Environmental and Experimental Botany 172 (2020) 103991

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Early season precipitation accounts for the variability of fine-root traits in a Tibetan alpine grassland

Jirong Cao[a,1], Li Lin[b,1], Shuang Pang[a], Xiaowei Guo[c], Guangmin Cao[c], Jin-Sheng He[b,d], Qibing Wang[a,*]

[a] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093, China*
[b] *Department of Ecology, College of Urban and Environmental Sciences and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, 100871, China*
[c] *Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, 810008, China*
[d] *State Key Laboratory of Grassland Agro-Ecosystems, College of Pastoral Agriculture Science and Technology, and Institute of Innovation Ecology, Lanzhou University, Lanzhou, 730000, China*

ARTICLE INFO

Keywords:
Alpine ecosystems
Fine roots
Non-growing season
Precipitation
Root traits
Root biomass
Specific root length

ABSTRACT

Root trait dynamics can reflect the adjustment in the strategy of plant roots in resource acquisition and energy storage when responding to climatic fluctuations. Under global change, the responses of root traits in climate sensitive ecosystems, e.g. high-elevation and cold Alpine ecosystems, remain unclear. To identify how climatic fluctuations drive the variations in the root traits in a Tibetan alpine grassland, we intensively investigated the temporal dynamic of root traits by biweekly measuring root length, root biomass and specific root length for three continuous years. The SRL showed strong seasonal patterns across three years, which did not support SRL considered as a constant in previous root system modeling, while as hypothesized, mean SRL in non-growing seasons was significantly higher than that in growing seasons by 17 %. The accumulative air temperature of growing or non-growing season exerted synchronic effects on the changes in root traits. Nevertheless, precipitation was observed to have the lag effects on root traits, showing that January-April accumulative precipitation was a major driver for the variations in the root length and root biomass respectively peaking in July and June each year. Distinguishingly, root length relied on the lag effect of precipitation; however, for root biomass, the continuous accumulative precipitation together with peak month, i.e. the January-June accumulative precipitation, was also significantly vital. Our results would have an important implication for predicting responses of belowground carbon cycling to global climate change.

1. Introduction

Root systems are vital for plants in carbohydrate storage and nutrients absorption, and thus root growth and turnover directly involve various belowground carbon and nutrient processes in terrestrial ecosystems (Matamala et al., 2003; McCormack et al., 2017; Norby and Jackson, 2000). Under global change, therefore, the responses of plant root traits have been increasingly focused on (Fort et al., 2015; McCormack and Guo, 2014; Mueller et al., 2016; Zhou et al., 2019). In different types of ecosystem, the effects of climatic variables on root traits would differ (Erktan et al., 2018). Moreover, root traits in growing season are proposed to be differential from those in non-growing season, and this difference can be more evident in the ecosystems with stronger climatic fluctuations between seasons (Gellesch et al., 2017). Therefore, although seasonal dynamics of root traits have been documented mostly in tropical/subtropical and temperate ecosystems (Miyatani et al., 2018; Montagnoli et al., 2019), it is still necessary to do more investigation because how different root traits will be between growing and non-growing seasons in climate-change sensitive ecosystems (e.g. cold ecosystems) is rarely reported and thus remains unclear.

The dynamics in root traits have been studied mainly during the

---

Abbreviation: AccumP-GS, accumulative precipitation of growing season; AccumP-NGS, accumulative precipitation of non-growing season; Mrl-GS, mean root length of growing season; Mbiom-GS, mean root biomass of growing season; Mbiom-NGS, mean root biomass of non-growing season; Msrl-NGS, mean specific root length of non-growing season; AccumT-GS, accumulative air temperature of growing season; AccumT-NGS, accumulative air temperature of non-growing season

[*] Corresponding author.

E-mail address: qwang@ibcas.ac.cn (Q. Wang).

[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.envexpbot.2020.103991
Received 14 January 2019; Received in revised form 24 December 2019; Accepted 16 January 2020

period when root activity is high, e.g. plant growing season (Fort et al., 2017), whereas much less attention has been drawn to them during the period when the roots are inactive, e.g. non-growing season, particularly the frozen winter. In addition, harsh condition for field work, especially the extreme condition such as high-elevation and cold alpine ecosystems, brings more difficulties for investigating non-growing season root traits. Morphological adaptations of the fine roots enable plants to optimize their nutrients even under harsh environmental condition (Ostonen et al., 2007a, b). Although non-growing season root activity is very low, it still has an ecological implication for a comprehensive understanding of the root traits in sensitive ecosystems in response to global change.

To understand how plants adjust the strategy of root growth in resource acquisition and energy storage from one to another season, specific root length (SRL, root length per unit root mass) is taken into consideration as one of essential root traits (Kramer-Walter et al., 2016; Ostonen et al., 2007b). Specific root length integrates root benefit in nutrients acquisition and cost in construction, and can comprehensively reflect root physiological status and dynamics in response to inter-seasonal climatic changes (Miyatani et al., 2018). Many previous studies and models equated SRL with a constant (Eissenstat et al., 2000; Eissenstat and Yanai, 1997; Ostonen et al., 2007b), and assumed that the seasonal patterns of root length were similar to those of root biomass. However, Ostonen, et al. (2007b) reported that SRL can be indicative of environmental changes (e.g. precipitation and temperature), suggesting that SRL may have seasonal dynamics in response to the seasonal shifts in a specific regional ecosystem. During growing season with the optimal temperature and precipitation, plants tend to increase biomass and length in the fine root system dominantly through nutrient acquisition (Poorter and Ryser, 2015). During non-growing season, particularly under the harsh environmental condition, there is only the consumption for roots to maintain the basic metabolism without photosynthate input (Wang et al., 2014). Therefore, we hypothesized that SRL could be a seasonal dynamic parameter rather than a constant, and it would be higher in non-growing season when compared with that in growing season in a cold ecosystem.

The Tibetan plateau is the largest and highest plateau on earth, which covers approximately 2.5 million km^2. The alpine grassland is the main vegetation type on the Tibetan plateau. Stable plant species composition, which means stable SRL at the community level with little human disturbance, provides a unique place to monitor fine-root dynamics and the effects of fluctuations in climatic factors of a certain period on root traits (Liu et al., 2018). Nevertheless, root-trait seasonal dynamics in these under-represented high-elevation and cold ecosystems were rarely reported, as noted above, largely because of harsh condition for field work during frozen seasons. It is reported that the accumulative precipitation of an early period was a major driver for the later peak grassland aboveground biomass (Bai et al., 2004). Would this phenomenon occur in belowground root system? Accumulative precipitation of non-growing season can potentially drive root resource acquisition and energy storage in the later season by altering root traits. In this study, we were interested to see whether precipitation (or air temperature) of a certain key period, e.g. non-growing season, could account for the later fluctuations in fine root traits in a Tibetan alpine grassland ecosystem. We hypothesized that precipitation (or temperature) would have a time lag effect on fine root traits.

2. Materials and methods

2.1. Study site

The experiment was conducted at the Haibei National Field Research Station of Alpine Grassland Ecosystem, which is located in the northeast of the Tibetan Plateau (101°19’E, 37°36’N, 3215 m a.s.l.). The site has a typical Plateau continental climate, which is affected by the southeast monsoon in summer and the Siberian cold in winter. Mean annual air temperature is -1.1 °C, and mean annual precipitation is 485 mm and over 84 % of it occurs during the growing season (May to September). The soil is classified as Mat-Gryic Cambisols in Chinese Soil Taxonomy and as *Borolls* in USDA Soil Taxonomy with clay content of 65.3 %, bulk density of 0.8 g cm^{-3}, pH of 7.8, total C of 78.2 g kg^{-1} and organic C of 63.1 g kg^{-1} in the top 10-cm layer. The plant community is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa pratensis*, *Carexscab rirostris* and *Scripus distigmaticus*. The average aboveground net primary production was 368.7 (± 45.6) g m^{-2} yr^{-1} from 1983 to 2012. The site is flat and has been free of disturbance by human activities for more than a decade.

2.2. The estimations of fine-root length, biomass and specific root length

Root traits were estimated through a sequential coring method every two weeks from May 2013 to September 2015. Soil samples containing roots were randomly taken at 0 − 10 cm soil depth from each of five plots (2.2 m × 1.8 m) in the experimental site using a 7-cm diameter drill. The samples were taken back to the laboratory and washed carefully by a 0.5 mm sieve through flowing water. All live fine-roots (diameter < 2 mm) were picked up by distinguishing root color, shape and flexibility, and were scanned using a Canon scanner (Canon CanoScan LIDE 220; Canon, Krefeld, Germany) at a resolution of 600 dpi. The scanned images were analyzed by Root snap CI-690 Software (CID Bio-Science Inc., Camas, WA, USA) to measure root length. After scanned, all live roots were cleaned using deionized water, dried at 65 °C for 48 h and then weighed for root biomass.

The SRL (m g^{-1}) was calculated following the Eq. (1) for each sample (Ostonen et al., 2007a, 1999).

$$\mathrm{SRL}= RL/RM \tag{1}$$

Where *RL* is the root length (m m^{-2}), and *RM* is the root mass (g m^{-2}).

2.3. Measurements of root carbon and nitrogen

Dried root samples were ground after weighed. Root carbon and nitrogen concentrations were determined by an Elemental Analyzer (Perkin Elmer instruments series II, USA).

2.4. Measurements of soil temperature and moisture

Soil temperature and moisture were monitored hourly using EM-50 devices and 5-TM sensors (Decagon devices, USA) at 5 cm and 10 cm depths, and were recorded by dataloggers.

2.5. Statistical analysis

All statistical analyses were performed in R 3.2.5. (http://cran.r-project.org). The effects of season or month on SRL were analyzed by a one-way ANOVA. Tukey’s HSD was used to determine if there were significant differences (α = 0.05) between seasons or months. Correlation analysis was used to examine relationships of SRL and abiotic or other biotic variables. The regression analysis was performed to evaluate the effects of precipitation and mean air temperature on fine-root traits in growing season and in non-growing season with the ‘corr.test’ function in package ‘psych’. The correlations between the mean fine-root traits of growing/non-growing season and climatic factors of growing/non-growing season were analyzed by the ‘corr.test’ function in package ‘psych’. The data were visualized by function ‘ggplot’ in package ‘ggplot2’. Based on one of important results from the former analyses that non-growing season accumulative precipitation had strong effects on root biomass and length of growing season, we further performed a series of regression analyses to identify the most important period accumulative precipitation for the peak root biomass and length, using the ‘lm’ function in package ‘stats’. The potential predictor variables mainly included the accumulative precipitations of

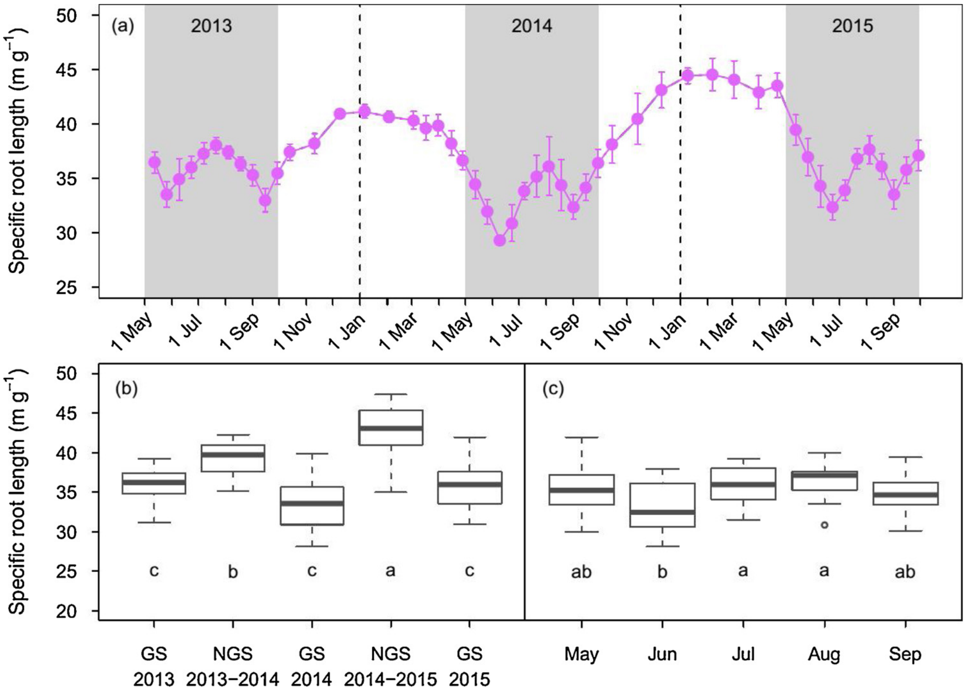

Fig. 1. Seasonal patterns of fine-root specific root length (SRL) from 2013 to 2015 (a), variations of SRL among seasons (b), and variations of SRL among months during the growing season, i.e. May-September (c). GS, growing season; NGS, non-growing season. Different letters mean significant differences at $P < 0.05$ level.

October-April (i.e. non-growing season from the last year October to the current year April), November-April, December-April, January-April, January-June and January-July.

3. Results

Specific root lengths showed a similar seasonal pattern across the three years (Fig. 1a). The SRL peaked both in the growing seasons (from May to September) and in the non-growing seasons (from October to the next April). The peak value of SRL appeared on 21 July in 2013 (38.1 m g^{-1}) across the growing seasons, and appeared on 6 February in 2015 (44.6 m g^{-1}) across the non-growing seasons. The minimum valley value of SRL occurred on 9 June in 2014 (29.3 m g^{-1}) across the growing seasons.

The mean SRL in the non-growing seasons was significantly higher than that in the growing seasons by 16.9 % across the three years (Fig. 1b). Among the five months of growing seasons, monthly mean SRL was the highest in August (36.3 m g^{-1}) and the lowest in June (33.0 m g^{-1}) (Fig. 1c).

The SRL had strong negative relationships with soil temperature and moisture (r^2 = 0.57 and 0.26, respectively; Fig. 2). The changes in SRL were also significantly associated with the shifts in plant root carbon and nitrogen (Fig. 3). The SRL decreased with an increase in root carbon concentration (r^2 = 0.19), whereas it was positively correlated with root nitrogen concentration (r^2 = 0.30).

Precipitation and mean air temperature showed significant effects on fine-root traits across the course of study ($p < 0.001$; Fig. 4). These climatic effects were distinct between growing season and non-growing season. During growing season, fine-root length, biomass and SRL all had significant correlations with precipitation (r = 0.45, 0.47 and -0.27, respectively) and mean air temperature (r = 0.48, 0.47 and -0.24, respectively). During non-growing season, however, only SRL showed a significant correlation with precipitation (r = -0.35, p = 0.014) and mean air temperature (r = -0.30, p = 0.037; Fig. 4), as well as accumulative air temperature (r = 0.86, p = 0.003; Fig. 5), suggesting that fine-root SRL could be a better indicator of environmental changes rather than root biomass or length alone. Non-growing season (or growing season) accumulative temperature showed synchronic effects on root traits of non-growing season (or growing season) (Fig. 5). It should be noted that the precipitation of non-growing seasons had no

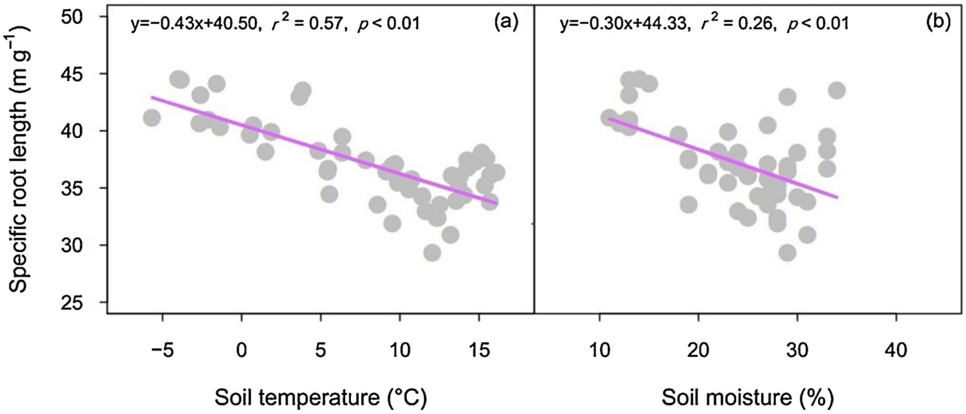

Fig. 2. Scatterplots for specific root length versus abiotic factors, i.e. soil temperature (a) and soil moisture (b) across the three years.

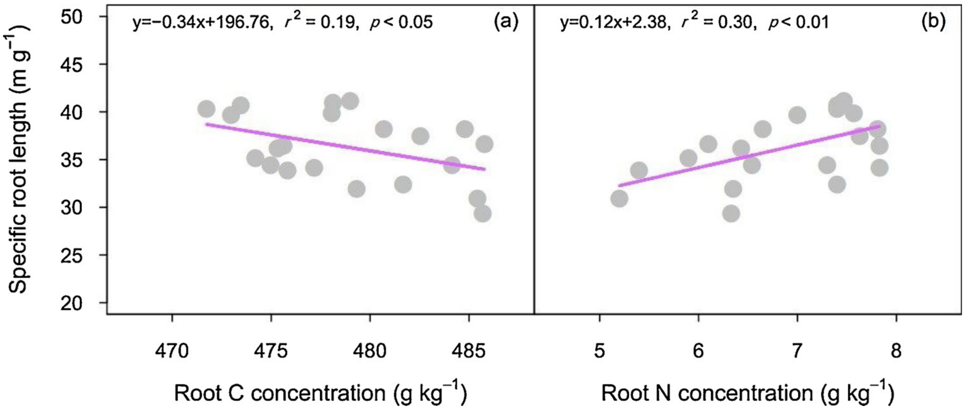

Fig. 3. Relationships of specific root length with root carbon (C) concentration (a) and root nitrogen (N) concentration (b).

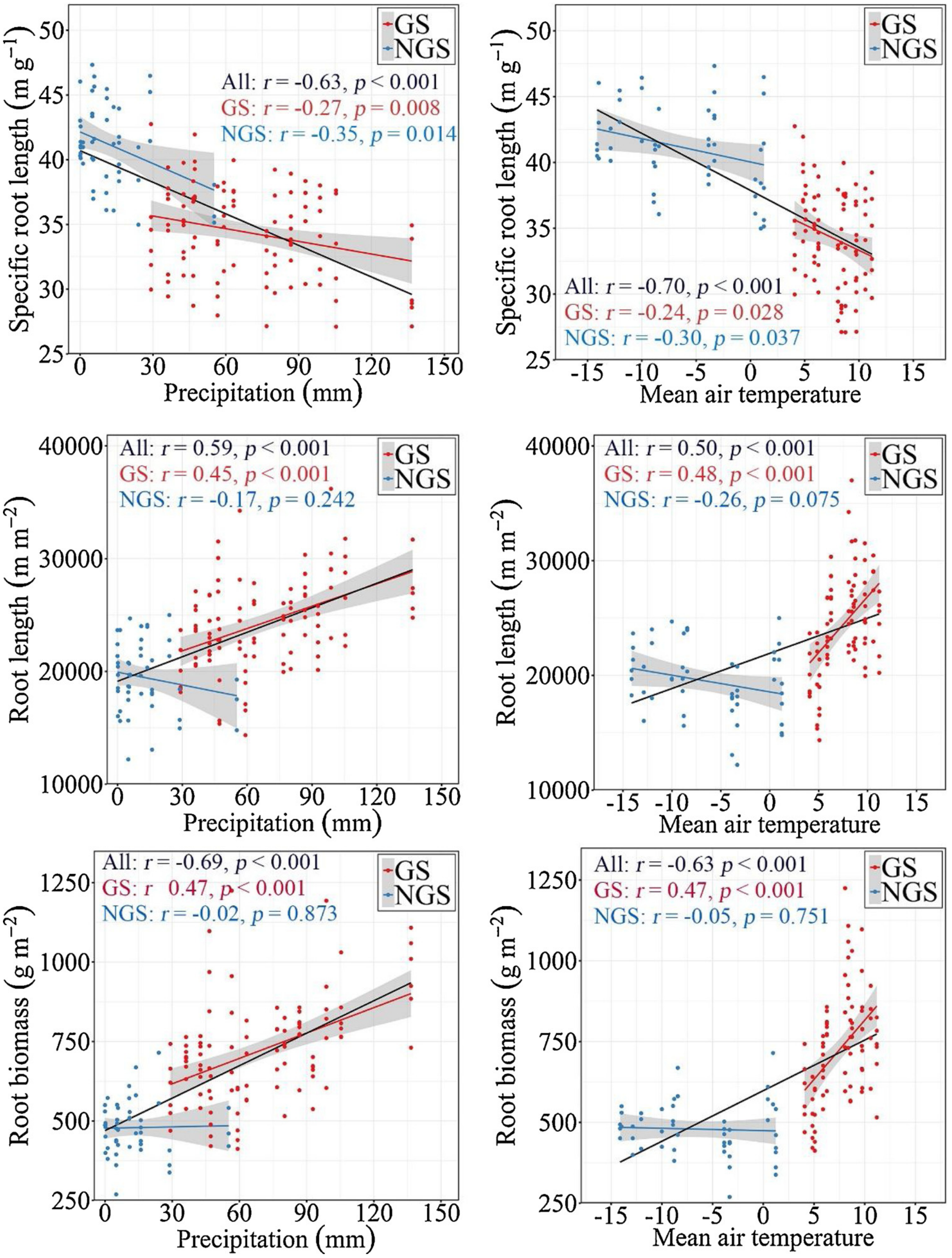

Fig. 4. Changes in fine-root traits along with precipitation and mean air temperature thorough a year (All), in growing season (GS) and in non-growing season (NGS) across the three measurement years.

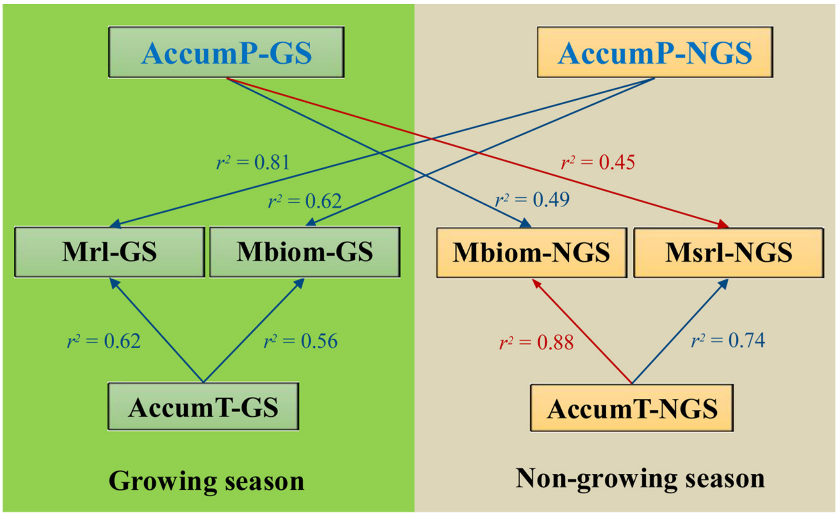

Fig. 5. The significant ($p < 0.05$) relationships of mean fine-root parameters of growing/non-growing season with accumulative precipitation and air temperature of growing/non-growing season. The blue and red lines denoted positive and negative relationships, respectively (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

significant effects on fine-root biomass and length of non-growing seasons ($r^2 = 0.00$ and 0.03, respectively; Fig. 4), but showed high relevance to root biomass and length of growing season ($r^2 = 0.62$, $p = 0.012$, and $r^2 = 0.81$, $p = 0.001$, respectively; Fig. 5), which suggested that the total precipitation of non-growing seasons could have a delay effect on root biomass and length.

To further identify whether non-growing precipitation would have the time lag effects on root biomass and length, we conducted a series of regression analyses, and found that the effect of precipitation on root length differed from that on root biomass (Table 1). The early season precipitation, i.e. the accumulative precipitation from January to April (slope = 84.31; $r^2 = 0.29$; $p = 0.021$), played a key role in the variation in the peak root length, which occurred in July each year, whereas the accumulative precipitation with peak month precipitation included, i.e. January-July precipitation, did not show a significant influence (slope = 22.31, $r^2 = 0.12$, $p = 0.16$, respectively). For the changes in the root biomass peaking in June each year, the early accumulative precipitation of January-April was the major driver as well (slope = 4.06; $r^2 = 0.29$, $p = 0.022$), and meanwhile, the accumulative precipitation including the peak month precipitation, i.e. January-June precipitation was also of importance (slope = 2.25; $r^2 = 0.25$, $p = 0.035$; Table 1).

4. Discussion

Specific root length was often used as a constant in ecological modeling, for example, data transformation from root length to root biomass (Eissenstat et al., 2000; Eissenstat and Yanai, 1997; Ostonen et al., 2007b). However, our results showed that there was significant seasonal dynamics in SRL in this high elevation and cold grassland ecosystem, indicating that SRL cannot be considered as a constant. It should be noted, as hypothesized, that mean SRL in the non-growing season was significantly greater than that in the growing season across the three measurement years. As the integrative parameter of fine roots, SRL can reflect how plants 'manage' economic benefit of the root system (Huang and Eissenstat, 2000). For example, during non-growing season, there is probably only consumption for roots to maintain their life but almost no photosynthate input (resource acquisition), which thus results in higher SRL relative to growing season (Geng et al., 2014). During the non-growing season, only SRL (neither fine-root biomass nor root length) was significantly associated with the fluctuations in climatic factors. The results suggested fine-root SRL was a sensitive indicator of climatic changes in Alpine grasslands, which was consistent with the observation in forest ecosystems (Ostonen et al., 2007b).

Table 1
The regression analysis results for the effects of the accumulative precipitation of a certain key period on the variations in peak root length and biomass. $\text{AccumP}_{\text{Jan-Apr}}$ and $\text{AccumP}_{\text{Jan-Jun}}$ indicate the accumulative precipitation of January-April and January-June, respectively.

Accumulative precipitation	**Root length** (mm m^{-2})			**Root biomass** (g m^{-2})		
	slope	p value	r^2	slope	p value	r^2
$\text{AccumP}_{\text{Jan-Apr}}$	84.312	**0.021**	0.291	4.064	**0.022**	0.287
$\text{AccumP}_{\text{Jan-Jun}}$	40.638	0.070	0.190	2.254	**0.035**	0.249

The p value in bold indicates the significance at $p < 0.05$.

Soil temperature and moisture were key predictors for the responses of fine-root SRL to climatic fluctuations. During the growing season, plants under warm and wet conditions would enhance net primary productivity by improving photosynthesis, which would also input more carbon into root and further make root diameter bigger (Comas et al., 2013; Fitters et al., 2018). This explanation was also supported by the result that root carbon concentration increased with a decrease in SRL. During non-growing season roots consume carbohydrate without a supply from aboveground, which led to the elevation in SRL. Dilution effect could explain why root nitrogen concentration was decreased with a decrease in SRL during growing season. As a result of rapid carbon accumulation and input from aboveground to belowground, root nitrogen concentration would be decreased (Caplan et al., 2019; Jarrell and Beverly, 1981).

The accumulative air temperature of a certain period exerted synchronic effects on root traits. Nevertheless, the accumulative precipitation of early season, e.g. the non-growing season, might have a lag effect on root traits. Our further regression analyses revealed this lag effect of precipitation on root traits, showing that January-April accumulative precipitation was a major driver for the variations in the root length and root biomass respectively peaking in July and June each year. Distinguishingly, root length relied on the lag effect of precipitation; however, for root biomass, the continuous accumulative precipitation together with peak month, i.e. the January-June accumulative precipitation, was also significantly vital, which was similar to the observation on grassland aboveground biomass that the peak biomass occurring in August highly depends on the January-July accumulative precipitation (Bai et al., 2004). The results can be attributed to plant economic strategy. As the increase in growing-season water availability, it was not necessary for plants to increase the root length to capture more water (Brunner et al., 2013; Johnson et al., 2001; Ostonen et al., 2005; Zhang et al., 2019). Therefore, the accumulative precipitation of early season played a crucial role in the peak root length.

However, different from root length growth, plants prefer to benefit from not only early season precipitation but also synchronic optimal growth conditions (precipitation and temperature) to enhance the biomass of root system for energy storage (Caplan et al., 2019; Mueller et al., 2016).

In conclusion, our results better reflect how climatic factors drive root dynamics in relation to plant economic strategy, which is rarely studied with non-growing season in such extreme environmental conditions, e.g. high elevation (> 3200 m a.s.l.) and cold weather with the minimum air temperature of approximately −30 °C, for three continuous years. The research we conducted in this underrepresented, yet broadly important Alpine ecosystem provides precious fine-root data, and our findings give a valuable insight into the responses of belowground carbon in a sensitive terrestrial ecosystem to global climate change.

Author contributions

L.L., J. H. and Q.W. conceived the ideas and designed methodology; L.L. conducted the experiment; G.C. and X.G. provided the meteorology data; L.L., J.C., S.P. and Q.W. analyzed the data; J.C. and L.L. led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

Acknowledgements

This study was supported by National Natural Science Foundation of China (41271316, 30670348) and the National Basic Research Program of China (973 Program) (2014CB954003, 2014CB954004). We thank the anonymous reviewers for their insightful comments, which considerably improved the manuscript.

References

Bai, Y., Han, X., Wu, J., Chen, Z., Li, L., 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431, 181–184.

Brunner, I., Bakker, M.R., Björk, R.G., Hirano, Y., Lukac, M., Aranda, X., Børja, I., Eldhuset, T.D., Helmisaari, H.S., Jourdan, C., Konôpka, B., López, B.C., Miguel Pérez, C., Persson, H., Ostonen, I., 2013. Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. Plant Soil 362, 357–372.

Caplan, J.S., Meiners, S.J., Flores-Moreno, H., McCormack, M.L., 2019. Fine-root traits are linked to species dynamics in a successional plant community. Ecology 100, e02588.

Comas, L., Becker, S., Cruz, V.M., Byrne, P.F., Dierig, D.A., 2013. Root traits contributing to plant productivity under drought. Front. Plant Sci. 4.

Eissenstat, D.M., Yanai, R.D., 1997. The ecology of root lifespan. In: Begon, M., Fitter, A.H. (Eds.), Advances in Ecological Research. Academic Press, pp. 1–60.

Eissenstat, D.M., Wells, C.E., Yanai, R.D., Whitbeck, J.L., 2000. Building roots in a changing environment: implications for root longevity. New Phytol. 147, 33–42.

Erktan, A., McCormack, M.L., Roumet, C., 2018. Frontiers in root ecology: recent advances and future challenges. Plant Soil 424, 1–9.

Fitters, T.F.J., Mooney, S.J., Sparkes, D.L., 2018. Sugar beet root growth under different watering regimes: a minirhizotron study. Environ. Exp. Bot. 155, 79–86.

Fort, F., Cruz, P., Catrice, O., Delbrut, A., Luzarreta, M., Stroia, C., Jouany, C., 2015. Root functional trait syndromes and plasticity drive the ability of grassland Fabaceae to tolerate water and phosphorus shortage. Environ. Exp. Bot. 110, 62–72.

Fort, F., Volaire, F., Guilioni, L., Barkaoui, K., Navas, M.-L., Roumet, C., 2017. Root traits are related to plant water-use among rangeland Mediterranean species. Funct. Ecol. 31, 1700–1709.

Gellesch, E., Arfin Khan, M.A.S., Jentsch, A., Beierkuhnlein, C., 2017. Grassland experiments under climatic extremes: reproductive fitness versus biomass. Environ. Exp. Bot. 144, 68–75.

Geng, Y., Wang, L., Jin, D., Liu, H., He, J.-S., 2014. Alpine climate alters the relationships between leaf and root morphological traits but not chemical traits. Oecologia 175, 445–455.

Huang, B.R., Eissenstat, D.M., 2000. Linking hydraulic conductivity to anatomy in plants that vary in specific root length. J. Am. Soc. Hortic. Sci. 125, 260–264.

Jarrell, W.M., Beverly, R.B., 1981. The dilution effect in plant nutrition studies. In: Brady, N.C. (Ed.), Advances in Agronomy. Academic Press, pp. 197–224.

Johnson, M.G., Tingey, D.T., Phillips, D.L., Storm, M.J., 2001. Advancing fine root research with minirhizotrons. Environ. Exp. Bot. 45, 263–289.

Kramer-Walter, K.R., Bellingham, P.J., Millar, T.R., Smissen, R.D., Richardson, S.J., Laughlin, D.C., 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. J. Ecol. 104, 1299–1310.

Liu, H., Mi, Z., Lin, L., Wang, Y., Zhang, Z., Zhang, F., Wang, H., Liu, L., Zhu, B., Cao, G., Zhao, X., Sanders, N.J., Classen, A.T., Reich, P.B., He, J.-S., 2018. Shifting plant species composition in response to climate change stabilizes grassland primary production. Proc. Natl. Acad. Sci. 115, 4051–4056.

Matamala, R., Gonzàlez-Meler, M.A., Jastrow, J.D., Norby, R.J., Schlesinger, W.H., 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science 302, 1385–1387.

McCormack, M.L., Guo, D.L., 2014. Impacts of environmental factors on fine root lifespan. Front. Plant Sci. 5, 205.

McCormack, M.L., Guo, D., Iversen, C.M., Chen, W., Eissenstat, D.M., Fernandez, C.W., Li, L., Ma, C., Ma, Z., Poorter, H., Reich, P.B., Zadworny, M., Zanne, A., 2017. Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. New Phytol. 215, 27–37.

Miyatani, K., Tanikawa, T., Makita, N., Hirano, Y., 2018. Relationships between specific root length and respiration rate of fine roots across stands and seasons in Chamaecyparis obtusa. Plant Soil 423, 215–227.

Montagnoli, A., Dumroese, R.K., Terzaghi, M., Onelli, E., Scippa, G.S., Chiatante, D., 2019. Seasonality of fine root dynamics and activity of root and shoot vascular cambium in a Quercus ilex L. Forest (Italy). For. Ecol. Manage. 431, 26–34.

Mueller, K.E., Blumenthal, D.M., Pendall, E., Carrillo, Y., Dijkstra, F.A., Williams, D.G., Follett, R.F., Morgan, J.A., 2016. Impacts of warming and elevated CO_2 on a semi-arid grassland are non-additive, shift with precipitation, and reverse over time. Ecol. Lett. 19, 956–966.

Norby, R.J., Jackson, R.B., 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytol. 147, 3–12.

Ostonen, I., Lõhmus, K., Lasn, R., 1999. The role of soil conditions in fine root ecomorphology in Norway spruce (Picea abies (L.) Karst.). Plant Soil 208, 283–292.

Ostonen, I., Lõhmus, K., Pajuste, K., 2005. Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: comparison of soil core and ingrowth core methods. For. Ecol. Manage. 212, 264–277.

Ostonen, I., Lõhmus, K., Helmisaari, H.-S., Truu, J., Meel, S., 2007a. Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests. Tree Physiol. 27, 1627–1634.

Ostonen, I., Puttsepp, U., Biel, C., Alberton, O., Bakker, M.R., Lohmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A.F.M., Pronk, A., Vanguelova, E., Weih, M., Brunner, I., 2007b. Specific root length as an indicator of environmental change. Plant Biosyst. 141, 426–442.

Poorter, H., Ryser, P., 2015. The limits to leaf and root plasticity: what is so special about specific root length? New Phytol. 206, 1188–1190.

Wang, Y., Liu, H., Chung, H., Yu, L., Mi, Z., Geng, Y., Jing, X., Wang, S., Zeng, H., Cao, G., Zhao, X., He, J.S., 2014. Non-growing-season soil respiration is controlled by freezing and thawing processes in the summer monsoon-dominated Tibetan alpine grassland. Global Biogeochem. Cycles 28, 1081–1095.

Zhang, B., Cadotte, M.W., Chen, S., Tan, X., You, C., Ren, T., Chen, M., Wang, S., Li, W., Chu, C., Jiang, L., Bai, Y., Huang, J., Han, X., 2019. Plants alter their vertical root distribution rather than biomass allocation in response to changing precipitation. Ecology 100, e02828.

Zhou, M., Wang, J., Bai, W., Zhang, Y., Zhang, W.H., Weiser, M., 2019. The response of root traits to precipitation change of herbaceous species in temperate steppes. Funct. Ecol. 33, 2030–2041.