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## Root size and soil environments determine root lifespan: evidence from an alpine meadow on the Tibetan Plateau

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**Abstract** We used a minirhizotron system to investigate the influence of three major factors—root morphology, root depth, and season of root emergence—on root survivorship and longevity in a *Kobresia humilis* meadow on the Tibetan Plateau during the growing season of 2009. Root longevity was assessed by survival analysis, Kaplan–Meier analysis, and Cox proportional hazards regression. Root longevity was correlated positively with root diameter. A 17.5 % decrease in the risk of mortality was associated with a 0.1-mm increase in diameter. Roots distributed in the top 10 cm of the soil had significantly shorter longevities than roots at greater depths, with a 48 % decrease of mortality risk for each 10-cm increase in soil depth from the surface to 40 cm. Of all the factors examined, the season of root emergence had the strongest effect on root lifespan. Roots that emerged in May and June had shorter longevity than roots that emerged later in the year, and roots that emerged in September and October were more likely to survive over winter. Our findings indicated that life-history traits of roots in *K. humilis* meadows are highly heterogeneous, and this heterogeneity should be considered when modeling the contribution of roots to carbon and nitrogen fluxes in this type of meadow ecosystem. Moreover, temporal, spatial, and compositional

variations in root longevity must be considered.

**Keywords** Minirhizotron · Alpine meadow · Root lifespan · Survival analysis · Seasonal dynamics

### Introduction

Fine roots—the most active fraction of root systems—are an integral component of ecosystem-level processes, especially carbon and nutrient cycling. Assuming that fine roots turn over once per year, the expense of fine root production accounts for nearly 30 % of total global annual net primary production (NPP) (Jackson et al. 1997). Moreover, in forest ecosystems as much as 40–50 % of annual NPP may be allocated to fine roots (Vogt et al. 1996). In addition to the important role of fine roots in the plant's carbon budget, the amount of nitrogen returned to the soil from fine root death and decomposition equals or exceeds that from leaf litterfall (Vogt et al. 1986). Although the importance of fine roots is well recognized, many questions remain regarding the variation in fine root lifespan among species and measuring methods, as well as which factors regulate fine root lifespan and the mechanisms underlying those factors (Eissenstat et al. 2000).

Root diameter is often used as a criterion to categorize root populations with very different lifespans. Studies of trees demonstrated that the lifespan varies several-fold within a narrow root diameter class, as reported in fruit trees (Wells and Eissenstat 2001; Wells et al. 2002) and in *Pinus palustris* Mill. (Guo et al. 2008). The relationship between root diameter and lifespan for woody species is relatively clear, but it is debatable whether this relationship exists in grasses. Several studies have reported a relationship between grass root diameter and longevity (Hendrick and Pregitzer 1996; Tingey et al. 2000; Krift and Berendse 2002; Peek et al. 2005; Steinaker and Wilson 2005), in contradiction to the common view that grass roots are homogeneous with respect to life-history traits. Gill et al. (2002) were

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the first to introduce minirhizotrons to a shortgrass steppe, and they showed that a 0.1-mm increase in diameter resulted in a 6 % decrease in grass root mortality. However, the relationship between root diameter and lifespan for grass roots is still poorly understood.

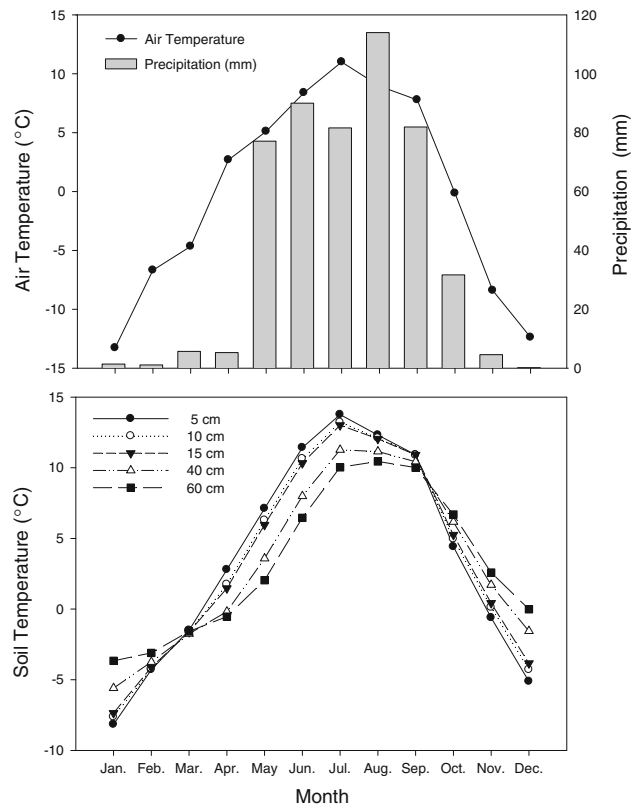
Root diameter, as an endogenous factor influencing root lifespan, should be used to partition the fine root guild for more precise lifespan estimates. Exogenous factors such as temperature, moisture, and soil nutrient availability may also affect root lifespan (Nadelhoffer et al. 1985; Pregitzer et al. 1993, 2000; Hendrick and Pregitzer 1997; Nadelhoffer 2000). Such knowledge is critical for identifying the factors that determine root mortality and lifespan under changing environments, which is also directly relevant to global climate change because of the carbon partitioning in roots. It is difficult to generalize from the few studies available, however, due to the large variations in both direction and strength of environmental effects on root lifespan. Moreover, it is likely that a combination of factors influences root lifespan interactively and site- or ecosystem-specifically. For example, water availability may have the largest impact on root longevity where water is most limiting, such as in a desert, whereas in more humid systems, nutrients may play a greater role (Nadelhoffer et al. 1985). However, few of the studies on grass root systems were similar, and even fewer have been conducted in alpine grasslands.

The purpose of this study was to use a minirhizotron system to examine how potentially important covariates of root longevity—root diameter, soil depth, and season of root emergence—influence root survivorship and longevity in a *Kobresia humilis* meadow on the Qinghai-Tibetan Plateau. We predicted that (1) root diameter would be correlated positively with root lifespan; (2) root lifespan would increase with increasing depth in the soil; and (3) the season of root emergence would strongly influence root lifespan because roots that emerge in different seasons may serve different ecological functions in this highly seasonal environment.

## Methods

### Site description

This study was conducted at the Haibei Alpine Meadow Ecosystem Research Station (37°29–45'N, 101°12–23'E), within an alpine *K. humilis* meadow on the northeastern edge of the Qinghai-Tibetan Plateau. The meadow is approximately 3,250 m in elevation, and its weather is dominated by the southeastern monsoon and the Siberian high pressure system. The area has a continental monsoon climate, with long severe winters and short cool summers. The annual average air temperature for 1981–2000 was  $-2^{\circ}\text{C}$ , with a maximum of  $27.6^{\circ}\text{C}$  and minimum of  $-37.1^{\circ}\text{C}$  (Li and Zhou 1998). Annual precipitation during the same period ranged from 426 to



**Fig. 1** Seasonal variation of monthly integrated air temperature, precipitation, and soil temperature at various depths in 2009

860 mm, 80 % of which fell during the short growing season from May to September (Li and Zhou 1998). The annual duration of sunshine was 2,462.7 h, or 60.1 % of the total possible duration (Yi and Yang 2006). According to the FAO classification system, the dominant soil is a Mat-Cryic Cambisol. The surface soil has high moisture and organic matter contents (Cao et al. 2004). Microclimatic conditions during the measurement period are presented in Fig. 1.

The plant community is dominated by the perennial sedge *K. humilis* (C. A. Mey.) Serg. Aboveground living biomass averaged  $342\text{ g m}^{-2}$  during 1980–1993 and peaked in July or August, when air temperature and precipitation were the highest of the year (Li and Zhou 1998). Since 1982, the study site had been used as winter pasture for sheep, with the grazing period from late September to the end of April. The grazing intensity was  $2.55\text{ sheep ha}^{-1}$  with only lambs. Almost all visible stubble and dead leaf materials were consumed during the winter period (Cao et al. 2004).

### Minirhizotron

A plot of  $250\text{ m}^2$  was set in the meadow, in which minirhizotrons (BTC-100X camera system and BTC I-CAP software, Bartz Technology Corp. Santa Barbara, CA)

were used to observe and photograph fine root dynamics. In September 2008, six clear polybutyrate tubes (inside diameter 4.4 cm, length 100 cm) were installed into 71-cm-deep auger holes at a 45° angle to the soil surface in the alpine meadow. This gave an effective maximum viewing depth of 50 cm, and about 40 images were collected per tube. The bottom of each tube was sealed to prevent soil water from entering the tube. The aboveground portion of the tube was covered with aluminum foil and wrapped with reflective tape to exclude light. The top end of each tube was sealed with a white PVC rubber stopper to minimize heat exchange between soil and the atmosphere and to prevent light from entering.

The minirhizotron tubes were left in place for 8 months before the first image collection to allow the root system to recover from the disturbance caused by their installation and to improve contact between the tube surfaces and soil. Images (frame size 18 mm × 14 mm) were recorded using a high-magnification video camera attached to a ratcheting handle (Bartz Technology Corp.). A hole was drilled in the tube on the top face just below the upper end, which allowed the camera to be fixed in an upward position during image collection. This ensured that the same positions in the soil were photographed consistently to allow comparison of images over time. Minirhizotron tube and frame numbers were logged directly on the video image during recording using an on-screen display. Images were collected at 2-week intervals from May to November 2009 and once in May 2010.

Images of roots intersecting the surface of each tube on the sequential sampling dates were reviewed by microvideo camera and used to construct a database of life-history information. The root image-analysis software WinRHIZO TRON (Regent Instruments, Canada, <http://www.regentinstruments.com>) was used to digitize the video images. Dates of individual root emergence and death were recorded, and the diameter was assessed. Roots were classified as dead when they appeared dark or disappeared, following the convention used in previous minirhizotron studies (e.g., Hendrick and Pregitzer 1993). Root diameter was measured only once, when an individual root first appeared in view.

#### Data analysis

A total of 435 individual roots that emerged during the observation period were included in the analysis, and roots that were not dead at the final observation were right-censored. Roots were divided into five diameter classes: <0.2, 0.2–0.3, 0.3–0.4, 0.4–0.5, >0.5 mm. Roots were also classified according to soil depth: 0–10, 10–20, 20–30, 30–40, 40–50 cm. Those roots that emerged during the growing season in 2009 were classified into three cohorts: spring cohort (emerged in May and June), summer cohort (emerged in July and August), and autumn cohort (emerged in September and October). It

was nearly impossible to obtain root images during winter because of icing on the tube walls.

Two survival analysis techniques were employed to assess the effects of root diameter, soil depth, and season of emergence on root lifespan. Kaplan–Meier analysis (Kaplan and Meier 1958) was used to plot root survival curves. This analysis also provided the median survival time, which represents the number of days for 50 % mortality of roots in the same class. Differences in survivorship of roots among diameter classes, soil depths, and root cohorts were assessed by pairwise comparisons using the log-rank test (Kaplan and Meier 1958).

The second analysis was a stratified Cox proportional-hazards regression (Cox 1972), which allowed us to estimate the effects of the three covariates (diameter, soil depth, and emergence time) on root lifespan. Further details on the design and interpretation of proportional-hazards regression were provided by Allison (1995) and Cantor (1997). In a proportional-hazards model, the hazard of an individual  $i$  at time  $t$ ,  $h_i(t)$ , is the product of an unspecified baseline hazard function ( $h_0$ ) and an exponential function of  $k$  covariates:

$$h_i(t) = h_0(t)e^{(\beta_i x_{i1} + \beta_k x_{ik})}$$

The Cox model estimates a  $\beta$  coefficient for each model covariate and tests the null hypothesis that  $\beta = 0$  using a Chi square statistic. This coefficient determines the effect of a covariate on the hazard function: a negative  $\beta$  coefficient corresponds to a decreased risk of death with the covariate increasing, whereas a positive  $\beta$  coefficient indicates the opposite. We also calculated a risk ratio ( $e^\beta$ ), which represents the death risk of roots at one level relative to that of roots differing by one unit of a covariate, controlling for all other covariates. For the variables we considered, the percent change in the likelihood of death for a one-unit change in either diameter or soil depth can be calculated by subtracting 1 from the risk ratio and multiplying by 100 (Allison 1995; Wells et al. 2002).

Statistical analyses were performed with SPSS version 11.5 (SPSS, IBM, Armonk, NY). In all cases, a  $P$  value < 0.05 was considered to be significant.

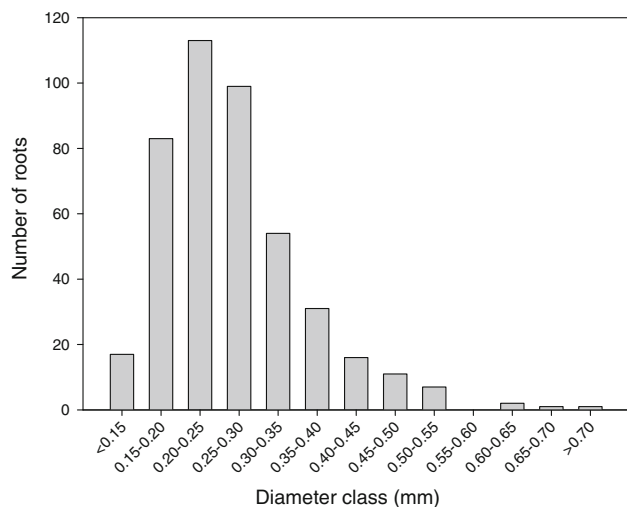
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## Results

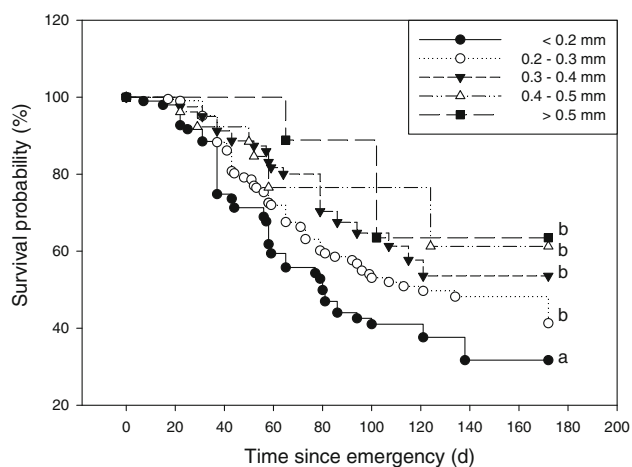
### Effect of root diameter on root survivorship

The mean diameter of roots monitored in our study was  $0.27 \pm 0.09$  mm (range 0.12–0.72 mm). The largest proportion of roots belonged to the 0.20- to 0.30-mm diameter class (Fig. 2). A majority (63.35 %) of the roots had a diameter between 0.15 and 0.30 mm.

The survivorship of roots increased with increasing diameter (Fig. 3). Roots <0.2 mm in diameter had a median survival time of 80 days, and only 31.7 % survived until the end of the observation period. In contrast, more than 50 % of roots >0.3 mm in diameter



**Fig. 2** The distribution of the number of roots in the various diameter classes in 2009. Diameter was measured on the date when a root first appeared



**Fig. 3** Survivorship for roots in the five diameter classes. Different letters indicate significant differences between root diameter classes according to a log-rank test ( $P < 0.05$ )

survived until the end of the observation period, with a median survival time of 79 days or more (Table 1). Roots  $< 0.2$  mm in diameter persisted for a significantly shorter period than roots of the other four diameter classes ( $P < 0.5$ ; Fig. 3), whereas the survivorship of the other four classes was similar.

Root diameter had a risk ratio of 0.825 ( $e^{-0.192}$ ) (Table 2). Therefore, a 0.1-mm increase in root diameter would decrease the risk of root mortality by 17.5 % [i.e.,  $100(1 - e^{-0.192}) = 17.5$  %], while controlling for the other covariates.

#### Effect of soil depth on root survivorship

About one-half of the roots (50.21 %) were distributed in the surface soil layer (0–10 cm), and 86.58 % of the

**Table 1** Mean root diameter ( $\pm 1$  SD) and survivorship data for the roots of the five diameter classes, five soil depths, and three root emergence seasons in 2009

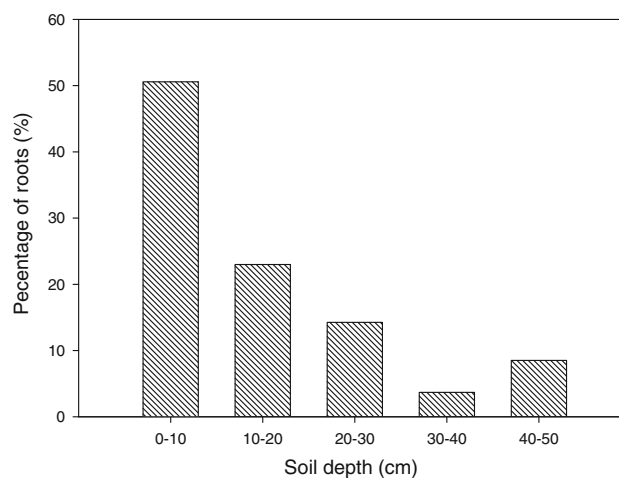
Variable	<i>n</i>	Mean diameter (mm)	Survival period <sup>a</sup> (days)		Final survivorship <sup>b</sup> (%)
			50 %	75 %	
<b>Diameter class (mm)</b>					
<0.2	100	0.18 $\pm$ 0.02	80	37	31.7
0.2–0.3	212	0.25 $\pm$ 0.03	121	58	41.3
0.3–0.4	85	0.35 $\pm$ 0.03	–	79	53.6
0.4–0.5	27	0.44 $\pm$ 0.03	–	124	61.2
>0.5	11	0.57 $\pm$ 0.08	–	102	63.5
<b>Soil depth (cm)</b>					
0–10	220	0.26 $\pm$ 0.09	79	43	27.4
10–20	100	0.29 $\pm$ 0.09	172	79	47.1
20–30	62	0.29 $\pm$ 0.10	–	121	63.9
30–40	16	0.33 $\pm$ 0.09	–	–	86.7
40–50	37	0.25 $\pm$ 0.06	–	172	72.3
<b>Root emergence</b>					
Spring	192	0.25 $\pm$ 0.07	79	43	31.9
Summer	150	0.30 $\pm$ 0.11	–	81	51.4
Autumn	93	0.28 $\pm$ 0.08	–	–	93.3

<sup>a</sup> Days when cumulative survivorship equaled 50 and 75 %, according to Kaplan–Meier analysis

<sup>b</sup> Percentage of roots in each class that survived to the end of the observation period

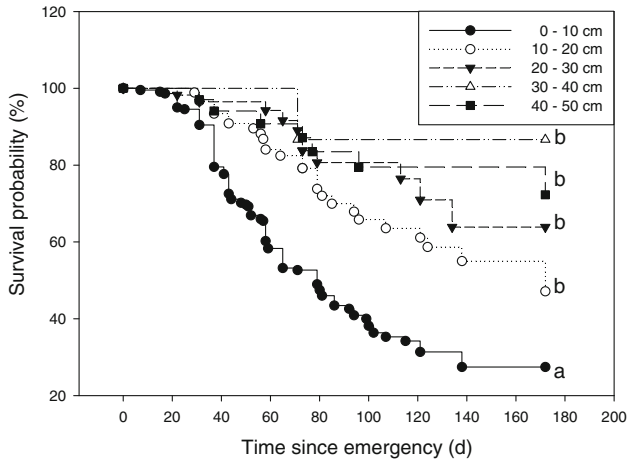
**Table 2** Proportional-hazards regression analysis for root survivorship based on data collected in 2009

Variable	df	Parameter estimate	SE	Wald Chi square	<i>P</i>	Risk ratio
Root diameter	1	–0.192	0.093	4.224	0.040	0.825
Soil depth	1	–0.654	0.126	26.901	<0.000	0.520
Season	1	–0.795	0.159	24.941	<0.000	0.452



**Fig. 4** Percentage of root numbers at five soil depths

roots were recorded in the top 30 cm soil. The number of roots generally decreased as soil depth increased, except that there were a few more roots in 40- to 50-cm layer than in the layer above it (Fig. 4).



**Fig. 5** Survivorship of roots distributed in the five soil layers. Different letters indicate significant differences between soil depth classes according to a log-rank test ( $P < 0.05$ )

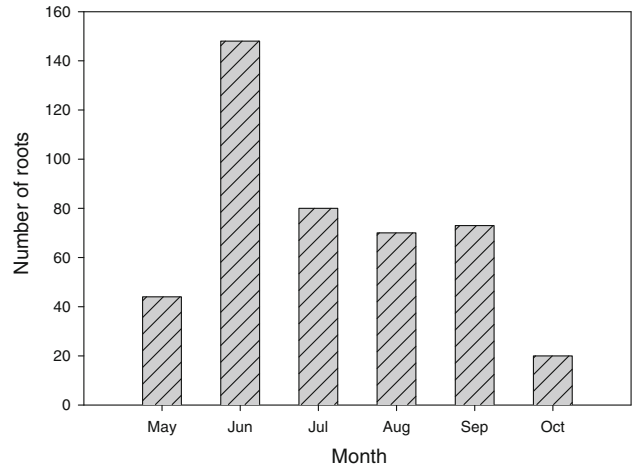
We hypothesized that the root turnover rate would be highest in the surface soil layers and decrease with depth because of variation in edaphic factors. This hypothesis was supported by the data from 0- to 40-cm soil depth. At the end of the observation period, the survivorship of roots in the top 10-cm layer was the lowest, only 27.4 %, compared to 47.1 % for root in 10- to 20-cm soil layer. More than 50 % of the roots in the lower three layers (20–50 cm) survived until the end of the observation period (Table 1). Therefore, the median survival times were calculated only for roots in the top two soil layers, and were 79 and 172 days, respectively. Root survivorship in the surface layer was significantly lower from that of the other four layers ( $P < 0.01$ ), whereas survivorship in the lower four layers was similar (Fig. 5).

Roots in deep soil had a lower risk of death than roots in shallow soil layers. The risk ratio for soil layers from 0 to 40 cm was 0.520 (Table 2), which corresponds to a 48 % decrease of death risk for each 10-cm increase in soil depth to 40 cm.

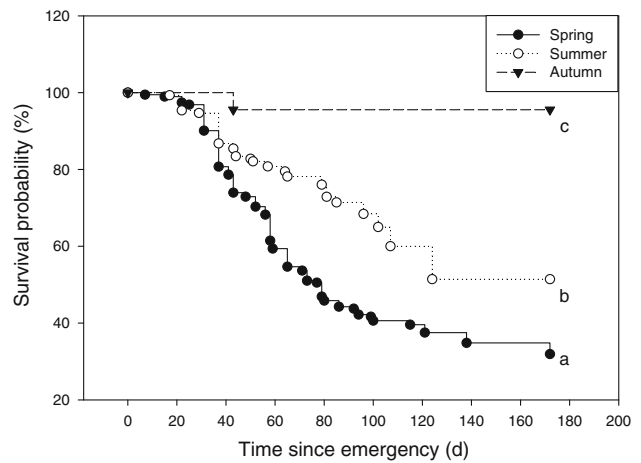
Effect of root emergence time on root survivorship

The highest percentage (34.0 %) of roots emerged in June (Fig. 6). We classified 44.14 % of roots as belonging to the spring cohort; this percentage may be underestimated, however, because roots present at the first imaging date were not included due to the uncertainty of their emergence time. Few roots emerged in October, such that the autumn cohort was the smallest.

The season of root production had a stronger effect on root survivorship than did root diameter and soil depth (Table 2). Roots that emerged in May and June, i.e., the spring cohort, had a significantly lower survival rate until the end of the observation period than the summer cohort ( $P < 0.01$ ). Moreover, the median survival time of the spring cohort was 79 days compared with more than that for the autumn cohort (Table 1).



**Fig. 6** The number of newly emerged roots in each month during the growing season



**Fig. 7** Survivorship of roots produced in the three seasons. Different letters indicate significant differences between root cohorts according to a log-rank test ( $P < 0.05$ )

Significant differences among root cohorts were also illustrated by survival curves (Fig. 7), which show that the autumn cohort persisted significantly longer than the spring cohort ( $P < 0.01$ ) and summer cohort ( $P < 0.01$ ).

**Discussion**

Root diameter in relation to root lifespan

The lifespan of roots in the alpine meadow varied considerably with root diameter, and a difference of 0.1 mm resulted in a large difference in lifespan. Roots with diameters of <0.2 and 0.2–0.3 mm had median survival times of 80 and 121 days, respectively. These thinner roots made up 71.7 % of the observed root population, whereas the smaller group of roots >0.3 mm in diameter persisted longer. This dataset provides the first evidence that root lifespan is highly correlated with root

diameter in an alpine meadow community with various graminoid and forb species. This result is consistent with reports of an active fraction of grass root systems with a shorter lifespan (Hendrick and Pregitzer 1996; Tingey et al. 2000), contrary to the conventional view that grass roots are homogeneous with respect to life-history traits.

Previous studies on the relationship between root diameter and lifespan focused mainly on woody species because of their distinct differences in physiological and morphological features among various root sizes (diameters). According to these studies, the root turnover rate decreased as diameter increased (e.g., Gill and Jackson 2000). A survey of apple trees found that turnover rate of roots <0.3 mm in diameter was 20 % more than that of roots 0.3–0.5 mm in diameter (Wells and Eissenstat 2001). Observation of a deciduous hardwood found that the turnover rate decreased by 16 % as fine root diameter increased by 0.1 mm (Baddeley and Watson 2005). Similar correlations were reported in a perennial Concord grape (Anderson et al. 2003). These findings suggest that root diameter is an important predictor of root longevity in woody species. However, these measurements demonstrated considerable variations in survival time among roots differing by only 0.1-mm in diameter, suggesting that woody fine roots cannot be categorized by common diameter criteria, such as <1 or <2 mm.

In most tree species, roots smaller than 0.5 mm in diameter may contain two or more branch orders (Pregitzer et al. 2002; Guo et al. 2004), which may help to explain the large variations in root lifespan within a narrow diameter range. A limited number of studies have shown that lower order roots have a shorter lifespan than those of higher orders (Wells et al. 2002; Guo et al. 2008). Several researchers suggested that root branch order, rather than root diameter, is the fundamental architectural feature influencing root lifespan (Pregitzer 2002; Wells et al. 2002; Guo et al. 2008). Picon-Cochard et al. (2012) also found that root branch order was the main determinant of root trait variation for grass species. However, it is still under debate which parameter, diameter class or branch order, is linked more closely to root lifespan.

Root diameter is perhaps the most widely accepted factor related to root longevity in forests, although it is not clear whether the turnover of grass roots is tightly coupled with root diameter. Several studies showed that a 0.1-mm increase in root diameter decreased the risk of mortality by approximately 6 % in a shortgrass steppe (Gill et al. 2002) and by 6.8 and 9.6 % for *Bromus tectorum* L. and *Agropyron desertorum* Schult., respectively (Peek et al. 2005). In our study, the risk of mortality was decreased by 17.5 %. Because alpine meadows and steppes differ considerably in species composition, our data provide important new evidence concerning the life-cycle dynamics of root systems in grasslands. Furthermore, grass root systems cannot be treated as a single homogeneous population for modeling ecosystem carbon and nitrogen cycling, as is the common practice

(Parton and Greenland 1987). Craine and Lee (2003) examined roots of 24 grassland species and found low specific root lengths and high C:N ratios associated with long-lived roots. However, few studies have explored the physiological and functional differences of grass roots of various diameters, and their ultimate link with root lifespan. Moreover, the role of carbon and nutrient return to soil from dying roots is influenced not only by the root turnover rate but also by tissue carbon and nutrient concentrations, as well as their resistance to decomposition. All of these factors deserve further research.

#### Root longevity across soil depths

Root lifespan increased with increasing depth in the soil, except in the 40- to 50-cm layer. Longer root lifespan at greater depths has also been reported in fruit trees (Kosola et al. 1995; Wells et al. 2002; Anderson et al. 2003; Baddeley and Watson 2005) and a Swiss grassland (Arnone et al. 2000). In contrast, Hendrick and Pregitzer (1992) observed that roots of sugar maple lived longer at shallow depths, and Gill et al. (2002) found no differences of root longevity across the soil profile.

Temporal variation in soil environmental factors along with soil depth may be the principal cause of the different lifespans of roots distributed in different soil layers. Numerous studies showed that soil temperature, nutrient availability, and moisture status control the timing and duration of root growth (Nadelhoffer et al. 1985; Vogt et al. 1986; Pregitzer et al. 1993, 2000; Hendrick and Pregitzer 1997; Nadelhoffer 2000; Brassard et al. 2009). Warmer soils were shown to be linked to higher root mortality in a field study of sugar maple (Hendrick and Pregitzer 1993), in an upland grassland (Fitter et al. 1999), and in a pot experiment with ryegrass (Forbes et al. 1997). The effect of available nitrogen was not consistent. For example, two studies reported that fine root turnover and production increased with higher nitrogen availability in Norway spruce (Majdi and Andersson 2005) and ponderosa pine (Johnson et al. 2000), whereas Burton et al. (2000) found greater root longevity with higher nitrogen availability in a northern hardwood forest dominated by sugar maple. Another study found no significant influence of different nutrient levels on root lifespan (Finér and Laine 1998). Previous studies on grass species showed that root lifespans of species from fertile habitats were significantly shorter than those from low-fertility habitats (Krift and Berendse 2002).

The effects of soil moisture on root lifespan appear to be species- and ecosystem-specific, making generalization difficult. Herbaceous roots were shown to be very sensitive to dry conditions. Grasses experienced substantial root mortality under lower water availability, as found in savannah bunchgrasses (West et al. 2004), both perennial and annual grasses (Peek et al. 2005), and in seven warm-season turfgrasses (Huang et al. 1997).

Similarly, other studies demonstrated that root lifespan was longer in irrigated patches in a hardwood forest community (Pregitzer et al. 1993) and in a perennial shrub (Peek et al. 2006). However, *Citrus* species retained their roots in dry soil (Kosola and Eissenstat 1994; Bryla et al. 1997; Espeleta and Eissenstat 1998), and root turnover rates were not affected when rainfall was experimentally reduced in a mixed hardwood forest (Joslin et al. 2000). Furthermore, a survey of global patterns of root turnover found no significant relationship between mean annual precipitation and fine root turnover in several ecosystems (Gill and Jackson 2000).

Among the soil environmental factors, the meadow root lifespan may be linked more closely to soil temperature, as root survivorship increased (Fig. 5) with decreasing soil temperatures across the soil vertical profile (Fig. 1). The climate of this alpine meadow is humid, and the soil surface layer usually had a high moisture content (Fig. 1; see also Cao et al. 2004; Li et al. 2004), indicating that the effects of soil moisture conditions on root lifespan may be less evident, because the plants were not severely water stressed. However, roots distributed in the surface soil experienced more fluctuations, even to an extreme extent, in moisture than in deeper soil horizons. Consequently, the median lifespan of surface roots was shorter than that of deeper roots. The effect of soil fertility on optimal root lifespan may depend on whether all the roots of the plant are exposed to uniformly fertile soil or whether a small portion of the roots are exposed to a fertile patch (Eissenstat and Yanai 1997). Thus, to explore the relationship between root lifespan and available nitrogen, future studies should examine the heterogeneity of the nutrient supply among the root axes. It is likely that a combination of related factors influences the pattern of fine root lifespan across the soil profile, including abiotic factors, such as temperature, moisture content, and available nitrogen, as well as biotic factors, such as herbivores and pathogens.

In addition, because we found that thinner roots had shorter lifespans (Fig. 3), the proportion of root diameters at various depths would also affect the variation of root longevity among soil depths. As illustrated in Fig. 8, more of the thinnest roots were distributed in the surface layer than in deeper layers, as also reported by Fukuzawa et al. (2007). However, in the 40- to 50-cm layer there were more thin roots (<0.2 mm) than in the layer above it. This may help to explain why roots in the 40- to 50-cm layer survived for a shorter period than those in the 30- to 40-cm layer.

#### Seasonal pattern of root survivorship

The root emergence time had a strong influence on root lifespan, and roots that emerged in May and June had the shortest lifespan. Similar results were also obtained in woody species. For example, pine roots that emerged in spring and summer had shorter lifespans than those

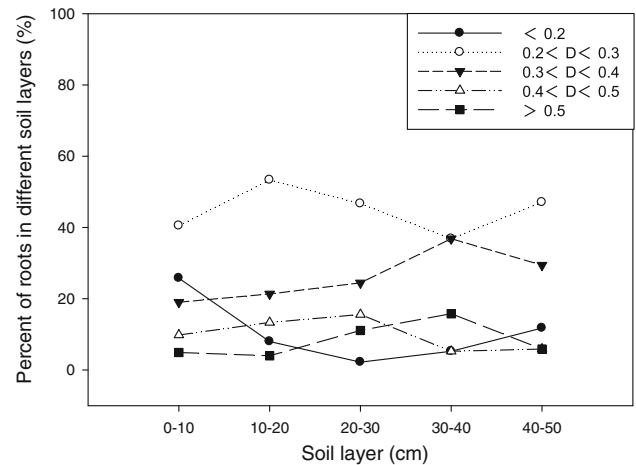


Fig. 8 Percent of root numbers of each root diameter class in the five soil layers

that emerged in autumn and winter (Johnson et al. 2000). In a cottonwood community, roots that emerged in spring had lower survivorship than those that emerged in summer and autumn (Kern et al. 2004). In a sugar maple stand, the annual mortality of fine roots that emerged in early spring was 46 %, as compared to 35 and 39 % for roots that emerged in July and October (Burton et al. 2000).

Seasonal variability in root lifespan is likely associated with the temporal variation of environmental factors. Hendrick and Pregitzer (1993) compared fine root mortality of sugar maple at two sites in Michigan and found that roots turned over faster at the less northerly site. Likewise, Self et al. (1995) found greater root longevity in a high-elevation *Festuca* grassland, as compared to a low-elevation site with a 5 °C higher annual temperature. Both studies suggest that temperature may be a critical factor in determining fine root lifespan. Other studies found that root turnover rates increased exponentially with increasing mean annual temperature (Gill and Jackson 2000; Yuan and Chen 2010). At our high-elevation study site with a very cold climate, root longevity may be linked strongly to the length of time that the soil is above a threshold temperature. As in warmer climates, plant maintenance respiration and microbial activities increase at higher temperatures, resulting in greater nutrient availability, such that the optimal lifespan for a root decreases. We could not identify how long the autumn cohort survived during the next growing season (after around 180 days) because we observed these roots only during the dormant period. However, the seasonal pattern of root lifespan is not clear. For example, Baddeley and Watson (2005) reported that roots of old wild cherry trees were more likely to die in the spring, whereas root mortality of young trees was greater in autumn. Other studies showed that some temperate deciduous tree roots produced in spring (Psarras et al. 2000) or in autumn (Kosola et al. 1995) had the greatest survival rate.

Thus, it appears that the relationship between season of emergence and fine root longevity is controlled by a myriad of endogenous (i.e., genetics, phenological features) and exogenous (i.e., temperature, precipitation, radiation) factors.

The amount of carbon allocated to roots may have a great effect on root lifespan. In Concord grape, Anderson et al. (2003) reported that roots that emerged in early spring had the shortest lifespan, and Bates et al. (2002) recorded the lowest starch level in fine roots that emerged near blooming time. These findings suggest that roots with less carbohydrates persist for shorter periods. The meadow at our study site started to green up around May, when carbon from the stored carbon pool in belowground parts was more likely to be removed for shoot budding than retained for root growth. It was not until the early growing season in July that carbon needed for root growth would be deficient, especially for previously emerged roots. The highest temperature and precipitation in July and August would support high carbon fixation activity. Because shoots achieve maximum biomass at that time, roots would receive a large proportion of assimilate and lifespan would be extended (Wu et al. 2011). In September and October, shoots gradually senesce and re-allocate their carbon and nutrients to roots as a storage pool. Therefore, roots that emerged during this period would be able to store carbon to survive the long cold winter and continue growing the following year. Thus, carbon demand and allocation between shoot and roots likely has an impact on root mortality. However, few experiments have directly addressed the issue of shoot carbon demand in relation to root lifespan in woody plants. The few such studies in grass species suggested that strong carbon demand in the shoot increased root mortality (Eissenstat and Yanai 1997), and the relationship between shoot carbon demand and root lifespan was complex and might be modified by environmental variables (Anderson et al. 2003).

Little information is available to discuss the mechanisms that control root lifespan, partly because plant phenological changes usually accompany seasonal climate changes, which confound the effects of a species' internal physiology with external environmental factors. Manipulative experiments are required to quantify the individual and interactive effects of environmental factors and plant internal cycling of carbohydrates and nutrients to fully understand and model root lifespan.

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