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Climate change drivers alter root controls over litter decomposition in a semi-arid grassland

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ABSTRACT

Plant roots are the primary source of soil organic carbon (C) and critically support the growth and activities of microbes in the rhizosphere. Climate change factors may, however, modify root-microbial interactions and impact C dynamics in the rhizosphere. Yet, the direction and magnitude of interactive climate change effects, as well as the underlying mechanisms, remain unclear. Here we show evidence from a field experiment demonstrating that warming and precipitation changes strengthen root controls over litter decomposition in a semi-arid grassland. While warming and precipitation reduction suppressed microbial decomposition of root litter regardless of the root presence, precipitation increase stimulated litter decomposition only in the absence of roots, suggesting that plant competition for water constraints the activities of saprophytic microbes. Root presence increased microbial biomass but reduced microbial activities such as respiration, C cycling enzymes and litter decomposition, indicating that roots exert differential effects on microbes through altering C or water availability. In addition, nitrogen (N) input significantly reduced microbial biomass and microbial activities (respiration). Together, these results showed that alterations in soil moisture induced by climate change drivers critically modulate root controls over microbial decomposition in soil. Our findings suggest that warming-enhanced plant water utilization, combined with N-induced suppression of microbes, may provide a unique mechanism through which moderate increases in precipitation, warming and N input interactively suppress microbial decomposition, thereby facilitating short-term soil C sequestration in the arid and semi-arid grasslands.

1. Introduction

Roots are the vital organ of terrestrial plants, supporting the aboveground plant and acquiring nutrients and water that are essential to plant growth. While live roots provide energy sources and favorable habitats for soil organisms (Wardle et al., 2004), root-derived organic materials (root deposition and dead roots) are also the primary source of soil organic carbon (C) (Gill and Jackson, 2000; Rasse et al., 2005; Sokol and Bradford, 2019), the largest active C pool on the Earth's surface (Chapin et al., 2011). Roots play a particularly important role in soil C dynamics in grasslands where plants allocate more than 50 percent of the net primary production (NPP) belowground (Chapin et al., 2011). Compared to the entire root system, fine roots (≤2 mm in diameter) usually have a higher turnover rate. The rapid turnover of fine roots in the grasslands (ca. 50% annually) brings high labile litter input to soil (Gill and Jackson, 2000). Fine roots are estimated to contribute about one third of the annual plant litter input in grasslands (Freschet et al., 2013). In addition, live fine roots affect dead root decomposition through modifying the surrounding soil environment. For example, live roots provide energy-rich labile C to microbes and stimulate microbial

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growth and enzyme production, enhancing microbial decomposition of indigenous soil organic matter (i.e., the priming effect) (Bastida et al., 2019; Cheng et al., 2014; Fontaine et al., 2007). Alternatively, live roots may out-compete saprophytic microbes for limiting resources such as nutrients and water (Chen et al., 2013; Hu et al., 2001) and reduce microbial growth and enzyme production (Cheng and Kuzyakov, 2005; Dijkstra et al., 2013; Malik et al., 2019), suppressing litter decomposition (Fig. 1).

Climate change factors may, however, alter interactions between roots and soil microbes (Bennett and Klironomos 2019; Pugnaire et al., 2019) and thus affect the decomposition of root-derived litter in soil (Hopkins et al., 2013). For example, root-induced rhizosphere priming may increase the temperature sensitivity of microbial decomposition (Hopkins et al., 2014; Zhu and Chen, 2011). Also, precipitation increase and reactive nitrogen (N) input can modulate root-microbial interactions directly through increasing water and/or nutrient availability that are required for microbial production of enzymes associated with litter decomposition (Schimel and Bennett, 2004) (Fig. 1). When water is plentiful and plants actively exploit soil nutrients, microbial growth in the rhizosphere is often limited by low availability of nutrients (N in particular). In arid and semi-arid ecosystems, however, water often functions as a primary limiting factor to microbes (Austin, 2011; Jackson et al., 1989), which further modulates the priming effect (Dijkstra and Cheng, 2007). In a semiarid temperate steppe, for example, Liu et al. (2009) showed that warming reduced soil water availability through increasing evapotranspiration, and subsequently suppressed microbial biomass and microbial respiration. Furthermore, climate change factors such as N input, warming and precipitation changes may alter plant photosynthate allocation belowground, and root growth, turnover and exudation, indirectly influencing microbial growth and activities (Coskun et al., 2017; Kuzyakov, 2010). Although climate change factors are known to modulate the impact of live roots over root litter decomposition via various mechanisms (Fig. 1), few experiments have directly characterized these effects, particularly in the field settings (Cheng et al., 2014).

Litter decomposition is an enzyme-mediated process that critically controls C turnover and balance, and nutrient cycling in terrestrial ecosystems, and represents an important source of CO_2 to the atmosphere (Hobbie, 1992; Wieder et al., 2013). Climate change factors such as warming, N input and rainfall change can critically affect decomposition (Bradford et al., 2016; Coûteaux et al., 1995; Silver and Miya, 2001). For example, N input often suppresses soil microbial growth (Treseder, 2008; Zhang et al., 2018), microbial enzyme activities, and CO_2 release (Chen et al., 2018; Liu and Greaver, 2010). Also, warming has been shown to alter the composition, biomass, activities and C use efficiency of the soil microbial community (Frey et al., 2013; Melillo et al., 2017; Sheik et al., 2011). Similarly, rainfall regime influences microbial growth and microbial decomposing activities (Austin, 2011; Martiny et al., 2017; Ren et al., 2017). Moreover, environmental change drivers may interact to affect plant-microbial interactions, microbial C utilization, and litter decomposition (Carrillo et al. 2018; Hu et al. 2001). For example, water availability critically affects the effects of warming and nutrient additions on microbial decomposition (Allison and Treseder, 2008; Quan et al., 2019; Zhong et al., 2017). A recent study has shown that enhanced summer warming reduced fungal decomposer diversity and litter mass loss more strongly in dry than in wet tundra (Christiansen et al., 2016). Nutrient (N in particular) availability may also mediate the impact of warming on microbial growth and activities (Conant et al., 2011). Although many studies have examined the direct effect of environmental changes on microbial decomposition (Christiansen et al., 2016; Liski et al., 2003; See et al., 2019), limited work has assessed how climate change factors affect litter decomposition through affecting the rhizosphere priming in field, particularly in arid systems where roots and microbes likely compete for

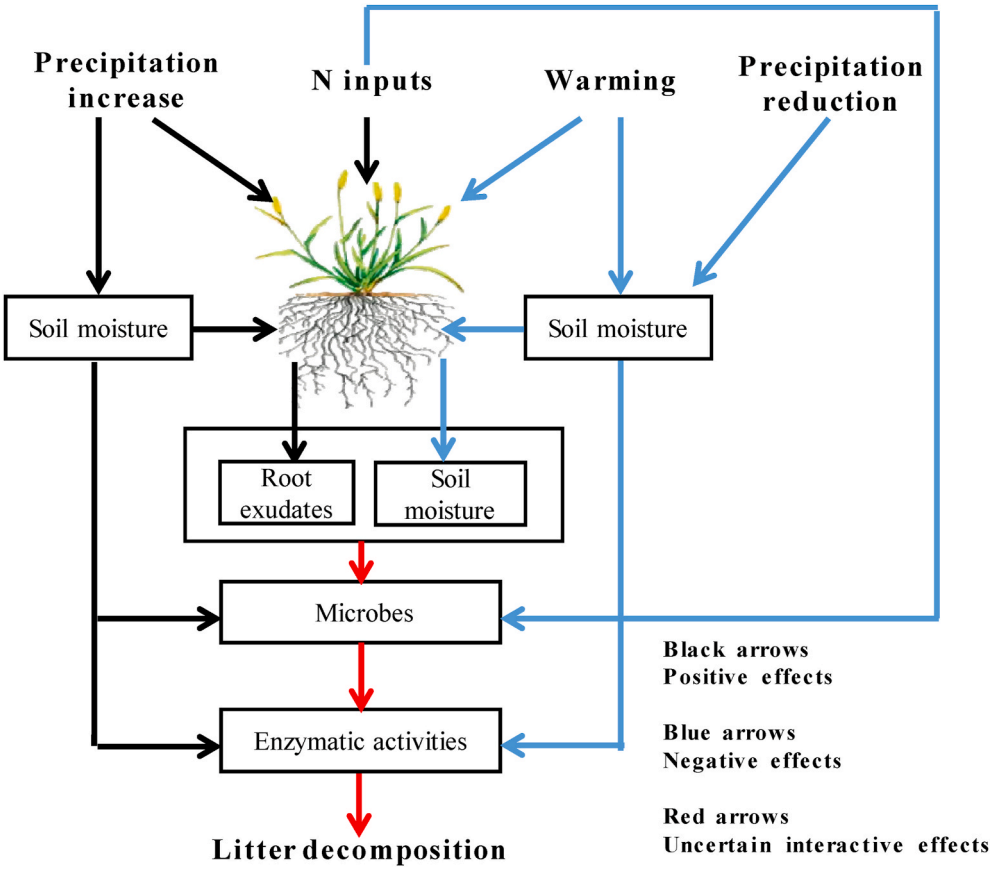

Fig. 1. A conceptual framework of interactive effects of precipitation alterations, warming and N input on root controls over microbial litter decomposition.

the limited water.

Understanding the effects of climate change factors on litter decomposition and C dynamics in arid and semiarid grasslands is particularly important as these grasslands cover ca. 40% of the Earth's land surface (White et al., 2000). Many semi-arid grasslands are experiencing climate warming and increased N deposition, as well as more periodic and extreme precipitation events (Jansson and Hofmockel, 2019). Also, arid and semi-arid grasslands have greater root:shoot ratios (Mokany et al., 2006), store relatively more organic C belowground (Chapin et al., 2011; Gill and Jackson, 2000), and are more sensitive to the climate change (Schröter et al., 2005; White et al., 2000) than other terrestrial ecosystems.

Taking advantage of a field experiment manipulating multi-climate change factors (namely, warming, N input and altered precipitation), we examined how these climate change drivers modulate the root control over litter decomposition in a semi-arid grassland on the Loess Plateau, Northwestern China. We hypothesized that (1) alterations in soil moisture in response to warming and precipitation change would exert a dominant effect on litter decomposition, (2) live roots would modulate microbial growth and microbial decomposition through controlling root exudation and soil moisture, (3) warming and precipitation reduction would promote root-mediated suppression of litter decomposition through reducing soil moisture, microbial growth and enzyme activities, and (4) precipitation increase and N input would enhance the rhizosphere priming of litter decomposition through promoting root growth and microbial activities.

2. Materials and methods

2.1. Site description

The study was conducted in a semi-arid grassland in Yunwu Mountains Natural Preserve (106°21′–106°27′E, 36°10′–36°17′N, 1800–2000 m a.m.s.l.) on the Loess Plateau, Guyuan, Ningxia Hui Autonomous Region, China. The sanctuary has been fenced since 1982 and the region is characterized by a semi-arid continental climate with an average annual temperature of 7.01 °C, the maximum mean monthly temperature at 22–25 °C in July and the minimum at −14 °C in January. Mean annual precipitation in that area is about 425 mm, with 60–75% of which being in July–September, and mean annual potential evaporation is 1330–1640 mm.

Three plant species, *Stipa grandis*, *Stipa przewalskyi* and *Artemisia sacrorum*, dominate the vegetation in this area, accounting for over 70% of the total aboveground biomass (Su et al., 2019). The type of soil is a mountain gray-cinnamon soil classified as a Calci-Orthic Aridisol according to the Chinese taxonomic system, equivalent to a Haplic Calcisol in the FAO/UNESCO system.

2.2. Field manipulation treatments

The field manipulation experiment included three (3) levels of precipitation (precipitation reduction by 30% (Pr), ambient (P0) and precipitation increase by 30% (Pi)), two (2) levels of warming (ambient (i.e. Unwarmed) and warming (Warmed)), and two (2) levels of N inputs (without N input and 12 g m $^{-2}$ yr^{-1} added N). A total of 12 field manipulation treatments (3 × 2 × 2) were then formed, and was arranged into a complete block in field with 4 replicates (Fig. 2a). The plots were 4 m × 4 m in size and 1.5 m away from each other within each block. The distance between each block was 5 m at least. Open top chambers (OTCs) with a maximum basal diameter of 150 cm were used (Fig. 2b), following the International Tundra Experiment (ITEX) protocol (Waldrop and Firestone 2006), to increase air temperatures in warming plots. Nitrogen (12 g N m^{-2} y^{-1}) was added as urea solution twice each year (6.0 g N m^{-2} y^{-1} each in May and June). In each Pr plot (n = 16 in total), a rain shelter was installed to intercept approximately 30% of precipitation. The rain shelter consisted of seven v-shaped transparent plexiglass and an iron hanger, which was placed 1 m above the soil surface in the south side and 1.5 m on the north side (Fig. 2c). Intercepted rain in each Pr plot was collected and then added into the nearest Pi plot, forming 16 pairs in total.

2.3. Field experimental design: randomized complete block split-plot design

Within each field plot, we installed two root-ingrowth chambers (one with 30 μm mesh for root exclusion, and another with 1 mm mesh allowing root penetration) (Fig. 2d). A split-plot design was then formed with the precipitation change, warming and N input being the three main plot factors and root (absence or presence) as the subplot factor (Jones and Nachtsheim, 2009). Consequently, there was a total of 24 (12 × 2) treatment combinations with 4 replicates for each combination, totaling 96 root chambers.

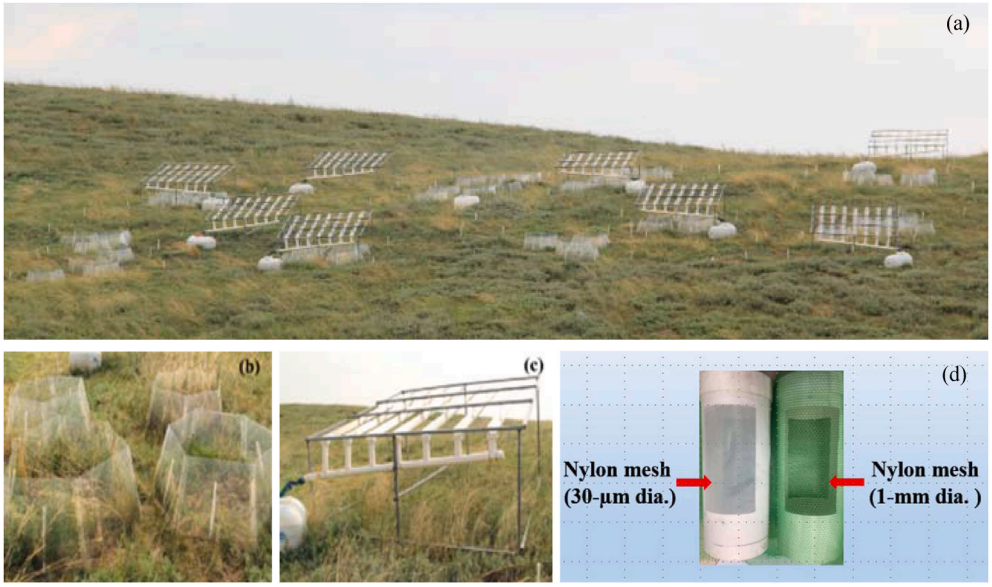

Fig. 2. The panoramagram of the field setup (a), open-top chambers for warming (b), and precipitation interception apparatus (c), and root-ingrowth chambers (d).

2.4. Preparation of root-ingrowth chambers

Roots of *Stipa grandis* and the topsoil sample (0–20 cm) were collected from the vicinity of the field experimental plots in early May 2017. All root materials (root diameter < 1 mm) were gently washed in tap water to remove soil particles and organic debris. They were air-dried to a constant weight at room temperature, and then cut into small pieces (2–3 cm) and thoroughly mixed. The topsoil sample was air dried and passed through a 1 mm sieve, and all visible organic materials (including live and dead roots) were removed to achieve maximum homogeneity. Subsamples (five each for the root material and the topsoil sample) were oven-dried at 70 °C for 48 h (for root) and 105 °C for 24 h (for soil) to determine their water contents.

We selected root-ingrowth chambers to assess root effects on litter decomposition for three reasons. First, although aboveground plant materials have often been used in the literature, it is root materials that are decomposed in soil, as most of aboveground litter in field has been decomposed by microbes before moving into soil (Sokol and Bradford, 2019). Second, the protection of soil matrix is key for high root contribution to the soil organic matter (Nguyen, 2003; Xia et al., 2015) and placing the soil-litter mixture into the root ingrowth chambers can avoid lumping litter materials together that usually happens in litterbags. Finally, placing litter materials into litterbags departs from *in situ* conditions, and likely underestimates fine-root decay rates (Dornbush et al., 2002). In comparison, root-ingrowth chambers allow root penetration and minimize disturbances to roots, soil, and rhizosphere microbes inside, providing an improved alternative for measuring root effects on litter decomposition. The root-ingrowth chambers made of PVC cylinders (12 cm height, 5 cm diameter) included two rectangular windows covering 65% of the total surface area (Cheng et al., 2012). The windows were then covered with nylon mesh (1 mm or 30 μm mesh size) to allow or prevent root penetration (Fig. 2d). The bottom of all chambers was sealed to prevent physical loss of litter particles. A root-soil mixture of 3.3 g air-dried roots and 190 g root-free topsoil (exactly equivalent to 2.0% dry root to dry soil) was placed into each chamber. The root-soil mixture was compressed with a metal bar to obtain a bulk density similar to that of undisturbed soil before the chamber were inserted 10 cm into the soil. In May 2017, two soil cores with the same size of the ingrowth chamber were randomly collected from each plot, and two chambers covered with different types of mesh (one each with 1 mm or 30 μm mesh size) were put into the holes left by soil sampling. This led to 96 root-ingrowth chambers in total.

Soil moisture and temperature were measured using two different approaches. The first approach was continuous measurements using SIN-R6000C (Hangzhou Liance Automation Technology Co., Ltd., Hangzhou, China). The second approach was to record field soil temperature and moisture (at 10 cm depth) of each plot once every week when soil respiration was measured. In the latter case, soil temperature was measured by a portable temperature meter and soil moisture was measured by TDR-100 (Spectrum Technologies, Inc., Plainfield, IL, USA).

2.5. Root and soil sampling and measurements

In September 2017, all root-ingrowth chambers were collected to estimate decomposition during the growing season. Collected chambers were placed on dry ice and delivered to Nanjing Agricultural University, Nanjing by the express mail. Live plant roots were collected from each chamber by passing the soil-litter mixture through a 1 mm sieve. Dead roots were distinguished from live roots based on the color and root tip of the fine roots (Fiala et al., 2017; Santantonio et al., 1987). Live roots have "white stele and turgid and unbroken root tips", while dead roots have "brownish stele and broken root tips". Collected roots were gently washed in tap water to remove any soil particles and then oven-dried to constant mass at 70 °C. The decomposition rate was calculated as mass remaining:

$$\text{Mass remaining } (\%) = M_t / M_0 \times 100\%,$$

Where M_t is the mass of the decomposing root litter at time t, and M_0 is the mass of the initial root litter (equivalent to 3g dry litter). Part of the sieved soil was immediately stored at −20 °C for subsequent analysis of the microbial community composition. The remaining sieved soil was stored at 4 °C for determinations of soil moisture, NO_3–N, microbial biomass C (MBC), microbial respiration and microbial enzyme activities. Soil moisture was determined by drying at 105 °C for 24 h. 12.5 g fresh soil was extracted with 50 mL 0.5 M K_2SO_4. Soil NO_3–N contents in the extracts were determined using a flow injection auto-analyzer (Skalar SAN Plus, Skalar Inc., Breda, The Netherlands).

2.6. Determinations of soil microbial biomass and activity (respiration), and soil enzyme activities

Microbial biomass C (MBC) was determined by the chloroform fumigation-extraction method (Vance et al., 1987). Briefly, a subsample (12.5 g fresh sieved soil) from each field sample was fumigated with ethanol-free chloroform for 48 h. Another subsample of 12.5 g was used as a non-fumigated control. Both fumigated and non-fumigated soils were extracted with 0.5 M K_2SO_4 solution and their dissolved organic C concentrations were determined by a Elementar TOC analyzer (Elementar Vario TOC cube, Hanau, Germany). The measured organic C was converted to MBC using conversion factor $k_{ec} = 0.33$. Soil microbial activity was determined by quantifying the CO_2 release during the 7-d incubation in dark (Hu and van Bruggen, 1997). The respired CO_2 was collected at the end of the incubation and determined by gas chromatography (Agilent Technologies 7890B, Palo Alto, CA, USA). The activities of C-hydrolase (Cellobiohydrolase, α-1,4-glucosidase, β-1,4-glucosidase, β-1,4-xylosidase) were measured using microplate fluorometric assay according to the protocol of (Bell et al., 2013).

2.7. Statistical analyses

To test the treatment effects on each parameter, linear mixed models (y ~ N*W*PRE*Root+(1|Block/plot)) were used with N input (N), precipitation (PRE), warming (W), root (Root) and their interactions as fixed effects, and block and plot were included as random effects with plot nested within block (mixed effects model; lmer function from the lme4 package). In this model, we used F tests to assess the evidence for how each fixed effect and interaction influenced the response variable, which is a practice that has been extensively used (Harris et al., 2020; Leverkus and Crawley, 2020; Wu et al., 2020). The complete ANOVA table for the 4-factor split-plot design in this study was listed in Table S1. The tested soil parameters include soil moisture in chambers, litter mass remaining, MBC, soil microbial respiration and C-acquiring enzyme activities (the sum of cellobiohydrolase, α-1,4-glucosidase, β-1,4-glucosidase, β-1,4-xylosidase).

We used linear mixed models with precipitation (PRE), warming (W), N input (N) and their interactions as fixed effects and block as random effects to test for treatment effects on soil NO_3–N, soil moisture and soil temperature. The Tukey's HSD test was used for post hoc comparisons of factors with more than two levels (glht function from the multcomp package). To interpret significant interactions, we used a simple main effects test (García-Palacios et al., 2016). Data were divided into subsets based on one of the factors of the interaction and were then subjected to ANOVA as appropriate (García-Palacios et al., 2016). In this study, we found that precipitation and plant roots significantly affected the decomposition of litter (Table 1). Therefore, the PRE × Root interaction was further analyzed. A separate ANOVA was conducted at each precipitation level to interpret the (marginally) significant PRE × Root interaction on several parameters (i.e., litter mass remaining ($P = 0.075$), microbial biomass C ($P < 0.05$) and C-acquiring enzyme activities ($P < 0.05$), Table 1). In addition, linear regression analysis was used

Table 1
P-values of four-way ANOVA on the effects of precipitation (PRE), warming (W), nitrogen input (N), and root (Root) on microbial biomass C (MBC), soil microbial respiration, C-acquiring enzyme activities and litter mass remaining.

Source of variation	Microbial biomass C	Soil microbial respiration	C-acquiring enzyme activities	Litter mass remaining
Among plots				
PRE	**0.003**	< **0.001**	0.378	< **0.001**
W	0.552	< **0.001**	0.109	**0.031**
N	**0.004**	< **0.001**	0.297	0.568
W × PRE	0.141	**0.025**	0.171	0.638
N × PRE	0.381	0.843	**0.028**	0.322
N × W	0.409	0.993	0.113	0.889
N × W × PRE	**0.039**	0.166	0.297	0.078
Within plots				
Root	< **0.001**	0.381	< **0.001**	< **0.001**
PRE × Root	**0.021**	0.149	**0.036**	0.075
W × Root	0.360	0.543	0.533	0.231
N × Root	0.434	0.186	0.051	0.242
N × W × Root	0.141	0.598	0.417	0.068
N × PRE × Root	0.544	0.589	0.159	0.628
W × PRE × Root	0.489	0.600	0.154	0.124
N × W × PRE × Root	**0.011**	0.939	0.139	0.266

to assess the responses of microbial respiration and mass remaining to soil moisture in root-ingrowth chambers.

We tested the normality of residual distribution and homogeneity of variances, and ln-transformed the data when necessary. All statistical analyses were performed using the R software version 4.0.2 (R Development Core Team, 2020).

3. Results

3.1. Climate manipulation effects on soil abiotic properties and root exclusion effects on root biomass

Soil moisture and temperature showed different trends of dynamics across the growing season. Soil moisture was highest at the end of the growing season when more rain events occurred (Fig. S1a). In contrast, soil temperature increased from the beginning of May to the highest in mid-July and then began to decline (Fig. S1b). Precipitation treatments had a significant effect on soil moisture (Table S2). Across the growing season, soil moisture under precipitation increase (Pi, n = 4) were 24% higher than under precipitation reduction (Pr, n = 4) (Fig. S2a). In addition to precipitation reduction, warming and plant roots also reduced soil moisture in root-ingrowth chambers (Fig. S3). In contrast, warming effect on soil temperature was dependent on the method and timing of the measurements. The weekly measurement by a portable temperature meter between 10 and 11 a.m. in the morning did not show a significant warming effect (Fig. S2b; Table S2). This null effect of warming was different from the significant increase (ca. 1.17 °C) obtained with continuous monitoring in field over the same time (Fig. S1b and Fig. S2b), suggesting that the effect of OTC on soil temperature may accumulate during the day but subside during the evening. Nitrogen input did not affect soil moisture and temperature, but significantly increased soil NO_3–N during the 2017 growing season (Fig. S4; Table S2). Root exclusion mesh effectively prevented root growth inside the chamber: The average live root biomass in root-ingrowth chambers (1-mm mesh) was at 0.07 g in dry weight, equivalent to 35.67 g m^{-2}, while no visible newly-grown roots were observed in chambers covered with the 30-μm mesh.

3.2. Effects of the climate manipulations and plant roots on microbial biomass C, soil microbial respiration, and microbial C-acquiring enzyme activities

Precipitation, warming, N input and plant roots differently affected microbial biomass C (MBC) (Table 1). Precipitation increase and root presence significantly increased MBC, and there was also a significant interaction between precipitation and plant roots (Fig. 3a; Table 1). Plant roots significantly increased MBC under ambient and precipitation increase treatments, but not in the precipitation reduction treatment. In contrast, warming did not significantly affect MBC, but N input significantly reduced MBC (Fig. 3b; Table 1).

Effects of four factors on soil microbial respiration were different from those on MBC (Table 1). Similar to its effect on MBC, precipitation increase significantly increased microbial respiration (Fig. 4a). In contrast, root presence had no significant effect on microbial respiration, although it increased MBC (Table 1). Also, both warming (Fig. 4b) and N input (Fig. 4c) significantly reduced microbial respiration. In addition, there was a significant interaction between precipitation and warming (Fig. 4b; Table 1). The combination of precipitation reduction and warming (PrW) led to the lowest microbial respiration, regardless of the root presence, indicating that low soil moisture exerted a dominant control.

Precipitation increase significantly enhanced C-acquiring enzyme activities in the absence of roots (Fig. 5a). However, plant roots significantly reduced C-acquiring enzyme activities by 36.4% (Fig. 5a). Warming had no significant effect on C-acquiring enzyme activities (Table 1). There was a significant interaction between N input and precipitation (Fig. 5b; Table 1).

3.3. Effects of the climate factor manipulations and plant roots on root litter decomposition

Precipitation increase significantly stimulated litter decomposition, leading to lower litter mass remaining, but plant root significantly inhibited the decomposition (Fig. 6a). Also, there was a marginally significant interaction between precipitation and root (P = 0.075; Table 1). Precipitation critically modulated the impact of live roots on litter decomposition: live roots significantly reduced litter decomposition by 21.6% and 19.9% in the control and precipitation increase treatments, respectively, but had no effect on litter decomposition in the precipitation reduction treatment (Fig. 6a). Warming significantly inhibited litter decomposition, and reduced the difference in the litter mass remaining between treatments with and without roots (Fig. 6b). N input has no significant effect on litter decomposition (Table 1).

Correlation analysis further showed that litter mass remaining was negatively related to soil moisture in the root-ingrowth chambers, and soil moisture in the root-ingrowth chambers explained 30% of the variation in the mass remaining (Fig. 7a) and 60% of the variation in microbial respiration for all treatments (Fig. 7b).

4. Discussion

Results from our field experiment in a water-limited grassland ecosystem showed that climate change factors, precipitation change and warming in particular, not only directly affected microbial decomposition of root litter in soil, but also altered root mediation of microbial decomposition (Fig. 6a and b; Table 1). Climate change factors may have affected microbial decomposition through modifying the complex interactions between roots and heterotrophic microbes that control microbial enzyme production and enzymatic activities in the rhizosphere (Allison, 2005; Pugnaire et al., 2019).

4.1. Microbial decomposition of litter and impacts of live roots

Litter decomposition is an enzyme-mediated process and

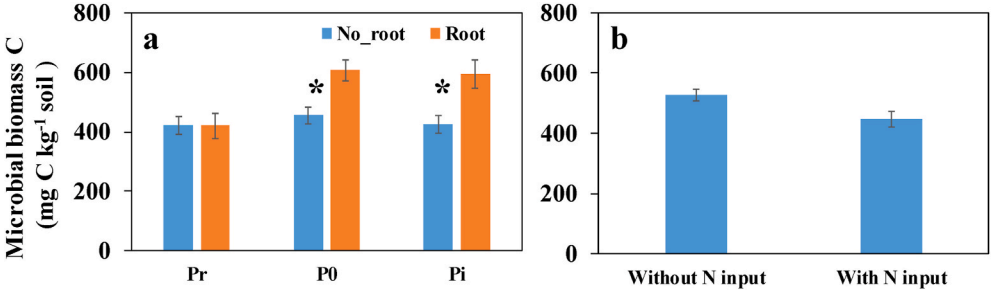

Fig. 3. Effects of live roots on microbial biomass C as influenced by different precipitation treatments (a) (n = 16 for each treatment); Effects of N input on microbial biomass C (b) (n = 24 for each treatment). Vertical bars represent mean values plus standard errors. * represent a significant difference ($P < 0.05$) between different color groups. No_root refers to the absence of roots (i.e., growth chambers with a mesh pore size of 30 μm that prevented root penetration). Root refers to the presence of roots (i.e., root-ingrowth chambers with a pore size of 1 mm that allowed root penetration). Pr represents a combined precipitation reduction treatment (n = 16; 2 warming levels × 2 N input levels × 4 blocks); P0 represents a combined control treatment (n = 16); Pi represents a combined precipitation increase treatment (n = 16). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

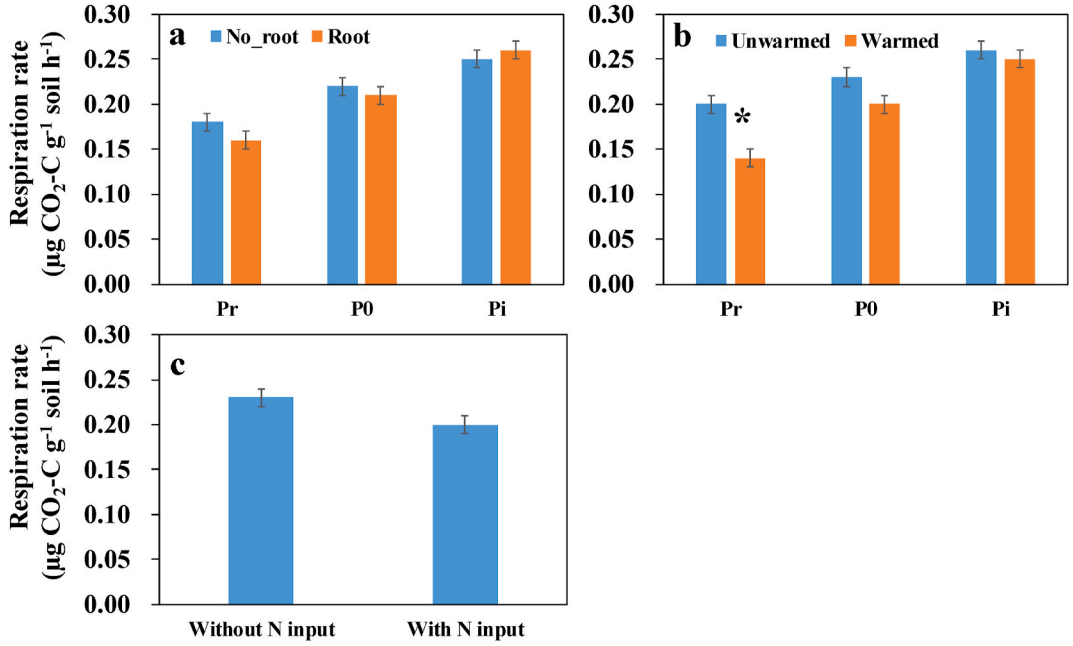

Fig. 4. Effects of live roots (a) and warming (b) on soil microbial respiration rate as influenced by different precipitation treatments (n = 16 for each treatment); Effects of N input on soil microbial respiration rate (c) (n = 24 for each treatment). Vertical bars represent mean values plus standard errors. Abbreviations for the treatments were same as in Fig. 3.

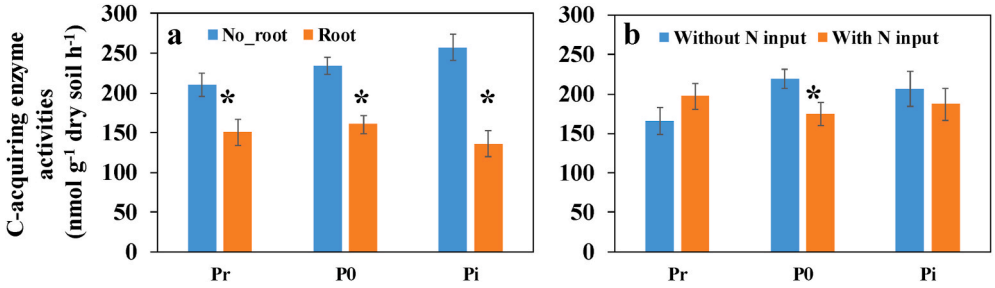

Fig. 5. Effects of live roots (a) and N input (b) on C-acquiring enzyme activities as influenced by different precipitation treatments (n = 16 for each treatment). Vertical bars represent mean values plus standard errors. * represent a significant difference ($P < 0.05$) between different color groups. Abbreviations for the treatments were same as in Fig. 3. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

environmental factors affect both microbial production of enzymes and their activities in soil (Allison et al., 2010; German et al., 2012; Henry et al., 2005; Sinsabaugh et al., 2009). Our results showed, as expected, that water scarcity is the dominant factor controlling litter decomposition in our semi-arid grassland ecosystem, as the release of water constraints under precipitation increase significantly enhanced decomposition (Figs. 6a and 7a). Soil microbes, bacteria in particular, need to attach water films to stay active, and environmental changes that reduce water availability likely suppress microbial activities and decomposition (Dijkstra and Cheng., 2007; Yahdjian et al., 2006). A decrease in the

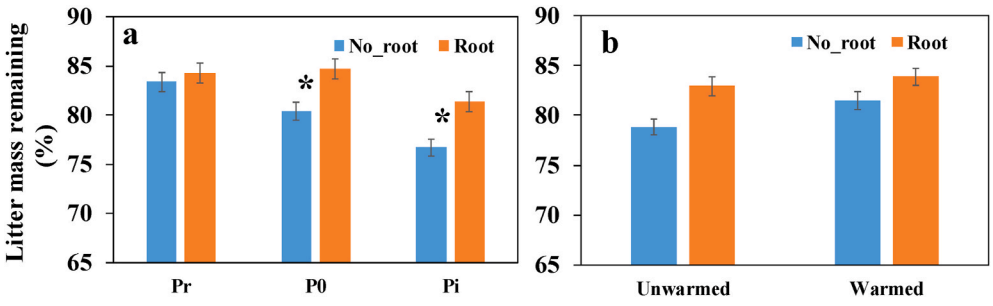

Fig. 6. Effects of live roots on litter mass remaining as influenced by different precipitation treatments (a) (n = 16 for each treatment) and by different warming treatments (b) (n = 24 for each treatment). Vertical bars represent mean values plus standard errors. * represent a significant difference ($P < 0.05$) between different color groups. Abbreviations for the treatments were same as in Fig. 3. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

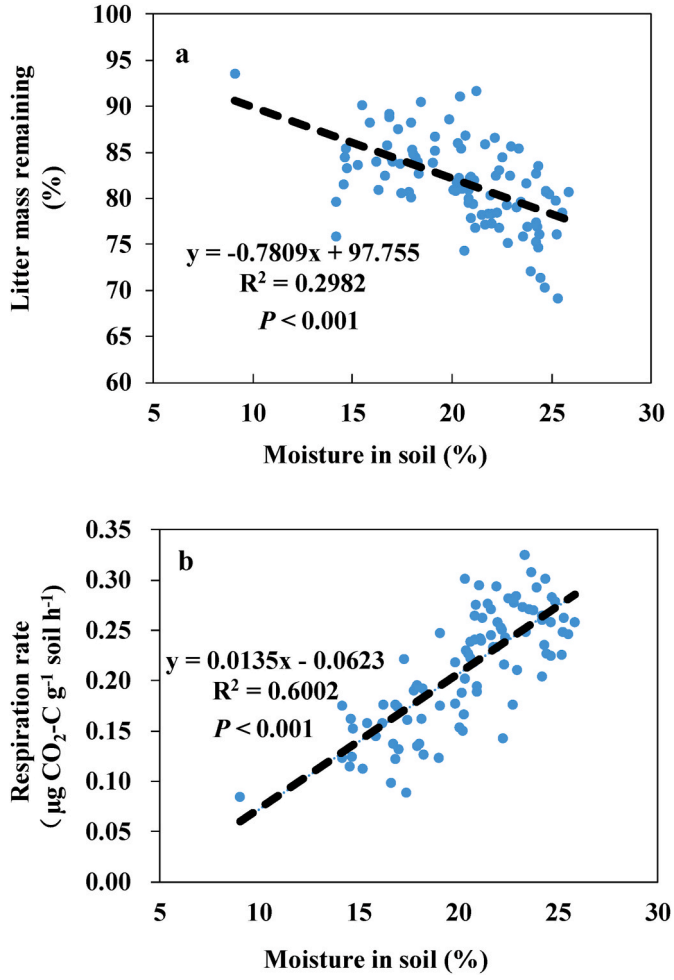

Fig. 7. Relationships between soil moisture in root-ingrowth chambers and litter mass remaining (a) or soil microbial respiration (b).

thickness of water films on soil or litter surfaces likely reduces the diffusion rate of substrates to microbes (Stark and Firestone, 1995) and of enzymes on the decomposing substrates (Allison, 2005; Manzoni et al., 2016). The negative effect of warming on microbial respiration, particularly under precipitation reduction (Fig. 4b; Table 1), indicated that even a low degree of warming may enhance evapotranspiration and reduce soil moisture, constraining the decomposition (Fig. 6b; Table 1). These results are consistent with those from other previous studies (Christiansen et al., 2016; Liski et al., 2003; Liu et al., 2009). When water was not a limiting factor, however, warming may stimulate litter decomposition through promoting microbial growth and enzyme activities (Frey et al., 2013; Hobbie, 1996; Sheik et al., 2011). Strong correlations between soil moisture and microbial respiration (Fig. 7b), and increased MBC and C-acquiring enzyme activities under increased precipitation (Figs. 3a and 5a) observed in our study further support our first hypothesis that changes in soil moisture in response to climate change may dominate C cycling processes, especially in arid and semi-arid ecosystems.

Contrasting to our hypothesis 2, the presence of live roots suppressed litter decomposition, likely through reducing production and activities of microbial enzymes (Fig. 1; Fig. 5a). Soil microbes are, in general, C-limited, and plant roots are often shown to enhance microbial growth and the decomposition of indigenous soil organic matter (i.e., the priming effect) (Fontaine et al., 2007). What is surprising was that although it increased microbial biomass (Fig. 3a), the presence of plant roots significantly inhibited litter decomposition (Fig. 6a; Table 1). This contradicts the results from many other studies (Bastida et al., 2019; Fontaine et al., 2007; Shi et al., 2018) and suggests that other mechanisms rather than root-enhancement of C supplies dominated the root effect on decomposition. One possibility is that microbes may prefer to utilize the readily available C derived from roots, rather than the complex organic compounds in residues, as the Preferential Substrate Utilization Hypothesis predicts (Cheng and Kuzyakov, 2005). This would reduce the need for microbes to produce exoenzymes, minimizing the energy costs for C-acquisition. Also, plant roots not only provide C sources to microbes, but also compete against microbes for water and nutrients (Chen et al., 2013; Cheng and Kuzyakov, 2005). Plants may out-compete microbes for water and/or nutrients in water-limiting environments, constraining the growth of microbes (Hu et al., 2001) and their gene expression (Shi et al., 2018), as well as reducing microbial enzyme production and diffusion of enzymes (Burns et al., 2013).

4.2. *Climate change drivers promote root suppression of litter decomposition*

Previous experiments have shown that live roots may have positive, negative or neutral effects on litter decomposition (Bastida et al., 2019; Zhu and Cheng, 2012). These diverse effects may stem from complex interactions between living roots and surrounding biotic and/or abiotic factors. In our study, the presence of roots (and their associated mycorrhizal fungi) in general reduced decomposition across the different treatments (Fig. S5; Table 1). While precipitation increase amplified the difference in litter decomposition between root and no-root chambers (Fig. 6a), warming reduced this difference (Fig. 6b). These results contrasted to our hypothesis 3 and highlight the importance of soil moisture in controlling litter decomposition. Since water is the primary limiting factor for both plants and microbes in arid systems, plant roots and microbes likely co-exist in a delicate balance. When soil water becomes even scarcer as a result of climate change, litter decomposition would remain being suppressed (Allison and Treseder, 2008), as in the cases of warming and rainfall reduction treatments in our study (Fig. S3). Increasing precipitation may, however, induce different responses through direct and indirect pathways (Austin, 2011). While plants may suppress microbes through directly out-competing microbes for water (Homyak et al., 2017), increased plant growth may

lead to more root exudates for microbes and subsequent stimulation of microbial activities, priming the decomposition (Cheng et al., 2014; Zhu and Cheng, 2011). Therefore, the net impact of precipitation increase on decomposition may likely depend on the tradeoff between these two effects (Fig. 1). In our study, precipitation increase stimulated above-ground ($P < 0.05$; Su et al., 2019) and below-ground (57.1 vs. 24.7 g m^{-2} in Pi and P0 plots, respectively; $P < 0.05$) plant biomass as water stress was partially relieved. Increased root biomass likely increases root exudates (Pausch and Kuzyakov, 2018) but also enhances plant transpiration. High plant transpiration likely exacerbates soil moisture deficiency and reduces the rate of enzyme diffusion on the decomposing substrates (Manzoni et al., 2016), suppressing litter decomposition.

The effect of N input was interesting as it increased aboveground biomass by 25% ($P < 0.05$) but reduced microbial biomass (Fig. 3b) and activity (Fig. 4c). Yet, it did not significantly affect litter decomposition (Table 1), which contradicts to our hypothesis 4. Reactive N input has often been documented to suppress microbial biomass (Treseder, 2008; Liu and Greaver, 2010) and microbial enzyme production (Chen et al., 2018). Our results also suggest that enhanced water limitation induced by increased aboveground plant growth under N input may in turn suppress microbial growth and activities. Taken together, these results indicate that precipitation increase to arid and semiarid grasslands may increase short-term soil C sequestration, as a result of increased plant-C inputs and the negative priming effect. Suppression of microbial biomass and activities by reactive N input (Figs. 3b and 4c; also see Treseder, 2008; Zhang et al., 2018) may further amplify the potential impact of precipitation on soil C dynamics. However, the long-term consequences of these climate change factors on microbial decomposition and soil C balance need to be further exploited.

5. Conclusions

Understanding mycorrhizosphere controls over decomposition of root litter as influenced by climate change factors is vital to predict the C dynamics and nutrient cycling in arid grasslands under future climate change scenarios. Our results provide direct evidence from a field experiment illustrating that climate change factors modulate the effects of plant roots on litter decomposition through altering the availability of both root-derived C and soil available water for microbes. While live roots enhanced microbial growth through increasing root exudates, they inhibited microbial enzyme production and constrained microbial decomposing activities likely by increasing plant water uptake and thus reducing water availability for microbes. Moderate warming alone did not affect root effects on microbial decomposition possibly because ambient water availability was already limiting to microbes. In contrast, precipitation increase stimulated microbial decomposition in the absence of roots but had no effects in the presence of roots, suggesting that plants out-compete microbes for the water that became available. High capacity for plant roots and their associated mycorrhizal fungi for water acquisition, plus N-suppression to microbes, may provide a unique mechanism through which moderate increases in N deposition and precipitation interactively facilitate soil C sequestration in the vast arid and semi-arid ecosystems across the globe.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108278.

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