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ORIGINAL ARTICLE

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Effects of root diameter, branch order, root depth, season and warming on root longevity in an alpine meadow

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Abstract Fine root is of importance in biogeochemical cycles especially in terrestrial ecosystems. The lack of understanding of the factors controlling root lifespan has made accurate prediction of carbon flow and nutrient cycling difficult. A controlled warming experiment was performed in an alpine meadow on the northern Tibetan Plateau (near Nagchu Town). We used a minirhizotron technique to measure root dynamics in situ during the growing season of 2013 and 2014 and survival analyses to assess root lifespan and the effects of root diameter, branch order, birth season, root depth and warming on root lifespan. Root diameter, branch order and root depth were all positively correlated with root lifespan. With an increase in diameter of 0.1 mm, mortality hazard ratio of roots declined by 19.3 %. An increase in one level in branch order was associated with a decrease of 43.8 % in root death ratio. Compared with roots born in May–mid-July, the mortality hazard ratio of roots born in late July–August and September–October reduced by 26.8 and 56.5 %, respectively. In warming treatments, roots tended to be thinner, less branched and deeper, and there was a higher proportion of roots born in spring compared to ambient conditions. Warming shortened the median root lifespan 44 days. However, in single warming condition, root diameter had no significant influence on root lifespan. Root diameter, branch order, root depth and season of birth were all factors affecting root lifespan in the alpine meadow; however, root branch order was dominant.

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Introduction

As one of the most active component of plants, fine roots play a substantial role in biogeochemical cycles in terrestrial ecosystems (Brunner and Godbold 2007; Finer et al. 2011). McCormack et al. (2015) estimated that fine roots account for roughly 20 % of global annual net primary productivity. Root lifespan, as an important root trait, not only regulates the capacity of a plant to absorb water and nutrients from the soil, but also determines the quantity and quality of root-derived organic matter transferred to soil (Guo et al. 2008). Notwithstanding its great importance to whole plants and ecosystem processes, understanding concerning the controls of root lifespan is lacking, hindering the prediction of carbon (C) flow and nutrient cycling dynamics at the ecosystem scale (McCormack and Guo 2014).

Previous studies have shown that root lifespan is related to endogenous factors such as root diameter, different seasons of birth, root depth, nitrogen (N) concentration (Baddeley and Watson 2005; Tjoelker et al. 2005; Gang et al. 2012; McCormack et al. 2012; Chen and Brassard 2013) and environmental factors such as temperature, water, nutrient availability and microbial activities, as well as competition (Tierney and Fahey 2001; Jones et al. 2003; Green et al. 2005; Beyer et al. 2013; Chen and Brassard 2013). Among endogenous factors, root diameter is often regarded as a key determinant of root lifespan and has attracted the most attention (Wells and Eissenstat 2001; King et al. 2002; Tierney and Fahey 2002). In a study in a temperate pine forest, Guo et al. (2008) showed that root branch order also dictates root lifespan. However, these trends have not been validated in alpine grasslands where the roots account for above 50 % of biomass, despite the considerable variation in branch structure in roots of many alpine plants (Yang et al. 2009). As root traits may be drivers of ecosystem processes (Bardgett et al. 2014; McCormack et al. 2015), and as branch order can be an important factor influencing root traits, considering root branch order when studying the controls of grassland root lifespan has become increasingly necessary.

Of the different environmental factors that often affect root and whole-plant physiology, temperature is one of the most important. There have been many studies on the effects of rising temperature on root lifespan. Most results indicated that root lifespan decreased with rising temperature (Forbes et al. 1997; King et al. 1999; Majdi and Ohrvik 2004; Leppälammi-Kujansuu et al. 2014); however, there is still some debate, as root lifespan was not altered in some cases (Fitter et al. 1999; Johnson et al. 2006) or even increased (Bai et al. 2012). Therefore, more work is needed to determine how warming influences root lifespan.

As the earth's 'third pole', the Qinghai–Tibetan plateau is suffering an unprecedented warming trend, which is much greater than the global average. This will likely have substantial effects on alpine ecosystems (IPCC 2013), as the alpine ecosystems in the plateau formed under long-term extreme environmental conditions tend to be simple, fragile and quite sensitive to climatic change (Zhou et al. 2006). Alpine meadow dominated by *Kobresia* spp. is a widely distributed vegetation type on the plateau, covering one-third of its area, and plays a critical role in uptake and storage of C (Kato et al. 2006; Yang et al. 2008). To better understand the effects of climatic change on alpine meadows, a number of warming experiments have been conducted to study multiple aspects of aboveground plant growth and soil respiration (Atkin et al. 2000; Xu et al. 2009; Luo et al. 2010; Lin et al. 2011; Wang et al. 2012). However, studies concerning effects of warming on belowground dynamics are insufficient (e.g., Wu et al. 2014). Root biomass has been suggested to account for nearly 90 % of total biomass in alpine grasslands (Yang et al. 2009). Thus, a lack of information regarding effects of warming on root turnover strongly limits comprehensive understanding of the effects of warming on alpine vegetation, and hinders our ability to predict how C sequestration will vary under future warming in alpine areas. Therefore, to further an understanding of how alpine ecosystems respond to climatic change it is critical to study effects of warming on root lifespan in alpine meadows.

The present study involved a controlled warming experiment applying open-top chambers (OTCs) in an alpine meadow on the central Qinghai–Tibetan plateau. We used the minirhizotron technique to measure root production and mortality in situ for two growing seasons. Based on each root axis measured in root images, we categorized root populations for each treatment by root diameter, branch order, root depth and season of birth. Then we applied survival analyses to assess effects of each factor above and warming on root lifespan in the alpine meadow. We aimed to determine what endogenous factors influence root lifespan and how warming affects root lifespan in the alpine meadow. According to previous studies (e.g., Guo et al. 2008; Wu et al. 2013, 2014), we hypothesized that: (1) root diameter, root branch order, root depth and season of birth would significantly influence root lifespan in the alpine meadow and (2) warming would shorten root lifespan.

Materials and methods

Site descriptions

The study was carried out at the Nagchu Alpine Grassland Ecosystem Research Station (31°38′43″N, 92°00′46″E, hereafter Nagchu Station), which belongs to the Institute of Geographical Science and Natural Resources, Chinese Academy of Sciences. Nagchu Station is located at high altitude (4585–4603 m) in the vital area of the Tibetan Plateau, where the climate is arid, cold and windy, with long winters and short summers. The growing season is from May or June to October. The mean annual temperature is −0.9 to −3.3 °C with mean temperature of the warmest month of 8.8 °C and that of the coldest −13.8 °C. The average annual relative humidity is 48–51 % and the mean annual precipitation is 400 mm (Su et al. 1994). There is a 60-ha experimental area in Nagchu Station, which has been enclosed by a 1.5-m-high metal fence since 2010 to prevent grazing. The soil is a typical alpine meadow soil: a sandy loam, with pH of 8.0–8.7 and thickness of 30–50 cm (Wang et al. 2015). Roots in topsoil form a sod layer of 5 cm beneath the ground surface.

The vegetation belongs to typical alpine meadow. The average height is 3–5 cm and the total coverage is 70–80 %. The dominant population is *Kobresia pygmaea* (coverage of 50–65 %), and the major accompanying species include *Potentilla saundersiana*, *P. bifurca*, *Stipa purpurea* Griseb., *Festuca ovina* L., *Leontopodium pusillum* and *Carex moorcroftii* (Wang et al. 2015).

Controlled warming experiment

The experiment was initiated in the experimental area of Nagchu Station in May 2012. A square sample area with sides of length 50 m was stochastically chosen in the area. Passive warming treatments were established using five OTCs that were randomly established in the area. The OTCs made of polycarbonate were regular octagons of 1.5 m both in length and height, vertical to the ground. The OTCs remained in place year round. Five control plots were randomly set up near the OTCs. The distance between any two plots was > 3 m.

Two microclimate automatic monitoring systems (CR200X-Series data logger, Campbell Scientific, Logan, UT, USA) were used to continuously measure air temperature and moisture, and soil temperature and moisture. With experimental warming, daily air temperature (Ta) increased by 0.46 °C, soil temperature in the top 10 cm increased by 1.6 °C and soil water content in the top 10 cm decreased by 15.1 % (2.8 % V/V) during June–October (growing season) 2013; correspondingly during May–October 2014 there was a 0.49 °C increase, 1.72 °C increase and 12.4 % decrease (2.9 % V/V).

Minirhizotron installation

A minirhizotron tube (inside diameter, 6.3 cm; outside diameter, 7 cm; length, 100 cm) was installed in each plot following the setting up of OTCs. First, an auger (diameter 7 cm) was used to drill a hole of length 80 cm at an angle of 30° with respect to the ground surface. The minirhizotron tube was then installed into the auger hole, with the bottom sealed with a black plastic cap to prevent soil and water entering. The aboveground portion of each tube was wrapped with 2–3 layers of aluminum foil to exclude light infiltration and heat loading. The top was then covered with a PVC stopper to prevent entry of dust, rain and light. Finally, soil was backfilled so as to minimize the voids surrounding the tube wall and to prevent rotation and sliding of the tube.

Root image capture

After an equilibrium period of 14 months, a CI-600 device (In-situ Root Scanning System, CID Inc., Camas, WA, USA) was used to capture root images. During each image-capture session, images (frame size 21.59 cm × 19.56 cm) were collected at 20-cm intervals along each tube. The effective length of each image was 20 cm, excluding the overlapping portion and, taking into account the 30° angle with the ground surface, the images represented depths of 0–10, 10–20 and 20–30 cm. Almost all roots in the alpine meadow were above a depth of 30 cm. Images were captured six times during July–September 2013, and 11 times during May–October 2014. In each growing season, the sampling interval was 14–17 days. From October 2013 to April 2014, root images were not captured because of dormancy of the roots.

Data analysis

The analysis software WinRHIZO TRON (Regent Instruments Canada Inc., 2013) was used to analyze the root images. Following the method of Hendrick and Pregitzer (1993), roots in all images were classified as 'alive', 'dead' or 'gone'. Roots of all vegetation species were treated together. If they were white or light brown, roots were recorded as 'alive'; if they had turned dark and showed no elongation in later sessions, they were classified as 'dead'; and if they had disappeared, they were classified as 'gone'. The required parameters, such as birth session and diameter of each root axis, were recorded automatically. In total, there were 4784 individual roots of different orders analysed in the control and 3820 individual roots in the warming treatment. All roots of each treatment were classified into five classes according to root diameters: 0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.4 and > 0.4 mm. Meanwhile, roots were classified into three classes according to root orders following Wells et al. (2002a)and Guo et al. (2008): root segments with zero, one and two orders of visible dependent laterals were considered first, second and third order roots, respectively (i.e., first order roots were terminal roots derived from second order roots, and second order roots were derived from third order roots). Roots were also classified into three categories according to root depth of 0–10, 10–20 and 20–30 cm; and three cohorts according to season of birth: spring (May to mid-July), summer (late July–August) and autumn (September–October).

A stratified Cox proportional hazards regression was used to predict the factors influencing root lifespan (Cox 1972; Guo et al. 2008) for each treatment. Factors of treatment, root diameter, root order, root depth and season of birth were taken as predictor covariates (Table 1).

$$h_i(t) = h_0(t)\exp(\beta_1\chi_{i1} + \beta_2\chi_{i2} + \cdots + \beta_p\chi_{ip})$$

In the Cox regression, $h_i\,(t)$ represents the mortality hazard for an individual root at time t. It is computed by an unspecified baseline hazard function (h_0) and an exponential function of p covariates. The model determines coefficient β for each covariate and tests the null hypothesis of $\beta = 0$ with a Chi square statistic. A positive β indicates that mortality rate will increase with increasing values of a covariate (Wells and Eissenstat 2001). The hazard ratio (e^{β}) represents the death risk of roots at one level. For a continuous covariate such as diameter or order, the parameter represents the risk change with a one-unit change of the covariate. For categorical covariates such as root depth and season of birth, the hazard ratio can be interpreted as the ratio of the hazard of root cohorts in 10–20 or 20–30 cm to that of root cohort in 0–10 cm.

Table 1 Predictor covariate tested in the Cox proportional hazards regression analysis of root lifespan

Variable	Coding and description
Treatment	Control, warming
Order	Categorical, 1 = first order, 2 = second order, 3 = third order or higher
Diameter	Continuous, root diameter at appearance (mm), 0.1 mm interval (0.0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.4, > 0.4)
Root depth	Continuous, soil depth at which a root appeared (0–10, 10–20, 20–30 cm)
Season of birth	Categorical, the season when a root axis first appeared: spring (May–mid July), summer (Late July–August), autumn (September–October)

Then Kaplan–Meier analysis was employed to plot root survival curves and predict median lifespan of each root cohort classified by different criteria and treatments (Kaplan and Meier 1958).

In addition, one-way ANOVA with warming as the main factor was applied to test the effects of warming on root diameters, branch orders and vertical locations (based on root numbers). Statistical analyses were performed with SPSS version 21.0 (IBM Inc., Armonk, NY, USA). In all cases, a significance level of $P < 0.05$ was accepted.

Results

Influence of root diameter, branch order, root depth, season and warming on root lifespan in the alpine meadow

According to the analysis of Cox proportional hazards regression, root diameter, branch order, season of birth and root depth all had a significant influence on root lifespan (Table 2). With an increase in diameter of 0.1 mm, mortality hazard ratio of roots declined by 19.3 % ($P < 0.001$). The death risk of roots decreased by 43.8 % with an increase of one level in branch order ($P < 0.001$). Compared with roots born in spring, the mortality hazard ratio of roots born in summer and autumn reduced by 26.8 and 56.5 %, respectively ($P < 0.001$). Compared with roots located 0–10 cm below the ground, the mortality hazard ratio of roots located 10–20 and 20–30 cm was reduced by 29.7 % ($P < 0.001$) and 20.4 % ($P = 0.001$), respectively.

Warming significantly increased the mortality hazard ratio of roots by 46.4 % ($P < 0.001$). Warming reduced the median root lifespan to 282 days, compared with 326 days for control plots (Fig. 1). From October 2013 to April 2014, root images were not captured for the dormancy of roots in the alpine meadow, so there is a plateau from day 100 to around 220 (Fig. 1). However, in single warming condition, root diameter had no significant influence on mortality risk ($P = 0.109$).

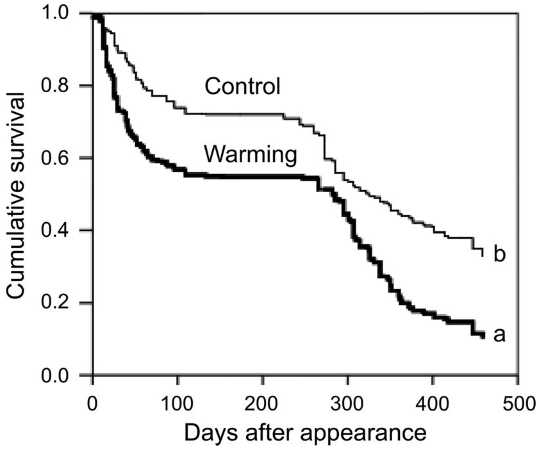

Fig. 1 Root survival probabilities under the control and warming conditions. *Different letters* (*a*, *b*) indicate significant difference ($P < 0.05$)

Effects of experimental warming on root architecture and root depth

In control plots, the range of root diameters was 0.08–0.78 mm, average diameter was 0.16 ± 0.08 mm and median diameter was 0.14 mm. The proportion of the number of roots <0.1 mm was the highest (39.4 ± 3.6 %) and, with increasing diameter class, the root number decreased. In warming conditions, the range of root diameter was 0.08–0.68 mm, and the average and median diameter reduced to 0.12 ± 0.07 and 0.08 mm, respectively. Among diameter classes, the proportion of the number of roots <0.1 mm in warming condition was double that in the control and the proportions of other diameter classes all decreased by over 50 % (Fig. 2a).

In control plots, first order roots accounted for a large proportion (58.4 ± 3.5 %). Root numbers decreased exponentially with branch orders. The total root number by order distribution yielded a ratio between the second and first order of 1.8, and between the third and second order of 3.2. Warming increased the proportion of first order roots by 22.1 % ($P < 0.01$), resulting in the ratio between the second and first order increasing to

Table 2 Results of Cox proportional hazards regression analyses for predictor variables of root lifespan for all roots

Factors	d.f.	Parameter estimate	SE	χ^2 value	*P*	Hazard ratio
Treatment	1	0.381	0.040	90.621	<0.001	1.464
Order	1	–0.576	0.036	258.100	<0.001	0.562
Diameter	1	–0.214	0.024	79.448	<0.001	0.807
Season (Ref* = spring)	2			188.160	<0.001	
Summer	1	–0.313	0.040	60.503	<0.001	0.732
Autumn	1	–0.833	0.062	182.522	<0.001	0.435
Depth (Ref* = 0–10 cm)	2			72.304	<0.001	
10–20 cm	1	–0.352	0.042	69.640	<0.001	0.703
20–30 cm	1	–0.228	0.069	11.009	0.001	0.796

Spring, Summer, and Autumn represents May–mid-July, late July–August, and September–October, respectively

* The reference season, depth to which lifespan of roots born in other seasons or located in other soil depths was compared

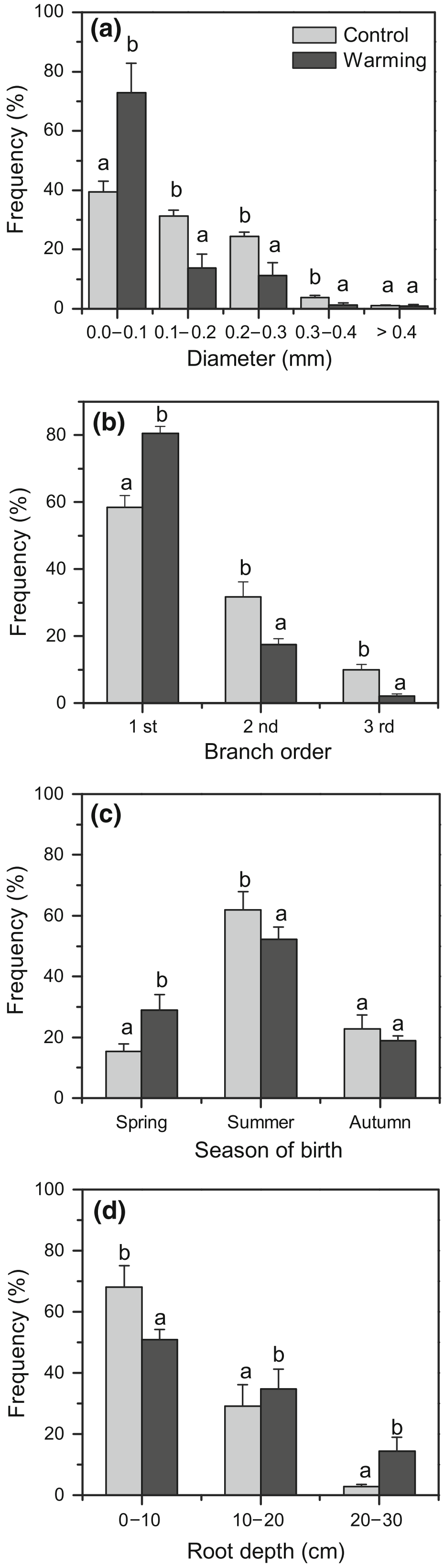

Fig. 2 Effects of warming on root diameters (**a**) branch order (**b**) root depth (**c**) and season of birth (**d**). Spring, summer, and autumn were in May to mid-July, late July to August, and September to October, respectively. *Vertical bars* correspond to standard error (n = 5). *Different letters* (*a*, *b*) indicate significant difference ($P < 0.05$)

4.6, and between the third and second order increasing to 8.3 (Fig. 2b).

Root number decreased dramatically with deeper soil layers. Under ambient conditions, root number proportion in top (0–10 cm), middle (10–20 cm) and bottom soil (20–30 cm) were 68.1 ± 6.9, 29.1 ± 7 and 2.8 ± 0.7 %, respectively. While in warmed plots, the proportion in top soil reduced by 17.2 % ($P < 0.01$) and in bottom soil increased by 11.5 % ($P < 0.01$, Fig. 2c).

Under ambient conditions, most roots were born in summer (61.8 ± 6 %), followed by autumn (22.7 ± 4.6 %) and the least were in spring (15.4 ± 2.4 %). Warming doubled the proportion of roots born in spring (29 ± 5.1 %) and reduced those in summer by 9.6 % ($P < 0.01$, Fig. 2d).

Discussion

Root diameter and branch order

The root lifespan across species in the alpine meadow was positively correlated with root diameter. The trend was consistent with many other studies on woody plants and in some forests (Wells and Eissenstat 2001; Anderson et al. 2003; Baddeley and Watson 2005; Pritchard et al. 2008; McCormack et al. 2012), shortgrass steppe (Gill et al. 2002) and alpine meadow (Wu et al. 2013). In general, root features such as root respiration rate and C and N contents differ with diameters (Bahn et al. 2006; Bardgett et al. 2014). Finer roots with faster respiration and more active physiology tend to have shorter lifespans (Pregitzer et al. 1998). Fine roots with higher N content are also likely more palatable to soil herbivores which may also contribute to their shorter lifespan (Gordon and Jackson 2000).

Previous studies showed that root diameter was a key factor influencing root lifespan (Wells and Eissenstat 2001; King et al. 2002; Tierney and Fahey 2002; Pilon et al. 2012; Wu et al. 2013). A survey of peach trees showed that influence of root order on lifespan was nearly equal to that of diameter (Wells et al. 2002a). For evergreen pine forest, Guo et al. (2008) found that root branch order was a stronger predictor of root lifespan than diameter. Our study showed that root lifespan markedly increased with increasing root order, and the relationship between root order and lifespan was stronger than for diameter (43.8 versus 19.3 % in control condition). This suggested that root branch order might be the more dominant predictor of root lifespan than root diameter in this alpine meadow.

According to the definition of root branch order, lower order roots were born on roots of the higher order. Once a root with higher order died, its branches must also be dead. Therefore, higher order roots must have longer lifespan than lower order roots as a result of branch order itself (Guo et al. 2008). Moreover, root traits (e.g., structural C and N contents and specific surface area) differ with root orders, affecting root lifespan (Pregitzer et al. 2002; Guo et al. 2004), like N or structural C content which is influencing the predation of soil herbivores (Sun et al.2011) and metabolism rate (Guo et al. 2008). McCormack et al. (2015) stated that root function was closely related with root branch order. Roots of lower orders mainly undertake functions of capturing water and nutrients, have more dynamic physiology and have shorter lifespans; in contrast, roots of higher orders mainly undertake functions of storage, support and transportation, have less dynamic physiology and survive longer. Specifically, root lifespan was positively related to root tissue density and average mass of an individual root, indicating the total amount of C a plant invests into its roots is positively related to root lifespan (Sun et al. 2016).

Season of birth

This study showed that roots born later in the growing season had longer lifespans than those born earlier (i.e., spring), consistent with previous studies on woody plants (Burton et al. 2000; Johnson et al. 2000; Kern et al. 2004) and an alpine meadow (Wu et al. 2013). This may be related to seasonal variation in temperature which is directly related with soil N mineralization resulting in more rapid respiration and physiological activity of roots, increasing their mortality hazard (Burton et al. 2000; Eissenstat et al. 2000; Pregitzer et al. 2000; Bai et al. 2010).

It was previously suggested that root lifespan was related to C allocation (Farrar and Jones 2000; Norby and Jackson 2000; Bai et al. 2012). More C allocated to aboveground parts could shorten the root lifespan. At the beginning of the growing season in alpine meadows, the resprouting and green-up of plants may consume many nutrients stored in roots. Therefore, substantial amounts of C may be transferred from belowground to aboveground parts, leading to a C shortage in new roots born in spring. As a result, their lifespan may be shortened. With growth deceleration of aboveground growth in summer, more C can be allocated to belowground structures, resulting in sufficient C resources for new roots (Wu et al. 2010). Therefore, in the alpine meadow, roots born in summer and autumn may survive longer than roots born in spring owing to greater availability of C resources later in the growing season.

In addition to the reasons above, the apparently longer lifespan of roots born in summer and autumn compared to spring may be due to a sampling artifact. Because image collection had to be halted during the non-growing season there were more complete data for roots born in spring and, conversely, more censored data (i.e., roots whose death dates could not be directly observed) for roots born in summer and autumn. Roots born in spring were generally more easily observed over a longer period throughout the growing season and directly classified as dead in later sessions. In contrast, roots born in summer and autumn more likely entered a dormancy period and were more likely to pass through the long non-growing season, resulting in a longer lifespan.

Root depth

The deeper roots tended to survive longer than those in shallow soil. These results were generally consistent with data from another alpine meadow (Wu et al. 2010) and most studies on woody species (Baddeley and Watson 2005; Guo et al. 2008), which all showed that fine root lifespan was moderately increased with root depth. However, these results contrast with Gill et al. (2002), who showed that root depth did not significantly alter root lifespan in a shortgrass steppe.

Overall, there is generally a positive, but sometimes weak relationship between root depth and root lifespan. This may be due to comprehensive environmental conditions resulting from root depths, including soil biotic and abiotic environments. Gill et al. (2002) proposed three mechanisms based on the assumption of relationships between root lifespan and soil temperature, N mineralization and soil herbivore activities. For each mechanism, deeper roots experience a more stable environment with smaller fluctuations.

Effects of warming on root lifespan

This study indicated that experimental warming significantly shortened overall lifespan of roots in the alpine meadow, consistent with most results of previous studies (Tierney and Fahey 2001; Jones et al. 2003; Majdi and Ohrvik 2004; Wu et al. 2014). Compared to Wu et al. (2014), the reduction in fine root lifespan was relatively large in our study (reduction of 44 days compared to 21 days in Wu et al. 2014). This may have been because of different warming amplitudes, different altitude and different sensitivities to warming of the different species between the two alpine meadows and different diurnal fluctuation.

Burton et al. (2002) found that root respiration rate was strongly and positively related to temperature. With increasing temperature, root metabolism and respiration, free radical formation and root maturing all accelerate and death risk is increased, resulting in an overall shortened lifespan. Some studies found that soil animals significantly influenced root dynamics (Wells et al. 2002b; Stevens and Jones 2006), and as warming may promote activities of soil herbivores, warming may also indirectly lead to increased root herbivory and shortened root lifespan. In the present study, when ignoring the influences of root architecture and vertical location of roots, warming still shortened the median root lifespan by 19 days (data not shown). Additionally, by comparing the same root cohorts classified by a single endogenous factor of the two different treatments, we found lifespan of each different root cohort (i.e., each diameter class and order, as well as those born in spring and summer) was shortened by warming.

The study was not consistent with a study in a semiarid temperate steppe (approximately 383 mm with 90 % of the precipitation falling from May to October in Inner Mongolia, China), which found day and continuous warming significantly prolonged root lifespan, while night warming had no significant influence on root lifespan as the interpretation of ecosystem C allocation (Bai et al. 2012). Day warming decreased soil moisture and resulted in proportionally more C allocated to roots, leading to longer root lifespans, but night warming did not (Farrar and Jones 2000; Norby and Jackson 2000). However, in the alpine meadow, our unpublished data showed that warming reduced the proportion of C allocated to belowground. This may be because of different adaptive strategies between alpine meadow and semiarid grassland for the different species compositions.

Warming may also indirectly influence root lifespan through other factors including water content (McCormack and Guo 2014). In addition to higher temperatures, experimental warming also reduced soil moisture in this study, which led to shifts in root architecture and root vertical location. Compared to Wu et al. (2014), we found a shift in root vertical location as the whole root zone became deeper rather than shallower. The opposite result may be ascribed to effects of warming on different modes of water and nutrient supply. Apart from the direct influence on roots, indirect influences through alternative community structure which showed lesser importance of shallower-rooted species (e.g., *K. pygmaea*) and greater importance of deeper-rooted species (e.g., *P. saundersiana*) also contributed to the shifts in root vertical location. We observed that the proportion of first order roots increased, roots were deeper and the proportion of roots born in spring increased. Furthermore, mean and median root diameters were reduced by 0.04 and 0.06 mm, respectively, and the proportion of extremely thin roots (diameter <0.1 mm) nearly doubled. Thinner roots are more economical to build (Chen and Brassard 2013; Carrillo et al. 2014) and have relatively larger specific surface area which may help improve water absorption capability of the total root system. This study also showed that warming increased the proportion of roots of first order by 23 % ($P < 0.01$). Because the main function of first order roots is absorbing water and nutrients (Long et al. 2013; McCormack et al. 2015), so a greater proportion of these roots would effectively boost the overall water absorbing ability of plant roots and enable adapting to water limitations.

Conclusions

Root diameter, branch order, root depth and season of birth were all positively correlated with root lifespan. Among these factors, root branch order was the strongest single predictor and determinant of root lifespan.

Warming significantly shortened root lifespan in the alpine meadow. On the one hand, warming may have directly shortened root lifespan by increasing physiological activity. On the other hand, experimental warming resulted in a greater proportion of thinner roots, first order roots and roots born in spring, which consequently shortened the overall root lifespan. We can conclude: in the alpine meadow, warming and drier environment will significantly accelerate root turnover and ecosystem C and N cycling.

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