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REGULAR ARTICLE

Simulating warmer and drier climate increases root production but decreases root decomposition in an alpine grassland on the Tibetan plateau

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Abstract
Background Future ecosystem structure and function will largely depend on root responses to climate change. However, few studies have explored the responses of root production and decomposition to simultaneous warming and altered precipitation in high-latitude and high-altitude ecosystems.
Methods Using ingrowth core and root bag methods, we investigated root production and decomposition dynamics from 2013 to 2015 in a full-factorial warming (control, 1.5 ~ 1.8 °C warming) and precipitation (dry (−50% precipitation), ambient, and wet (+50% precipitation)) experiment established in 2011 in a Tibetan alpine grassland.
Results Warming and precipitation effects on root production were independent. Dry plus warming treatments increased root production, while wet treatments did not significantly affect root production. In contrast, root decomposition accelerated along the increasing precipitation gradient. Warming tended to decrease root decomposition under dry treatments but did not affect root decomposition under wet treatments. The different responses of root production among the treatments were mainly driven by changes in soil moisture, whereas those of root decomposition were mainly due to the changes in the root carbon nitrogen ratio, soil microbial biomass and soil moisture.
Conclusions Given that altered precipitation had contrasting effects on root production and decomposition, our findings indicate that root-derived carbon may accumulate in soils on the Tibetan Plateau where precipitation decreases but not in the areas with projected increasing precipitation under future warming.

Keywords Global warming · Precipitation · Root dynamics · Alpine ecosystems · The Tibetan plateau

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Introduction

Due to the buildup of carbon dioxide and other greenhouse gases, the global land surface temperature is expected to increase by 1.0 ~ 3.7 °C by the end of this century (IPCC 2013). This unprecedented global warming has also accelerated hydrological circulation and led to dramatic changes in precipitation regimes in terrestrial ecosystems (Buytaert et al. 2015; Ernakovich et al. 2015). Plant roots are of pivotal importance for linking above- and belowground carbon processes (Norby et al. 2004), and play fundamental roles in controlling ecosystem carbon cycling (Kou et al. 2018; Sun et al. 2018). Root production and decomposition are expected to be highly responsive to changes in temperature and precipitation, given that these two factors are important in determining plant growth and decomposer activity (Gimbel et al. 2015; Jonsdottir et al. 2005; Liu et al. 2017; Wilcox et al. 2017). However, our knowledge of the responses of root production and decomposition to climate warming and altered precipitation remains rudimentary, especially in alpine ecosystems.

Root production accounts for ~50% of terrestrial net primary production and has implications for carbon sequestration and nutrient cycling (Iversen et al. 2015; Mokany et al. 2010). Climatic changes including increases in air temperature and changes in precipitation regimes, could have a significant influence on root production (Padilla et al. 2019; Stuart-Haëntjens et al. 2018; Wu et al. 2011). Several studies indicate that plant root production varies in response to climate warming, with reported decreases (Majdi and Öhrvik 2004; Wan et al. 2004), increases (Alvarezuria and Körner 2007; Dawes et al. 2015; Liu et al. 2017; Xia et al. 2012), or no change (Kandeler et al. 1998). Altered precipitation can also strongly influence root production. For instance, increased precipitation enhanced root production in a semiarid steppe and in a desert grassland (Niu et al. 2010; Phillips et al. 2006). However, increased root production was observed under drought in an alpine grassland (Zhang et al. 2017). The contradictory results among different studies may arise from the variations in other environmental factors, such as soil moisture conditions and vegetation types. In particular, contrasting responses of root production to warming with and without altered precipitation have been detected in many ecosystems (Bai et al. 2010; Liu et al. 2017). Consequently, it is less clear how concurrent climate warming and altered precipitation affect root production in alpine grasslands.

Vast studies have documented how experimental warming or altered precipitation affect root production in many ecosystems, but the responses of root decomposition are less well understood. Globally, root decomposition has been found to be positively related to annual air temperature (Silver and Miya 2001). Elevated temperature has also been shown to have a major effect on root decomposition through changes in soil microbes and the decomposition environment (Allison et al. 2010; Sardans et al. 2008). The effects of altered precipitation on root decomposition are inconclusive. The majority of studies have found that increased precipitation could accelerate root decomposition by promoting microorganismal growth and accelerating soil enzyme activity (Austin 2002). Nevertheless, other studies have found that increased precipitation did not affect root decomposition or even had a negative effect (Lavelle et al. 1993). Warming and altered precipitation can alter root decomposition in a diverse way (King et al. 2005; Rustad 2008; Xu et al. 2015), additionally, they may affect root decomposition differently across decomposition time, as with the changes in substrate quality (Day et al. 2010). To date, only a few studies have investigated the combined effects of warming and precipitation on root decomposition, which further impedes our understanding of how root decomposition affects ecosystem carbon and nutrient cycling under recent climate change.

The Tibetan Plateau is the largest and highest plateau on earth, covering approximately 2.5 million km^2 (Zhang et al. 2007). The Tibetan Plateau is experiencing rapid climatic warming and changes in precipitation regimes (Dong et al. 2012). An increase in precipitation has been reported in most parts of the Tibetan Plateau, however, a decrease in precipitation has been found in many other regions, such as in our study site, which is located in the northeastern part of the Tibetan Plateau (Chen et al. 2013). Many carbon cycling processes in alpine grasslands have been well investigated, such as aboveground litter production and decomposition (Luo et al. 2010; Xu et al. 2010), but there is a dearth knowledge regarding how root production and decomposition respond to climate warming and altered precipitation. Here, we used a field warming and altered precipitation experiment to investigate their main and interactive effects on root production and decomposition. We hypothesized that warming effects on root production depend on precipitation, as a previous study found that soil moisture is the primary factor driving plant growth in this alpine grassland (Liu et al. 2018). In particular, warming may decrease root production under dry treatments but increase root production under wet treatments. Second, we hypothesized that warming and increased precipitation may increase root decomposition by stimulating soil microbe activity, whereas dry treatments may have the opposite effects.

Materials and methods

Study site

This study was conducted at the Haibei National Alpine Grassland Ecosystem Research Station (37°36′N, 101°19′E, 3215 m a.s.l.) in Qinghai Province, China. The site is affected by a continental monsoon and has a short, cool summer and a long, cold winter. Climatological records at this site show that the annual mean air temperature and annual precipitation were − 1.2 °C and 489.0 mm, respectively, from 1980 to 2014. The annual mean air temperatures at Haibei station were − 1.08, −1.36, and − 0.79 °C in 2013, 2014, and 2015, respectively (Fig. S1A). The annual mean precipitation was 403.4, 573.0, and 406.1 mm in 2013, 2014, and 2015, respectively (Fig. S1A). The experimental site has become warmer and drier during the past four decades (Liu et al. 2018). The soils are mollisols according to the US Department of Agriculture Soil Taxonomy and are classified as Mat-Gryic Cambisols according to Chinese Soil Taxonomy. The soil bulk density and organic carbon content were 0.8 g cm^{-3} and 63.1 g kg^{-1}, respectively, in the 0–10 cm layer (Lin et al. 2016). The community of this alpine grassland is dominated by *Elymus nutans*, *Helictotrichon tibeticum*, *Gentiana straminea*, *Tibetia himalaica*, and *Kobresia humilis*.

Experimental design

Our study was conducted in a warming and precipitation experiment that was established in 2011. Two temperature and three precipitation levels were applied in a full factorial design. Each treatment had six replicates; overall, 36 2.2 m × 1.8 m plots were randomly arranged into six blocks. The two temperature levels were the control and warming (elevated soil temperature by 1.5 ~ 1.8 °C), and the three precipitation levels were ambient, −50% precipitation (dry) and + 50% precipitation (wet). Model projections showed that air temperature would increase by 2.6 ~ 5.2 °C, and the changes in precipitation would vary in a wide range from 38 to 272 mm on the Tibetan plateau by 2100 (Chen et al. 2013). Based on the model results, our experimental design was used to simulate future climate warming and extreme precipitation conditions in the next 100 years. To increase the temperature in the warming plots, two medium-wave heaters (220 V, 1200 W, 1.0 m long, and 0.22 m wide) were installed in each warming plot, and two dummy heaters were installed in each control plot. Four transparent Panlite sheet channels (PC-1151; Teijin Chemicals) were installed at 15° angles above each plot to control the precipitation amount. The −50% precipitation treatment was controlled by nonslotted channels; the intercepted rainfall was sprinkled into the +50% precipitation plots with slotted channels immediately after the rain event. The control plots were also installed with dummy channels. Metal plates were inserted into the soil to 15 cm to prevent runoff.

EM 50 sensors (EM 50, Decagon Devices Inc., Pullman, WA, USA) were installed into three blocks to monitor the soil temperature and moisture at 5 cm depths hourly in three blocks. Additional details regarding the experimental design are provided in Liu et al. 2018.

Aboveground net primary productivity of different functional groups and root production measurements

Aboveground production from different functional groups was measured by using the harvest method at the peak of growing season (late August) from 2011. The plants in each plot were seperated to species and oven-dried to constant weight. The species were then classified into grasses, forbs and sedges, the details are described in Liu et al. 2018. The ingrowth core method was used to estimate root production in this study. In September 2012, the preexisting root biomass was taken from the soil by using a hand drill (5 cm diameter and 50 cm deep). The soils sieved with polyester mesh bags from the same soil depths outside the plots were filled back to the soil holes. The filled soils were compressed to a density that was comparable to the original soils. The collected soil was divided into five segments according to soil depth (0–5, 5–10, 10–20, 20–30 and 30–50 cm). Root samples were put into marked plastic bags and stored at −30 °C before further processing. To remove attached soil and black debris, root samples were washed carefully through 0.5 mm diameter sieves under gently flowing water. Then, the root samples were oven-dried at 65 °C to constant weight and weighed to calculate root production at different depths.

Minirhizotrons were also used to estimate root production in this study. In October 2012, transparent acrylic minirhizotron tubes were vertically inserted at a soil depth of 80 cm. The tube end was capped by a rubber cover, and the part remaining aboveground was painted black inside to prevent the light from entering the tube. Seven months after installation, a scanner (CI-600, CID Bio-Science Inc., Camas, WA, USA) was used to collect root images. The root images were scanned every two weeks during the growing season (from May to September). At each time point, four images in the horizontal direction were obtained from along the tube and then combined into one picture. Then, each combined picture was divided into 5 separate images according to the soil depths in the vertical direction, e.g., 0–10, 10–20, 20–30, 30–40, and 40–70 cm. Root Snap CI-690 software (CID Bio-Science Inc., Camas, WA, USA) was used to analyze the images to obtain root length. In this study, only 0–40 cm root production was used because of the limited root production at 40–70 cm. Root production was estimated by summing all new root lengths during the two monitoring intervals, and the method has been used in previous studies (Burton et al. 2000; Majdi and Öhrvik 2010).

Root decomposition measurements

The root decomposition experiment was conducted by using the traditional root bag technique from October 2013 to October 2015. Fresh roots were taken at 0–10 cm depth using soil cores from the same stand adjacent to the experimental plots. The root samples were washed, and fine roots (diameter < 2 mm) were separated from coarse roots. Equally weighed air-dried fine roots (1.7 g) were placed into a root bag that was 0.1 mm mesh. Root decomposition was measured in 5 replicates across 30 plots. In total, 210 root bags were prepared for seven times of measurements. The prepared root bags were placed at a depth of 5 cm and staked on the soil surface in each plot. One bag was randomly taken in April, July and October in 2014 and 2015 from each plot. During each measurement, 30 root samples were removed and analyzed. Once taken, the remaining roots were washed under a 0.1 mm sieve to remove the soil particles in the laboratory and then oven dried at 65 °C to constant weight.

Root substrate quality and soil sample analysis

All the dried samples were milled to powder to analyze the substrate quality. The total carbon and nitrogen concentrations were analyzed by using an elemental analyzer (Perkin Elmer Instruments Series II, USA). The total phosphorus concentration was analyzed by using a flow autoanalyzer (Seal AutoAnalyzer 3 (AA3), Germany). A common sequential extraction technique was used to analyze the hemicellulose, cellulose, and lignin concentrations (Lin and King 2014). First, 0.6 g of 0.1 mm sieved root litter samples was weighed and subjected to neutral detergent, defoamer and anhydrous sodium sulfite. The heating digestion method was used to calculate the proportion of neutral detergent fiber. Second, 0.6 g of 0.1 mm sieved root litter samples was subjected to acid detergent, defoamer and anhydrous sodium sulfite to calculate the proportion of acid detergent fiber by using the heating digestion method. Then, 72% concentrated sulfuric acid was added to the acid detergent fiber to calculate the content of lignin and ash by using the heat digestion method. The ash content was then determined by the calcination method. The hemicellulose content was determined by the difference between the neutral and acid detergent fiber. The cellulose content was determined by the difference between acid detergent fiber and lignin and ash. The flow diagram for root carbon fractions measurement was shown in Fig. S1.

In August 2013 and 2015, one soil core (5 cm diameter and 70 cm depth) was taken per plot. A portion of fresh soil was air dried and sieved to measure soil total carbon, soil organic carbon and soil nitrogen. Another portion of soil was stored in iceboxes and subsequently taken to the laboratory for measuring soil microbial biomass. Soil microbial biomass carbon and nitrogen were analyzed by using the chloroform-fumigation extraction-flow analyzer method (Seal AutoAnalyzer 3 (AA3), Germany). Extractable C and N were extracted with K_2SO_4 solutions from the non-fumigated and fumigated soils. The microbial biomass carbon and nitrogen were calculated using the conversion factors of 0.45 and 0.54. At the same time, soil pH, soil temperature at 5 cm and soil moisture at 5 cm were measured.

In our study, overall root production and root production at different depths were measured in 6 replicates across all 36 plots. However, root decomposition was measured only in 5 replicates across 30 plots. Soil total carbon, soil total nitrogen and soil microbiological characteristics were measured only in 4 replicates across 24 plots.

Calculations and statistical analysis

Here, the remaining mass, substrate content and substrate remaining were used as measures of root decomposition, and the equations are as follows:

$$\text{Remaining mass } (\%) = \frac{Final\ mass\ (g)}{Initial\ mass\ (g)} \times 100 \quad (1)$$

$$\text{Substrate content} = \text{Remaining mass (g)} \times Substrate\ concentration\ \left(g\ kg^{-1}\right) \quad (2)$$

$$\text{Substrate remaining } (\%) = \frac{Remaining\ mass\ (g) \times Substrate\ concentration\ (g\ kg^{-1})}{Initial\ mass\ (g) \times Initial\ substrate\ concentration\ (g\ kg^{-1})} \quad (3)$$

A single exponential model was used to determine the decomposition constant (k), and the equation is as follows (Olson 1963):

$$\ln\frac{M_t}{M_0} = -kt \quad (4)$$

where M_t is the mass of roots remaining at time t, M_0 is the initial root mass, k is the decomposition constant and t is time in months.

We used the mixed linear model to explore the effects of warming and altered precipitation on root decomposition constants, in which warming and altered precipitation were fixed factors and block was a random factor. We also used a mixed linear model to investigate the effects on soil temperature, moisture, overall root production, root production at different depths and root chemical characteristics, in which warming, altered precipitation and year (or sampling time) were fixed factors and year nested in block was a random factor. A mixed linear model was constructed using the "nlme" package in R software. One-way analysis and Tukey's honest significant difference test were used to determine whether there were significant differences between the treatments.

Mean decrease accuracy (%IncMSE) based on random forest was calculated to rank the importance of ecological and environmental factors for the total root production, the percentage of root production at different depths and root decomposition constant. A higher %IncMSE represents a higher variable importance for these variables (Han et al. 2016). Linear regressions were used to analyze the relationships between root production and soil temperature and moisture and aboveground production of different functional groups. Linear regressions were also used to evaluate the relationships between the root decomposition constant and soil total carbon, soil total nitrogen, pH, microbial biomass nitrogen, microbial biomass carbon, root C:N, soil moisture and soil temperature. Significance level was set at $P \leq 0.05$ unless otherwise stated. All statistical analyses were carried out with R 3.2.2 (R Core Team 2015).

Results

Soil temperature and moisture

Warming increased the mean soil temperature at a depth of 5 cm by 1.5 °C from April to October during the three experimental years (Fig. S2B). However, altered precipitation did not significantly influence soil temperature. There was no interactive effect on the mean soil temperature between warming and altered precipitation (Fig. S2B). During the experiment, the warming and dry treatments decreased the mean soil moisture at a 5 cm depth by 3.7% and 4.9%, respectively, while the wet treatment increased soil moisture by 4.0% from April to October. No interactive effect between warming and altered precipitation on soil moisture was detected (Fig. S2C).

Root production

The ingrowth core method showed that altered precipitation significantly affected total root production (Table 1). Compared to the control, the dry treatments increased total root production by 28.7% whereas both the wet treatment and warming did not significantly influence total root production (Fig. 1 and Table 1). Dry plus warming treatments had the highest root production across all three experimental years, which was 862.15 ± 66.70 g m^{-2}. The minirhizotron approach showed the same pattern of root production (Fig. S3).

Table 1 Results of linear mixed model on the effects of warming (W), altered precipitation (P), years (Y) and their interactions on total root production and percentage of root production at 0–20 cm and 20–50 cm to total root production from 2013 to 2015 ($n = 6$)

Variables	W	P	W * P	Y	W*Y	P*Y	W*P*Y
Root production							
df	1, 75	2, 75	2, 75	2, 10	2, 75	4, 75	4, 75
F	2.53	4.74	0.82	17.59	1.60	1.35	1.12
P	0.12	0.01*	0.44	<0.001***	0.21	0.26	0.36
Root production$_{_0–20\ cm}$							
df	1, 75	2, 75	2, 75	2, 10	2, 75	4, 75	4, 75
F	5.01	3.09	2.25	1.13	1.53	2.20	0.98
P	0.03*	0.05*	0.11	0.36	0.22	0.08	0.43
Root productionn$_{_20–50\ cm}$							
df	1, 75	2, 75	2, 75	2, 10	2, 75	4, 75	4, 75
F	5.01	3.09	2.25	1.13	1.53	2.20	0.98
P	0.03*	0.05*	0.11	0.36	0.22	0.08	0.43

*, ** and ***: statistically significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$

In addition, altered precipitation and warming significantly affected root distribution. The warming and altered precipitation effects on root distribution were independent (Table 1). Compare to control, the dry and warming treatments decreased the percentage of root production at 0–20 cm but increased the percentage of root production at 20–50 cm (Fig. 1; Table 1 and Table S1). The wet treatments did not significantly affect the percentage of root producton either at 0–20 cm or 20–50 cm (Fig. 1).

Root decomposition

By using linear mixed models, we found that altered precipitation significantly interacted with warming in affecting the root decomposition process (Table 2). Warming inhibited root decomposition in the dry plots but accelerated root decomposition in the wet plots (Fig. 2 and Table 2). The root decomposition constant increased from dry to ambient to wet along the precipitation treatments, the wet treatments changed the root decomposition constant more than dry treatments (Fig. 2b, c). Following three years of decomposition, root remaining was highest in the warming plus dry treatment (71.4%) and lowest in the warming plus wet treatment (62.8%) (Table S2).

The carbon content gradually decreased with experimental time under all treatments (Fig. 3A). The carbon content was significantly affected by altered precipitation. The initial root litter carbon content was 853.0 ± 2.0, 852.1 ± 1.8 and 855.1 ± 2.7 mg and the final root litter carbon content was 770.5 ± 6.7, 738.8 ± 5.6 and 719.8 ± 13.3 mg in the dry, ambient and wet plots. After three years of decomposition, the root litter carbon remaining (values are expressed as % of initial carbon content) was 90.3 ± 0.60%, 86.7 ± 0.64% and 84.2 ± 1.44% in the dry, ambient and wet plots, respectively (Fig. 3A). The nitrogen and phosphorus remianing increased with experimental time across all treatments (Fig. 3B, C). Thus, the root litter carbon nitrogen ratio decreased with time, and the largest decrease was found in the wet treatments (Fig. 3D). However, warming and altered precipitation did not affect the final nitrogen and phosphorus content percentages (Table 2).

Residual cellulose and hemicellulose remaining were affected by altered precipitation but were not influenced by warming (Table 2). The residual cellulose remaning was 89.2 ± 0.97%, 86.4 ± 0.54% and 83.2 ± 0.70% for the dry, control and wet treatments, respectively, while the residual hemicellulose remaining was 92.7 ± 0.80%, 92.5 ± 0.84% and 87.5 ± 0.62% for these three treatments, respectively (Fig. 4A, B). The residual lignin was not affected by warming or by altered precipitation (Fig. 4C).

Drivers of root production and decomposition

By using random forest, we ranked the relative importance of the ecological and environmental drivers for root production and root decomposition. Among the

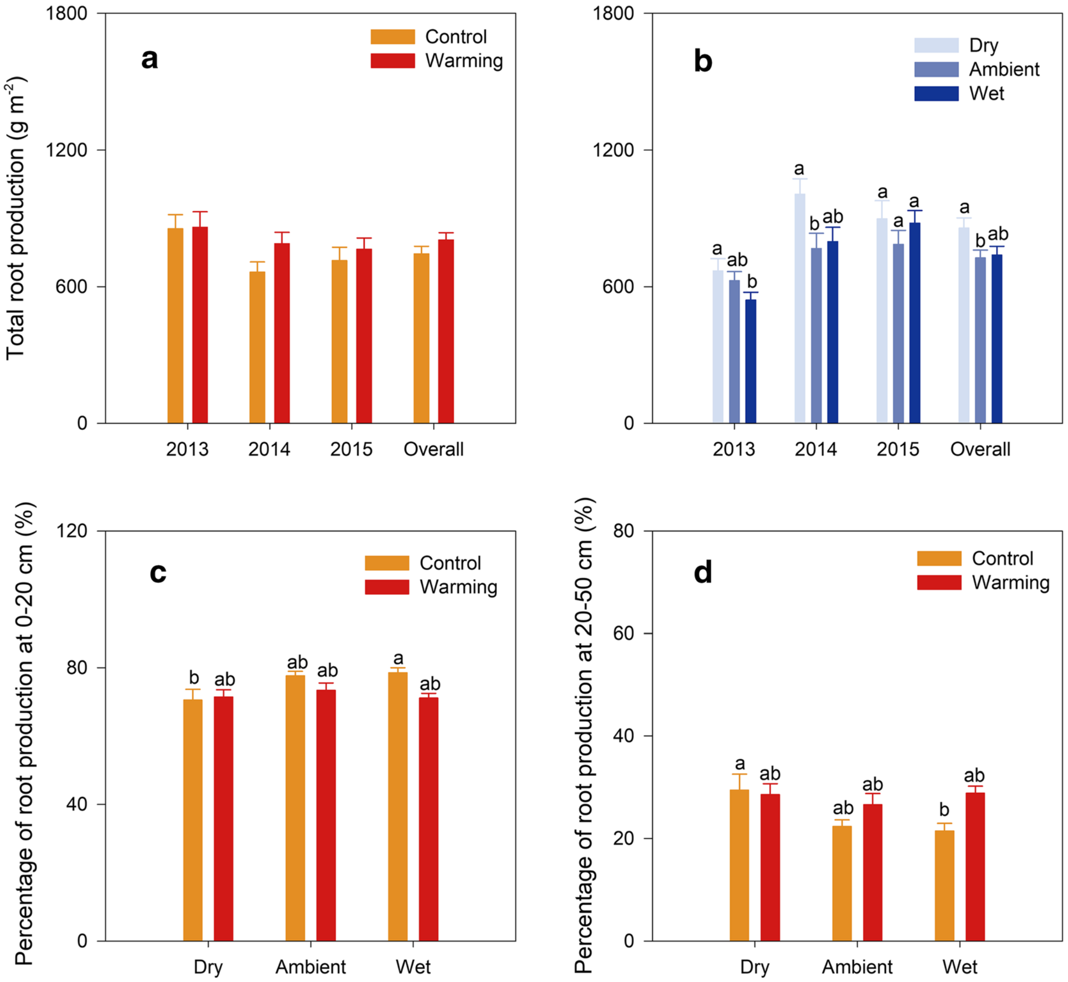

Fig. 1 Effects of warming and altered precipitation on total root production, percentage of root production at 0–20 cm and 20–50 cm soil depths to total root production from 2013 to 2015. Different letters indicate significant differences between treatments at the $P \leq 0.05$ level. Values are shown as the mean ± SE ($n = 6$)

examined factors, the most relevant factors with root production were soil moisture at 5 cm depth and forb production (Fig. 5a). Total root production was negatively correlated with soil moisture at the 5 cm depth (Fig. 5, $P = 0.01$). Meanwhile, the percentage of root production at 0–20 cm was positively related to forb production and soil moisture at 5 cm depth (Fig. 5f, h). The percentage of root production at 20–50 cm was negatively related to forb production and soil moisture at 5 cm depth (Fig. 5j, l).

The root decomposition process was significantly affected by many factors. The factors that influenced the process from the highest to lowest level were root carbon nitrogen ratio, microbial biomass nitrogen, soil moisture, soil pH, soil total carbon, soil total nitrogen, microbial biomass carbon and soil temperature (Fig. 6a). The microbial biomass nitrogen and soil moisture were positively related to the root decomposition constant, whereas the root carbon nitrogen ratio was negatively related to the root decomposition constant (Fig. 6b–d). Soil pH, soil total carbon, soil total nitrogen and soil temperature at the 5 cm depth had no significant relationships with the root decomposition constant (Fig. 6e–i).

Discussion

Warmer and drier climate stimulated root production

Our results showed that the dry treatments increased root production, whereas the wet treatment did not affect root production. This result was not in agreement with

Table 2 Results of linear mixed model on the effects of warming (W), altered precipitation (P), sampling date (D) and their interactions on root decomposition constant, root remaining mass and root chemical characteristics from 2013 to 2015 ($n = 5$)

Variables	W	P	W * P	D	W*D	P*D	W*P*D
Root decomposition constant							
df	1, 20	2, 20	2, 20	–	–	–	–
F	0.00	15.65	6.22	–	–	–	–
P	1.00	0.0001***	<0.01**	–	–	–	–
Root mass remaining							
df	1, 140	1, 140	2, 140	6, 24	6, 140	12, 140	12, 140
F	0.11	32.27	4.04	153.00	0.21	1.90	0.96
P	0.75	<0.001***	0.02*	<0.001***	0.97	0.04*	0.49
C remaining							
df	1, 140	1, 140	2, 140	6, 24	6, 140	12, 140	12, 140
F	0.47	56.48	11.32	231.35	0.72	5.32	2.58
P	0.49	<0.001***	<0.001***	<0.001***	0.64	<0.001***	<0.01**
N remaining							
df	1, 140	1, 140	2, 140	6, 24	6, 140	12, 140	12, 140
F	4.51	7.25	2.43	114.90	0.77	0.55	0.52
P	0.04*	<0.01**	0.09	<0.001***	0.59	0.88	0.90
P remaining							
df	1, 140	1, 140	2, 140	6, 24	6, 140	12, 140	12, 140
F	2.40	0.79	3.20	114.71	0.21	0.30	0.29
P	0.12	0.45	0.04*	<0.001***	0.97	0.99	0.99
Hemicellulose remaining							
df	1, 140	1, 140	2, 140	6, 24	6, 140	12, 140	12, 140
F	1.70	40.09	2.45	44.44	0.96	2.02	0.49
P	0.19	<0.001***	0.09	<0.001***	0.46	0.03*	0.92
Cellulose remaining							
df	1, 140	1, 140	2, 140	6, 24	6, 140	12, 140	12, 140
F	2.86	43.04	7.00	188.11	0.43	3.28	0.87
P	0.09	<0.001***	<0.01**	<0.001***	0.86	<0.001***	0.58
Lignin remaining							
df	1, 140	1, 140	2, 140	6, 24	6, 140	12, 140	12, 140
F	1.10	0.29	0.88	5.46	0.76	0.29	0.63
P	0.30	0.75	0.42	<0.01**	0.60	0.99	0.82

*, ** and ***: statistically significant at $P \le 0.05$, $P \le 0.01$ and $P \le 0.001$

the results of studies located in semiarid grasslands (Bai et al. 2010). In water-limited ecosystems, increased precipitation can improve soil water conditions and thus enhance plant growth, whereas reduced precipitation can weaken plant photosynthesis and thus decrease root production (Bai et al. 2010). However, our results were supported by the results of many other studies, and the optimal portioning theory, which indicates that plants can produce more root biomass when face a scarcity of soil resources within a reasonable range (van Wijk 2011). A previous study at the same experimental site showed that dry treatments shifted the species composition from shallow-rooted sedges and forbs to deep-rooted grasses, which could contribute to increased root production in the deeper soil profile (Liu et al. 2018).

We found that warming tended to increase root production, but the increase was not up to the significant level, which was consistent with previous results from

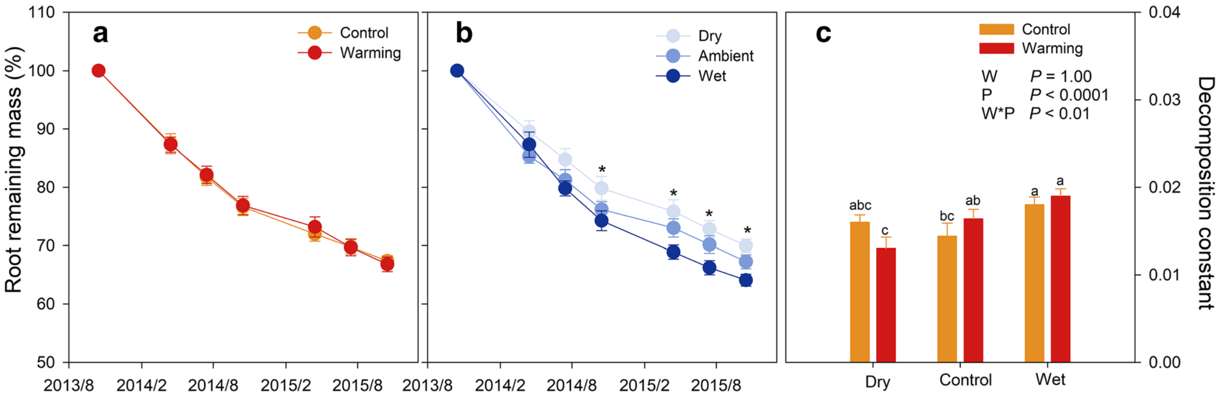

Fig. 2 Effects of warming and altered precipitation on root mass remaining (**a**, **b**) and root decomposition constant (**c**). A higher root decomposition constant indicates a higher decomposition rate. Different letters indicate significant differences between treatments at the $P \leq 0.05$ level. Values are shown as the mean ± SE ($n = 5$)

the same experimental site (Liu et al. 2018). No response of root production to increase in air temperature in our site may be attributed to the adaptation of the plants to the large temperature differences between

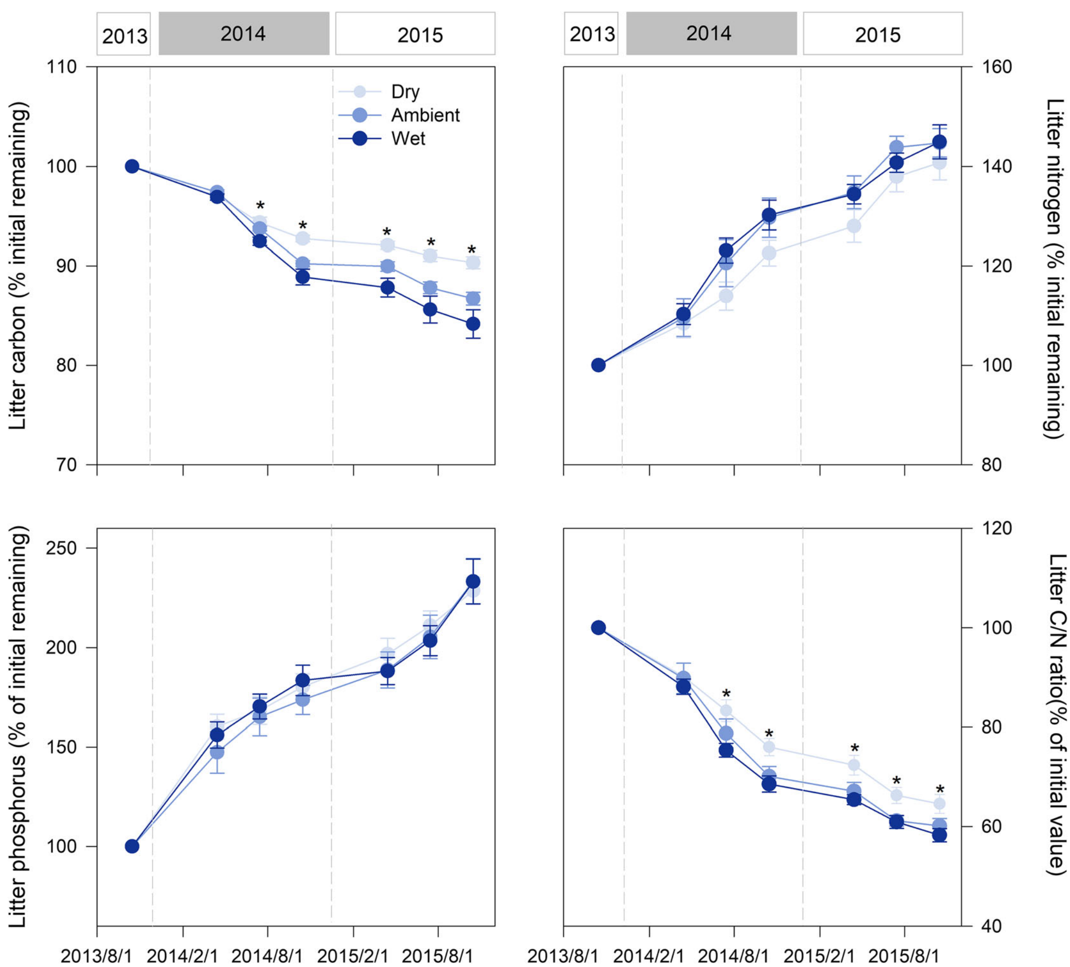

Fig. 3 Effects of altered precipitation on percentage change in carbon (A), nitrogen (B), phosphorus (C) remaining and the carbon and nitrogen ratio (D). Values are shown as the mean ± SE ($n = 5$)

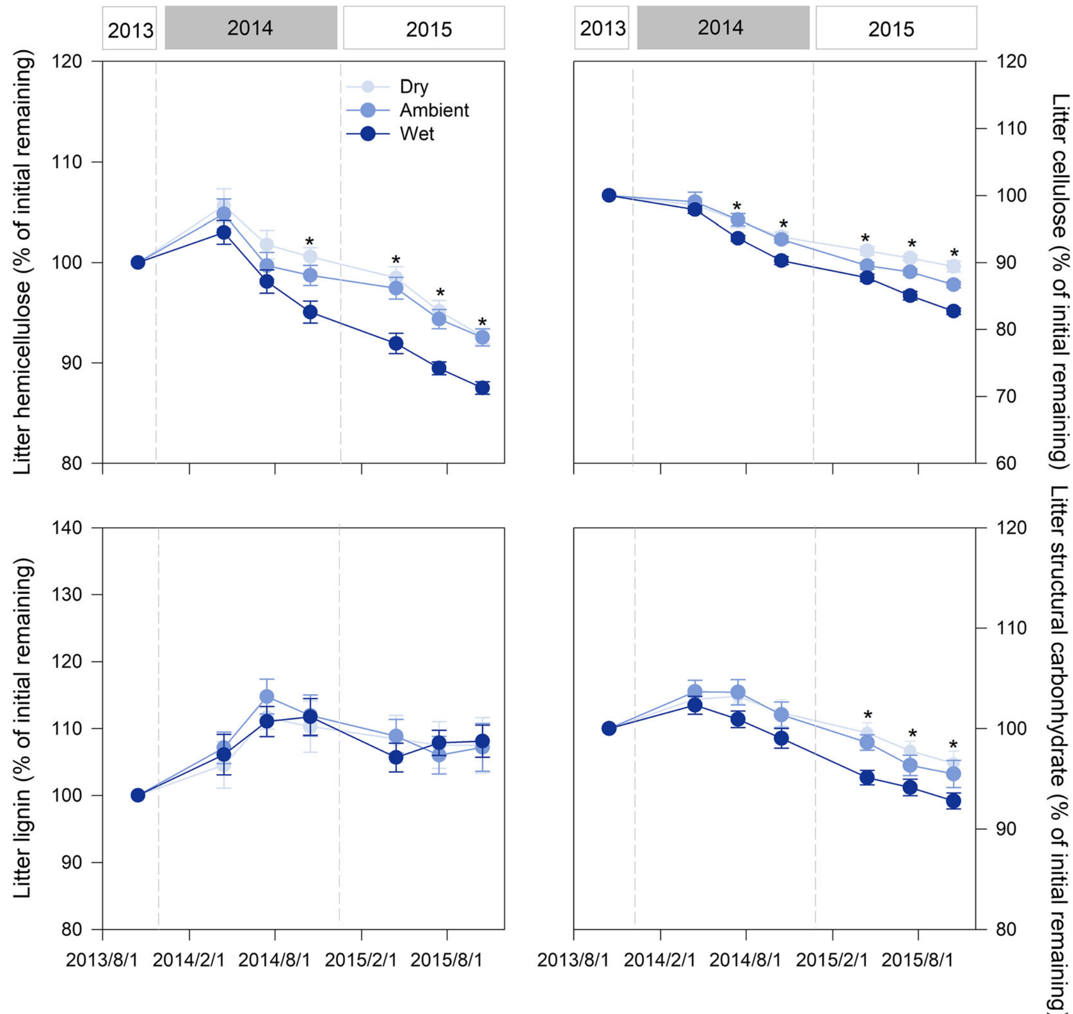

Fig. 4 Effects of altered precipitation on the percentage change in hemicellulose (A), cellulose (B), lignin (C) and overall structural carbohydrate remaining(D). Values are shown as the mean ± SE ($n = 5$)

daytime and nighttime. The gap between diurnal temperature and nocturnal temperature can be as high as 13 °C during the growing season in our site. Plants may have already adapted the dramatic temperature swings. Then the 1.5 °C increment of experimental warming may not affect the plant root productivity too much. This view was supported by a previous study in alpine grassland reporting that the plants have a lower temperature optimum for shoot and root growth than temperate plants (Chapin 1983).

Warmer and drier climate inhibited root decomposition

We found that warming had no influence on the root decomposition constant, remaining carbon and nitrogen contents or structural carbohydrate conents, which was in contrast to the results of a study showing that air temperature was the main factor controlling litter decomposition at the global scale (Silver and Miya 2001). Previous literature documented that warming could stimulate litter decomposition in many ways, such as by increasing microbial biomass and enzymatic activity or shifting microbial composition (Allison et al. 2010). In arcic or alpine regions, warming could also accelerate litter decomposition by extending freezing and thawing days and strengthening the fragmentation effect (Chapin et al. 2011). On one hand, warming may accelerate root decomposition by directly elevating soil temperature. On the other hand, warming simultaneously decreased soil moisture and soil microbial biomass, which could

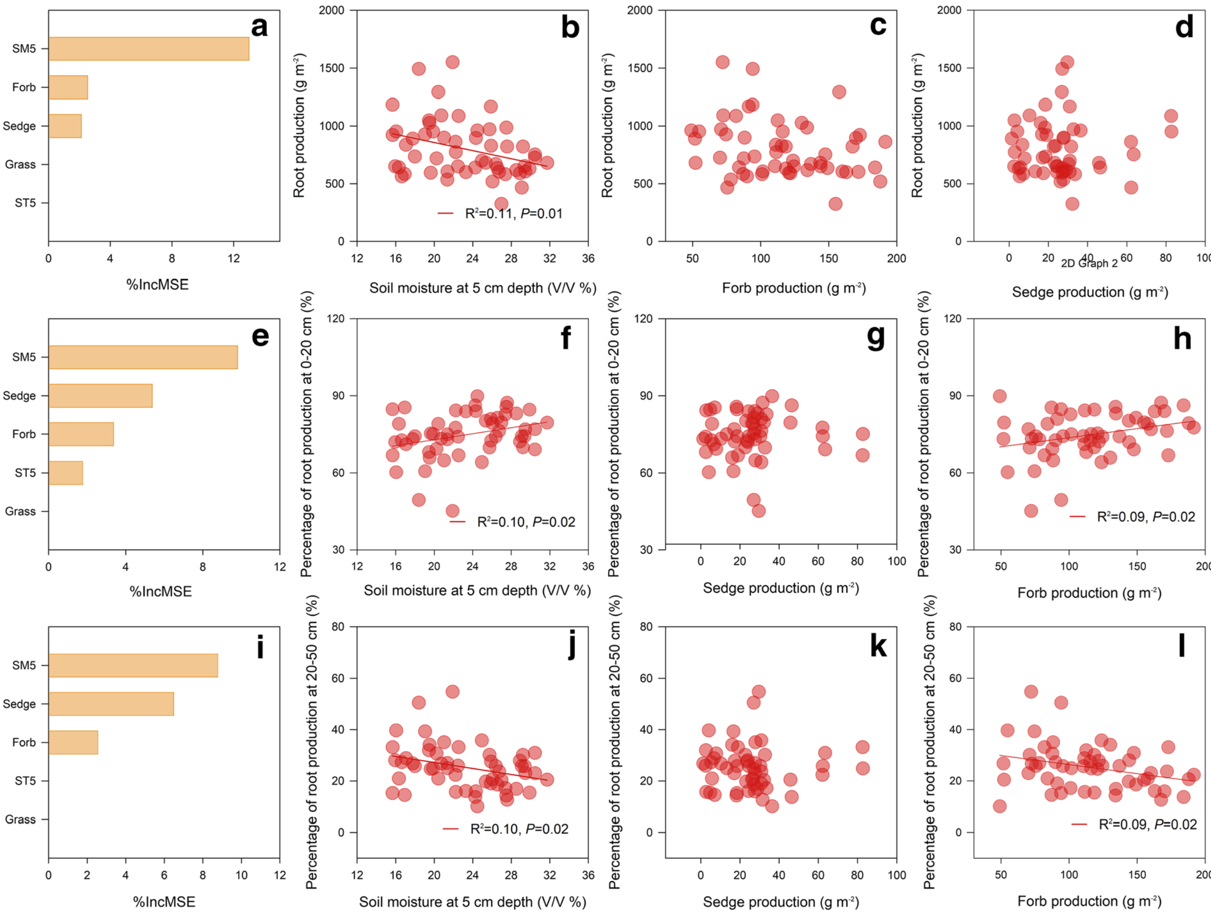

Fig. 5 Relative importance of soil temperature and soil moisture at the 5 cm depths, aboveground biomass of different functional groups (forb, sedge and grass production) to the total root production, the percentage of root production at 0–20 cm and 20–50 cm (**a**, **e**, **i**) and their relationships with root production and root distribution (**b**, **c**, **d**, **f**, **g**, **h**, **j**, **k** and **l**). ST5, SM5, Forb, Sedge and Grass mean soil temperature at 5 cm depth, soil moisture at 5 cm depth, forb production, sedge production and grass production. A higher mean decrease accuracy (%IncMSE) value means a higher importance for root decomposition. When %IncMSE is less than 0, the value is not shown. Solid lines represent $P \leq 0.05$

have a negative effect on root decomposition (Lin et al. 2016). The unresponsiveness of root decomposition to warming at our site may be because the positive warming effect on temperature was cancelled by the negative warming effect on soil moisture and soil microbe biomass. In addition, the differences in litter types and experimental methods could also have caused contrasting results. In most previous studies, leaf litter was placed at the soil surface to conduct decomposition experiments (Xu et al. 2010), however, root litter was buried at a 5 cm soil depth in the current study. As soil can buffer the warming effect, it was not surprising to observe a neutral response.

Consistent with the results of previous studies (Allison and Treseder 2008; Whitford and Duval 2019), we found that increased precipitation stimulated root decomposition, whereas decreased precipitation had the opposite effect. The results may be attributed to the following reasons. First, changes in precipitation could affect root decomposition via changes in soil microbial biomass (Liu et al. 2017). Indeed, we found that the soil microbial biomass increased along the precipitation gradient (Lin et al. 2016). Second, by analyzing the mean values of carbon remaining, nitrogen remaining and carbon nitrogen ratio over time, we found that both root carbon release and root nitrogen fixation increased and carbon nitrogen ratio decreased across all treatments, which indicated that the litter quality improved over time. Root litter had a lower carbon nitrogen ratio under wet treatments than that

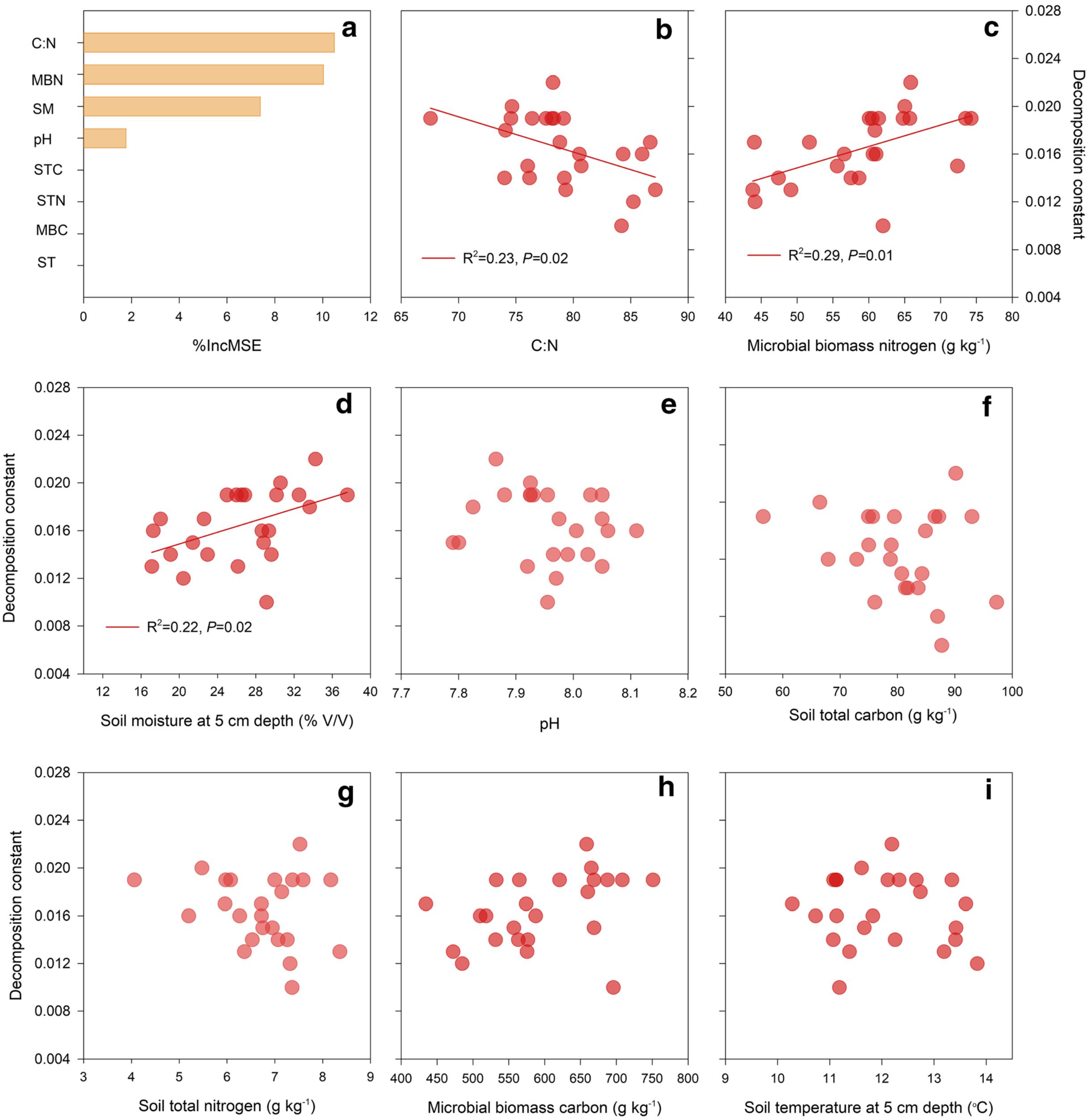

Fig. 6 Relative importance of the root carbon nitrogen ratio (C:N), microbe biomass nitrogen (MBN), soil moisture (SM), soil pH, soil total carbon (STC), soil total nitrogen (STN), microbe biomass carbon (MBC), soil temperature (ST) to root decomposition constant (**a**) and their relationships with the root decomposition constant (**b**–**i**). A higher mean decrease accuracy (%IncMSE) value means a higher importance of root decomposition. When %IncMSE is less than 0, the value is not shown. Solid lines represent $P \leq 0.05$

under other treatments at the end of the experiment, the more improved litter quality in wet plots may also lead to a faster decomposition process (Day et al. 2010).

Here we found that root decomposition was more affected by wet treatments than dry treatments, which may because soil microbial biomass changed to a greater extent in wet plots at our experimental site (Lin et al. 2016). The wet treatments may have disproportionately positive impacts on root decomposition because larger precipitation amount could enhance microbial growths by stimulating soil mineralization (Knapp et al. 2017). In addition, some soil microbes could resist to drought by promoting water use efficiency (de Vries et al. 2020), thus reduced precipitation could have less effects on microbial biomass and root decomposition.

An interactive effect of warming and altered precipitation on root decomposition was observed in our study. Warming suppressed root decomposition under drought conditions but did not affect root decomposition under wet treatments. We identified two possible reasons to explain this phenonemon. First, warming and drought together decreased the soil moisture the most, and severe drought conditions inhibited root decomposition (Kemp et al. 2003; Lin et al. 2016). Second, we found that microbial carbon and nitrogen were significantly lower in the warming and drought plots than in the other treatments (Lin et al. 2016), and restrained soil microbe metabolism could also reduce root decomposition (Liu et al. 2017).

Warmer and drier climate inhibited hemicellulose and cellulose decomposition but did not affect lignin decomposition

The decomposition of hemicellulose and cellulose was slowest at the end of this experiment in the warming and drought plots, while lignin decomposition did not show differential responses to simulated warming and altered precipitation. The reason that hemicellulose and cellulose decomposed more slowly in under warmer and drier conditions may be because of the lower litter carbon nitrogen ratio and lower soil moisture across the experimental time, which could create unfavorable conditions for microbial decomposer growth (Kemp et al. 2003).

Compared to hemicellulose and cellulose, lignin is a complex macromolecular compound that is difficult to decay (Brown and Chang 2014). The contrasting responses between these compounds to climate change may be because the differences in the environmental conditions and soil microbes between the treatments were not enough to result in differential decomposition rates of lignin. In addition, altered precipitation could affect hemicellulose and cellulose content by soil leaching; however, lignin content is not easily affected by leaching due to its hydrophobic property (Whitford and Duval 2019).

Concluding remarks

In conclusion, our results provide a thorough understanding of root responses to climate change and showed that simulating warmer and drier climate increased root production but decreased root decomposition in an alpine grassland on the Tibetan Plateau. This finding has important implications for predicting ecosystem carbon dynamics under future climate change. First, the increase in root production we observed can enhance the input of root exudates and thus influence soil organic carbon composition. At the same experimental site, a previous study reported that increased root production accumulates more new soil carbon (e.g., sugar and lipids) but decomposes more old carbon (e.g., lignin) by enhancing the priming effect (Jia et al. 2019). Second, the increased production and decreased decomposition of alpine plant roots can influence ecosystem nutrient cycling by enhancing soil nutrient absorption but reducing nutrient release (Pausch and Kuzyakov 2017). Given the important roles of roots in determining soil carbon composition and nutrient cycling, our findings could help us better predict carbon feedbacks to future climate change in alpine grassland ecosystems.

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