellatum*, *Phlox* spp.).

2.2. Experimental design

We quantified the spatial structure of soil respiration using a 3/7 cyclic sampling scheme as shown in Fig. A1 (Appendix). The 3/7 cyclic sampling design resulted in 144 plots within a grid of 12 m × 12 m with a minimum and maximum plot center separation of 0.5 m and 16.97 m respectively. Soil respiration points were randomly located within each circular plot (Diameter = 0.5 m) and the coordinates of these points were recorded. The advantages of this sampling technique are that it reduces the coefficient of variation for each lag distance among pairs of points and minimizes the number of measurements required in obtaining dependable spatial statistical results (Burrows et al., 2002). For details on the cyclic sampling design, refer to Burrows et al. (2002).

2.3. Data collection

Soil respiration was measured with a portable infrared gas analyzer (IRGA, model EGM-4, PP Systems International, Inc., Amesbury, MA, USA) with a 0.1 m diameter soil respiration chamber (SRC-1, PP Systems International, Inc., Amesbury, MA, USA). Adjacent to the respiration measurement points, soil temperature (HI 9053, Hanna Instruments, Smithfield, RI, USA) and volumetric soil moisture (HH2 Moisture Meter, Delta − T Devices, Cambridge, England) at 0.06 m depth were measured. Soil moisture at 0.06 m depth and soil temperature at 0.1 m depth was also recorded at 30-min interval for the whole period of study at a nearby location (Model CS616, Campbell Scientific, Logan, Utah, USA). Since precipitation data was not available, we used data for Rawlins, WY (Elevation − 2073 m), located 146.45 km away from the study site (www.ncdc.noaa.gov/oa/ncdc.html). Soil samples from 32 of the 144 points were used to determine the percentage clay amount using laser diffraction method. In this paper we have reported the mean of 3 subsamples.

Soil respiration measurements were conducted four times during the summer season in 2009. The first set of measurements was collected in the last week of June, the second set in the first week of July and the third and fourth sets were collected in the last week of July. These four sets of measurements henceforth are referred as R_1, R_2, R_3, and R_4 respectively. Except for R_1, all measurements were conducted within the time frame of 9 am to 12-noon with an error margin of 30 min in order to avoid temporal variation. Due to early morning precipitation, the measurements on R_1 were delayed until afternoon immediately after the precipitation event. Because of the labor intensiveness of the measurement protocol, soil respiration measurements were made at an average of 70 plots on each of the four measurement days. Nonetheless, the number of point pairs in each semivariogram class was much more than the recommended 30 point pairs (Rossi et al., 1992).

At each plot, vegetation cover was estimated using the line intercept method. The non-destructive Point Center Quarter (PCQ) method of vegetation analysis (Fig. A2) was employed to calculate the distance of each shrub from the measurement point (Cottam and Curtis, 1956). At each measurement point a compass was used to define the four quadrants. At each of the four quadrants, the nearest shrub to the measurement point was identified and the distance of the canopy to the measurement points as well as bearing were recorded. The distance and bearing were used to calculate the coordinates of the shrubs located within the four quadrants. The dimensions of the sagebrush in each of the four quadrants that we measured included the height and the two widest stems and canopy widths which were perpendicular to each other. We used the elliptical crown volume to calculate canopy volume (Cleary et al., 2008; Vora, 1988). Natural log of elliptical crown volume (C_V) was used to calculate total aboveground leaf

biomass (kg plant^{-1}) (Cleary et al., 2008; Vora, 1988). The allometric relationships we used for total and leaf biomass were the same across three sagebrush sites in Wyoming, and thus we assume they are applicable to the present study area. Total aboveground leaf biomass was used as surrogate of labile plant photosynthate (Ekblad and Hogberg, 2001).

Root biomass estimates were made at each of the 144 plots at the end of the four measurement periods. Soil samples were collected using polyvinyl chloride (PVC) cores (diameter = 0.05 m) to 0.1 m depth. Each sample was sealed in a separate bag and stored in a cooler until they were returned to the lab where they were immediately weighed to get the total field moist weight. The samples were then oven-dried at 70 °C for 48 h and reweighed to estimate the water content. The soil samples were subsequently sieved using a 0.002 m sieve. Coarse root fragments collected at the top of the sieve were removed and weighed separately. Large roots from the <0.002 m fraction were picked out and added to the roots collected at the top of the sieve. The roots were then weighed to get an estimate of the root biomass at the 144 respiration measurement points. Root mass was converted to per unit area by dividing it by the circular area of the PVC cores.

2.4. Influence of plant vegetation

In order to determine whether carbon flux at each measurement point within the 12 m × 12 m grid was influenced by sagebrush in close proximity, a circular plot of radius 0.5 m was placed at the center of each measurement point. All shrubs, whose majority of the crown cover (≥50%) were within the 0.5 m circular plot were included. Leaf biomass (kg plant^{-1}) was converted to an aerial basis by dividing it by the circular area of the plot. The process was repeated by expanding the radius of the circular plot to 0.75 m, 1 m, 1.5 m and 2 m. A 0.5 m radius was used as the base value since the minimum average distance between two measurement plot centers was 0.5 m. Leaf biomass of the shrubs within 0.5 m, 0.75 m and 1 m from the measurement point has been referred as $LB_{0.5}$, $LB_{0.75}$ and LB_1 respectively.

2.5. Statistical analysis

We used geostatistical techniques to analyze the spatial structure of soil respiration, soil moisture, soil temperature, vegetation cover and aboveground and belowground biomass. Semivariance (γ) provides a measure of the spatial correlation between two points. Semivariance can be calculated as follows:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} (z_i - z_{i+h})^2 \quad (1)$$

where N is the number of observations at lag distance h and z_i and z_{i+h} are the scalar values at point pairs separated by a distance h. While we employed both Restricted Maximum Likelihood (REML) and Ordinary Least Squares (OLS) methods to fit curves to the empirical semivariograms, we have only reported results from the REML curve fitting procedure. We used the REML curve fitting procedure as it has been documented to be least sensitive to outliers and thereby provide less biased parameter estimates (Schabenberger and Gotway, 2004). We used parameters from OLS curve fitting procedure as initial parameter estimates for the REML curve fitting procedure (Angstmann et al., 2012). Likfit function in the spatial package of the R statistical software was used for our curve fitting procedure (R Development Core Team, Vienna, Austria, Version 2.10.1). The covariance models fitted to the empirical semivariogram included the exponential model (Equation (2)), linear model (Equation (3)) and the nugget model (Equation (4)):

$$\gamma(h) = C_0 + C\left(1 - e^{-\frac{3h}{a}}\right) \quad (2)$$

$$\gamma(h) = C_0 + C^*h \quad (3)$$

$$\gamma(h) = C_0 \quad (4)$$

where the parameters include nugget (C_0) which accounts for unexplained trends or measurement errors at lag distance h, sill (C) which accounts for total variability (i.e. the semivariance at which the curve saturates) and range (a) incorporates the distance in meters at which autocorrelation ceases to exist. Spatial dependence has been classified as strong ($C_0/C \leq 0.25$), moderate ($0.25 < C_0/C \leq 0.75$) and weak ($C_0/C > 0.75$) (Lopez-Granados et al., 2004). The exponential model provides a specific range of autocorrelation from the semivariogram while a nugget model would imply absence of spatial autocorrelation. A linear model fit indicates no effective range and spatial autocorrelation occurs across the entire spatial domain measured. The models were also evaluated for anisotropic behavior which occurs when the semivariogram displays different spatial autocorrelation in different directions. The REML curve fitting technique quantified anisotropy by providing the angle (ψ_A) and magnitude (ψ_R) of anisotropy. The ratio of isotropic versus anisotropic model likelihood values was then used to decide between isotropic (not direction-dependent) versus anisotropic models (Schabenberger and Gotway, 2004). The 95% confidence intervals (CI_{95}) of the empirical semivariograms were generated as shown below (Cressie, 1993):

$$CI_{95} = 1.96\frac{\sqrt{2\gamma}}{\sqrt{N}} \quad (5)$$

where γ and N are the average semivariance and number of point pairs at each lag distance.

2.6. Analyzing drivers of soil respiration

Spatial drivers of soil respiration were determined by 3 different analyses: 1) Cross-variogram analysis in order to determine whether spatial autocorrelation existed between soil respiration and the measured covariates, 2) REML curve fitting technique where covariates were added until the range of soil respiration approached zero (i.e. no spatial autocorrelation) (Angstmann et al., 2012) and 3) Generalized least squares (GLS) regression modeling in order to analyze the relationship between soil respiration and the covariates.

Before the analysis, we calculated the correlation coefficient between different variables. Variables which displayed high degree of collinearity (correlation coefficients >0.8) were excluded from our analysis. As a result the variables that we included in our analysis were soil moisture (θ), soil temperature (T), vegetation cover, root biomass (measured) and plant leaf biomass ($LB_{0.5}$ and $LB_{0.75}$). Biomass of shrubs located1 m, 1.5 m and 2 m away from the measurement point were removed from our analysis. After the significant variables were identified, they were combined to identify the optimal model structure. AIC (Akaike Information Criterion) values were used to identify the optimal model. A model validation process was then applied to the final model which included examination of the model residuals for spatial dependence. Wherever the model residual exhibited spatial autocorrelation, a spatial autocorrelation structure was incorporated into the model. The spatial model was then compared to the aspatial model using AICto

determine if it improved the model structure and whether the significance of the regression coefficients changed. We have reported ΔAIC in this paper, defined as the difference between the spatial and non-spatial model to emphasize the improvement of the spatial model over the aspatial model. The objective of the spatial model was to provide a more robust identification of the spatial drivers of soil respiration.

When soil respiration was not spatially autocorrelated, we conducted multiple regression analysis to analyze the influence of the biotic and abiotic drivers of soil respiration on carbon flux. Given 32 random soil samples to determine soil texture, we conducted univariate statistics to determine the relationship between soil texture and soil respiration. Cross-variogram analysis and OLS curve fitting procedure of the empirical semivariograms were conducted in GS+ (version 7, Gamma Design Software, Plainwell, MI, USA). REML curve fitting procedure as well as GLS modeling were done in R (R Development Core Team, Vienna, Austria, Version 2.10.1).

3. Results

3.1. Climate and vegetation structure

Surface soil moisture (0.06 m depth) across the site from May (DOY 122) until end of July (DOY 213) fluctuated between a high value of 0.12 m^3 $m^{-3}$and low value of 0.09 m^3 m^{-3} (Fig. 1). The corresponding soil temperature values at 0.1 m depth varied between 24.9 °C and 6.15 °C (Fig. 1). Surface soil texture (10 cm depth) across the site was sandy loam, with a water holding capacity of only 14%. Our soil respiration measurements captured both the high (R_1) and low end members of soil moisture (R_4) (Fig. 1).

The average measured root biomass across the grid was 0.106 kg m^{-2} with the maximum and minimum values ranging between 0.603 and 0.004 kg m^{-2} respectively. Vegetation cover ranged between 0 and 100% and averaged 36.82%. The relative vegetation cover of shrubs, forbs and grass averaged 17.6%, 13.8% and 3.7% respectively. REML curve fitting found total aboveground biomass (Fig. 2A) to have a moderate spatial dependence with a range (a) of 2.22 m with the proportion of nugget variance from the sill (C_0/C) being 0.14 (Table 1). No spatial dependency was found for root biomass (Table 1 & Fig. 2B) or vegetation cover (Table 1 & Fig. 2C).

3.2. Spatial pattern of soil respiration

Soil respiration (Fig. 3A & Table 2, $a = 2.51$ m), soil temperature (Fig. 3B & Table 2, $a = 7.71$ m) and soil moisture (Fig. 3C & Table 2, $a = 8.04$ m) displayed spatial structure for R_1. As shown in Table 2, for R_1, the spatial dependency was moderate for soil respiration ($C_0/C = 0.27$), strong for soil temperature ($C_0/C = 0$) and weak for soil moisture ($C_0/C = 0.78$). Covariate addition methodology, cross variogram analysis and GLS regression analysis (Table 3) have found that soil temperature, vegetation cover and leaf biomass of shrubs located within 0.5 m explained the spatial pattern of soil

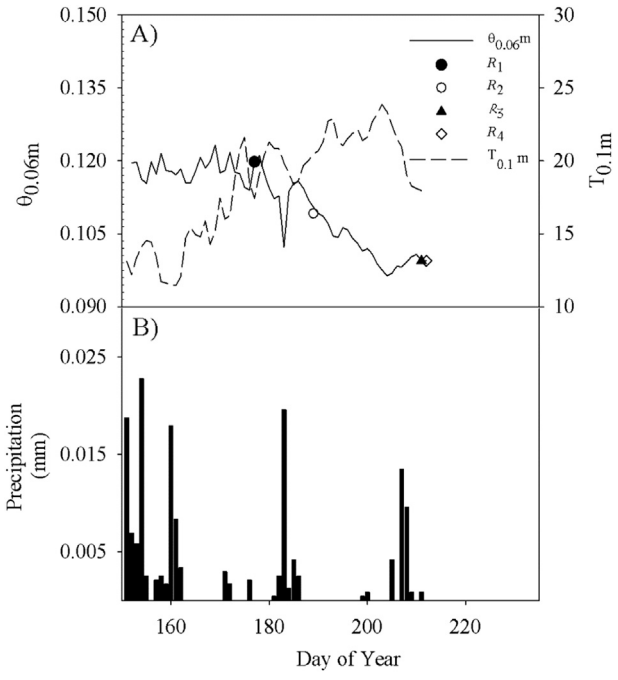


Fig. 1. Time series (DOY 121–212) of the A) average soil moisture at 0.06 m depth ($\theta_{0.06m}$) and average soil temperature at 0.1 m depth ($T_{0.1m}$) and also the days (R_1, R_2, R_3, R_4) when soil respiration measurement were conducted and B) Average precipitation in May, June and July. Soil moisture and soil temperature data were collected near the experimental site and precipitation data was obtained from Rawlins, WY, located 146.45 km away from the site (www.ncdc.noaa.gov/oa/ncdc.html).

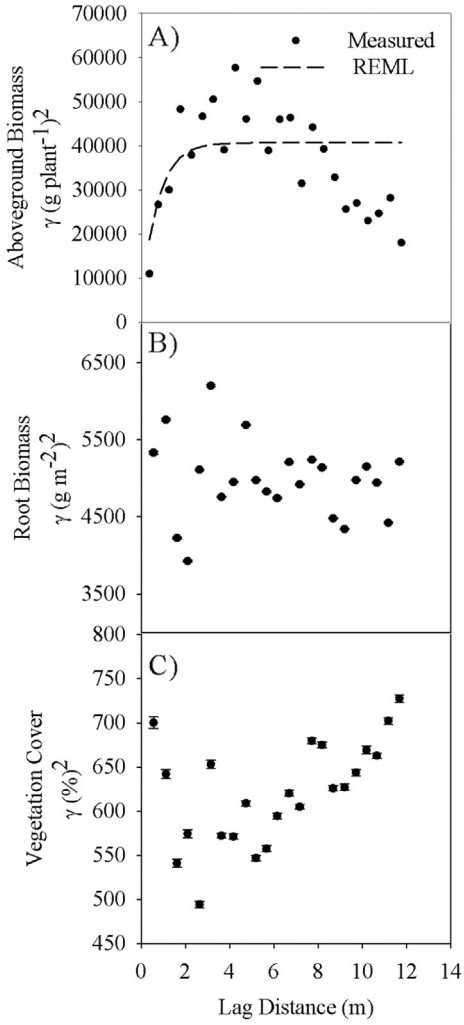


Fig. 2. Semivariogram of A) aboveground biomass (g $plant^{-1}$) of the shrubs, B) root biomass (g m^{-2}) and C) vegetation cover (%). Each point in the empirical semivariogram has at least 30 sample points and the error bars represent 95% CI. Parameters of the exponential model fit (Equation (2)) based on REML curve fit procedure has been reported in Table 1.

Table 1
Summary of the geostatistical parameters of aboveground plant biomass of shrubs, root biomass of shrubs and vegetation cover (Based on REML curve fitting procedure). The r^2 are reported fit of the exponential model (Exp.) fit and significance of the regressions (P) is * for $P < 0.05$. For explanation of the parameters, see Equation (2). A value of NA indicates that the value of the parameter was not relevant.

Parameter	Equation	Fit	C_0	$C + C_0$	a	C_0/C	r^2	p-Value
Aboveground Plant biomass (g plant^{-1})	Exp.	REML	4849	40702	2.22	0.14	0.23	*
Root biomass (g m^{-2})	NA	REML	NA	NA	NA	NA	NA	NA
Vegetation cover (%)	NA	REML	NA	NA	NA	NA	NA	NA

respiration. While soil temperature (T_s) (Coefficient = −1.348, Table 3) and vegetation cover (Coefficient = −2.177, Table 3) negatively influenced soil respiration, $LB_{0.5}$ was a weak positive driver of respiration (Coefficient = 0.021, Table 3). Only soil temperature and $LB_{0.5}$were statistically significant. Range decreased from 2.51 m to 0.82 m when the three covariates were incorporated.

For R_2, we fit a linear covariance model for soil respiration (Table 2, $r^2 = 0.58$) and soil temperature (Table 2, $r^2 = 0.71$) while soil moisture had no spatial trend (Table 2, a = NA). Stepwise regression analysis found soil temperature (Table 3, Coefficient = 0.152), measured root biomass (Table 3, Coefficient = −0.007) and biomass of shrubs (Table 3, Coefficient = 0.002) located within 0.5 m best explained the model structure. Soil temperature and root biomass were statistically significant.

For R_3, only soil respiration displayed spatial pattern (Fig. 3G & Table 2, a = 3.55 m) with a strong spatial structure (Table 2, $C_0/C = 0$). Spatial pattern of soil temperature (Table 2, $r^2 = 0.61$) and soil moisture (Table 2, $r^2 = 0.38$) were however best explained by a linear relationship. A combination of soil temperature and vegetation cover in R_3were negatively correlated with respiration even though GLS regression analysis (Table 3) found none of the parameters to be statistically significant. Range was reduced from 3.55 m to 2.13 m when vegetation cover was added as a covariate.

For R_4, we found both soil respiration (Fig. 3J & Table 2, a = 8.82 m) and soil temperature (Fig. 3K & Table 2, a = 2.31 m) to be spatially heterogeneous. The spatial structure was stronger for the latter (Table 2, $C_0/C = 0.11$) compared to the former (Table 2, C_0/C = 0.58). Soil moisture however displayed no spatial trend (Table 2, a = NA). Soil temperature and biomass of shrubs located within 0.5 m of the plot influenced the spatial pattern of soil respiration (Table 3). Soil temperature, biomass of shrubs within 0.5 m and vegetation cover reduced the range from 8.82 to 5.3 m. In case of R_1, R_3 and R_4, the addition of spatial autocorrelation structure improved the model structure as evident from the positive ΔAIC values (Table 3).

As shown in Fig. 1, we found spatial patterns of soil respiration to be strong at high soil moisture (R_1) and low soil moisture (R_3&R_4) condition but non-existent when soil moisture was intermediate (R_2). The R_1 measurement was conducted immediately after a precipitation event while R_3 and R_4 measurements were conducted one and two days after the pulse event (Fig. 1). R_2 on the other hand was conducted five days after a precipitation event (Fig. 1). For R_1, soil moisture measurements conducted at 0.06 m depth before and immediately after the precipitation event within the 12 m × 12 m grid averaged 5.6 m^3 m^{-3} and 14.2 m^3 m^{-3}respectively. No

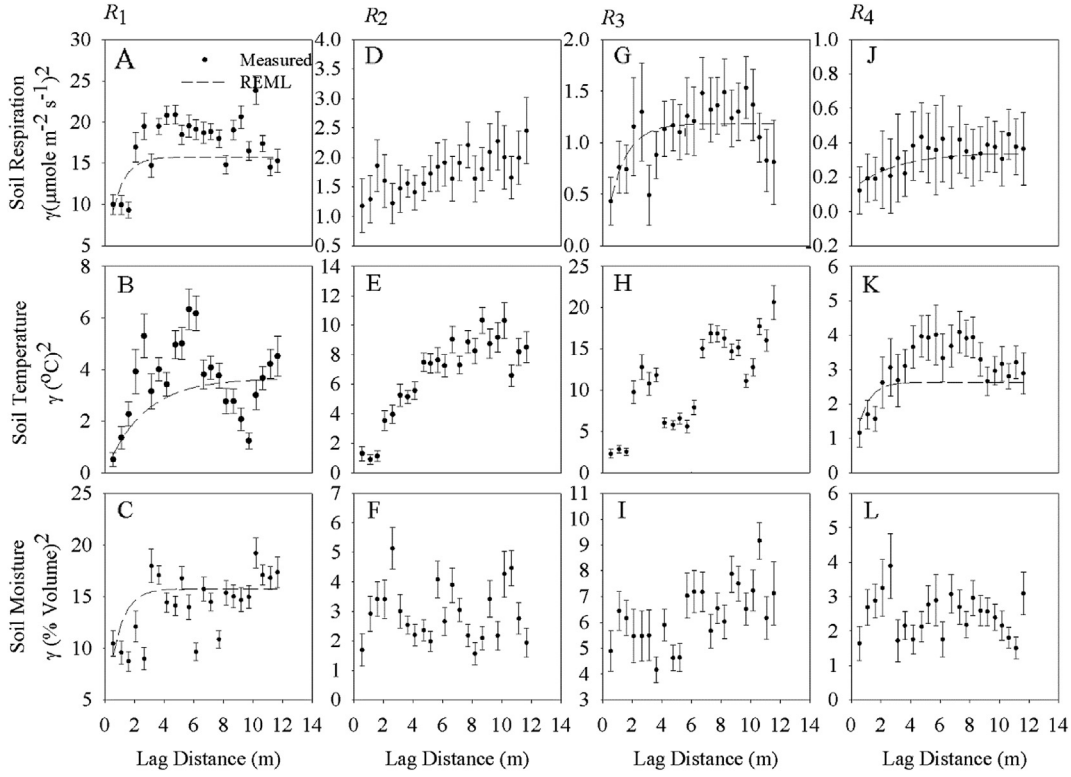


Fig. 3. Semivariogram of Soil Respiration, Soil Temperature and Soil Moisture for the four days (R_1, R_2, R_3, R_4) when the respiration measurements were conducted. Measurements were conducted within 9 am–12 noon with an error margin of 30 min in order to avoid temporal variation. Each point in the empirical semivariogram has at least 30 sample points and the error bars represent 95% CI. Parameters of the exponential model fit (Equation (2)) based on REML curve fit procedure has been reported in Table 2.

Table 2
Summary of the geostatistical parameters of the empirical semivariogram of soil respiration, soil temperature and soil moisture based on REML fitting procedure. The geostatistical parameters were generated based on the four days (R_1, R_2, R_3, R_4) when soil respiration measurement were conducted. The r^2 are reported fit of the exponential (Exp.) and linear (Lin.) model fit and significance of the regressions (P) is * for $P < 0.05$. A value of NA indicates that the parameter was not relevant.

Parameter	Eq.	Fit	C_0	$C + C_0$	a	C_0/C	r^2
R_1							
Soil Respiration	Exp.	REML*	3.34	15.77	2.51	0.27	0.49
Soil Temperature	Exp.	REML*	0	3.652	7.71	0	0.17
Soil Moisture	Exp.	REML*	7.17	16.58	8.04	0.78	0.26
R_2							
Soil Respiration	Lin.	REML*	1.43	2.76	NA	NA	0.58
Soil Temperature	Lin.	REML*	0.02	4.93	NA	NA	0.71
Soil Moisture	NA	REML	NA	NA	NA	NA	NA
R_3							
Soil Respiration	Exp.	REML*	0	1.184	3.55	0	0.41
Soil Temperature	Lin.	REML*	2.757	37.07	NA	NA	0.61
Soil Moisture	Lin.	REML*	5.6	10.447	NA	NA	0.38
R_4							
Soil Respiration	Exp.	REML*	0.125	0.341	8.82	0.58	0.545
Soil Temperature	Exp.	REML*	0.26	2.626	2.31	0.11	0.58
Soil Moisture	Exp.	REML	2.417	0	0	NA	NA

significant relationship between soil respiration and clay content was observed (data not shown).

4. Discussion

4.1. Aboveground vegetation exhibits spatial structure

Our study demonstrates the presence of spatial patterns in sagebrush canopies as evident from Table 1 and Fig. 2A and contributes to the growing body of literature on 'vegetation pattern' (D'Odorico et al., 2007). Models of vegetation dynamics have documented the formation of patterns to facilitation and competition between plants with the former leading to water storage and the latter to explain water consumption by plants (Barbier et al., 2006). Spatial structure of the landscape in semiarid regions has exacerbated the problem of accurately predicting changes in the carbon pool (Christensen, 1996). The ecological significance of the spatial distribution of aboveground biomass (and other resources) lies in its capacity to influence the net ecosystem productivity as well as its role in influencing the pattern of biological activity across the biome (Shmueli et al., 2007).

4.2. Spatial structure in the soil environment

Both soil moisture and soil temperature have been documented to be important primary drivers of soil microbial activities which contribute to the soil respiration flux. The spatial pattern demonstrated by soil temperature (R_1 and R_4) and soil moisture (R_1) can potentially be attributed to the patch dynamics of semiarid ecosystems which allows greater concentration of resources beneath canopy compared to interspaced bare soil modulated primarily by lateral root movement and movement of soil (Housman et al., 2007). The lack of spatial autocorrelation in the measured root biomass (Fig. 2B) therefore was contrary to expectation considering that aboveground biomass was auto correlated, and that soil respiration had a spatial structure. More importantly, it highlights the methodological challenge of biomass root estimation in a patchy landscape. We believe a different approach to root biomass estimation that would have incorporated estimation of coarse root biomass beneath the shrubs could have yielded a different outcome. A root biomass study found sagebrush roots to be only concentrated near the soil surface but also at depths of 8–23 cm with their taproots extending well below the soil surface (Rau et al., 2009). The role of roots (at depths greater than 10 cm) as well as that of taproots in modulating the spatial structure of soil respiration should be investigated as part of future research. Another potential explanation can be attributed to water limitation as dry soil maximizes root occupation, thereby inhibiting spatial autocorrelation. Considering the fact that roots are an important contributor to organic matter in soil vis-a-vis exudates and dead roots (Fonte et al., 2012), this result is in contrast with other studies that have found belowground carbon distribution in desert ecosystems to be closely linked to the plant distribution (Mouratov et al., 2001). Separate analysis of the spatial pattern of shrub, grass and forb cover displayed random pattern (Refer Appendix, Fig. A3). This could be potentially attributed to their low overall cover within the study grid. The lack of spatial trend in the overall vegetation cover (Fig. 2C) was consistent with a similar study conducted in a sparsely vegetated sagebrush ecosystem at a different site that had experienced succession following burning about 20 years prior (Ewers and Pendall, 2008). The timing of the last disturbance at the present study site was unknown. We speculate that spatial autocorrelation in vegetation can be observed only above a certain threshold cover value, approximately 40% in sagebrush steppe (Ewers and Pendall, 2008).

4.3. Spatial autocorrelation of soil respiration and its relation to biotic and abiotic factors

We found that the spatial autocorrelation of soil respiration varied within the growing season and that the drivers of the spatial patterns changed over the four measurement periods. Specifically, our results suggest that spatial pattern in soil respiration was critically modulated by precipitation events.

High soil respiration immediately after the precipitation event in case of R_1 can be attributed to a host of factors including physical displacement of CO_2 molecules from the entrapped soil pores, increased availability of soil nutrients, increased physiological activity of the microbes (Schwinning and Sala, 2004) or chemical reactions (Glinski and Stepniewski, 1985). Which of these factors dominated the release of CO_2 remains unclear. The negative relationship between temperature soil respiration (Table 3, T_s coefficient $= -1.24$) suggests that soil temperature exceeded the optimum value for soil respiration on this day. Alternatively, the

Table 3
Coefficients of the optimum spatial model of soil respiration for the four (R_1, R_2, R_3, R_4) days when measurement were conducted. GLS regression analysis was conducted for R_1, R_3 & R_4 while linear regression analysis was conducted for R_2. Significance of the GLS regression analysis has been reported as the difference in the Akaike Information Criterion between the spatial model and the aspatial model (ΔAIC). Significance of the regression analysis has been reported by p-value and r^2. Coefficients include both biotic (Vegetation Cover, Root Biomass, $LB_{0.5}$, $LB_{0.75}$) and abiotic (Soil Temperature & Soil Moisture) drivers of soil respiration. $LB_{0.5}$ and $LB_{0.75}$ are plant leaf biomass of shrubs located 0.5 and 0.75 m away from the soil respiration measurement point. Significance of the regressions (P) are *, **, or *** for $P < 0.05$, 0.01, and 0.001, respectively. A value of NA indicates that the parameter was not relevant.

Time	Soil temperature	Soil moisture	Vegetation cover	Root biomass	$LB_{0.5}$	$LB_{0.75}$	ΔAIC	r^2	p-Value
R_1	−1.348*	NA	−2.177	NA	0.021*	NA	17.09		
R_2	0.152**	NA	NA	−0.007***	0.002	NA	NA	0.27	<0.05
R_3	−0.008	NA	−0.43	NA	NA	NA	20.47		
R_4	0.02	NA	NA	NA	−0.003	NA	16.0		

high nugget value (Table 2, $C_0 = 3.34$) at this short spatial scale could also be related to atmospheric mixing. The soil respiration measurement was conducted immediately after the pulse input in June and degassing has been known to occur for a couple of hours after precipitation (Luo and Zhou, 2006).

Apart from soil temperature, root biomass and aboveground leaf biomass ($LB_{0.5}$) were found to be drivers of soil respiration for R_2. Aboveground biomass can be considered as an indicator of photosynthesis. This result is therefore consistent with isotope analysis by previous researchers who have shown a strong link between photosynthesis and soil respiration that originates from roots (Ekblad and Hogberg, 2001). The role of root exudates from taproots as a potential driver of the spatial structure of soil respiration cannot be discarded. The role of $LB_{0.5}$ as a driver of soil respiration was also consistent with the overall idea that vegetation play a crucial role in influencing soil respiration (Raich and Tufekcioglu, 2000). Vegetation influences soil respiration in various ways which would include alteration of the structure of the soil and its corresponding microclimate which in turn would change soil temperature and moisture as well as the flow rates of substrate through and out of roots (Raich and Tufekcioglu, 2000). A significant fraction of the carbon assimilated by plants is allocated belowground which is then released to the atmosphere after varying lag times (Leake et al., 2006). Our study supports a growing body of evidence where the link between photosynthesis and respiration has been documented including grasslands (Johnson et al., 2002), deciduous (Liu et al., 2006) and evergreen (Irvine et al., 2005) temperate forest ecosystems. The negative coefficient of root biomass (Table 3, −0.007) was contrary to expectation since root respiration is typically a major source of soil respiration.

Soil respiration measurements in the last week of July (R_3 and R_4) were conducted when overall soil moisture conditions were lower compared to earlier measurements. We believe the strong spatial autocorrelation in R_3 and R_4 are the effects of increased spatial resource partitioning under shrub canopies during dry conditions (Schlesinger and Pilmanis, 1998). The biogeochemical processes were probably stronger in R_4 compared to R_3 as evident from the large value of the range in R_4 ($a = 8.82$) compared to R_3 ($a = 3.55$).

The presence of linear relationship (Table 2) for soil respiration (Fig. 3D), soil temperature (Fig. 3E and H) and soil moisture (Fig. 3I) suggests that the spatial pattern for the abovementioned variables were evident across all range and our study plot was not sufficient to capture the range (Anderson et al., 2004; Ewers and Pendall, 2008). Similar linear trend have been observed in the basal cover for graminoids in the grasslands (Anderson et al., 2004; Rahman et al., 2003). Further empirical studies are required to further elucidate the presence of linear patterns within our data sets.

Low biological activity during some periods may have contributed to the lack of statistical significance of vegetation cover (R_1&R_3) or $LB_{0.5}$ (R_1&R_4). Root activity is dependent on sufficient prior precipitation, and microbial activity also requires adequate moisture. A lack of significance of soil temperature could be related to reduced microbial activity in hot dry soils.

Our geospatial models may not have included all the parameters potentially influencing spatial structure. The exponential covariance structure was included in the soil respiration model to improve the model fit and none of the combination of covariates reduced the range of soil respiration to zero in the REML curve fitting technique. This suggests there were additional variables influencing the spatial pattern (McIntire and Fajardo, 2009). We speculate that additional factors which control the strength of resource islands like biological soil crusts, nutrients, growth form of plant species, root distribution (especially below 10 cm), animal activity and erosion caused by wind could have influenced the spatial pattern. Biological soil crusts, an important characteristic of desert ecosystems have the ability to not only increase the fertility of soil but also their capacity to store moisture on account of their dust trapping capacity which leads to increase in nutrients like nitrogen, phosphorus and potassium (Belnap, 2003). Biological soil crusts also act as carbon sink in those landscapes in semiarid ecosystem where the vegetation cover is not dense (Belnap et al., 2001; Beymer and Klopatek, 1991). The patchy distribution of vegetation in the dryland ecosystem in general and sagebrush ecosystem in particular creates different microclimatic condition and allows for greater distribution of mineral nutrients like nitrogen, phosphorus beneath canopies compared to interspaced bare soil (Ewing et al., 2007). These mineral nutrients influence the soil microbial community which in turn can modulate the soil respiration process (Ewing et al., 2007). Future research work should focus on the effects of biological soil crusts and spatial distribution of soil nutrients like nitrogen and phosphorus in modulating the spatial pattern of soil respiration.

4.4. Implications of the spatial pattern of soil respiration

The fact that the conventional temporal driver of soil respiration (soil temperature) was also the spatial driver of soil respiration should simplify our attempt to develop a mechanistic model of upscaling soil respiration to large landscape level. One caveat to our spatial pattern study is that the soil respiration measurements were conducted from the last week of June. The sagebrush ecosystem is characterized by high percentage of forb and grass cover during the early spring season on account of snowmelt (Ewers and Pendall, 2008). This could potentially underestimate the influence of vegetation cover vis-à-vis spatial pattern of soil respiration in our study.

We suggest incorporation of the spatial range of soil respiration during the sampling design of point measurements of soil respiration which is not only important from the perspective of the analysis of the drivers of soil respiration but also from the point of view of upscaling respiration to large landscape level. The current approach of upscaling, whereby point measurements of soil respiration are multiplied by representative fractions of the functional components of the ecosystem respiration has been found to over-estimate respiration at ecosystem level in mixed temperate forest (Goulden et al., 1996) and boreal coniferous forests (Lavigne et al., 1997). One possible approach suggested by researchers to overcome the disparities between eddy-covariance and point measurements includes incorporation of sufficient point measurements of soil respiration to ensure not only the temporal variation of soil respiration but also the spatial heterogeneity of the landscape was well documented (Rayment and Jarvis, 2000). Aggregating spatial heterogeneity over large spatial scale can be achieved by use of either a lumped model, deterministically distributed model, statistically distributed model or by spatial integration (Harvey, 2000). Moreover, intensive temporal measurements can be time consuming and prohibitive, especially where fetch can extend up to hundreds of meters. Establishment of a study design that would correlate point measurements with metrics obtained at large spatial scale (Example − NDVI.) can help to extrapolate carbon flux across large spatial scales (Lee et al., 2011).

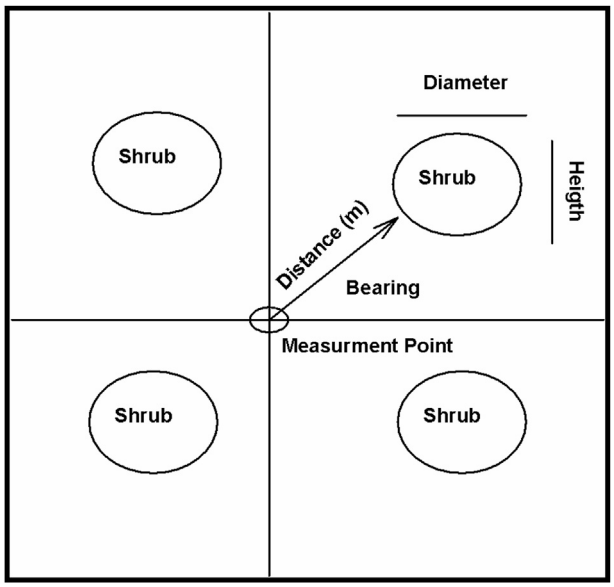
5. Conclusions

Spatial pattern in soil respiration was found to change during the four measurement periods. The pattern was modulated primarily by soil temperature. The role of aboveground biomass in influencing the spatial pattern of soil respiration should be further investigated in order to determine if feedback processes at short term scales can be used to develop process based models of soil respiration. This would pave the way for the development of more

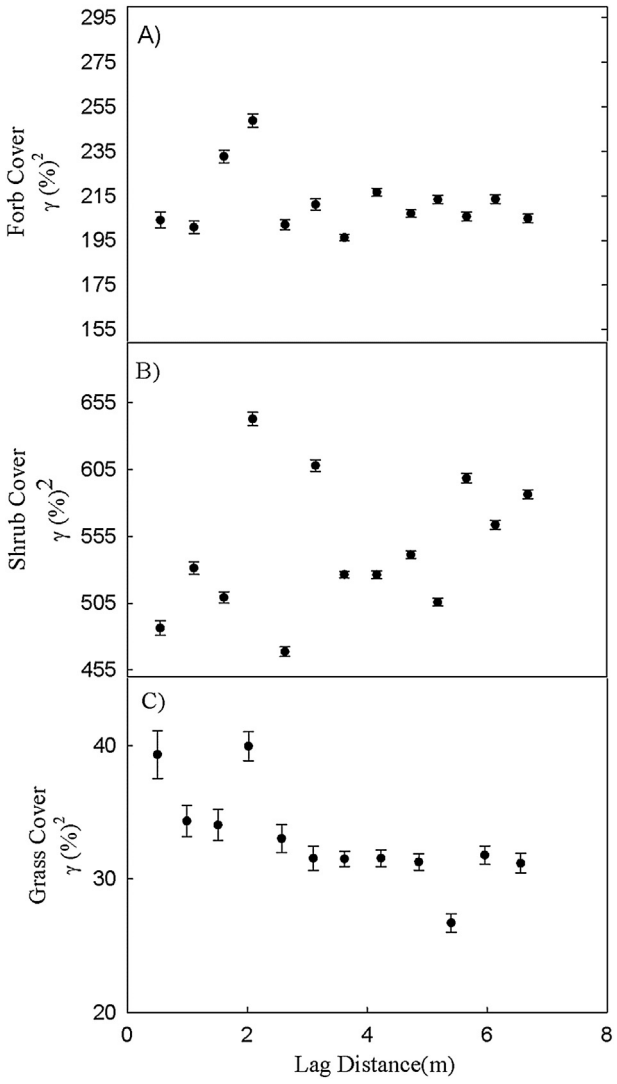
mechanistic soil respiration models, which could then be used to compare and explain respiration fluxes across different ecosystems as well as reduce uncertainty in the estimation of soil respiration at the landscape and ecosystem level.

A1	A2	A3	B1	B2	B3	C1	C2	C3	D1	D2	D3
A4	A5	A6	B4	B5	B6	C4	C5	C6	D4	D5	D6
A7	A8	A9	B7	B8	B9	C7	C8	C9	D7	D8	D9
E1	E2	E3	F1	F2	F3	G1	G3	G3	H1	H2	H3
E4	E5	E6	F4	F5	F6	G4	G5	G6	H4	H5	H6
E7	E8	E9	F7	F8	F9	G7	G8	G9	H7	H8	H9
I1	I2	I3	J1	J2	J3	K1	K2	K3	L1	L2	L3
I4	I5	I6	J4	J5	J6	K4	K5	K6	L4	L5	L6
I7	I8	I9	J7	J8	J9	K7	K8	K9	L7	L8	L9
M1	M2	M3	N1	N2	N3	O1	O2	O3	P1	P2	P3
M4	M5	M6	N4	N5	N6	O4	O5	O6	P4	P5	P6
M7	M8	M9	N7	N8	N9	O7	O8	O9	P7	P8	P9

Appendix Fig. A1. Depiction of the 3/7 Cyclic sampling strategy whereby 3 plots out of every 7 plots was used to analyze the spatial structure of soil respiration. The sampling scheme was repeated within a grid framework of 12 m by 12 m resulting in 144 sample points.



Appendix Fig. A2. Depiction of the Point Center Quadrant (PCQ) method employed to find the distance and bearing of the soil respiration measurement point to the nearest sagebrush at each of the four quadrants. This method was repeated for each of the 144 respiration measurement point within the 12 m × 12 m grid.



Appendix Fig. A3. Empirical semivariogram of A) Forb Cover, B) Shrub Cover and C) Grass Cover. The semivariogram were plotted based on the 144 measurement points within the 12 m × 12 m grid. All three covariates were randomly distributed. Each point in the empirical semivariogram has at least 30 sample points and the error bars represent 95% CI calculated from Equation (5).

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