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Hot spots, hot moments, and spatio-temporal controls on soil CO_2 efflux in a water-limited ecosystem

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ABSTRACT

Soil CO_2 efflux is the primary source of CO_2 emissions from terrestrial ecosystems to the atmosphere. The rates of this flux vary in time and space producing hot moments (sudden temporal high fluxes) and hot spots (spatially defined high fluxes), but these high reaction rates are rarely studied in conjunction with each other. We studied temporal and spatial variation of soil CO_2 efflux in a water-limited Mediterranean ecosystem in Baja California, Mexico. Soil CO_2 efflux increased 522% during a hot moment after rewetting of soils following dry summer months. Monthly precipitation was the primary driver of the seasonal trend of soil CO_2 efflux (including the hot moment) and through changes in soil volumetric water content (VWC) it influenced the relationship between CO_2 efflux and soil temperature. Geostatistical analyses showed that the spatial dependence of soil CO_2 efflux changed between two contrasting seasons (dry and wet). During the dry season high soil VWC was associated with high soil CO_2 efflux, and during the wet season the emergence of a hot spot of soil CO_2 efflux was associated with higher root biomass and leaf area index. These results suggest that sampling designs should accommodate for changes in spatial dependence of measured variables. The spatio-temporal relationships identified in this study are arguably different from temperate ecosystems where the majority of soil CO_2 efflux research has been done. This study provides evidence of the complexity of the mechanisms controlling the spatio-temporal variability of soil CO_2 efflux in water-limited ecosystems.

1. Introduction

Water-limited environments occupy nearly 40% of terrestrial habitats (Loveland et al., 2000), and changes in timing and magnitude of precipitation pulses will influence the biophysical mechanisms that regulate the carbon cycle in these globally distributed ecosystems (Schimel, 2010). These ecosystems are defined by high variability in seasonal and inter-annual precipitation, high rates of potential evapotranspiration, and precipitation pulses that drive biotic activity until available water is depleted (Noy-Meir, 1973; Reynolds et al., 2004; Collins et al., 2008). It is estimated that 241 Pg C is stored in these ecosystems (Lal, 2005), which represent nearly 16% of total terrestrial organic carbon in the first meter of soil (Post et al., 1982; Jobbagy and Jackson, 2000).

A high-priority objective in carbon cycle science is to understand the spatial and temporal controls of CO_2 dynamics in terrestrial ecosystems. Identifying these controls is important for improving model architecture (i.e., mathematical equations that represent biophysical processes) and parameterization (Luo et al., 2008; Carvalhais et al., 2010). Failing to properly represent these controls could over- or under-estimate CO_2 fluxes in terrestrial ecosystems. For example, a recent meta-analysis has shown that process-based ecosystem models tend to misrepresent ecosystem respiration in water-limited ecosystems (Vargas et al., 2013a). Therefore, more information about the temporal and spatial controls of different components of ecosystem respiration is needed to better represent ecosystem CO_2 dynamics.

The largest component of ecosystem respiration is soil CO_2 efflux (i.e., soil respiration). This flux is the main source of CO_2 emissions from terrestrial ecosystems to the atmosphere with a

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potential flux of 98 Pg C yr^{-1} (Bond-Lamberty and Thomson, 2010). Soil CO_2 efflux varies temporally in water-limited ecosystems and these variations have been linked to changes in timing and intensity of precipitation (Thomey et al., 2011; Vargas et al., 2012), soil temperature (Cable et al., 2010), and plant phenology (Barron-Gafford et al., 2011). Furthermore, precipitation pulses create "hot moments" in these ecosystems when metabolic activity is increased (Jenerette et al., 2008) and higher soil CO_2 efflux rates are observed (Kim et al., 2012). Hot moments are defined as short periods of time that show disproportionately high soil CO_2 efflux relative to longer intervening time periods, and could be important for the annual carbon balance in water-limited ecosystems. The concept of hot moments is important in water-limited ecosystems because they are considered to be areas with low metabolic activity. Nonetheless, the rate of change from baseline soil CO_2 efflux could be >9000% during a hot moment; typically associated with a precipitation pulse following a dry period in water-limited ecosystems (Kim et al., 2012).

Hot spots are spatially defined areas that show disproportionately high soil CO_2 efflux relative to the surrounding area. Several studies have linked spatial variability of soil CO_2 efflux in water-limited ecosystems to changes in soil texture (Cable et al., 2008), soil organic matter fractions (Almagro et al., 2013), vegetation types (Maestre and Cortina, 2003; Vargas et al., 2010), and inter-canopy spaces (Barron-Gafford et al., 2011). To quantify and predict the spatial variability of soil CO_2 efflux many studies have applied geostatistical approaches (e.g., semivariograms, kriging); however, few studies have been conducted in water-limited ecosystems (La Scala et al., 2000; Stoyan et al., 2000; Panosso et al., 2009; Herbst et al., 2011).

The primary objective of this study was to determine the temporal and spatial variation of soil CO_2 efflux in a Mediterranean water-limited ecosystem. Specifically, we explored hot moments (i.e., sudden temporal high fluxes) and hot spots (i.e., spatially defined high fluxes) of soil CO_2 efflux within this ecosystem. We used an array of simple empirical models to represent the temporal variability of soil CO_2 efflux, as well as principal component analysis and geostatistical techniques to identify spatial relationships among variables and to quantify the degree of spatial dependence. Based on previous knowledge of water-limited ecosystem we postulate three hypotheses. First, soil CO_2 efflux will follow a temporal pattern driven primarily by soil water content and secondarily by soil temperature. This statement is based upon the understanding that soil water content modulates the plant and microbial contribution to soil CO_2 efflux and the temperature dependence of this flux in water-limited ecosystems (Almagro et al., 2009; Cable et al., 2010; Carbone et al., 2011; Vargas et al., 2012). Second, the beginning of the rainy season will trigger a hot moment of high soil CO_2 efflux, potentially driven by a priming effect after the dry-hot summer months (Kuzyakov, 2010). Third, soil CO_2 efflux spatial dependence will change between dry and wet seasons as a result in changes in soil moisture, plant activity (associated with root biomass and leaf area index), or soil temperature. Therefore, it is likely that soil CO_2 efflux spatial dependence would be higher during the wet season as a result of higher ecosystem metabolic activity when water is not a limiting factor.

2. Materials and methods

2.1. Study site

The study site, El Mogor, is located at 406 m.a.s.l. in the Valle de Guadalupe, Baja California (32.03017N and 116.604219W), Mexico. The climate at El Mogor is semiarid Mediterranean, with warm-dry summers and cool-wet winters. Chaparral vegetation is characteristic of Mediterranean shrublands and these ecosystems are common across California and Baja California in North America (Hellmers et al., 1955; Minnich and Chou, 1997). The mean annual temperature is 17 °C and mean annual precipitation is 309 mm (average of years 1980–2009, Fig. 1). Rainfall typically occurs during the cool-wet winters (November–April) with mean monthly temperatures of 11–14 °C and monthly precipitation of 18–63 mm. Meanwhile, the warm-dry months (May–October) have mean monthly temperatures of 16–21 °C and monthly precipitation of 1–6 mm (Fig. 1a). Soils at the study site are shallow (approximately 30 cm of depth) and developed from granitic parent material. Soil texture is sandy loam (75% sand, 14% silt, and 11% clay). For a detailed description of soils at the study site see Franco-Vizcaino and Sosa-Ramírez (1997). The study site El Mogor is part of the Mexican eddy covariance network (MexFlux; Vargas et al., 2013b).

Vegetation at El Morog is characterized by a mixture of chaparral and less-sclerophyllous species with a mean height of 1 m. The species with the greatest ground cover at the study site are: *Adenostoma fasiculatum*, *Ornithostaphylos oppositifolia*, *Cneoridium dumosum*, *Salvia apiana*, and *Lotus scoparius*. The site was severely burned in 1988 and has recovered rapidly over the last 24 years; however, wildfires are an expected feature of the natural cycle of chaparral (Franco-Vizcaino and Sosa-Ramirez, 1997; Keeley and Fotheringham, 2001).

We established a 100 × 50 m sampling area within a representative location of the ecosystem in September 2011. Within this

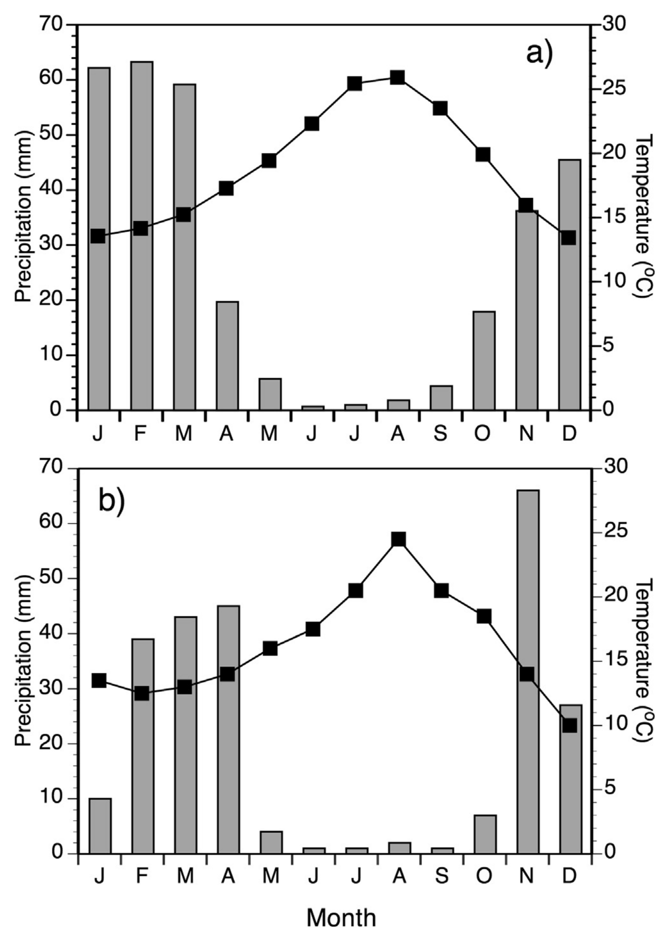

Fig. 1. Mean monthly precipitation (mm) and mean monthly temperature (°C) during the period 1980–2009 (a) and during the study period (September 2011–August 2012; b) at El Mogor, Baja California, Mexico. The *x*-axis label is the first letter of each month.

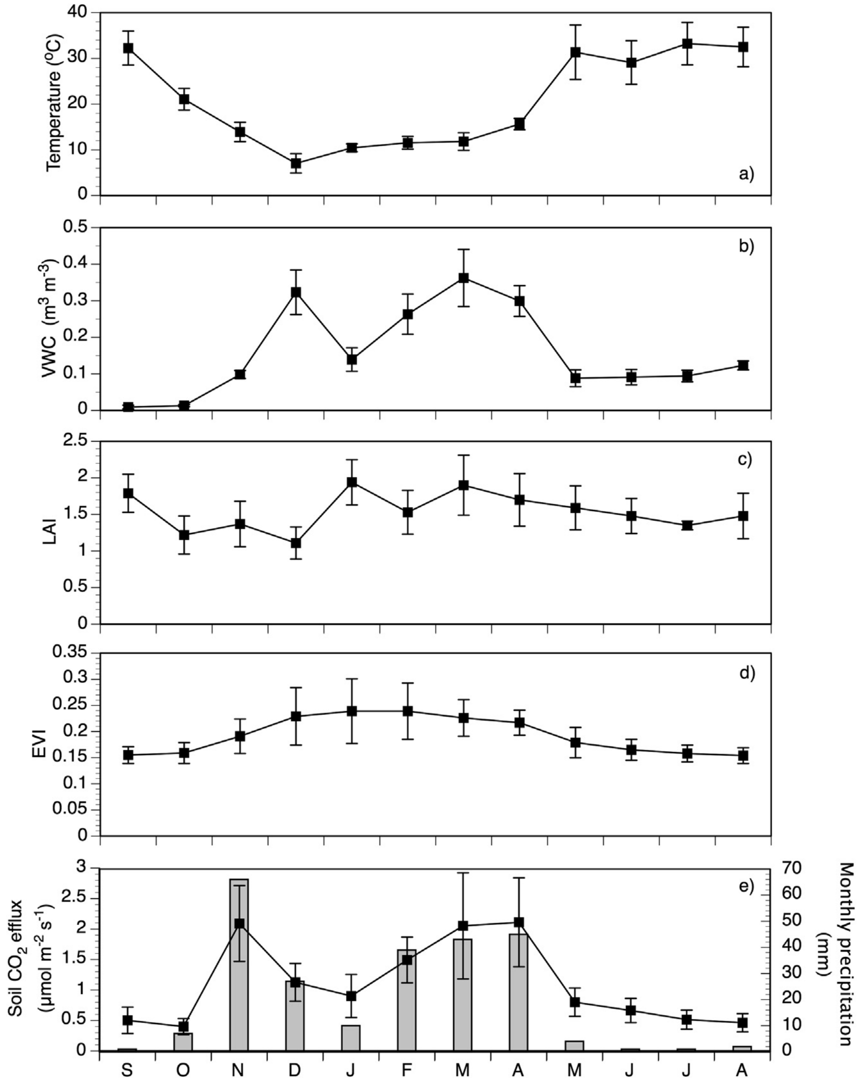

Fig. 2. Temporal variation of soil temperature (at 10 cm depth; a), soil volumetric water content (VWC; 0–15 cm depth; b), leaf area index (LAI; c), enhanced vegetation index (EVI; d), and soil CO_2 efflux with monthly precipitation (e). Each point represents the mean ± 1 standard deviation of 50 measurements within a 0.5 ha plot. The *x*-axis label is the first letter of each month between September 2011 and August 2012.

0.5 ha we marked a grid with 50 survey points with intervals ranging between 5 and 10 m. At each of these points we collected litter, soil samples, fine roots (<5 mm), and we measured soil temperature and moisture, soil CO_2 efflux, and leaf area index (LAI) as described below.

2.2. Belowground biomass and soil analyses

Plant litter and soil samples were collected at the end of the dry season (September 2011) and at the middle of the wet season (February 2012). Samples were taken within a 20 cm radius of the soil CO_2 collars (see Section 2.3) at each one of the 50 survey points. First, plant litter was collected from 30 cm^2 micro-plots. Litter was cleaned by hand to remove small rocks and soil aggregates, and the clean litter samples were oven dried (65 °C for 48 h) to calculate total litter biomass. After removing the litter, soil samples were taken with a soil core (8 cm diameter) to a depth of 10 cm (502.6 cm^3). Soil samples were transported to the laboratory and first analyzed for soil density and pH. A second set of soil samples were air-dried, sieved through a 2-mm mesh, and all fine roots (dead and alive) were hand-picked from the sieved soil and the sieve using forceps. The largest fine roots had a diameter of 5 mm, however, over 90% of them were <2 mm in diameter. Fine roots were washed with deionized water to clean attached soil and then oven dried (65 °C for 48 h) to determine the dry weight. Soil samples were ground to pass through a 250 μm sieve, and analyzed via dry combustion for total carbon and nitrogen using a Thermo Finnigan Flash EA1112 N/C analyzer (Thermo Scientific, USA).

2.3. Soil CO_2 efflux, volumetric water content, and temperature

Soil CO_2 efflux was measured monthly at the 50 sampling points using a LI-8100 (Licor, Lincoln, NE) and a 10 cm survey chamber (model 8100-102; using 10 cm diameter PVC collars inserted into the soil). Changes in soil CO_2 concentrations within the soil chamber were measured for 2 min to calculate soil CO_2 efflux rates at each sampling point. In addition soil volumetric water content (VWC, using Theta Probe type ML2x) and soil temperature were measured at 10 cm depth inside each soil collar. All measurements were done between 9 and 11 am to avoid large changes in temperature during the day, and after at least 3 days of a precipitation event to avoid bias on higher soil moisture rates.

2.4. Vegetation parameters

Leaf area index (LAI) was measured monthly at the 50 sampling points using a LAI-2200 (Licor, Lincoln, NE). LAI measurements were carried out under diffuse sky conditions early in the morning (between 6 and 7 am) using a 90° view cap to avoid the appearance of the operator on the sensor and to block direct light. The operator stood between the sensor and the rising sun at all times following protocols for Mediterranean ecosystems with open canopy (Ryu et al., 2010).

Enhanced vegetation index (EVI) was calculated to complement the temporal patterns of vegetation dynamics (Huete et al., 2002). We used MODIS Land Product Subsets for a 2 × 2 km area around the study site; average EVI was calculated for the four MODIS pixels for 8-day temporal resolution within this area. These data were derived from MODIS products generated from Collection 5 from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC). Details about preparation of subsets including MODIS data reprocessing, methods, and formats are available online (DAAC, 2011). Temporal interpolation was used to replace pixels that had quality control flags indicating poor quality.

2.5. Data analyses

First, we explored the temporal variability of soil CO_2 efflux, VWC, temperature, EVI, and LAI. Data from each for the 50 sampling points was averaged to calculate a mean for the particular sampling date. For EVI, the 8-day values were used to calculate monthly averages between September 2011 and September 2012. Our measurements do not attempt to represent complete monthly means or to be used to calculate an annual flux, but rather to describe general temporal trends between September 2011 and September 2012. Previous reviews have discussed the importance of continuous measurements of soil CO_2 efflux for describing high temporal resolution of rewetting events and interannual patterns for accurate calculation of annual estimates (Vargas et al., 2011; Kim et al., 2012).

Empirical linear models were used to determine the temporal relationship between monthly measurements of soil CO_2 efflux with monthly measurements of soil VWC, soil temperature, and precipitation. Simple empirical linear models assume high dependence of soil CO_2 efflux with temperature in temperate ecosystems (Lloyd and Taylor, 1994), but there is increasing evidence that moisture plays a primary role in water-limited ecosystems (Almagro et al., 2009; Carbone et al., 2011). These linear models were complimented with regression tree analysis to identify how predictor variables influenced the magnitude of soil CO_2 efflux over the course of the year (Breiman et al., 1984). This analysis partitions the data into two clusters, optimizing the use of predictor variables (e.g., LAI, temperature, soil VWC, precipitation) to best classify the sources of variability of CO_2 efflux. The process was repeated on each branch until a significant partition cannot be made of the remaining variability using a minimum node size of 10; no node with fewer than 10 data points was split, following the criterion of other soil CO_2 efflux studies (Vargas et al., 2010).

Second, we explored the spatial variability of soil CO_2 efflux, VWC, temperature, LAI, fine roots and litter biomass, total soil carbon and nitrogen, soil density, air-filled pore space, and soil pH for two contrasting seasons (dry and wet). Spatial variability of the 50 sampling points was described by applying descriptive statistics (e.g., mean, standard deviation, minimum, maximum, skewness, kurtosis), and a student *t*-test was used to identify significant differences ($p < 0.05$) between seasons. The coefficient of variation (CV) was used to quantify spatial variability.

The spatial dependence was analyzed by applying geostatistical techniques (Webster et al., 1990) to soil CO_2 efflux, soil moisture,

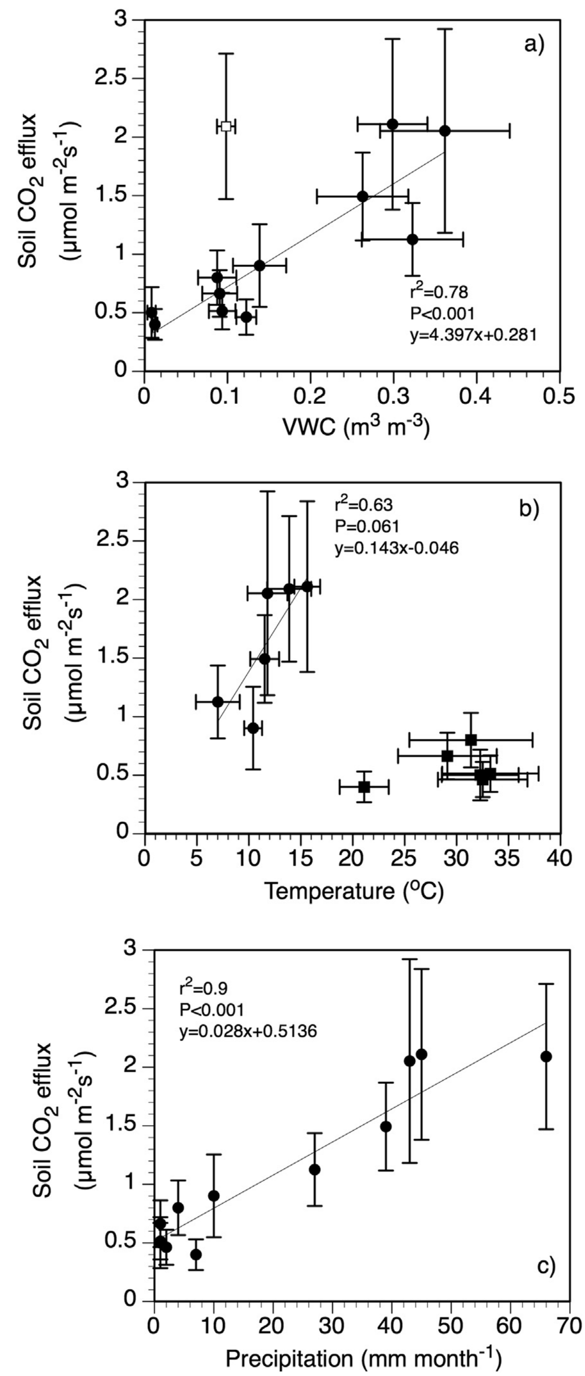

Fig. 3. Relationships of monthly measured soil CO_2 efflux with: soil volumetric water content (VWC; a), soil temperature (b), and total monthly precipitation (c). The white square represents the soil CO_2 efflux measured during the month of November at the beginning of the wet season and represents a hot moment of this flux. Each point represents the mean ± 1 standard deviation of 50 measurements within a 0.5 ha plot. Regression line in panel (a) was fitted without including the measurements during November (i.e., hot moment).

soil temperature, and LAI measurements, by using a semivariogram according to Eq. (1):

$$\widehat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(x_i) - Z(x_i + h)]^2 \quad (1)$$

where $\widehat{\gamma}(h)$ is the semivariance at separation distance h; N is the number of pairs separated by h distance; $Z(x_i)$ is the value of

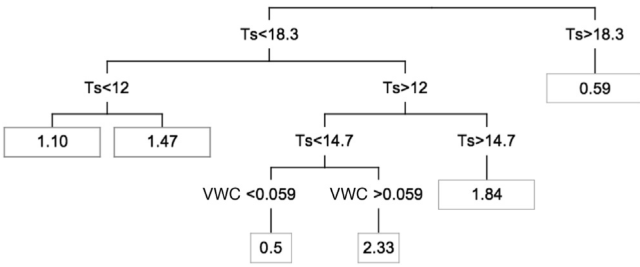

Fig. 4. Regression tree soil CO_2 efflux at the study site ($n = 600$; measurements are from September 2011through August 2012). Soil temperature and soil volumetric water content were the most important variables for describing the temporal variability of soil CO_2 efflux. Terminal points of the tree indicate mean soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) of the cluster. Abbreviations are: Ts = soil temperature (°C); VWC = soil volumetric water content (m^3 m^{-3}).

variable Z at point x_i; and $Z(x_i + h)$ is the value of variable Z at point $x_i + h$. Plotting $\hat{\gamma}(h)$ against h gives the semivariogram, which either exhibits purely random behavior or some systematic behavior described by theoretical models (linear, spherical, exponential, Gaussian, and power law) (Burrough and McDonnell, 1988). Model coefficients were determined by best-fitting to all the semivariance data. For variables that depend on separation distance, it was expected that the values of $Z(x_i) - Z(x_i + h)$ would increase with the distance h up to a given distance, after which point the values would stabilize. The semivariance value in which the semivariogram curve stabilized is called sill (i.e., $C + C_0$). The distance in which the stabilization of semivariogram occurred (a; range distance) was defined as the spatial dependence limit. The C value represents the structured spatial variability of data. The nugget effect (C_0) is the semivariance value found at the intercept with the y-axis. Theoretically, this value should be zero for a lag distance (h) of zero; however, sampling error measurements and short-scale variability may cause a deviation from zero. Therefore, the nugget effect represents the amount of variance not explained or modeled as spatial correlation. We applied a cross validation procedure to verify the reliability of the mathematical model. The final chosen model was the one with the highest correlation coefficient between the observed and estimated values and was closer to the bisectrix (Isaaks and Srivastava, 1989).

Estimates of variables in non-sampled places were performed by ordinary kriging using adjusted models (Trangmar et al., 1985). The weights (λ_i) for each neighboring point were determined based on an adjusted semivariogram model, so that the variance of the estimates was minimized leading to a linear system of equations according to Eq. (2):

$$\hat{Z}(x_0) = \sum_{i=1}^{N(h)} \lambda_i Z(x_i), \quad \text{with} \quad \sum_{i=1}^{N(h)} = 1 \tag{2}$$

where $\hat{Z}(x_0)$ is the estimated value of the property at a non-sampled place; N is the number of values used for prediction; λ_i is the weighting associated with each value; and $Z(x_i)$ is the observed value at the ith point.

For classification of spatial data within each season, three exploratory approaches were used: hierarchical, non-hierarchical cluster analysis, and principal component analysis (PCA). The goal of these analyses was to provide information about the relationship among all variables during the wet and dry season, and how data may cluster depending on the relevance of different variables during the different seasons (Tabachnick and Fidell, 2001). Prior to conducting analyses all quantitative variables were standardized to zero mean and unit variance. *A priori*, the structure of groups contained in the original data was evaluated by cluster analysis adopting Euclidean distance as the similarity measure between samples and Ward's method for connecting groups. After taking a number of groups that best characterized the structure contained in the original data, we applied a cluster analysis by using the non-hierarchical k-means algorithm that allows the characterization of default variables for the group considered. PCA was applied to the variables in order to reduce the dimensionality into a smaller set of orthogonal variables (Tabachnick and Fidell, 2001). All geostatistical analyses were done using GS+ (Gamma Design Software, Plainwell, Michigan), and remaining data analyses were done with MATLAB R2007a (MathWorks, Natick, Massachusetts, USA).

3. Results

3.1. Temporal variation

During the year of measurements mean annual temperature and precipitation were 15.9 °C 245 mm, respectively, with the heaviest rains during November (Fig. 1b). Soil temperature varied between 21 and 34 °C during the dry months (May to October) and between 7 and 16 °C during the wet months (November to April; Fig. 2a). Mean soil VWC for the dry months was <0.09 and between 0.14 and 0.36 m^3 m^{-3} for the wet months (Fig. 2b). Mean LAI and EVI were 1.4 and 0.16 for dry months, and 1.6 and 0.24 for the wet months, respectively (Fig. 2c, d). Soil CO_2 efflux varied from 0.4 to 0.8 (during the dry months) and from 0.9 to 2.1 μmol CO_2 m^{-2} s^{-1} (during the wet months, Fig. 2e).

There was a significant positive linear relationship ($r^2 = 0.53$, $p = 0.007$) between the monthly soil CO_2 efflux and monthly soil VWC (Fig. 3a). When the hot moment of soil CO_2 efflux (i.e.,

Table 1
Descriptive statistic and Student's *t*-test between measured variables during the dry season (i.e., September) and the wet season (i.e., February). Values in bold and letters represent significant differences ($P < 0.01$) between dry and wet season.

Variables	Dry season								Wet season							
	Mean		SD	Min	Max	CV	Skewness	Kurtosis	Mean		SD	Min	Max	CV	Skewness	Kurtosis
Soil CO_2 efflux (μmol m^{-2} s^{-1})	**0.49**	**b**	0.22	0.23	1.65	44.9	0.38	−0.85	**1.45**	**a**	0.05	0.90	2.56	3.4	0.91	0.75
Root biomass (kg m^{-2})	0.49	a	0.43	0.04	2.46	87.8	2.30	5.27	0.57	a	0.62	0.01	3.67	108.8	3.90	16.45
Soil Moisture (m^3 m^{-3})	**0.01**	**b**	0.007	0.001	0.03	70.0	1.54	2.69	**0.26**	**a**	0.04	0.16	0.37	15.4	0.30	−0.51
Soil Temperature (°C)	**32.3**	**a**	3.8	23.4	38.0	11.8	−0.46	−0.74	**11.5**	**b**	0.4	9.6	13.99	3.5	0.44	−0.94
Soil Density (g m^{-3})	0.82	–	0.07	0.61	0.93	8.5	−0.39	−0.10	0.82	–	0.07	0.61	0.93	8.5	−0.39	−0.10
LAI	0.65	a	1.21	0	4.42	186.2	2.05	3.47	0.81	a	1.08	0.00	4.30	133.3	1.20	0.55
pH	6.5	a	0.42	5.6	7.5	6.5	−0.05	−0.10	7.5	a	1.1	6.1	8.4	14.6	0.3	−0.6
Air-filled pore space (%)	**0.68**	**a**	0.02	0.64	0.74	2.9	0.10	−0.56	**0.43**	**b**	0.04	0.37	0.52	9.3	0.17	−0.83
Total soil porosity (%)	0.69	–	0.03	0.65	0.77	4.3	0.45	0.01	0.69	–	0.03	0.65	0.77	4.3	0.45	0.01
Litter Biomass (kg m^{-2})	0.66	a	0.81	0.06	4.52	122.7	2.09	5.89	0.39	a	0.50	0.03	2.22	128.2	1.85	3.54

Note: $N = 50$; means followed by the same letters on rows do not differ (Student's *t*-test; $p < 0.01$). Soil density and total soil porosity was not measured during the wet season as was assumed to be the same as during the dry season.

Table 2
Principal component analysis of selected variables for the dry season (i.e., September) and the wet season (i.e., February).

	PC1	PC2	PC3
Dry Season			
Eigenvalues	2.05	1.37	1.13
Explained variance (%)	29.3	19.57	16.1
Correlation			
CO_2 efflux	0.03	−0.52*	0.34
Root biomass	0.56*	−0.62*	0.03
Soil Moisture	0.87*	−0.1	−0.01
Soil Temperature	−0.43	−0.43	−0.62*
Total soil porosity	0.77*	0.16	0.04
Soil N	−0.13	−0.69*	−0.04
Soil C	−0.41	−0.14	0.79*
Wet season			
Eigenvalues	1.74	1.47	1.35
Explained variance (%)	24.81	20.95	19.24
Correlation			
CO_2 efflux	0.37	0.4	−0.65*
Root biomass	−0.15	−0.1	−0.85*
Soil Moisture	0.75*	0.26	−0.11
Soil Temperature	−0.18	0.86*	0.16
Total soil porosity	0.72*	−0.54*	−0.04
Soil N	−0.53*	−0.43	−0.19
Soil C	−0.44	0.1	−0.35

PC means principal component. (*) represents significant correlations between the measured variable and each PC ($p < 0.05$).

measurements during November) was eliminated from the equation the strength of the relationship increased ($r^2 = 0.78$, $p < 0.001$; Fig. 3a). During the wet months there was a significant positive linear relationship between the monthly CO_2 efflux and monthly soil temperature ($r^2 = 0.63$, $p = 0.061$; Fig. 3b). In contrast, there was no significant relationship between these variables during the dry months (Fig. 3b). Finally, there was significant positive linear relationship ($r^2 = 0.9$, $p < 0.001$) between monthly soil CO_2 efflux and total monthly precipitation even when the hot moment of soil CO_2 efflux was included in the analysis. Notably, the spatial variability (represented by the error bars in Fig. 3) increased with soil CO_2 efflux rates.

Regression tree analysis was used to identify thresholds ($p < 0.001$) of soil temperature and soil VWC for soil CO_2 efflux (Fig. 4). Soil temperatures >18.3 °C and between 12 and 15 °C but with low soil moisture were associated with the lowest soil CO_2 efflux rates. In contrast, temperatures between 12 and 18 °C with higher soil water content (>0.06 $m^3 m^{-3}$) were associated with the highest soil CO_2 efflux rates. The linear models and the regression tree analyses show that seasonal patterns of precipitation, and therefore soil VWC, regulated soil CO_2 efflux rates and the relationship with soil temperature.

3.2. Spatial variability in dry and wet seasons

Soil CO_2 efflux, soil temperature, soil VWC, and soil air-filled pore space were the only variables with significant differences

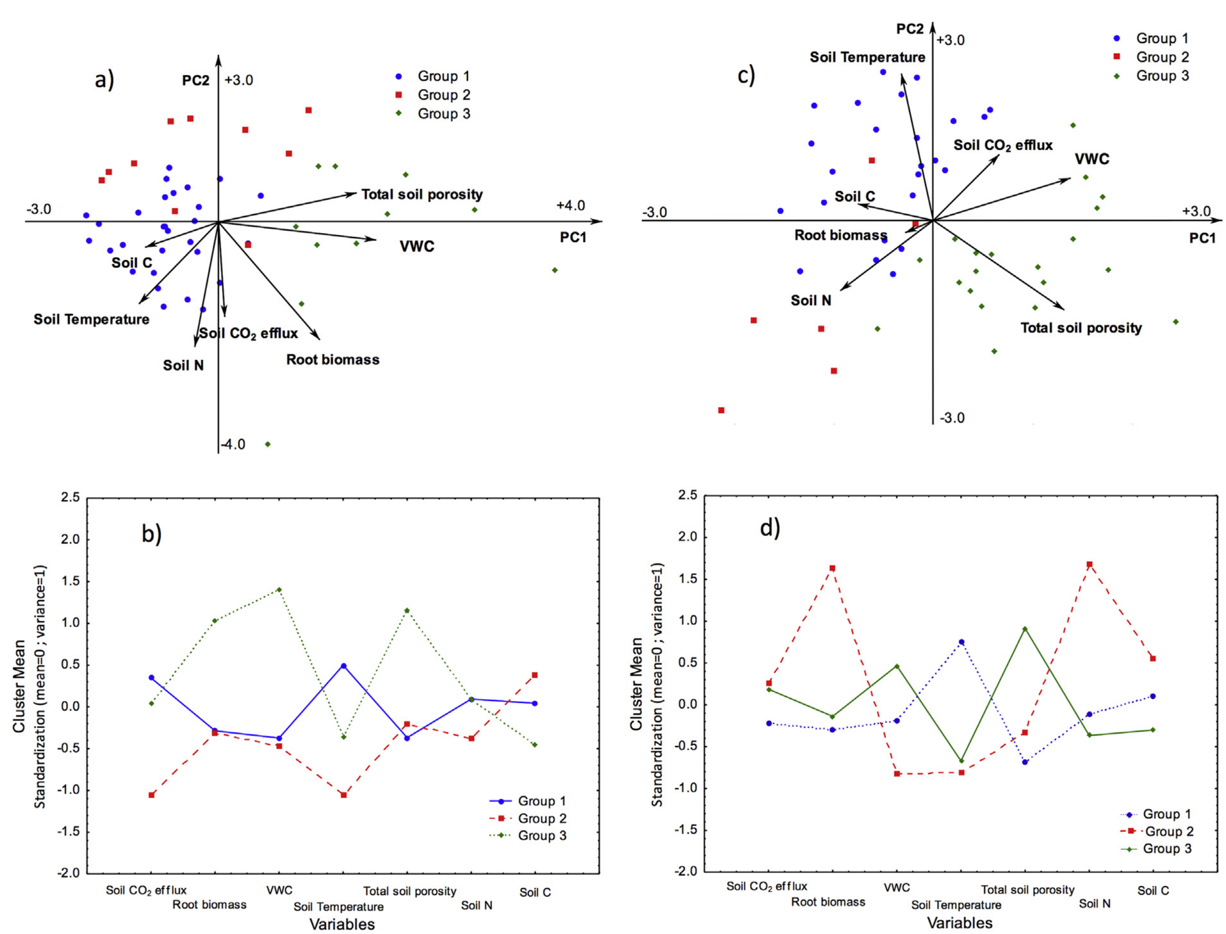

Fig. 5. Principal component analysis (PCA) and k-means grouping analysis for the spatial sampling during the dry season (September; a, b) and the wet season (February; c, d). VWC means soil volumetric water content. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Fitted estimated parameters and models of experimental semivariograms for soil CO_2 efflux, soil moisture, soil temperature and LAI in dry (i.e., September) and wet (i.e., February) seasons.

Variable	Nugget	Sill	Range	Residuals	r^2	$C/(C + C_0)(\%)$	Model
Dry season							
Soil CO_2 efflux	0.00714	0.01154	54.26	4.33E-06	0.79	61.78	Spherical
Soil moisture	0.00001	0.00006	16.1	5.75E-10	0.43	85.71	Spherical
Soil temperature	4.27	13.5	46.2	9.84E+00	0.75	75.97	Exponential
LAI	0.368	1.466	15.1	7.60E-02	0.56	79.93	Spherical
Wet season							
Soil CO_2 efflux	0.06831	0.12746	41.98	7.87E-04	0.70	65.107	Spherical
Soil moisture	–	–	–	–	–	–	Pure Nugget Effect
Soil temperature	0.98249	2.01314	53.85	4.25E-02	0.90	67.203	Exponential
LAI	0.1652	1.2642	24.73	5.71E-02	0.87	88.443	Spherical

($p < 0.01$) in their spatial means between seasons (Table 1). The coefficient of variation was substantially higher for soil CO_2 efflux, soil VWC, LAI, and soil temperature during the dry season; however, higher for soil pH and soil air-filled pore space during the wet season (Table 1).

PCA for the dry season showed that the first two principal components (PC) explained nearly 50% of the variance. The PC1 was positively correlated with root biomass, soil VWC, and total soil porosity; whereas PC2 was negatively correlated with soil CO_2 efflux, root biomass, and soil nitrogen (Table 2). The PCA and k-means showed that soil VWC was associated with the group of higher soil CO_2 efflux during the dry season (Fig. 5a, b).

For the wet season the first two principal components (PC) explained nearly 46% of the variance. PC1 was positively correlated with soil VWC and total soil porosity, however negatively correlated with soil nitrogen (Table 2). PC2 was positively correlated with soil temperature and negatively correlated with total soil porosity (Table 2). The PCA and k-means showed that root biomass was associated with higher soil CO_2 efflux during the wet season (Fig. 5c, d).

There was spatial dependence for soil CO_2 efflux, soil temperature, soil VWC, and LAI (Table 3). The spatial dependence of these variables changed between the dry and the wet seasons, though most notably for soil VWC. Using ordinary kriging we found a north to south gradient for soil CO_2 efflux during the dry season related to the slope of the terrain (Fig. 6a). During the wet seasons there was a hot spot of CO_2 efflux associated with higher LAI but independent of soil temperature and soil VWC (Fig. 6).

4. Discussion

In contrast to expectations for more widely studied temperate ecosystems, monthly precipitation was the primary driver of the seasonal trend of soil CO_2 efflux in this water-limited ecosystem. Instantaneous measurements of soil VWC did not fully explain the instantaneous variability of soil CO_2 efflux. Although there is evidence of the importance of soil VWC in regulating soil CO_2 efflux (Almagro et al., 2009) there is also evidence that lags exist between these variables as a result of rewetting and drying events in water-limited ecosystems (Vargas et al., 2012). Furthermore, monthly precipitation and not soil VWC explained the higher soil CO_2 efflux observed during a hot moment in the month of November. This was the wettest month (>65 mm) for the year of 2011–2012 and followed the dry months of July through October. Measured soil CO_2 efflux for November increased 522% with respect to the rates observed one month prior to the end of the dry season. We propose that this increase in soil CO_2 efflux rate could have been driven by a priming effect triggered by higher water availability following the long dry-hot summer months (Kuzyakov, 2010). Similar hot moments in carbon fluxes have been observed in other water-limited ecosystems and contribute to a substantial portion of annual site-specific soil carbon fluxes (Huxman et al., 2004; Xu et al., 2004; Almagro et al., 2009).

Our results support the hypothesis that precipitation and therefore soil VWC limits the strength of the relationship between temperature and soil CO_2 efflux in this water-limited ecosystem. These results contrast with the common observation of a strong exponential relationship between soil temperature and soil CO_2 efflux in temperate ecosystems (Lloyd and Taylor, 1994) that is widely used to model soil and ecosystem respiration (Reichstein et al., 2005; Mahecha et al., 2010). Previous studies have shown how soil moisture influences the temperature sensitivity of soil CO_2 efflux in water-limited ecosystems (Almagro et al., 2009; Carbone et al., 2011). Unfortunately, ecosystem process models are still limited in their ability to represent ecosystem respiration under drought conditions, arguably due to a misrepresentation of how soil moisture influences the temperature sensitivity of this process (Reichstein et al., 2002; Vargas et al., 2013a). It is known that soil temperature and soil moisture are independent but also confounding controls of soil CO_2 efflux in temperate forests (Davidson et al., 1998). We argue that the confounding effects of these variables could be stronger in water-limited ecosystems and therefore it is critical to understand how soil moisture and drought conditions influence the temporal and spatial dynamics of soil CO_2 efflux.

Although water-limited ecosystems are areas with relatively low metabolic activity we provide evidence of how spatial variability of soil CO_2 efflux changed between two contrasting seasons (wet vs. dry). During the dry season we were able to model most of the spatial dependence of soil CO_2 efflux (Table 3), but during the wet season there was a small sampling error due to short-scale variability (therefore larger spatial heterogeneity) as the nugget in the semivariogram increased (Table 3). These results provide evidence that an increase in metabolic activity is related to higher soil CO_2 efflux and changed the spatial dependence of this variable. Therefore, sampling designs should accommodate changes in spatial dependence of soil CO_2 efflux accordingly to the metabolic state of the ecosystem. For example, with higher metabolic rates and higher spatial heterogeneity (wet season) a denser network of sampling points will be needed to better represent the spatial dependence of different variables.

There was a clear spatial trend in soil CO_2 efflux from north to south related to the slope of the terrain during the dry season. Although this trend could not be explained by the spatial dependence of other variables (see Fig. 6) the PCA demonstrated that higher soil CO_2 efflux was related to higher soil VWC during this season (Fig. 5). Our results show a strong spatial dependence and the emergence of a hot spot of soil CO_2 efflux during the wet season. The emergence of a hot spot during this season was associated with the spatial dependence of LAI (Fig. 6), and the PCA demonstrated that higher root biomass was associated with higher soil CO_2 efflux

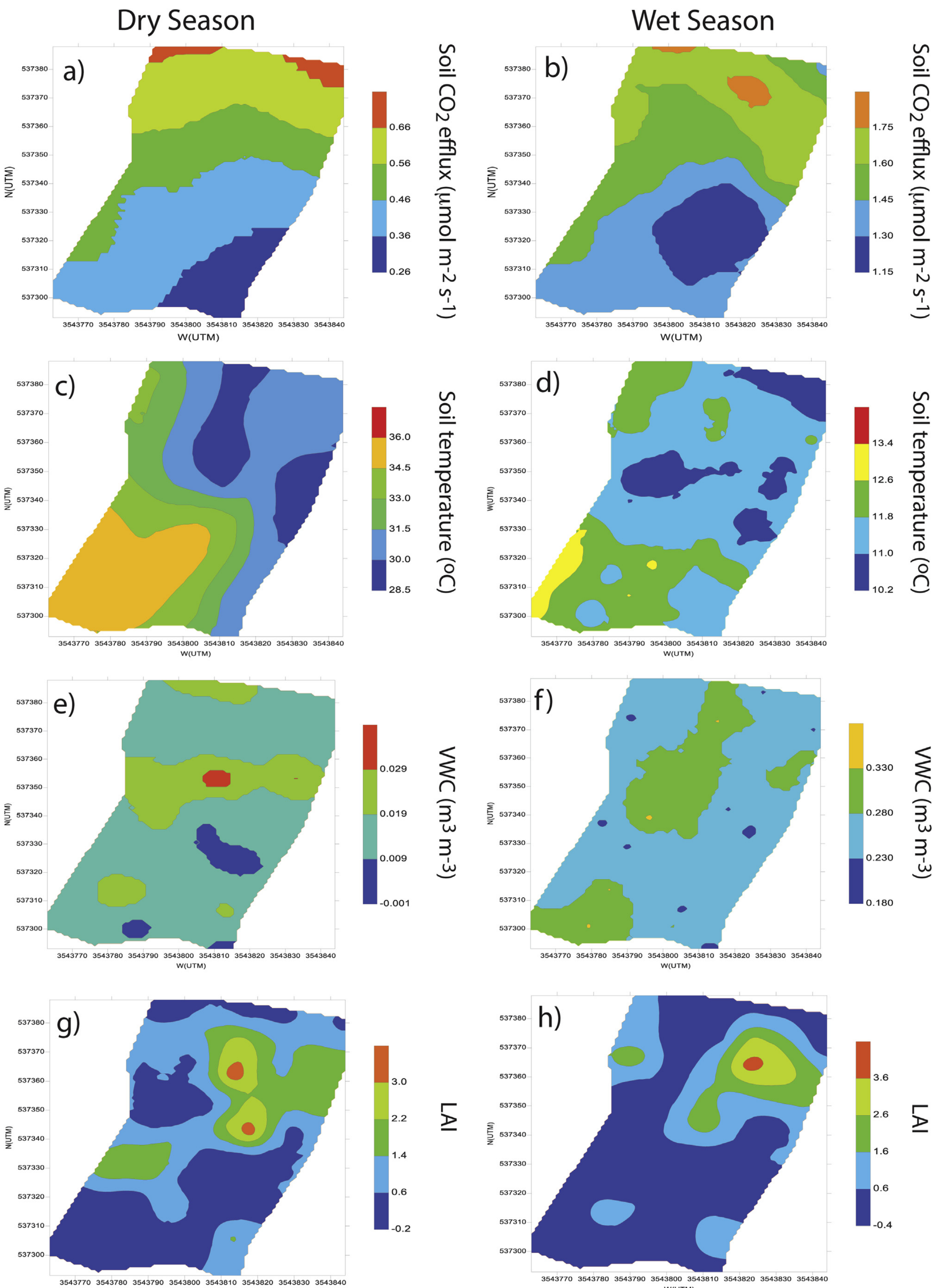

Fig. 6. Spatial patterns generated by ordinary kriging for the dry season (September) and the wet season (February) for soil CO_2 efflux (a, b), soil temperature (c, d), soil volumetric water content (VWC; e, f), and leaf area index (LAI; g, h).

rates (Fig. 5). Based on these results, we speculate that the spatial dependence of soil CO_2 efflux could be driven by heterotrophic respiration during the dry season when plants are dormant and soil CO_2 efflux is mainly driven by variability in soil moisture; and by autotrophic respiration during the wet season when plants are metabolically active and hot spots of soil CO_2 efflux are explained by root biomass and leaf area index.

These results bring attention to the complexity of the underlying mechanisms controlling the spatio-temporal variability of soil CO_2 efflux rates in this water-limited ecosystem. We recognize that higher spatial and temporal sampling may be needed to capture full dynamics of hot spots and hot moments, especially when spatial dependence of measured variables changes between seasons. It is likely that higher spatial resolution is needed for previously observed controls of soil CO_2 efflux such as: soil texture (Cable et al., 2008), different soil organic matter fractions (Almagro et al., 2013), soluble carbon pools (Scott-Denton et al., 2003), and litter decomposition rates (Stoyan et al., 2000). Likewise, it is critical to have high temporal frequency of soil CO_2 efflux measurements to capture full dynamics of the temporal variability and hot moments (Vargas et al., 2011). Unfortunately, as effort is invested in spatial sampling less effort is applied to temporal sampling and *vice versa*; this paradox should be addresses to fully understand the spatio-temporal variability of soil CO_2 efflux.

5. Conclusion

Our results provide evidence that common expectations derived from studies in temperate ecosystems could not be applied to explain spatial and temporal variation of soil CO_2 efflux in water-limited ecosystems. Soil moisture was a good predictor for the seasonal trend of soil CO_2 efflux, but could not explain a hot moment of soil CO_2 efflux following the dry months. Monthly precipitation was the main driver of the seasonal trend of soil CO_2 efflux, including a hot moment, and through changes in soil VWC it influenced the relationship between CO_2 efflux and soil temperature. There were differences in the spatial dependence of soil CO_2 efflux between two contrasting seasons. During the dry season high soil VWC was associated with high soil CO_2 efflux, and during the wet season the emergence of a hot spot of soil CO_2 efflux was associated with higher root biomass and LAI. These results suggest that spatial sampling designs should accommodate for changes in spatial dependence of soil CO_2 efflux (and other variables) accordingly to the metabolic state of the ecosystem. Finally, this study adds to the increasing evidence that soil CO_2 efflux dynamics in water-limited ecosystems are more complex than previously thought (when compared to temperate ecosystems), and require a better understanding to accurately represent them in global change models.

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