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Effect of plateau pikas disturbance and patchiness on ecosystem carbon emission of alpine meadow on the northeastern part of Qinghai-Tibetan Plateau

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Abstract

Plateau pikas (*Ochotona curzoniae*) disturbance and patchiness intensify the spatial heterogeneous distribution of vegetation productivity and soil physicochemical properties, which may alter ecosystem carbon emission process. Nevertheless, previous researches have mostly focused on the homogeneous vegetation patches rather than heterogeneous underlying surface. Thus, this study aims to improve our understanding of the difference in ecosystem respiration (Re) over heterogeneous underlying surface at the plot scale in an alpine meadow grassland. Six different land surface: large bald patch, medium bald patch, small bald patch, intact grassland, above pika tunnel and pika pile were selected to analyze the response of Re to pikas disturbance and patchiness, and the key controlling factors. The results showed that (1) soil moisture (SM) under pika pile and bald patches was 2-11% less than intact grassland despite pikas disturbance increased water infiltration rate, while soil temperature (ST) under pika pile and bald patches was 1-3°C higher than intact grassland; (2) soil organic carbon (SOC) and total nitrogen (TN) density under above pika tunnel were 2.45-3.31 and 2.10-3.72 times higher than other surface types; and (3) Re under intact grassland and above pika tunnel were 0.22-1.07 times higher than pika pile and bald patches, and Re was significantly correlated with SM, TN and vegetation biomass ($P<0.05$). Our results suggested that pikas disturbance and patchiness altered ecosystem carbon emission pattern, which was mainly attributed to the reduction of soil water and supply of substrates. Given that the wide distribution of pikas and large area of bald patches, the varied Re under heterogeneous underlying surfaces should not be neglected for estimation of ecosystem carbon emission at plot or region scale.

Keywords: pikas disturbance; patchiness; ecosystem respiration; alpine meadow; the Qinghai-Tibetan Plateau

Introduction

Ecosystem respiration (Re) is the key process to determine the carbon budget in the terrestrial ecosystem. Thus, even a small imbalances between CO_2 uptake via photosynthesis and CO_2 release by ecosystem respiration can lead to significant interannual variation in atmospheric CO_2 (Schimel et al., 2001; Cox et al., 2000; Grogan and Jonasson, 2005; Oberbauer et al., 2007; Warren and Taranto, 2011). Dependent on autotrophic (plant) and heterotrophic (microbe) activity, ecosystem respiration is mainly controlled by abiotic factors (primarily temperature and water availability) (Chimner and Welker, 2005; Flanagan and Johnson, 2005; Nakano et al., 2008; Buttlar et al., 2018), and supply of carbohydrate and other substrates (Janssens et al., 2001; Reichstein et al., 2002). Therefore, any external disturbance altering environmental conditions and affecting vegetation growth would exert profound influence on ecosystem carbon emission.

One of the basic function of terrestrial ecosystem is to regulate carbon balance between the atmosphere and ecological system (Canadell et al., 2007; Le Quéré et al., 2014; Ahlström et al., 2015). However, this balance would be broken by widespread land degradation (Post and Kwon, 2000; Dregne, 2002), which accompanied with the reduction of photosynthetic fixed carbon dioxide from atmosphere and carbon sequestration by soils (Defries et al., 1999; Upadhyay et al., 2005). It was estimated that land degradation had resulted in 19-29 Pg C loss worldwide (Lal, 2001). Over the past decades, grasslands have experienced patchiness throughout the world and this process is still ongoing (Baldi et al., 2006; Wang et al., 2009; Roch and Jaeger, 2014). Other than climate change (Yi et al., 2014), vegetation self-organization (Rietkerk et al., 2004; Venegas et al., 2005; McKey et al., 2010) or anthropogenic disturbances (Kouki and Löfman, 1998; Yi et al., 2016), rodents burrowing activities were also considered as the origin of the patchiness (Wei et al., 2007; Davidson and Lightfoot, 2008). Patchiness generally refers to a landscape that consists of remnant areas of native vegetation surrounded by a more heterogeneous and patchy situation (Kouki and Löfman, 1998). This spatial heterogeneity led to the changing of the structure and function of the original ecosystem (Herkert et al., 2003; Bestelmeyer et al., 2006; Lindenmayer and Fischer, 2013). For instance, there is abundant evidence that patchiness not only intensified the spatial heterogeneous distribution of ecosystem organic carbon (C) and vegetation productivity (Yan et al., 2016; Qin et al., 2018) but also altered the pattern of coupled water and heat cycling between the land surface and the atmosphere (Saunders et al., 1991; You et al., 2017; Ma et al., 2018). Consequently, this may alter ecosystem carbon emission process (Juszczak et al., 2013).

Plateau pikas (*Ochotona curzoniae*, hereafter pikas) are small mammals endemic to the alpine grasslands on the Qinghai-Tibetan Plateau (QTP) (Smith and Foggin, 1999; Lai and Smith, 2003). Living in underground, they excavated deep layer soil to surface through foraging and digging activities (Lai and Smith 2003) and led to substantial bald piles on the ground. The bald pile was considered to gradually become bald patches under soil erosion, gravity, freeze-thaw and other factors (Chen et al., 2017; Ma et al., 2018). As a consequence, natural vegetation patches and adjacent bald patches with different sizes, and pikas piles represent the most common landscape pattern in the alpine meadow grassland on the QTP. Previous studies have demonstrated that pikas disturbance and patchiness weaken the function of alpine meadow as a carbon sink (Liu et al., 13; Peng et al., 2015; Qin et al., 2018) and accelerated ecosystem carbon emission rate (Qin et al., 2015a). Nevertheless, most of these studies have mainly focused on the homogeneous underlying surface rather than heterogeneous underlying surfaces. It remains unclear what the differences of Re are among heterogeneous underlying surfaces, especially under the disturbance of pikas and patchiness. Thus, the specific aims of this study were to (1) quantify soil and vegetation properties of the heterogeneous underlying surface; (2) investigate the response of ecosystem respiration (Re) to pikas disturbance and patchiness; and (3) illuminate key factors affecting Re of an alpine meadow grassland in the northeastern part of Qinghai-Tibetan Plateau (QTP).

Materials and methods

Site description

This study was conducted at the permanent plots at Suli Alpine Meadow Ecosystem Observation and Experiment Station (98°18'33.2", 38°25"13.5", 3887 m a.s.l.), Northwest Institute of Eco-Environment and Resources, Chinese Academy of Science. The study area is characterized by a continental arid desert climate, with low mean annual air temperature, little rainfall, and high evaporation (Wu et al., 2015). The mean annual air temperature was approximately -4 ℃ and the annual precipitation ranged from 200 to 400mm, respectively

(Chang et al., 2016). The permafrost type at our site is transition and the active layer depth is 2.78 ± 1.03 m (Chen et al., 2012). The dominant species in the study area was *Kobresia capillifolia*, *Carex moorcroftii* (Qin et al., 2014). Soils was classified as “felty” with a pH of 8.56, 30.96 % silt and fine, 57.52 % fine sand and 10.68 % coarse sand, and soil bulk density is 1.41 g cm^{-3} within a 0-40 cm depth of the soil layer (Qin et al., 2015b). The grassland in this area suffered from degradation due to permafrost degradation and external disturbance from grazing livestock and small mammals, i.e. plateau pikas (Yi et al., 2011, Qin et al., 2015a). As a result, a mosaic pattern of vegetation patches, bald patches with different sizes and pika piles was common.

Field observation

At early June 2016, three 100 m × 100 m plots were established as replicates. In each plot, six representative underlying surfaces were selected: (1) large bald patch with size larger than 9.0 m^2 (LP), (2) medium bald patch with size of 1.0-9.0 m^2 (MP), (3) small bald patch with size of less than 1.0 m^2 (SP), (4) intact grassland patch (IG), (5) above pika tunnel (PT), (6) old pika pile (PP) (Figure 1). For each surface type, nine 1 m × 1 m quadrats were set up, of which three was used for soil temperature and soil moisture measurement, three for soil saturated hydraulic conductivity measurement and three for soil hardness measurement, soil and vegetation sampling. We also set up three 2 m × 2 m quadrats in each surface type in a 100 m × 100 m plot for measuring ecosystem respiration.

(Insert Figure 1 here)

Soil temperature and moisture at 10 cm were measured with an auto-measurement system (Decagon Inc., USA).The system consisted of an EM50 logger and five 5TM sensors. The Data logged automatically every 30 min. Soil saturated hydraulic conductivity was measured by Dual Head infiltrometer (Decagon Inc., USA). The measurement process included soak time 15 min, hold time 20 min at low pressure head (5 cm) and high pressure head (15 cm) with 2 cycles. Each measurement takes 95 min altogether. Soil hardness was measured with TJSD-750 (Hangzhou Top Instrument co., LTD, Hangzhou, China) from the soil surface to 10 cm depth. Ecosystem respiration rates were measured using the LICOR-8150 Automated Soil CO_2 Flux System equipped with LICOR-8100-104 long-term chambers (LICOR, Inc., Lincoln, NE, USA). To measure ecosystem respiration, polyvinyl chloride collars with a 20 cm inner diameter and a 12 cm height were inserted into the soil with 3-4 cm exposed to the air (Qin et al., 2013). All of the collars were installed at least 24 h before the first measurement to reduce disturbance-induced ecosystem CO_2 effluxes.

Soil and vegetation sampling

Soil samples were determined during the periods of late July to early August 2016. In each surface type of each plot, five soil cores were collected using a stainless-steel auger (5 cm in diameter) at depths of 0-10, 10-20, 20-30 and 30-40 cm, and bulked as one composite sample for each depth. Another five soil cores were sampled by cylindrical cutting ring (7 cm in diameter and 5.2 cm in depth) to determine soil bulk density. Soil samples were firstly air-dried, then removed gravel and stone with manual sieving and finally weighed. The remaining soil samples with diameter less than 2 mm were ground to pass through a 0.25 mm sieve for analysis of soil organic carbon (SOC) and soil total nitrogen (TN) concentration. SOC was measured by dichromate oxidation using Walkley-Black acid digestion (Nelson and Sommers, 1982). TN was determined by digestion and then tested using a flow injection analysis system (FIAstar 5000, Foss Inc., Sweden). Aboveground and belowground biomasses were determined within a 1 m × 1 m quadrat on 4 August 2016 during peak biomass and species diversity. Aboveground biomass was sampled by clipping all above-ground living plants at ground level, drying (oven-dried at 65 ℃ for 48 h) and weighing. Belowground biomass was sampled by collecting five soil columns, each 5 cm in diameter and 40 cm in depth. Soil cores were washed with a gentle spray of water over a fine mesh screen until soil separated from the roots, and then drying (oven-dried at 65 ℃ for 48 h) and weighing.

Statistical analysis

The soil organic C (kg m^{-2}) and total N (kg m^{-2}) densities in different underlying surface were calculated using the equation (1) and (2):

$$\mathrm{SOC} = \sum_{i=1}^{n} \rho * (1 - \sigma_{gravel}) * C_{SOC} * D_i \quad (1)$$

$$\mathrm{TN} = \sum_{i=1}^{n} \rho * (1 - \sigma_{gravel}) * C_{TN} * D_i \quad (2)$$

where SOC is soil organic C density, TN is soil total N density, ρ is the soil bulk density (g cm^{-3}), σ_{garvel} is the relative volume of gravel (% w/w), C_{SOC} is soil organic C content (g kg^{-1}), C_{TN} is soil total N content (g kg^{-1}) and D_i is soil thickness (cm) at layer i, respectively; i=1, 2, 3 and 4.

The data were presented as mean ± standard deviation. Statistical analyses were performed using the SPSS 17.0 statistical software package (SPSS Inc., Chicago, IL, USA). One-way analysis of variance (ANOVA) and a multi-comparison of a least significant difference (LSD) test were used to determine differences at the p=0.05 level. The relationships of ecosystem respiration with biotic and abiotic factors were analyzed by regression analysis using R.

Results

Microclimate and soil hydrothermal characteristics

Mean temperature and total rainfall during the growing seasons from 1 May to 30 September in 2016 were 6.18 ℃ and 343.4 mm, respectively (Figure 2). Soil temperature and moisture were significantly different (P<0.001) among various surface types (Table 1). The monthly average soil temperature was in a range of 8.20-13.72 ℃ during June to August, which was approximate 1-3 °C higher under pika pile and bald patches than the intact grassland (Figure 3a, P<0.05). The monthly mean soil moisture from June to August was approximate 30% for intact grassland and above pika tunnel, 25% for small patch and pika pile, and 20% for larger and medium patch (Figure 3b). Soil saturated hydraulic conductivity also showed significant variation under different underlying surface types (P=0.027, Table 2). Soil saturated hydraulic conductivity of pika piles was 2.58 cm h^{-1}, while it ranged from 1.53 to 2.13 cm h^{-1} for other surface types (Figure 4).

(Insert Table 1, Figure 2 to 4 here)

Soil and vegetation properties

Both pikas disturbance and patchiness significantly affected soil hardness, SOC density, TN density and vegetation biomass (Table 2) (P<0.001). Soil hardness was over 0.30 in intact grassland patch and above pika tunnel, approximate 0.20 for bald patches and less than 0.10 for pika pile (Figure 5), respectively. SOC and TN density showed significant variation under different underlying surface types (P=0.027, Table 2). Mean SOC and TN density under above pika tunnel were 14.54 and 0.98 kg m^{-2}, while they were 4.40 to 5.94 kg m^{-2} and 0.22 to 0.47 kg m^{-2} for other five surface types (Figure 6). Aboveground and belowground biomass were approximate 155 to 200 g m^{-2} and 2.5 to 3 kg m^{-2} for intact grassland and above pika tunnel, while they were less than 100 g m^{-2} and 2 kg m^{-2} for other surface types (Figure 7a, b).

(Insert Table 2, Figure 5 to 7 here)

Ecosystem respiration and influence factors

Pikas disturbance and patchiness had significant effects on ecosystem respiration (Table 1, $P<0.001$). During the growing season, ecosystem respiration has a maximum value in August and minimum value in June (Figure 8). In June, ecosystem respiration under intact grassland, above pika tunnel, small patch and pika pile had no significant difference and the lowest ecosystem respiration were found under large and medium patch (Figure 8). Average ecosystem respiration under intact grassland and above pika tunnel were in a range of 4.03 μmol m^{-2} s^{-1} and 3.77 μmol m^{-2} s^{-1}, which were 23.23 % to 102.50 % higher than other surface types both in July and August (Figure 8). Regression analysis showed that ecosystem respiration had no significant correlation with soil temperature, whereas it was sharply correlated with soil moisture ($P<0.01$), soil total nitrogen ($P<0.05$), aboveground ($P<0.05$) and belowground biomass ($P<0.05$) (Figure 9).

(Insert Figure 8 and 9 here)

Discussion

Effect of pikas disturbance and patchiness on soil hydrothermal properties

This study indicated evident response of soil hydrothermal properties to pikas disturbance and patchiness. Consistent with previous studies which demonstrated that pikas burrowing activity increased water infiltration rate (Hogan, 2010; Wilson and Smith, 2015), our results also showed that soil saturated hydraulic conductivity in pika pile was significantly higher than bald and vegetation patches (Figure 3). It was considered that the increased water infiltration rates on pika-occupied sites reduced local runoff and minimized the potential for down-slope water erosion (Hogan, 2010; Wilson and Smith, 2015). Nevertheless, the increased water infiltration was unable to increase soil moisture under pika pile. For example, soil moisture under pika pile was approximate 10% lower than intact grassland and above pika tunnel (Figure 3). Our result was discrepant with previous studies reported old pika mound had the highest soil moisture during the summer (Ma et al., 2018) and moderate pika burrowing activities increased surface soil moisture (Li and Zhang, 2006). This difference may be contributed to the high pika density in alpine meadow (Guo et al, 2017). Moreover, pika piles were loose (Figure 5) with less vegetation cover (Figure 7), which was not beneficial for soil moisture storage. Previous studies had reported that the soil compaction of bald patches decreased the rate of water infiltration (Wuest et al., 2006; Wilson and Smith, 2015). Our results also found that bald patches had less saturated soil hydraulic conductivity (Figure 4). In addition, soil moisture under bald patches was less than other surface types as well (Figure 3b). Low vegetation cover under bald patches was not beneficial for water retention and utilization, where most of soil water was mainly lost as a way of evaporation (Yi et al., 2014). Soil temperature under pika pile and bald patches was approximate 1 to 3 °C higher than intact grassland (Figure 3), which mainly resulted from the heterogeneity of surface albedo, surface soil water retention and heat conduction properties (Beringer et al., 2005; Pielke, 2005; You et al., 2017). It was suggested that pikas disturbance create a better soil temperature buffer for them to avoid the extreme cold in winter (Ma et al., 2018), whereas high soil temperature under bald patch was a disadvantage for the recovery of vegetation.

Effect of pikas disturbance and patchiness on ecosystem carbon and nitrogen

It was reported that pikas burrowing activities increased oxygen content in deep soil, which contributed to the decomposition of soil organic matter (Martin, 2003). The deposition of urine and feces by small herbivorous mammals could also promote ecosystem nutrition circulation (Clark et al., 2005). Indeed, SOC and TN densities reached up to 14.54 and 0.98 kg m^{-2} in above pika tunnel, which was 2.45 and 2.10 times, 2.90 and 3.72 times, 2.82 and 3.68 times, and 3.31 and 3.26 times higher than those of intact grassland, bald patches and pika piles (Figure 7), respectively. The consistent results reported that the contents of available soil nutrients around the pikas burrow were higher than those in control sites on an alpine meadow (Zhang et al., 2016). However, we also found that SOC and TN densities under pika pile decreased 13.35 % and 42.93 % than intact grassland. These results indicated that SOC and TN densities showed different response to pikas disturbance under their piles and burrows. Therefore, it was improper to evaluate the effect of pikas disturbance on SOC based only on the results from their piles or burrows. Different from pikas disturbance, patchiness caused evident loss of SOC and TN (Figure 6) due to decreasing in C input from vegetation and increasing in C output from soil erosion (Qin et al., 2018). Given the large area covered by bald patches in alpine grasslands (Yi et al., 2016), patchiness was more susceptible to erosion and exert greater influence on soil C loss than pikas disturbance. Recent study has also reported that bald patches of various sizes on the grasslands played a much more important role than pikas direct disturbance in reducing vegetation cover, aboveground biomass, soil carbon and nitrogen (Yi et al., 2016).

Effect of pikas disturbance and patchiness on ecosystem respiration

Field observation explained excreta deposited by pikas and frequently haunted in or near their burrows supplied organic C available to microbial decomposition with an increase in ecosystem CO_2 emission (Cao et al., 2004). Our results also found high SOC and TN under pika tunel (Figure 6). However, no significant difference of Re was found between intact grassland and above pika tunnel, while Re under pika pile and bald patches were less than intact grassland and above pika tunnel (Figure 8). The similar result was also found in an alpine meadow on the QTP (Peng et al., 2015), which indicated that ecosystem respiration decreased with increasing of pika holes because of grassland biomass regulated soil C and N with increasing number of pika holes. These results confirmed that pikas disturbance did not increase ecosystem carbon emission directly, but facilitated CO_2 emission into the atmosphere through pika holes (Qin et al., 2015a), while patchiness clearly resulted in significant reduction of ecosystem carbon emission. Nevertheless, the decline of ecosystem respiration induced by pikas disturbance and patchiness did not completely offset the sequestration of C fixed by photosynthesis because of the lower vegetation cover under bald patches and pika piles.

Most previous studies showed that soil temperature explained most of the temporal variation of ecosystem respiration on the alpine grassland on the QTP (Lin et al, 2011; Qin et al., 2015c; Zhang et al., 2017). However, no an obvious relationship between Re and soil temperature was found in the present study (Figure 9), which suggested that other factors involved in controlling Re induced by pikas disturbance and patchiness. Our results showed that Re were positively correlated with soil moisture, soil total nitrogen, aboveground and belowground biomass (Figure 9). Pikas disturbance and patchiness led to the drying and loosening of soil (Figure 3 and 5). It was considered that loose, dry surface sediments and strong winds were the primary factors responsible for soil erosion (Dong et al., 2010b) and wind erosion was especially common in arid and semi-arid regions (Figure 2; Zhang and Dong, 2014). This resulted in the reduction of soil organic carbon, total nitrogen and vegetation biomass (Figure 6 and 7). The decreasing in autotrophic respiration accompanied with reduction of vegetation biomass was one potential mechanism for the decrease of Re. Meanwhile, pikas disturbance and patchiness affected ecosystem carbon and nitrogen storage by altering input rates of organic matter produced by plant assimilation, decreasing soil organic carbon and total nitrogen available to microbial decomposition, and thus decreasing ecosystem respiration.

Conclusions

In this study, we investigated soil physicochemical properties, vegetation biomass and ecosystem respiration (Re) under six underlying surfaces originating from pikas disturbance and patchiness. We also analyzed the dominant factors regulated the Re. Our results showed that pikas disturbance and patchiness decreased soil moisture but increased soil temperature, which may be conducive to pikas survive in cold season but disadvantage for vegetation growth. Patchiness caused evident decreasing in SOC and TN density, while both SOC and TN density showed different response under pika piles and burrows. Both pikas disturbance and patchiness decreased ecosystem carbon emission, and ecosystem respiration sharply correlated with soil moisture, TN and vegetation biomass. Our results indicated that pikas disturbance and patchiness led to the changing of ecosystem respiration process owing to the drying of soil and the reduction of substrate supply. However, the decline of ecosystem respiration may not able to offset the sequestration of C fixed by photosynthesis.

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Table 1. ANOVA results of the effect of patches fragmentation and small mammal activities on soil temperature, soil moisture and ecosystem respiration.

	Soil temperature			Soil moisture			Ecosystem respiration		
	June	July	August	June	July	August	June	July	August
F	8.614	10.955	1.806	387.472	210.878	97.060	5.270	10.447	8.855
P	<0.001	<0.001	0.106	<0.001	<0.001	<0.001	0.001	<0.001	<0.001

Table 2. ANOVA results of the effect of patches fragmentation and small mammal activities on soil hardness, aboveground biomass, belowground biomass, soil hydraulic conductivity, SOC and TN density.

	Soil hardness	Aboveground biomass	Belowground biomass	Saturated hydraulic conductivity	SOC density	TN density
F	81.506	6.193	12.925	2.752	145.942	50.567
P	<0.001	0.002	<0.001	0.027	<0.001	<0.001

Figure legends

Figure 1. An aerial photo of field observation of ecosystem respiration at six surface types: (1) Large bald patch (LP), (2) Medium bald patch (MP), (3) Small bald patch (SP), (4) Intact grassland patch (IG), (5) above pika tunnel (PT) and (6) old Pika pile (PP).

Figure 2. Daily air temperature and precipitation of the study site.

Figure 3. Soil temperature and soil moisture under different surface types: (1) large bald patch (LP), (2) medium bald patch (MP), (3) small bald patch (SP), (4) intact grassland patch (IG), (5) above pika tunnel (PT) and (6) old pika pile (PP).

Figure 4. Soil saturated hydraulic conductivity (SHC) under different surface types: (1) large bald patch (LP), (2) medium bald patch (MP), (3) small bald patch (SP), (4) intact grassland patch (IG), (5) above pika tunnel (PT) and (6) old pika pile (PP).

Figure 5. Soil hardness under different surface types: (1) large bald patch (LP), (2) medium bald patch (MP), (3) small bald patch (SP), (4) intact grassland patch (IG), (5) above pika tunnel (PT) and (6) old pika pile (PP).

Figure 6. Soil organic carbon (SOC) (a) and total nitrogen (TN) (b) density of different surface types: (1) large bald patch (LP), (2) medium bald patch (MP), (3) small bald patch (SP), (4) intact grassland patch (IG), (5) above pika tunnel (PT) and (6) old pika pile (PP).

Figure 7. Aboveground biomass (AGB) (a) and belowground biomass (BGB) (b) under different surface types: (1) large bald patch (LP), (2) medium bald patch (MP), (3) small bald patch (SP), (4) intact grassland patch (IG), (5) above pika tunnel (PT) and (6) old pika pile (PP).

Figure 8. Ecosystem respiration of different surface types: (1) large bald patch (LP), (2) medium bald patch (MP), (3) small bald patch (SP), (4) intact grassland patch (IG), (5) above pika tunnel (PT) and (6) old pika pile (PP).

Figure 9. The relationships between ecosystem respiration and biotic and abiotic factors

518 **Figure 1.**

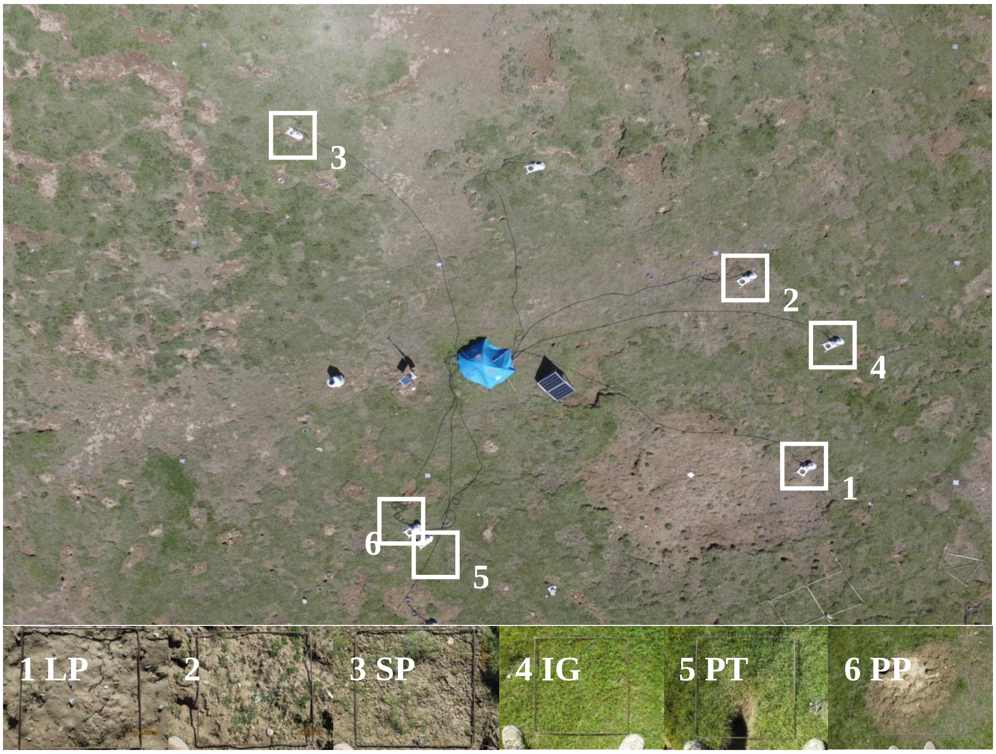


Figure 2.

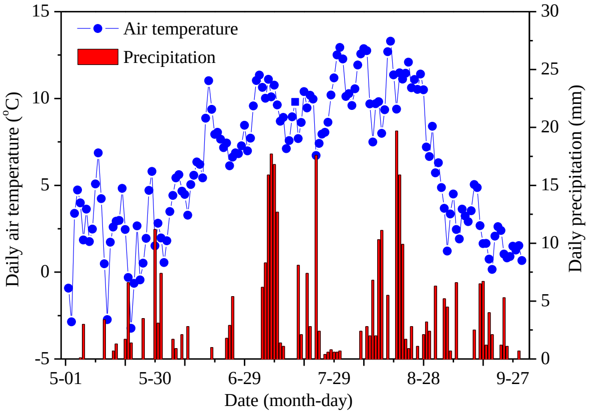
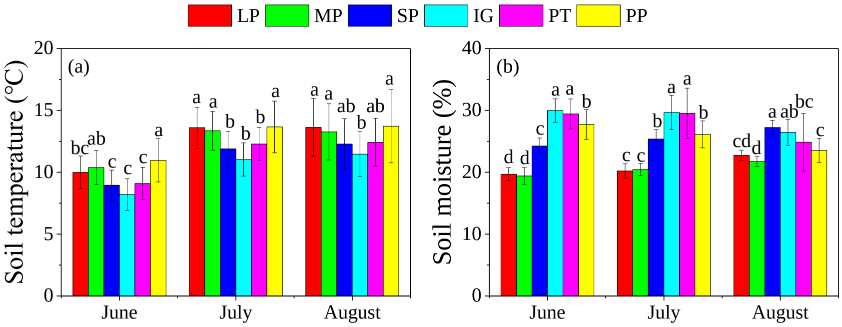
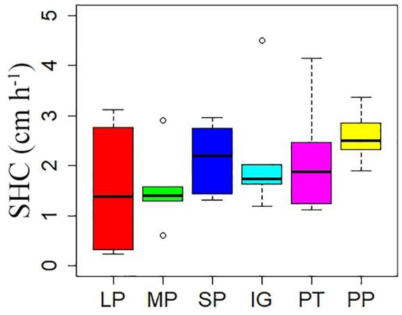

Air temperature
Precipitation
Daily air temperature (°C)
Daily precipitation (mm)
15
10
5
0
-5
30
25
20
15
10
5
0
5-01
5-30
6-29
7-29
8-28
9-27
Date (month-day)

Figure 3.


LP
MP
SP
IG
PT
PP
(a)
Soil temperature (°C)
0
5
10
15
20
bc ab c c c a
a a b b b a
a a ab b ab a
June
July
August
(b)
Soil moisture (%)
0
10
20
30
40
d d c a a b
c c b a a b
cd d a ab bc c
June
July
August

527 **Figure 4.**



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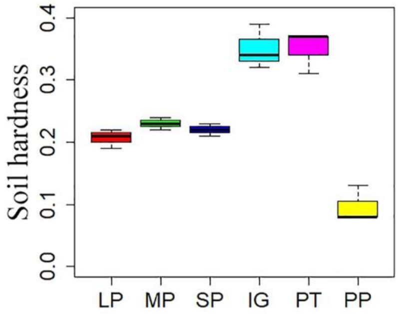
530 **Figure 5.**



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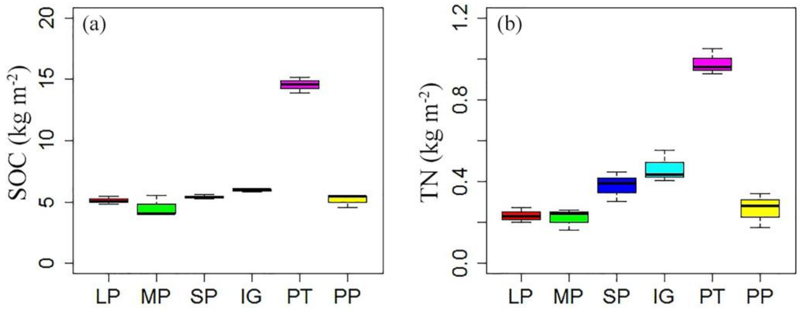
532 **Figure 6.**



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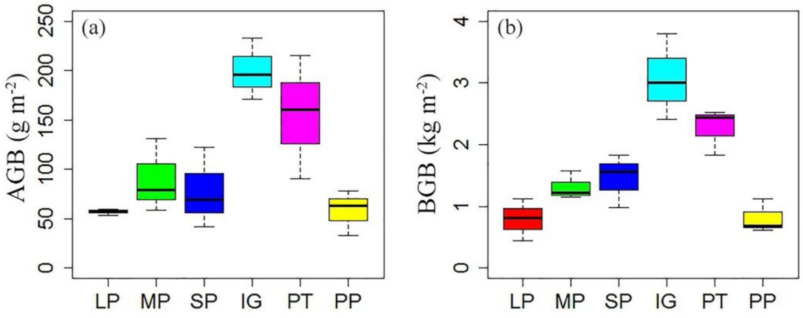
534 **Figure 7.**



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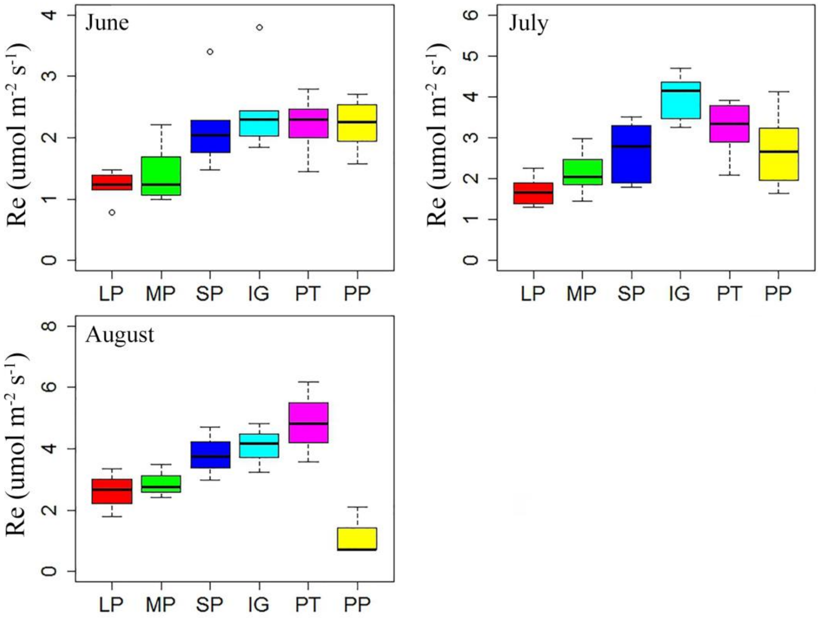
537 **Figure 8.**



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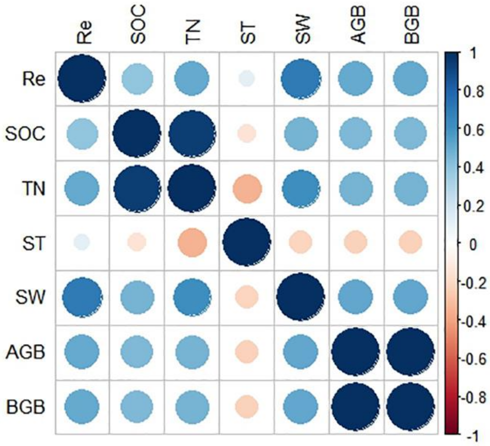

539 **Figure 9.**