



Research paper

Physical and biogeochemical controls on soil respiration along a topographical gradient in a semiarid forest

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ABSTRACT

Soil respiration is a dynamic and fundamental process across all terrestrial ecosystems. However, how physical and biogeochemical factors control seasonal variation and annual rates of soil respiration remains poorly understood. A topographical gradient in a semiarid forest was chosen as the study site to assess how both biogeochemical and physical factors control respiration rates. Parameters measured include soil respiration, litterfall, fine root biomass, soil physical and chemical properties, soil bacteria and archaea gene abundance, ectomycorrhizal fungi abundance and richness, and soil carbon isotope signatures. The results showed that increases in soil temperature and moisture exponentially and linearly promoted root activity, driving seasonal variation of total soil respiration. Seasonal variation of heterotrophic respiration was driven by soil moisture in a second-order polynomial pattern. Autotrophic respiration only contributed to 20% of the total soil respiration, and seasonal variation in the soil respiration rate was driven by heterotrophic respiration. Utilizing soil moisture as a scalar, the values of Q_{10} and R_{10} in different positions on the slope indicated soil respiration was controlled by interaction of soil temperature and moisture, and a new transformation of the R_{10} function inducing soil moisture was proposed. Along the topographical gradient, the long-term average soil temperature and moisture significantly varied from the top to the bottom of a slope. This variation in physical processes induced differences in plant productivity and biomass accumulation, leading to varying organic matter accumulation across the gradient. The topographical position also induced differences in the size of the soil organic matter aggregates, archaea and bacteria gene abundances, and ectomycorrhizal fungi abundance and richness. The aforementioned parameters are interrelated due to their association with the long-term average soil temperature and moisture, and the interrelation of these parameters ultimately affects annual rates of soil respiration.

1. Introduction

Soil respiration (R) is one of the major processes controlling the carbon budget of terrestrial ecosystems (Schlesinger and Andrews, 2000). Seasonal variation and the annual rate are the most important properties for soil respiration, as understanding what drives seasonal variation and the annual rate of soil respiration is vital to determining terrestrial carbon budgets (Luo and Zhou, 2006). Seasonal variation of soil respiration rates reflects localized shifts in the environment, and ultimately dictates the annual rate of soil respiration (Kuzyakov, 2011).

In recent decades, drivers of soil respiration have been investigated

across various ecosystems (Luyssaert et al., 2007; Pregitzer and Euskirchen, 2004; Raich and Tufekcioglu, 2000; Shi et al., 2014). Multiple hypotheses have been proposed to explain the mechanisms that control soil respiration: soil temperature (Davidson and Janssens, 2006; Lloyd and Taylor, 1994), soil moisture (Grünzweig et al., 2009; Xu and Qi, 2001), soil microbial community composition (Monson et al., 2006), ecosystem biomass (Li et al., 2006; Liu, 2013), root activity (Shi et al., 2011), photosynthesis (Hogberg et al., 2001; Kuzyakov and Gavrichkova, 2010), SOM pools (Birge et al., 2015; Liu, 2013), and the stoichiometry of soil nutrients (Manzoni et al., 2012; Spohn and Chodak, 2015). Although varied and diverse, the above drivers of soil

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respiration can be divided into two categories, physical processes (temporal variation of soil temperature and moisture) and soil biogeochemical properties (soil organic carbon (SOC), soil structure, and soil nutrients). These abiotic factors combine with the biotic components (microbes and plants) of the system to govern rates of soil respiration.

Many studies investigating the drivers of soil respiration either focus on seasonal variation of respiration or annual rates rather than examining both in tandem. Studies have demonstrated that temporal variation of physical processes drive seasonal variation of soil respiration (Li et al., 2008; Lloyd and Taylor, 1994; Xu and Qi, 2001), but what remains unknown is how temporal variation of physical processes affects the biotic components of the ecosystem to influence both heterotrophic and autotrophic soil respiration.

The physical and biogeochemical factors of an ecosystem control soil C cycling processes (Fang et al., 2009). For example, the parameters controlling the soil respiration are affected by topography, either directly through the dynamics of surface and subsurface water, nutrient availability, and organic matter content, or indirectly via soil texture and vegetation (Arias-Navarro et al., 2017). A topographic gradient was selected for this experiment as physical processes and biogeochemical properties range widely across topographic relief, presenting an opportunity to determine what drives seasonal variation and annual rates of soil respiration.

This study is one part of the “Gonglu Mountain Experiment”. “Gonglu Mountain Experiment” is a long-term and integrative ecological research on water and nutrient cycling in the arid and semiarid ecosystems of Loess Plateau. In our study, the soil respiration of an oak forest ecosystem along a topographical gradient in the semiarid Loess Plateau was measured for four years. To better understand the inter-annual and the intra-annual rates of respiration, we measured soil physical and biogeochemical properties. We hypothesized that the physical and biogeochemical parameters control seasonal variation and annual rates of soil respiration along a topographical gradient in a semiarid forest. The objective of this study was to investigate the relative importance of both soil physical processes and biogeochemical processes in control the inter-annual and the intra-annual rates of soil respiration.

2. Materials and methods

2.1. Study area and experimental site

The study site was located in semi-arid natural forests located on Mt. Gonglushan, near Yan'an city of Shaanxi province, China (36°25.40'N, 109°31.53'E; 1245–1395 m a.s.l.). On the Loess Plateau, the amount of precipitation and the occurrence of forests gradually decreases moving northwest, and the present study site was located in the forest–grassland transition zone (Cheng and Wan, 2002). In this area, the natural forests are dominated by *Quercus liaotungensis*, which is the climax community of this area. The natural oak forests are 60–70 year-old secondary forests (Du et al., 2007). The 40-year averages (1971–2010) of annual precipitation and annual mean air temperature are 504.7 mm and 10.1 °C, respectively (Shi et al., 2014). Most of the rainfall occurs from July to September, immediately following the dry season which occurs from early spring to early summer. The growing season of deciduous species is from April to October (Zhang et al., 2013). Topography around the study site is characterized as the hill and gully region of Loess Plateau (Xu et al., 2014). The soils are classified as Calcic Cambisols, which are derived from silt textured loess parent materials (Wang et al., 2003).

In August of 2009, three north slopes (slopes 1, 2, and 3) with a declination of 22–26° and dominated by *Quercus liaotungensis* were selected as the sites for this study. The main experimental plots (20m × 20m) were established at three positions on each slope: the upper position located on the summit of the slope, the middle position,

located on the middle of slope, and the bottom position located in the gully and adjacent area to the slope. Experimental plots were described in detail by Tateno et al. (2007), Du et al. (2007), and Zhang et al. (2013). In each plot of slope 1, five 5 m × 5 m subplots were established at the four corners and the center. A specially designed polyvinyl chloride (PVC) collar was placed in the central part of each subplot for measurements of soil CO₂ efflux. Diameter at breast height (DBH) was recorded for all trees larger than 4.5 cm. Tree census was conducted twice in mid-August during 2009 and 2010.

2.2. Sampling and laboratory analyses

Soil CO₂ efflux, soil temperature, and soil moisture: Soil respiration was measured using an automated soil CO₂ flux system (LI-8100, LI-COR, USA) equipped with a portable chamber (Model 8100-103). A PVC collar (20.3 cm in diameter and 10 cm in height) was inserted into the forest floor to a depth of 2.5 cm at each sampling point, about two months before the first measurement. Small litter and branches were left in the collar while large items were removed. All collars were left at the site for the entire study period.

Soil respiration was measured over the four year period from 24 March 2011–2 March 2015, approximately once every 30 days during April–October (growing season), and once every 45 days during November–March (dormant season). Due to logistic constraints, soil respiration rates were only conducted on slope 1. Specifically, soil respiration sampling events had to occur between 8:30 and 11:30 due to data quality concerns, therefore only one site could be adequately measured.

Temporal soil temperature and moisture near each collar were recorded at the same time as soil respiration measurements along the plots of slope 1. Soil temperature was measured at a depth of 12 cm using a handle thermocouple probe, while the soil volumetric water content was measured at 0–12 cm depth, using a time domain reflectometry moisture meter (TDR200, Spectrum, USA).

Litterfall production, litterfall organic carbon, and litterfall total nitrogen: Three litter traps (0.25m² in area) were placed on center lines at 4 m intervals. Litterfall was collected monthly or bimonthly from late April 2013 to late April 2014. All collections were sorted into oak leaves, leaves of other species, twigs, and other organs. Each litterfall fraction was weighted after drying at 70 °C. The concentrations of total organic carbon in litterfall were analyzed by TOC VWP (Shimadzu, Japan), and total nitrogen was analyzed using 2300 kjeltec analyzer unit (FOSS TECATOR, Sweden).

Fine root standing biomass: To measure fine root biomass (< 2 mm in diameter) we sampled five soils from the depths 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, and 30–50 cm using a cylindrical soil core sampler (20 cm² in area) during August 2009 from all three slopes (45 samples total). Fine roots in the soil core sample were sieved and washed using 0.5 mm nylon mesh bag. We sorted fine roots into living and dead root based on the morphology and condition. The fine roots were weighted after drying at 70 °C for 72 h.

Soil physical and chemical properties: Five representative soil samples (0–20 cm) were collected from four corners and the center of each plot along slope 1 in August 2012 within the period of peak plant growth. Measurements of soil bulk density, aggregate size distribution, soil organic carbon (SOC), soil total nitrogen (STN), soil total phosphorus (STP), and δ¹³C in the soil organic matter were conducted on these samples. Soil bulk density was measured at the 0–20 cm depths of each plot using a stainless steel cutting ring 5.0 cm high by 5.0 cm in diameter. The soil cores were dried at 105 °C. Aggregate size classes were separated by wet sieving through 0.25 and 0.053 mm sieves following the procedures described by Cambardella and Elliott (1993). The macroaggregate (> 0.25 mm), microaggregate (0.25–0.053 mm), and silt + clay (< 0.053 mm) fractions were dried in an oven at 50 °C for 24 h and then weighed. Soil samples were air-dried, and then ground to pass through a 2 mm sieve to measure SOC and STN in aggregate of

different size. SOC and STN were measured using the TOC VWP (Shimadzu, Japan) and 2300 Kjeltex analyzer unit (FOSS TECATOR, Sweden), respectively. Soil organic carbon stock was calculated as the product of soil bulk density and soil organic carbon concentration. The natural abundance of $\delta^{13}\text{C}$ in the soil organic matter was analyzed with a MAT 252 isotope ratio mass spectrometer (Thermo Fisher Scientific, USA) interfaced with an automated carbonate inlet device. Sample isotope ratios are expressed as a permil (‰) deviation relative to the VPDB standard.

Partitioning soil respiration: A soil respiration partitioning experiment was carried out from May to December in 2010. An experimental plot (20m × 20 m), located in the oak forest, was in close proximity to upper plot of slope 1 (approximate 10 m distance). The experimental procedures in detail were described by Shi et al. (2012a). This experiment was named as “PE” in this study.

Gene abundances of soil bacteria and archaea: Four representative soil samples (0–10 cm) were collected from center of four subplots of each plot in September 2015 and combined to form a composite sample for each plot across all slopes. Total nucleic acids were extracted from ~0.25 g fresh weight of soil using the MoBio Powersoil DNA kit (MoBio Laboratories, Carlsbad, CA, USA) according to manufacturer's instructions. The 16S rRNA gene abundances of soil bacterial and archaeal communities were quantified by real-time PCR using a Light Cycler Nano Instrument (Roche) with FastStart Essential DNA Green Master (Roche). For the bacterial 16S rRNA gene we utilized the forward primer 338f (ATTACCGCGGCTGCTGG) and reverse primer 518r (ATTACCGCGGCTGCTGG) (Long et al., 2012). For the archaeal 16S rRNA gene, we used forward primer A109f (ACKGCTCAGTAACACGT) and reverse primer A334r (TCGCGCCTGCTGCTCCCGT) (Long et al., 2012). The reaction conditions were as follows: an initial denaturation at 95 °C for 900 s, followed by 40 cycles of 95 °C for 60 s, 53 °C for 30 s and 72 °C for 60 s.

2.3. Model analysis

Seasonal variation of soil respiration over the 4 years was fitted to soil temperature with exponential functions given in Eq. (1) to describe the dependence of soil respiration (R) on soil temperature (T) (Shi et al., 2014).

$$R = \alpha \times e^{\beta T} \quad (1)$$

where R and T are soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and soil temperature (°C), and α and β are constant coefficients. The temperature sensitivity (Q_{10}) of soil respiration is based on Eq. (1) was calculated as:

$$Q_{10} = e^{10 \times \beta} \quad (2)$$

And the R_{10} (soil respiration rate at 10 °C) of soil respiration was calculated as (Lloyd and Taylor, 1994):

$$R = R_{10} \times e^{308.6 \times \left(\frac{1}{56.02} - \frac{1}{T+46} \right)} \quad (3)$$

A polynomial function was established to describe the effect of soil moisture (W) on soil respiration (Xu and Qi, 2001):

$$R = \alpha + W \times \beta + W^2 \times \gamma \quad (4)$$

where W is the soil volumetric water content (%), and α , β , and γ are constant coefficients. The theoretical threshold values of soil volumetric water (W_{TT}) in different position were calculated by differential derivation of Eq. (4). When soil moisture was lower than the threshold, soil respiration increased with an increase in soil moisture. If soil moisture was higher than the threshold, further increases in soil moisture lead to a decrease in respiration (Gaumont-Guay et al., 2006; Shi et al., 2011; Xu and Qi, 2001). Therefore, The W_{TT} could be used as a scalar to indicate effect of soil moisture on soil respiration.

2.4. Estimates of annual rate of soil respiration

Annual rate of soil respiration were estimated by interpolating the average soil respiration rates between sampling dates, and computing the sum of the products for the average flux rate and the time between respective sampling dates for each measurement period (Shi et al., 2014; Shi et al., 2012b; Sims and Bradford, 2001) as follows:

$$SR = \sum F_{m,k} \Delta t_k \quad (5)$$

Where $\Delta t_k = t_{k+1} - t_k$, which is the number of days between each field measurement within the year; SR is total soil CO_2 emitted in the measurement period, and $F_{m,k}$ is the average soil respiration rate over the interval $t_{k+1} - t_k$ recorded by the LI-8100 Soil CO_2 Flux System.

2.5. Statistical analyses

Repeated measures ANOVA (RMANOVA) with Turkey's HSD test were performed to examine the difference in soil temperature, soil moisture, and soil CO_2 efflux among the three slope positions for the study period.

One-way ANOVA was applied to test the significance of soil properties among different positions using Tukey's HSD test at $p < 0.05$. The relationships between soil respiration, soil temperature, and soil moisture were explored via regression analyses at $p < 0.05$.

3. Results

3.1. Soil respiration, temperature, and moisture

Soil respiration in different slope positions showed the same strong seasonal pattern with a peak in the summer and a trough in the winter (Fig. 1a). The results of RMANOVA indicated that the soil respiration rate was not significantly different among slope positions ($p < 0.05$). According to our estimation via the interpolating method, the annual rate of soil respiration (SCE) by position was 97.87 ± 15.31 , 95.56 ± 9.44 and $102.70 \pm 11.35 \text{ g C m}^{-2}$ in upper, middle and bottom position, respectively (Fig. 1b). These annual rates were not significantly different from one another ($p > 0.05$).

In contrast to soil respiration, the soil temperature (T) and soil moisture (W) on different slopes were significantly different based on RMANOVA result ($p < 0.05$). Fig. 1c shows the four-year average of soil temperature decreasing down the slope. As expected, the soil moisture four year averages show the opposite trend, with soil increasing soil moisture values moving down the slope.

3.2. Response of soil respiration seasonal variation to soil temperature and moisture

The seasonal variation of soil respiration can be explained by the temporal variation of soil temperature and moisture (Fig. 2). Fig. 2a, c & e showed that the R^2 of the relationship between soil respiration and soil temperature increased with lowering position based on an exponential function ($p < 0.05$). However, when polynomial function was used, the trend of the R^2 of the relationship between soil CO_2 efflux and soil moisture was opposite that of the exponential function (Fig. 2b, d & f $p < 0.05$).

Utilizing the soil respiration partitioning method, the response of RA and RH to soil temperature and moisture was investigated (Fig. 3). Fig. 3a & c showed a significant exponential correlation between soil temperature and both RA and RH ($p < 0.05$). However, RA and RH displayed differing responses to soil moisture. RA showed a positive linear relationship with soil moisture, while RH displayed a polynomial relationship with soil moisture. (Fig b & d, $p < 0.05$).

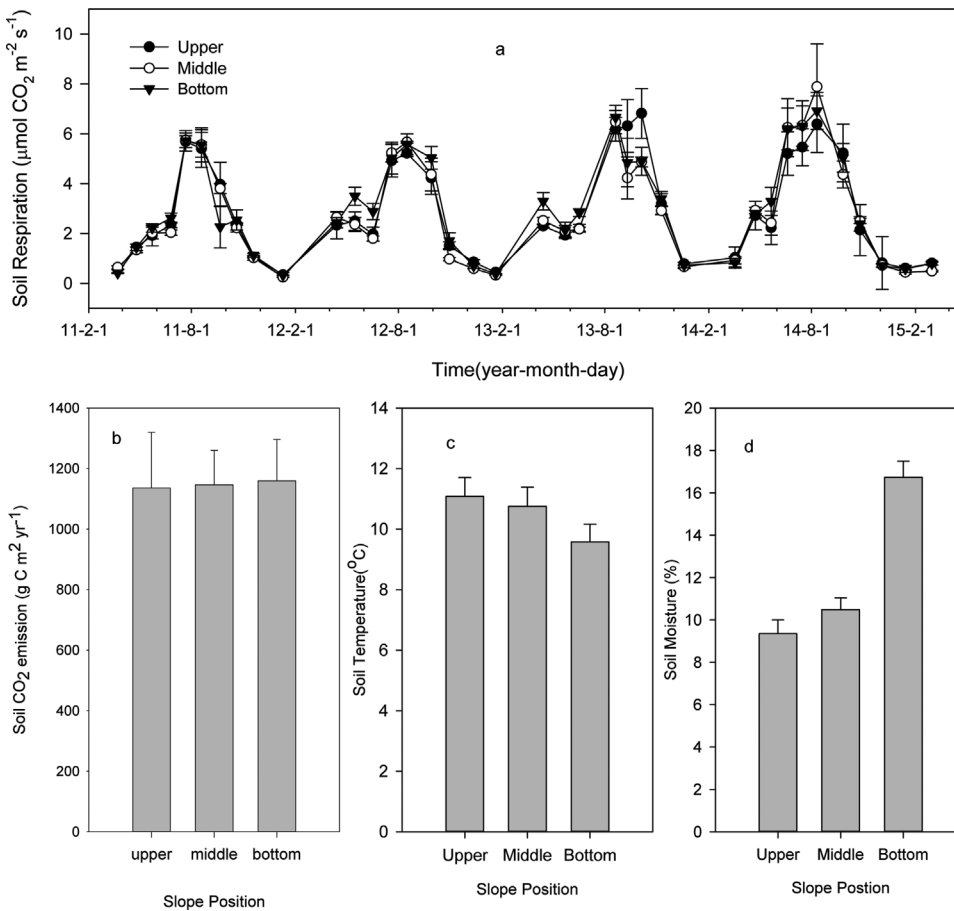


Fig. 1. (a) Variations in soil CO₂ efflux from 24 March 2011–2 March 2015 at different slope position (upper, middle, bottom) (mean \pm SE, $n = 5$). (b) Averaged annual soil CO₂ emissions at upper, middle and bottom position during 5 years using interpolation method (mean \pm SE, $n = 5$). (c) Annual means of soil temperature and (d) moisture at upper, middle and bottom position during 5 years (mean \pm SE, $n = 5$).

3.3. Physical, chemical, and microbial characteristics of soil

SOC in the bottom slope position was significantly greater than the other two slope positions (Fig. 4a, $p < 0.05$). SOC was concentrated in the form of macroaggregates ($> 0.25 \text{ mm}$) and microaggregates ($0.25\text{--}0.053 \text{ mm}$). The percent of SOC in macroaggregates decreased with decreasing slope position, while the percent of SOC in macroaggregates presented an opposite trend to microaggregates in terms of slope position (Fig. 4b). The C/N and C/P was lowest in the silt & clay ($< 0.053 \text{ mm}$) size class, and greatest in the microaggregates (Fig. 4c & d). The $\delta^{13}\text{C}$ in the soil organic matter significantly increased with increasing slope position (Fig. 4e, $p < 0.05$). Soil bacteria (16 s rRNA) showed lower abundances at the lower slope positions compared to the upper positions, with the archaea abundances following the same pattern (Fig. 5a & b, $p < 0.05$).

3.4. Plants

Forest structure was investigated based on stand density and mean DBH. Fig. 6a & b indicated that the stand density significantly increased with elevation, but the mean DBH showed the opposite relationship ($p < 0.05$). Although litterfall production in upper position was greater than the other positions (Fig. 6c), no significant difference was detected among the slope positions ($p > 0.05$). C/N and C/P of litterfall showed a decreasing trend moving down the slope, but were not significantly different across positions. (Fig. 6d & e). Fine root biomass at the bottom slope position was significantly lower than the other slope positions (Fig. 6f).

4. Discussion

4.1. Seasonal variation of soil respiration

Previously, a large number of studies have used the interaction of T and W to explain the seasonal variation of R (Chang et al., 2014; Davidson and Janssens, 2006; Davidson et al., 2000; Gaumont-Guay et al., 2006; Reichstein et al., 2003; Yuste et al., 2003). Xu and Qi (2001) indicated that the relationship between soil respiration and soil temperature was significantly controlled by soil moisture. Shi et al. (2011) also found that after precipitation, following dry periods, the soil temperature gradually became the dominant factor controlling soil respiration. Wang et al. (2014) suggested that soil moisture modifies the response of soil respiration to temperature. According to the previous studies, it could be concluded that soil respiration is controlled by the interaction of T and W.

In this four-year long study, we consolidated previous conclusions and found that when W is limiting, in comparison to T, the seasonal variation of R was dominantly driven by W variation (Fig. 2). This finding demonstrates that the limitation of any single factor (T or W) can change the relative importance of the factor to seasonal variation of R. Table 1 showed the Q_{10} , R_{10} and W_{TT} in different position. The W_{TT} value at the bottom position was nearly two-fold greater than the W_{TT} values at the middle and upper slope positions. This pattern of W_{TT} values across slope positions suggests that soil respiration is limited by soil moisture at the upper and middle positions, but not at the lower position. The W_{TT} values increased moving up the slope, showing the opposite trend for T limitation in comparison to W limitation. This suggests that soil respiration is more sensitive (Q_{10}) to T when W is not limiting.

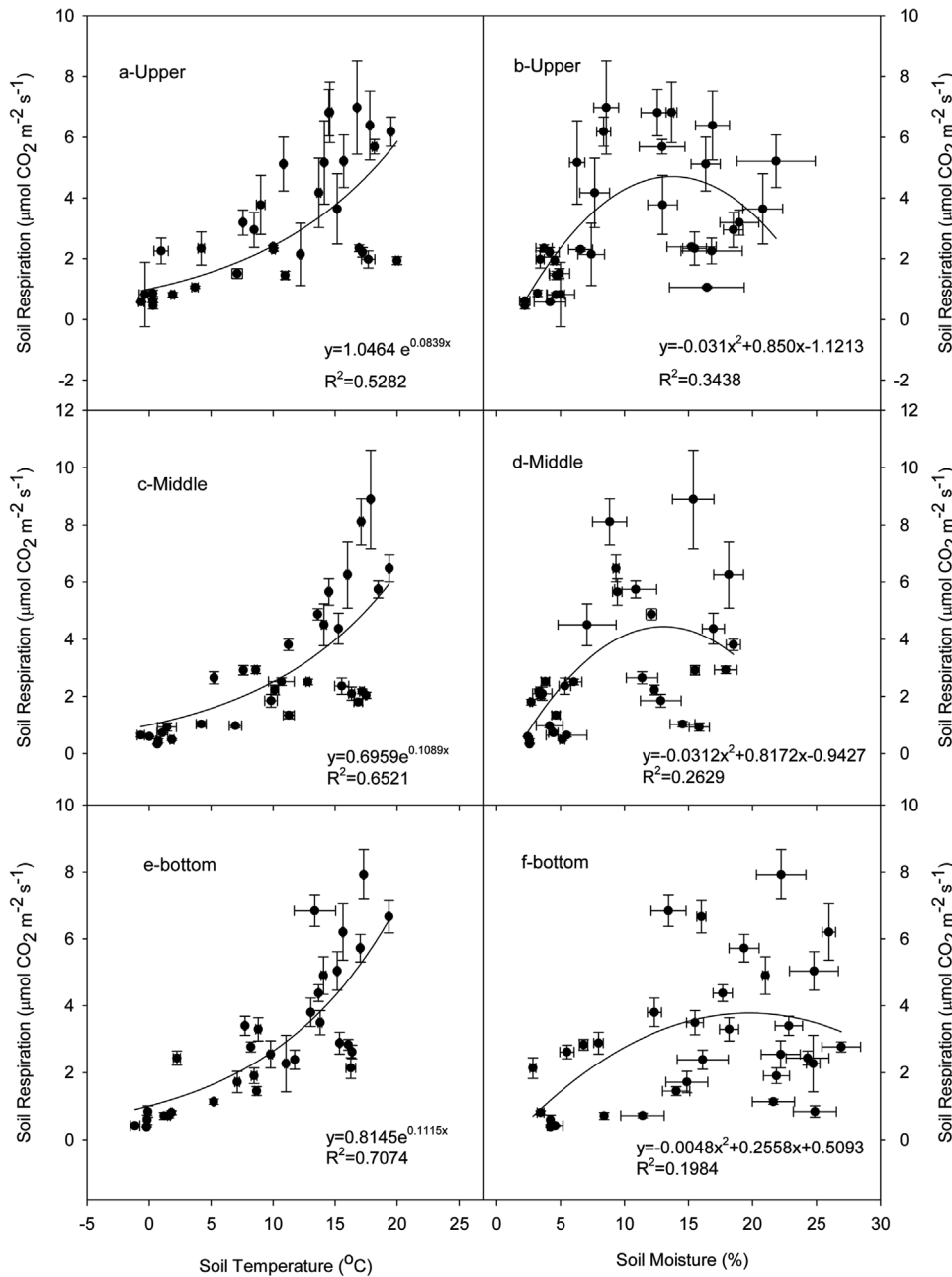


Fig. 2. Relationships between soil respiration and soil temperature and moisture at (a, b) upper, (c, d) middle and (e, f) bottom position ($p < 0.05$).

Based on the R_{10} function (Eq. (3)), every measurement of soil respiration rate was generalized into a R_{10} value. In this case, the relationship between R_{10} and W was obtained without the effect of T (Fig. 7 and Eq. (6)).

$$R_{10} = \alpha \times W^\beta \quad (6)$$

Fig. 7 showed the power function relationship between R_{10} and W , and Eq. (6) describes the physical process of the soil respiration rate with variation of W . This highlighted that the rate of soil respiration would not increase indefinitely with an increase in W , but would approach an asymptote towards a certain limiting or final values when controlling for soil temperature. In fact, the model (Eq. (6)) is suitable for semiarid or arid regions as these regions are defined by the limited availability of water.

Considering the generalization of this model for applications to other ecosystems, a new transformation of R_{10} function combined with soil moisture (W) was obtained as:

$$R = \alpha \times W^\beta \times e^{308.6 \times \left(\frac{1}{56.02} - \frac{1}{T+46} \right)} \quad (7)$$

where R , R_{10} , T and W are soil respiration (μmol m⁻² s⁻¹), soil respiration at 10 °C soil temperature (μmol m⁻² s⁻¹), soil temperature (°C) and soil moisture (%) respectively, and α and β are constant coefficients.

Soil respiration was partitioned into two sources: autotrophic respiration (RA) and heterotrophic respiration (RH) (Boone et al., 1998; Kuzyakov, 2006). The seasonal variation of R was essentially controlled by the dynamics of RA and RH. Borkhuu et al. (2015) reported that the dynamics of RA are controlled by the variation in fine root activity and biomass. In this study, the fine root biomass was not significantly different between August 2004 and August 2009 at the same long-term monitoring plot (Fig. 8). This finding agrees with a prior study in which the fine root biomass did not significantly change with temporal variation, rather RA was driven by root activity (Fukuzawa et al., 2013). Our study in the PE experiment demonstrated that T and W affect the root activity, thus driving seasonal variation of R (Fig. 3).

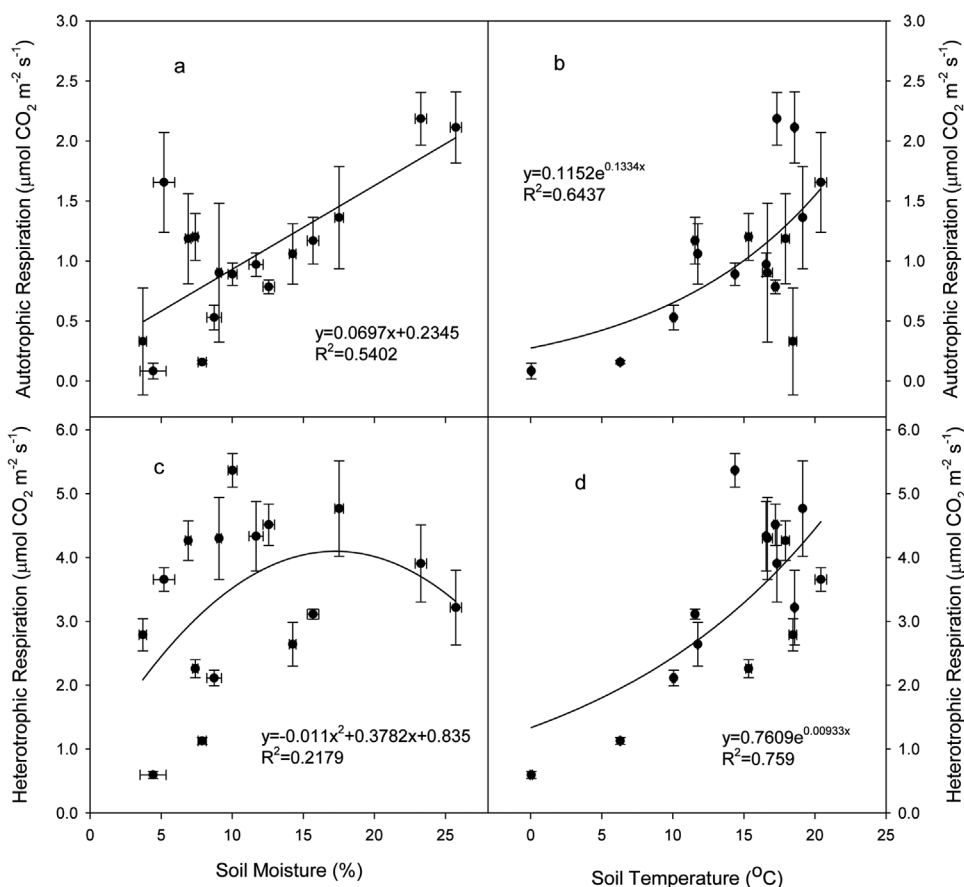


Fig. 3. Relationships between autotrophic respiration (RA) & heterotrophic respiration (RH) and soil temperature & moisture in soil respiration partition experiment (PE) during May to December in 2010 ($p < 0.05$).

The dynamics of RH depended on the soil carbon-use efficiency which was adjusted for by microbial abundance and richness, (Allison et al., 2010; Blagodatskaya and Kuzyakov, 2013) (Lange et al., 2015; Rousk et al., 2010). Soil microbes are not a static but a dynamic entity, and are seasonally influenced by T and W variation (Bell et al., 2010; Kramer et al., 2013; Monson et al., 2006; Wardle, 1998). Soil temperature has drastic effects on the microbial community; Allison et al. (2010) found that the dynamics of RH were driven by the soil temperature processes resulting from the interaction of the microbial biomass and microbial community composition. Monson et al. (2006) suggested that winter forest soil respiration rates were controlled by the microbial community composition, which was shaped by soil temperature. However, other studies have shown no effect of soil temperature on soil microbial communities (Moche et al., 2015). In this study, the dynamics of RH were exponentially driven by T. The abundance of archaea, bacteria, ectomycorrhizal taxa number, and species richness of ectomycorrhiza decreased moving down the slope. This decrease in the microbial community parameters also matched the decrease of T. Therefore, we could conclude that the RH dynamics were influenced by T through changes in soil microbial structure and processes.

In addition to the soil carbon, soil moisture is known to be a key driver of RH. Some studies reported that the influence of soil water processes had little effect on the total microbial biomass, but were highly correlated with the soil microbial community composition (Chen et al., 2007; Drenovsky et al., 2004). However, other studies suggest that soil water processes have a significant relationship with the monthly dynamics of the biomass and structure of soil microbial communities (Moche et al., 2015). Our study indicated that the RH dynamics were driven by the soil water processes in a second-order polynomial pattern. The abundance of archaea, bacteria, ectomycorrhizal taxa number, and species richness of ectomycorrhizal fungi decreased down slope as W increased. It is possible that W is the driver of

the soil microbial processes, hence indirectly controlling the RH dynamics. In this study, T and W coincidentally varied with the measured microbial community parameters, so we cannot definitively attribute T or W to changes in the microbial community. Further studies need to clarify the effects of T and W on the microbial abundance and the microbial community composition and/or richness. Finally, according to PE experiment (partitioning soil respiration experiment), we found that our site was dominated by heterotrophic respiration (80% total respiration). These results suggest that soil respiration was dominated by heterotrophic respiration, whose seasonal variation was governed by the physical processes of soil.

4.2. Annual rate of soil respiration

The mean annual of T (MAT) and W (MAW) are known to be important factors that control the carbon stock of soils (Karhu et al., 2014; Thomsen et al., 1999). In our study along a topographical gradient, MAT and MAW varied significantly from the top to the bottom of the slope (Fig. 1c & d). This typical variation of soil temperature and water, especially soil water in semiarid or arid regions, resulting from topography would induce differences in the stand structure of the forest across the slope. Our study showed that the density of the trees significantly decreased from the top to the bottom, but mean DBH displayed the opposite relationship with slope position (Fig. 6a & b). Interestingly, litter production did not differ significantly across the gradient (Fig. 6c). This supports that aboveground plant productivity is not different among the three slope positions, despite difference in stand density and DBH. Our results also showed that the C:N:P is not different along the slope (Fig. 6d & e), which indicated that the topographical position did not affect aboveground carbon input based on the biomass or the chemical composition of the litter. Nevertheless, the fine root biomass significantly decreased from the top to the bottom along the slope (Fig. 6f). Based on this, we conclude that variation in

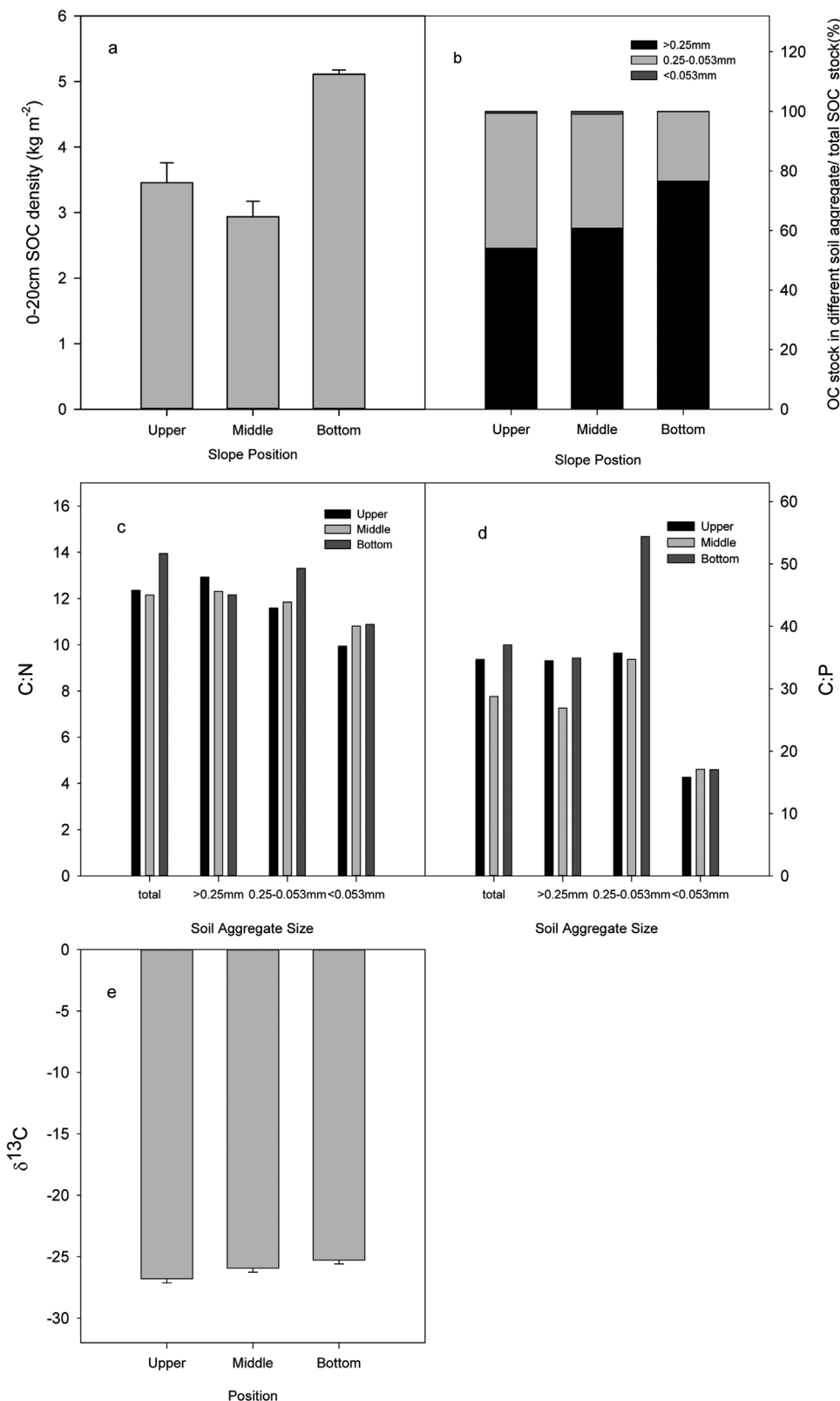


Fig. 4. (a) soil organic carbon content, (b) the percent of organic carbon stock of different size soil aggregate in total soil organic carbon stock, (c) C:N in different size aggregate and total soil and (d) C:P in different size soil aggregate and total soil and (e) δ¹³C in the soil organic matter at upper, middle and bottom position (mean ± SE, n = 5).

the SOC pool was due to belowground biomass, such as fine roots, and not variation in aboveground biomass composition or abundance.

Though our study found that the carbon biomass accumulation at the bottom position was the lowest (Fig. 6), the soil organic carbon stock in the bottom position was greater than the other two positions (Fig. 4a). This could suggest that soil carbon sequestration is not only dependent on carbon inputs, but also on SOC turnover. The soil physical

and biogeochemical properties generally play a dominant role in the SOC turnover of this system.

Our study found that topographical position induces differences in the size of the soil organic matter aggregates and soil C:N or C:P ratio. Generally, the soil C pools are dominated by organic carbon (Jobbagy and Jackson, 2000), but not all of this organic C is effectively turned over. This has been demonstrated by the models of the fast, slow, and

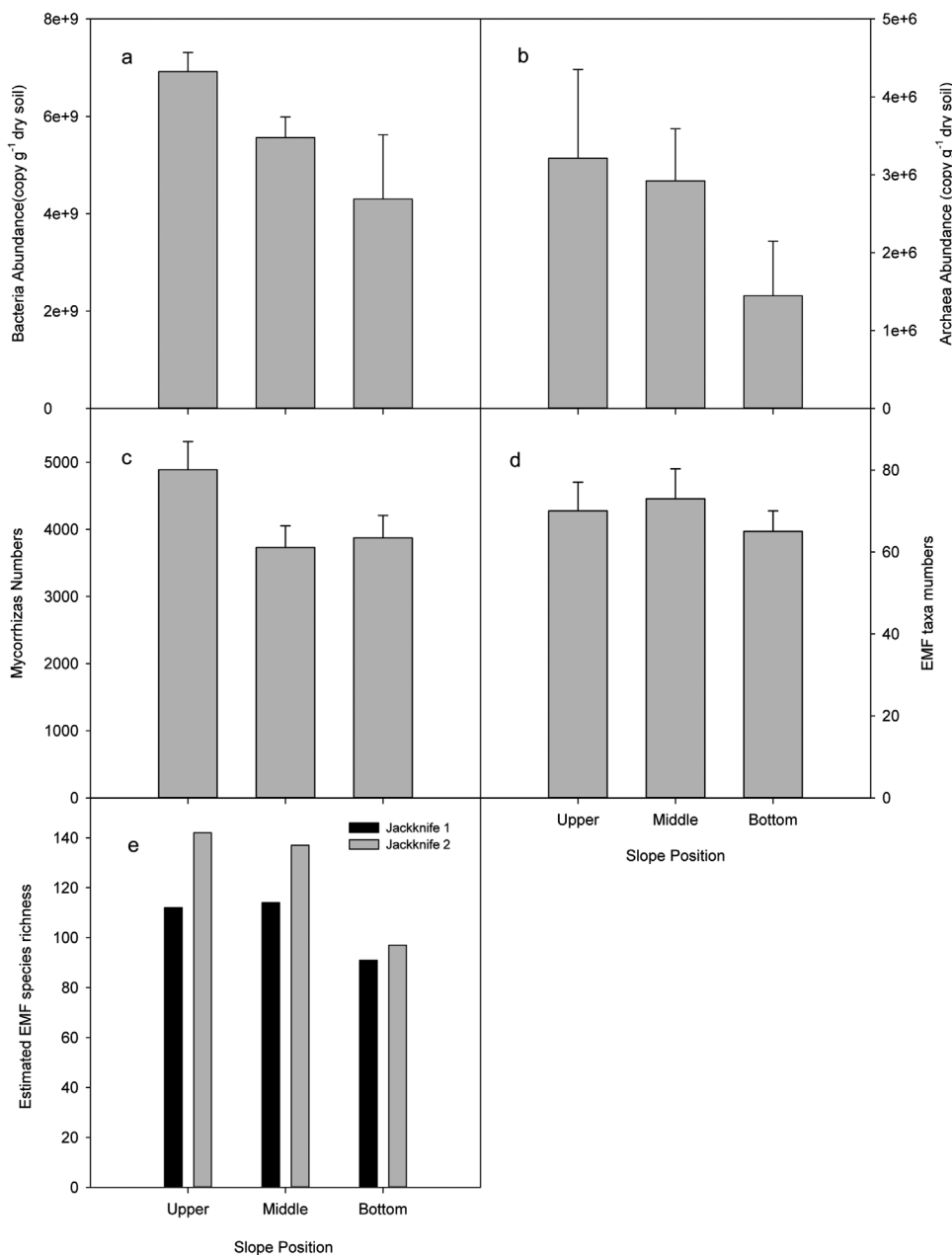


Fig. 5. (a) bacteria abundance, (b) archaea abundance, (c) mycorrhizas numbers, (d) ectomycorrhizal fungi (EMF) taxa numbers and (e) estimated EMF species richness value at upper, middle and bottom position. Mycorrhizas numbers, ectomycorrhizal fungi (EMF) taxa numbers and estimated EMF species richness were calculated from data of Zhang et al. (2013).

passive SOC pools (Andren and Katterer, 1997; Sierra et al., 2012). Some studies have found that soil respiration was limited by low C:N or C:P ratios and increased with increasing soil C:N or C:P ratios (Manzoni et al., 2012; Spohn and Chodak, 2015). In our study, the C:N or C:P ratios at the bottom position were the highest out of the three slope position, which would suggest that the soil respiration might be the highest at the bottom position (Fig. 4a, c & d). However, the annual rate of R was not significantly different across slope positions. To better understand the mechanism by which increased SOC, C:P, or C:N concentrations don't correspond to an increased rate of soil respiration, the soil aggregates were investigated as soil aggregates are structural units within the soil that control the dynamics of soil organic matter and nutrient cycling (Six et al., 2004). In this study, the SOC in silt & clay fraction contributed little (< 5%) to the total SOC and also showed the lowest C:N and C:P ratio of any soil fraction. The C:P ratio of the microaggregates in the bottom was significantly greater than all other ratios across all soil fractions for the three slope position. The C:N ratio of the microaggregates from the bottom slope position was the lowest among the slope positions (Fig. 4c & d). This indicated that the soil

organic carbon of the microaggregates in the bottom was prone to be used preferentially to macroaggregates. However, the macroaggregates make up 60 – 80% of the total organic carbon stock across slope positions. SOC of microaggregates at the bottom was 1.5–2 times lower than the SOC concentrations at the other two slope positions. Therefore, in regards to the effect of soil structure on soil respiration, we infer that the varying size of the SOC pool across soil fractions and the soil stoichiometric properties along the topographical gradient effectively influence SOC use efficiency, thereby decreasing the annual rate of R at the lower position. To test this inference we also investigated the variation of $\delta^{13}\text{C}$ in the soil along the slope as the $\delta^{13}\text{C}$ signature is regarded as an indicator of soil carbon turnover. The more positive a $\delta^{13}\text{C}$ value is, the slower the soil carbon turnover rate (Bernoux et al., 1998). Our study showed that the $\delta^{13}\text{C}$ gradually increased from top to bottom, indicating a decrease in SOC turnover moving down the topographic gradient (Fig. 4e).

We conclude that the synergistic interactions of the soil substrate structure and the soil microbial community drives soil respiration. Our results indicated that the topographical position induced differences in

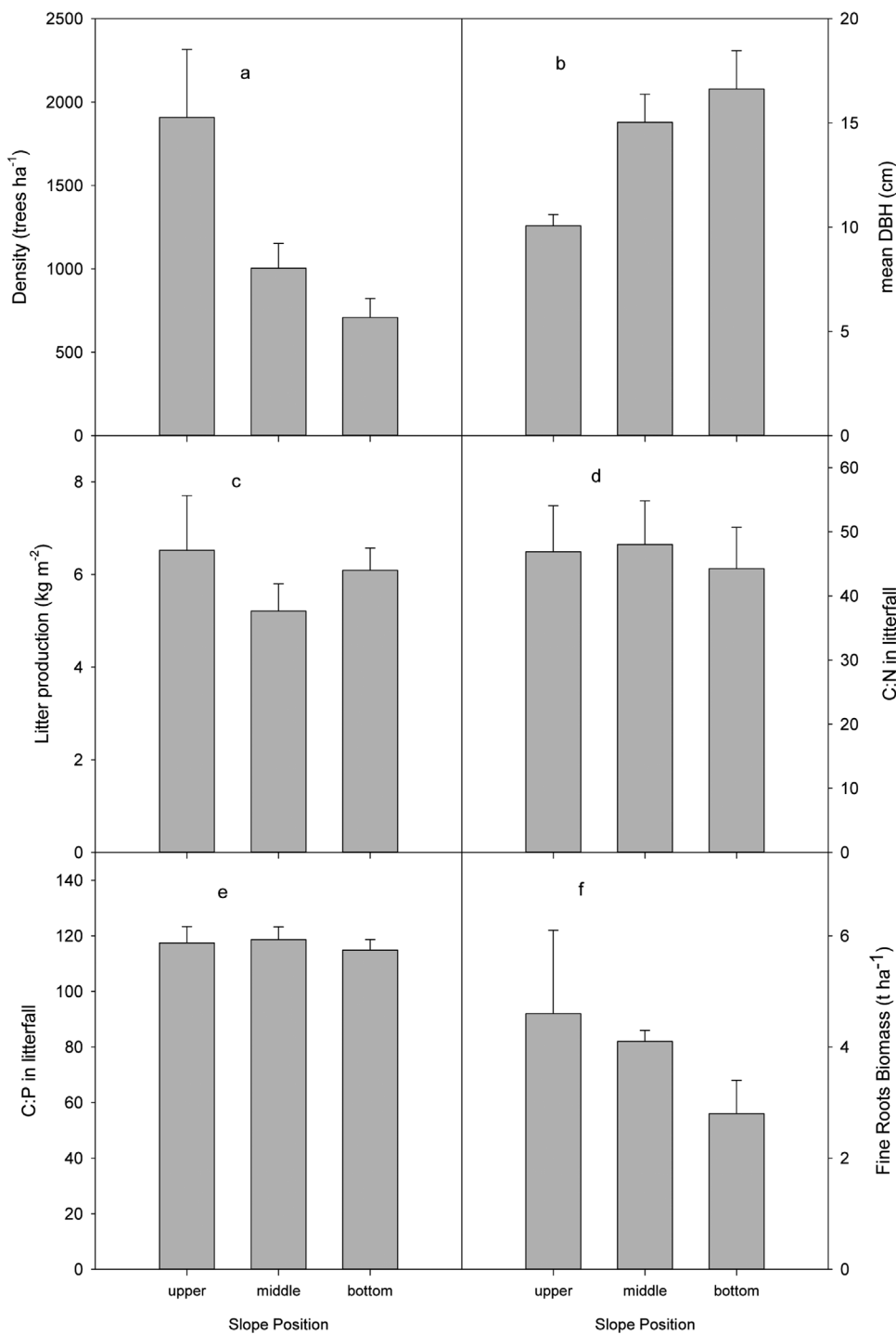


Fig. 6. (a) Stand density, (b) mean DBH, (c) litter production, (d) C:N in litterfall, (e) C:P in litterfall and (f) fine roots biomass at upper, middle and bottom position (mean \pm SE, n = 5).

Table 1
The Q_{10} , R_{10} and W_{TT} in different position.

Position	Q_{10}	R_{10}	W_{TT}
Upper	2.31	2.59	13.7
Middle	2.76	2.39	13.1
Bottom	3.05	2.88	26.6

All regressions were significant at $p < 0.05$.

the soil microbial population, including the rhizosphere dwelling microorganisms. The variation of the microbial population could result from the physical environment of the topographical gradient. As has

been established in prior work, heterotrophic respiration emits approximately 60 Pg annually from the global SOC pool, which is largely controlled by microorganisms, and a decrease in the microbial abundance could significantly decrease rates of heterotrophic respiration RH (Bradford, 2013). We suggest that even though the SOC concentration at the bottom position was greater than the other slope positions (Fig. 4 a), the SOC could not be effectively mineralized due to the lower abundance of soil microorganisms compared to the higher slope positions.

In addition, rhizosphere microorganisms were also investigated in the study as they could play a more important role in soil C balance compared with other soil microbes (Schweigert et al., 2015), due to their plant associations. Ectomycorrhizal fungi (EMF) were investigated

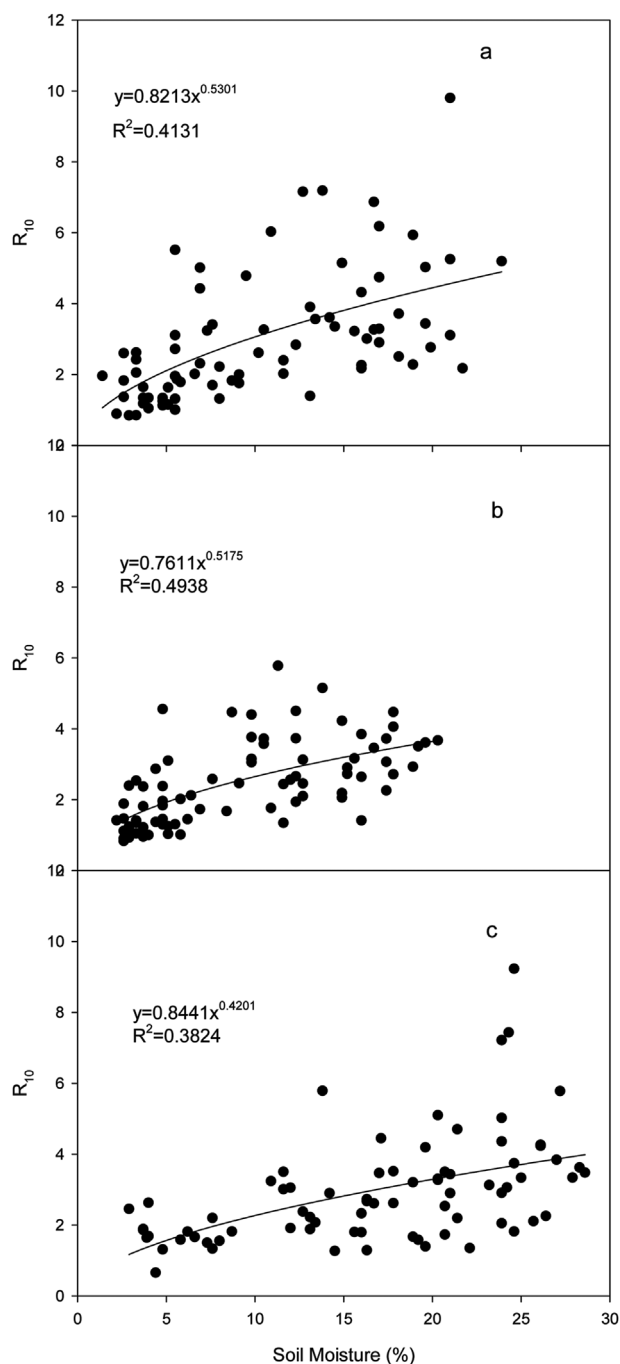


Fig. 7. the relationship between of R_{10} and soil moisture at (a) upper, (b) middle and (c) bottom position ($p < 0.05$).

as the typical rhizosphere microorganisms (Zhang et al., 2013), because EMF are widespread across forest ecosystems, and can make up 95% of the microbes associated with fine plant roots (Taylor et al., 2000). The ectomycorrhizal fungi abundances were significantly greater at the upper position than those of the middle and the bottom positions. (Fig. 5c, $p < 0.05$) In addition, the EMF taxa number and EMF species richness (both Jackknife 1 and 2) were both the lowest at the bottom position of the slope. (Fig. 5d, 5e, $p < 0.05$). Similarly to the other metrics of the soil microbial community, the rhizosphere microbes decreased in abundance and richness moving down the slope, further suggesting a decrease in microbial activity at lower slope positions.

Overall, these parameters are interrelated due to their association with the long-term average soil temperature and moisture, especially for soil moisture due to the semiarid environment. The physical and

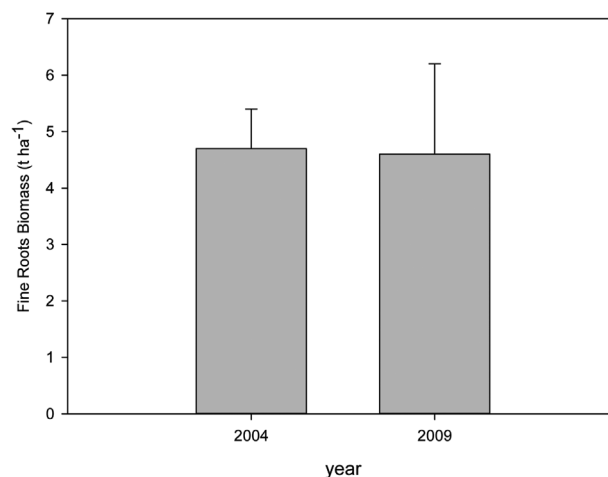


Fig. 8. comparison of fine roots biomass between 2004 and 2014.

biogeochemical parameters measured in this study are known to affect soil respiration, and it was the synergistic interaction of these parameters lead to similar annual rates of R across the topographical gradient.

5. Conclusions

This study examined the annual rate of soil respiration and seasonal variation via a long-term and integrative field monitoring in a typical semiarid ecosystem. Seasonal variation of heterotrophic respiration was driven by the soil water processes in a second-order polynomial pattern. Along the topographical gradient, the long-term average soil temperature and water differed significantly from the top to the bottom of a slope. This variation induces differences in plant productivity and biomass accumulation, leading to varying accumulations of soil organic matter accumulation in the soil. The topographical position also induces differences in the size of the soil organic matter aggregates, the overall soil microbial abundances, and the abundances of rhizosphere microorganisms. These parameters are interrelated due to their association with the long-term average soil temperature and moisture. The interrelation of these parameters ultimately affects the annual rate of soil respiration such that despite the varying physical and biogeochemical properties of the soil across the topographic gradient, soils respiration did not differ across the three slope positions selected in this study.

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