

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

Differences in spatial and temporal root lifespan of temperate steppes across Inner Mongolia grasslands

W.-M. Bai¹, M. Zhou^{1,2}, Y. Fang^{1,2}, and W.-H. Zhang¹

¹State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, Beijing, China

²Graduate School of Chinese Academy of Sciences, Yuquanlu, Beijing 100049, China

Received: 16 November 2015 – Accepted: 4 December 2015 – Published: 15 December 2015

Correspondence to: W.-H. Zhang (whzhang@ibcas.ac.cn)

Published by Copernicus Publications on behalf of the European Geosciences Union.

BGD

12, 19999–20023, 2015

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Abstract

Lifespan of fine roots plays important roles in regulating carbon (C) cycling in terrestrial ecosystems. Determination of root lifespan and elucidation of its regulatory mechanism in different plant communities are essential for accurate prediction of C cycling from ecosystem to regional scales. Temperate steppes in Inner Mongolia grasslands have three major types, i.e., *Stipa krylovii*, *Stipa grandis* and *Stipa breviflora* grasslands. There have been no studies to compare the root dynamics among the three types of grasslands. In the present study, we determined root lifespan of the three grasslands using the rhizotron. We found that root lifespan differed substantially among the three types of grasslands within the temperate steppes of Inner Mongolia, such that root lifespan of *Stipa breviflora* > *Stipa grandis* > *Stipa krylovii* grasslands. Root lifespan across the three types of grasslands in the Inner Mongolian temperate steppes displayed a similar temporal pattern, i.e. lifespan of the roots produced in spring and autumn was shortest and longest, respectively, whereas lifespan of summer-produced roots was between that of roots produced in spring and autumn. The spatial and temporal differences in root lifespan across the three types of grasslands were mainly determined by contents of soluble sugars in roots of the dominant species. The differences in root lifespan across the major types of grasslands and different seasons highlight the necessity to take into account these differences in the prediction of C cycling within grassland ecosystem by the simulating model.

1 Introduction

Root is a major source of the organic carbon pool in soils. Approximately half of the annual photosynthetic products of plants can be utilized by their roots (Vogt et al., 1986; Hendrick and Pregitzer, 1993; Peek, 2007). Root turnover is an important trait to link plants to organic carbon pool in soils (Loya et al., 2004; Strand et al., 2008). Thus, knowledge about the dynamic processes associated with root turnover and its

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



regulatory mechanisms are of importance for our understanding C cycling within the ecosystems (Aerts et al., 1992; Norby et al., 2004). However, these processes have been poorly understood in terms of C cycling within the terrestrial ecosystems (Iversen and Brien, 2010). The lack of detailed information on root turnover increases the uncertainty about the modeling-based prediction of C cycling within the terrestrial ecosystems (McCormack et al., 2013; Warren et al., 2015).

Root lifespan is a critical parameter that determines root turnover, C flux from plants into soils, and physiological processes associated with uptake of water and nutrients by roots (McCormack et al., 2012; McCormack and Guo, 2014). Root lifespan is highly variable among the inter-biomes, intra-biomes, and inter-species in a given ecosystem, and root lifespan for an individual plant species can also vary in different spatial and temporal scales (Eissenstat and Yanai, 1997; Burton et al., 2000; Withington et al., 2006; Bai et al., 2008; Peek, 2007; McCormack and Dali Guo, 2014). Several extrinsic and intrinsic factors have been shown to have impacts on root lifespan, including those extrinsic factors such as precipitation, temperature, soil moisture and nutrient availabilities in soils, and those intrinsic factors of plant life forms, nutrient contents in roots, root diameter and branching order (Peek, 2007; Chen and Brassard, 2013; McCormack and Guo, 2014). However, there have been few studies to directly evaluate how these factors interactively affect root lifespan. In particular, under the naturally environmental conditions, different types of vegetation often occur in different edaphic and climatic conditions. Therefore, root lifespan of different plant communities may reflect their overall biotic, edaphic and climatic characteristics in a regional scale. However, few studies have quantified root lifespan and compared the spatial difference in lifespan among different types of plant communities within a given ecosystem (McCormack et al., 2013). Moreover, a single value of root lifespan or root turnover determined in a limited types of community within a ecosystem has often been used to predict the ecosystem C cycling by modeling, rendering the model-projected C cycling less accurate and reliable (McCormack et al., 2013; Warren et al., 2015). In addition, several studies have suggested that lifespan of roots produced in different seasons may differ significantly

BGD

12, 19999–20023, 2015

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



because roots generated in different seasons can have varying functions (López et al., 2001; Anderson et al., 2003; Bai et al., 2008). Root lifespan may exhibit temporal differences within a ecosystem as suggested by variation in lifespan of roots produced in different seasons. Quantitative determination of lifespan of fine roots is technically challenging because of difficulties associated with direct observations of roots in situ under field conditions. Therefore, knowledge on how the botanic, edaphic and climatic factors impact root lifespan in regional and temporal scales is scarce in the literature.

The Inner Mongolia temperate steppe is a major temperate grassland in Northern China, with total area of $5.85 \times 10^6 \text{ hm}^2$. It plays an important role in the regulation of C cycling and climate changes (Ma et al., 2006). There are three major types of grasslands in the Inner Mongolia steppes, *Stipa krylovii*, *Stipa grandis* and *Stipa breviflora* grasslands, which account for 18.6, 30.1 and 13.3 % of total area in Inner Mongolia, respectively. The three types of grasslands differ in their dominant species, soil traits, and climatic features such as annual precipitation and temperature. However, little is known whether and how the root metrics of the three types grasslands differ. The development of rhizotron and minirhizotron technologies makes it possible to directly monitor dynamics of individual roots in situ in the grassland ecosystems (Majdi et al., 2005; McCormack and Guo, 2014), thus allowing us to evaluate the roles of extrinsic and intrinsic factors in the regulation of root lifespan across different types of grasslands. In the present study, we compared root lifespan of the three types of grasslands in the temperate steppes of Inner Mongolia using the rhizotron. We further explored the temporal patterns of root lifespan of the three grasslands by measuring lifespans of roots produced in different seasons. The factors that may contribute to the differences in the root lifespan across the different grassland-types and seasons are discussed.

2 Materials and methods

2.1 Study site

Stipa krylovii grassland is one of the representatives of the typical subtypes of grasslands among different types of grasslands in the Inner Mongolia temperate steppe. This type of grassland occurs in the middle and westward region of Inner Mongolia Autonomous Region with total area of 1.09×10^6 hm², accounting for 18.6 % of the total area of Inner Mongolia temperate steppe. Our study site was in the Duolun Restoration Ecology Experimentation and Demonstration Station, Institute of Botany, the Chinese Academy of Sciences (DREEDS, 116°17' E, 42°02' N; 1324 m.a.s.l.), which is a typical *Stipa krylovii* grassland (Fig. 1). The area is located in the temperate climatic zone, and its mean annual temperature is 2.1 °C with mean monthly temperature ranging from -17.5 °C in January to 18.9 °C in July. Mean annual precipitation is 382.2 mm, and approx. 90 % of the precipitation occurs from May to October. The soil in this area is classified as chestnut according to the Chinese classification and Haplic Calcisols based on the FAO classification. Vegetation in this area is a typical steppe community and the dominating species are perennials, including *Stipa krylovii*, *Artemisia frigida*, *Cleistogenes squarrosa* and *Leymus chinensis* (Yang et al., 2011).

Stipa grandis grassland is a zonal representative of the typical subtypes of grasslands in the temperate steppes, and located in the middle of in Inner Mongolia temperate steppe with area of 1.76×10^6 hm², accounting for 30.1 % of total area of the grasslands in Inner Mongolia. The *Stipa grandis* grassland used in the present study is located in Inner Mongolia (116°42' E, 43°38' N; 1100 m.a.s.l.; Fig. 1). This area is characterized by a continental, semi-arid climate, and its mean annual temperature is 0.7 °C. Mean annual precipitation is 335 mm, and approx. 70 % of the precipitation occurs from June to September. The soil type is Calcic-orthic Aridisol according to the US soil classification system. Dominant species in the typical steppe community are the perennial bunchgrass, including *Stipa grandis*, and the perennial rhizomatous

BGD

12, 19999–20023, 2015

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



grass, *Leymus chinensis*, as well as those associated species of *Artemisia frigida*, *Cleistogenes squarrosa*, *Carex korshinsky* and *Agropyron cristatum* (Bai et al., 2004).

Stipa breviflora grassland is one of the zonal subtypes of the desert steppe in the Inner Mongolia temperate steppes. The *Stipa breviflora* grassland used in the present study is located in the westward region of the Inner Mongolia temperate steppe (111°53' E, 41°47' N; 1450 m a.s.l.; Fig. 1). The *Stipa breviflora* grassland covers 0.78×10^6 hm², accounting for 13.3% of the overall grassland in Inner Mongolia. This type of the grassland is distinguished by a temperate continental climate with a relatively short growing season and long cold winter and mean annual temperature of 3.4°C (monthly temperature ranging from -15.1°C in January to 19.6°C in July). Mean annual precipitation in the *S. breviflora* grassland is approximately 280 mm with approx. 75% of the precipitation occurred from June to September. The soil type is Kastanozem with a loamy sand texture. Dominant species in the *S. breviflora* grassland are perennial *Stipa breviflora*, *Artemisia frigida*, *Cleistogenes songorica*, and associated species of *Convolvulus ammannii*, *Heteropappus altaicus*, *Neopallasia petinata*, *Caragana stenophylla* (Li et al., 2008).

2.2 Experimental design

In September 2010, the representative plant communities that were excluded from grazing in these three studied sites were selected to set the experimental plots. The plots were 6 m × 8 m and separated by 2 m-wide buffer strips with 6 replicated plots for each type of grassland.

2.3 Measurement of root dynamics

On 3 September 2010, one glass root-window was installed in each plot. The glass window (0.4 cm thick) of 35 cm in height and 20 cm in length was installed vertically into the soil. On each glass window, a 35 cm × 20 cm panel (with 5 cm distance to the bottom and 5 cm to the right and left sides) was separated into three 10 cm × 10 cm

BGD

12, 19999–20023, 2015

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



squares by carving the glass. In order to minimize the impacts of light on root growth, the upper edge of the glass window was installed under the soil surface and a piece of dark iron (20 cm in length, 1.5 cm in breadth and 0.5 mm in thickness) was covered on the top of the glass. A hole was dug in each plot with a vertical profile for the glass window to be installed. The glass window was put tightly to the trench and fixed with one iron stick at each side. After the root-windows were inserted, soil was backfilled as tightly as originally. The soil was closely attached to the glass throughout the whole study period.

A digital camera was used to monitor root growth. Observations began on 10 May 2011, which was about 8 months after the installation of glass windows, and lasted until 20 October 2012 with sampling intervals of 15 d. On each sampling date, the soil on one side of the glass window was removed and the screen was cleaned with tissue paper. One digital picture was taken for each of the three 10 cm × 10 cm numbered squares. Removed soil was carefully backfilled again after pictures were taken as described previously (Bai et al., 2008, 2012).

Appearance and disappearance of roots were analyzed by the software of Mapinfo Professional (5.0; Pitney Bowes Mapinfo Corporation, New York, US) as described previously (Bai et al., 2008, 2012). For the initially collected images, each root was assigned with an identification number and distinguished it as living or dead based on its colors as described in our previous paper (Bai et al., 2008). For the following image sets, the tracings from the previous date were compared with the new images, thus allowing previously existing roots to be identified. Newly emerged roots were also identified and numbered. Roots that had disappeared at subsequent images were assumed to be dead and decomposed. Complete records were kept for all roots, even for those that were classified as dead.

2.4 Measurements of aboveground net primary productivity (ANPP)

Aboveground biomass was clipped at the ground level in a randomly selected quadrat (1 m × 1 m) in each plot in mid-August each year, and both living aboveground biomass

and standing litter in the current year belonging to a same species were included. Plant samples were oven-dried at 70 °C for 48 h and then separately weighed for determination of ANPP.

2.5 Measurement of soil traits

5 In each plot, three fresh soil samples at the soil depths of 0–30 cm were taken in the mid of August of 2012, and inorganic N (NH_4^+ -N, NO_3^- -N) concentrations were measured using a continuous-flow ion auto-analyzer (Scalar SAN plus segmented flow analyzer, the Netherlands). A portion of each soil sample was ground with a mill and passed through a 0.18 mm sieve for determination of organic C concentrations. The organic carbon concentration was estimated using a CHNOS Elemental Analyzer (Vario EL III). To determine the available phosphorus contents, 0–30 cm soil was digested with NaHCO_3 and then was determined by molybdenum-stibium colorimetry method with a UV-visible spectrophotometer (UV-2550, SHIMADZU Corporation, China). To determine the available potassium contents, 0–30 cm soil was digested with NH_4OAc (soil: NH_4OAc solution; 1 : 10). Soil bulk density was measured using the soil cores (volume 100 cm^3) obtained from the three layers in each plots. Gravimetical soil water contents at 0–30 cm soil depths were measured on the same day when root images were collected. A soil core (3 cm diameter) of fresh soil from 0–30 cm soil layer was randomly sampled in August of 2012, then air-dried soil was passed through a 2 mm sieve for determination of soil pH. Soil pH was determined with Russell RL060P portable pH meter (Thermo Electron Corporation 166 Cummings Center, USA), and the water/soil ratio was 1 : 2.5.

2.6 Measurements of soluble sugars and of roots

15 In each plot, we scooped roots of plants community in the soil layer of 0–30 cm. The roots with diameter < 1 mm were selected and the soluble sugars concentrations were

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



determined by the anthrone method with a UV-VIS7500 spectrophotometer (Techcomp, Shanghai, China) as described by Ranwala and Miller (2008).

2.7 Data analysis and statistics

Root lifespan was calculated as the date on which roots were observed as black or disappeared minus the date on which roots were initially observed on the window. The date of root appearance or disappearance was estimated as the date midway between the sampling periods because they might have occurred on any day during the approx. 15 d sampling interval between two consecutive observations (López et al., 2001; Anderson et al., 2003).

We selected a total of 13 307 new roots germinated in spring (1–30 May), summer (1–31 July) and autumn (20 August to 10 September) of 2011 and 2012 to analyze the effects of different grassland types on their survival rates and longevity. We calculated their mean longevity through a survival curve using the Kaplan–Meier method with SPSS (12.0) software, and compared the root survival rates by Log-rank test.

The one-way ANOVAs were used to examine the effects of different grassland types on soil parameters, aboveground net primary production, and root soluble sugar content and root longevity. Bivariate correlations were used to determine the correlation of root longevity with aboveground net primary production, root soluble sugar content, soil water content, soil organic matter, soil inorganic N concentration, soil available phosphorus contents (AP), soil available potassium contents (AK), bulk density and soil pH. Stepwise multiple linear regressions were further used to identify the most important factor affecting root longevity after the different grassland types. All statistical analyses were conducted with SAS software (SAS Institute Inc., Cary, NC, USA).

BGD

12, 19999–20023, 2015

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



3 Results

3.1 Soil metrics in the three grasslands

Soil pH values in the three types of grasslands of *S. krylovii*, *S. grandis* and *S. breviflora* grasslands were ranged from 6.9 to 8.1, with the soil pH in *S. breviflora* grassland and *S. krylovii* grassland highest and lowest, respectively (Table 1). Soil organic matters in *S. krylovii* grassland was the highest, whereas soil organic matters in *S. breviflora* grassland was the lowest ($P < 0.05$). While there was no significant difference in soil inorganic nitrogen (N) contents between the *S. krylovii* and *S. grandis* grassland, they both were significantly higher than that in soil of *S. breviflora* grassland ($P < 0.01$). The available phosphorus (P) contents in soil of *S. grandis* grassland were significantly lower than those of *S. krylovii* and *S. breviflora* grasslands ($P < 0.05$). In contrast to soil P and inorganic N contents, there were no significant differences in both soil potassium contents and soil bulk density among the three types of grasslands ($P > 0.05$). During the experimental period, soil water contents in *S. grandis* grassland were significantly higher than in *S. krylovii* and *S. breviflora* grasslands, and soil water contents in *S. breviflora* grassland were the lowest among the three grasslands ($P < 0.01$; Table 1).

3.2 Root lifespan in the three types of grasslands

In the Inner Mongolia temperate steppes, survival rates and root lifespan of plant communities in the three types of grasslands differed significantly (Fig. 2). Among the three types of grasslands studied, the survival rates and root lifespan of *S. krylovii* grassland were the lowest ($P = 0.021$), followed by those of *S. grandis* grassland, while the survival rates and root lifespan of *S. breviflora* grassland were the highest ($P = 0.0001$). Accordingly, the mean root lifespan in the *S. grandis*, *S. grandis* and *S. breviflora* grasslands was estimated to be 98, 125 and 146 days, respectively (Fig. 2).

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



3.3 Lifespan of roots produced in different seasons

To further investigate the differences in root survival rates and lifespan of roots in these grasslands, we monitored the responses of survival rates and lifespan of roots produced in the three different seasons of spring, summer and autumn, in 2011 and 2012.

5 Roots produced in the three growing seasons in the three types of grasslands exhibited the comparable survival rates and lifespan (Fig. 3). Log-rank test revealed that survival rates and root lifespan for the roots initiated in spring were significantly shorter than those initiated in summer and autumn ($P < 0.01$; Fig. 3a). In contrast, survival rates and lifespan for those roots initiated in autumn were significantly longer ($P < 0.01$;
10 Fig. 3c) than those born in summer and spring. The survival rates and lifespan of those roots born in summer were between those of roots born in spring and in autumn (Fig. 3b). For those roots produced in spring, no significant difference in root lifespan between *S. krylovii* and *S. grandis* grassland was detected, while root lifespan in the two types of grasslands were both significantly shorter than that of *S. breviflora* grassland ($P < 0.01$). For those roots initiated in summer and autumn, root lifespan in *S. krylovii* grassland was the shortest ($P < 0.05$; Fig. 3c), followed by those roots in *Stipa grandis* grassland ($P < 0.01$). The root lifespan in *S. breviflora* grassland was the longest ($P < 0.001$).

3.4 ANPP and contents of soluble sugars in the three types of grasslands

20 ANPP in the *S. krylovii* grassland was the highest, whereas ANPP in the *S. breviflora* grassland was the lowest ($P < 0.001$). While there was no significant difference in ANPP between the *S. breviflora* and *S. grandis* grasslands (Fig. 4a). Among the three types of grasslands, soluble sugar contents in roots of *S. krylovii* grassland were the lowest, followed by those of *S. grandis* grassland, while the root soluble sugar contents
25 of *S. breviflora* grassland were the highest ($P < 0.001$) (Fig. 4b).

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



3.5 Correlations between root lifespan and botanic and abiotic factors

To elucidate the mechanisms by which the root lifespan differed among the three types of grasslands, we evaluated the roles of soil organic matter, soil inorganic N contents, aboveground net primary production (ANPP), and root soluble sugar contents of dominant species in the three types of grasslands. As shown in Fig. 5, across different plots in the two growing seasons, root lifespan was negatively correlated with soil organic matter ($P = 0.0004$), soil inorganic N concentration ($P = 0.0025$) and ANPP ($P = 0.0004$). In contrast, root lifespan was positively correlated with soluble sugar contents of roots ($P = 0.0003$). Stepwise multiple regression analyses revealed that root soluble sugar contents accounted for 57.1% ($r^2 = 0.571$, $P = 0.0003$) of variation in root longevity among the different grassland-types.

4 Discussion

To the best of our knowledge, no study has directly measured and compared root lifespan across different grassland types in the Inner Mongolia temperate steppes. Our results show, for the first time, that root lifespan in the three types of grasslands in the Inner Mongolia steppes differed significantly (Fig. 2), suggesting that within the temperate grassland ecosystem in Inner Mongolia, root turnover in different types of grasslands can differ substantially, and that no consistent patterns for root turnover across different types of grasslands occur within the Inner Mongolia steppes. These results highlight that the prediction of C cycling by modeling under the widely used assumption that the identical root turnover among the different types of grasslands should be treated with caution. For example, the estimated root turnover rate of Inner Mongolia steppes can differ by 48.6% using our determined root lifespan for *S. krylovii* and *S. breviflora* grasslands. Therefore, the use of root lifespan or root turnover of multi-community types rather than a single community type is highly recommend for accurately predicting C cycling in the temperate steppes of Inner Mongolia. In the forest

BGD

12, 19999–20023, 2015

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



ecosystem, McCormack et al. (2013) reported the root lifespan of a temperate tree species across the eastern part of the states in the regional scale. They found that root lifespan in the North Central states is shorter, whereas it is longer in the Southeastern states. They also found distinct patterns for the root lifespan across the studied areas, and attributed their observations to relatively high abundance of certain tree species (McCormack et al., 2013).

A number of intrinsic and extrinsic factors may be involved in the control of the root lifespan. These include the climatic factors, e.g., temperature and rainfall, the edaphic factors, e.g., soil inorganic N, and the intrinsic factors such as plant species composition, soluble sugars and N contents in plant roots. These factors can directly and/or indirectly determine root lifespans by affecting growth and death of plant roots (Peek, 2007; Chen and Brassard, 2013; McCormack and Guo, 2014). Thus, the factors involved in the control of root lifespan for different plant communities across a regional scale within the grassland ecosystem are more complex than those for a single plant community in an individual site due to interleaving effects of these factors on root metrics.

In the Inner Mongolia temperate steppes, we found that among three different types of grasslands, root lifespan in the three grasslands followed the orders of *S. breviflora* > *S. grandis* > *S. krylovii* grasslands. Attempts were made to explore the mechanisms underlying the differences. Our results showed that the overall root lifespan in Inner Mongolia temperate steppes was negatively correlated with the contents of soil organic matter and inorganic N, and ANPP of grasslands, while root lifespan exhibited a significantly positive correlation with contents of soluble sugars in roots of dominant species (cf. Fig. 5). It has been demonstrated that the availability of soil N is an important factor controlling growth and lifespan of roots (Burton et al., 2000), such that root lifespan is longer when grown in infertile soils compared to that grown in nutrient-rich soils (Eissenstat and Yanai, 1997; Van der Krift and Berendse, 2002; West et al., 2003; McCormack and Guo, 2014). Our results are consistent with this proposition. For example, we found that root lifespan in *S. breviflora* grassland was the longest among

**Spatial and temporal
root lifespan of
steppe**

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the three grasslands, while soil organic matter and soil inorganic N contents in the *S. breviflora* grassland was the lowest (Table 1, Fig. 2). In addition, the differences in root lifespan among the three types of grasslands may also be explained by their different patterns of C allocation. It has been well documented that root lifespan is closely related to C supply from shoot to root (Eissenstat et al., 2000; Anderson et al., 2003). A decrease in C allocation to root has been suggested to shorten the root lifespan (Eissenstat and Yanai, 1997; Bai et al., 2008, 2010). We found that ANPP and contents of soluble sugars in roots of the dominant species in the communities among the three types of grasslands differed significantly (Fig. 4). The findings that there was a negative correlation between root lifespan across different types of grasslands and ANPP and the positive correlation between root lifespan and contents of soluble sugars in roots are in line with this hypothesis (Fig. 5c and d). Moreover, the environmental factors can also have important impacts on root lifespan (Chen and Brassard, 2013; McCormack and Guo, 2014). In our studies, the mean multi-year precipitation in the three types of grasslands differed with the order of *S. krylovii* (382 mm) > *S. grandis* (335 mm) > *S. breviflora* grasslands (280 mm). However, across the experimental period, the mean soil water contents in the *S. grandis* grassland were actually the highest. This may result from unevenness in precipitation inter-annually, and may account for the observation of no significant correlation between root lifespan and soil water contents. The mean annual temperature in *S. breviflora* grassland was the highest among the three grasslands. Given the negative correlation between root lifespan and temperature (McCormack and Guo, 2014), a shorter root lifespan in *S. breviflora* grassland is expected. However, we found that root lifespan in the *S. breviflora* grassland was longest among the three types of grasslands. These results suggest that the mean multi-year atmosphere temperature may not be a key determinant for root lifespan in the Inner Mongolia steppe. We further conducted stepwise multiple regression analyses, and found that the changes in contents of soluble sugars in roots accounted for 57.1 % of variation in the root lifespan among different types of grasslands. Therefore,

contents of soluble sugars in roots of different types of grasslands play an important role in the determination of root lifespan in the temperate steppes.

It has been reported that root lifespan is closely related to the seasons when roots were initially born (López et al., 2001; Anderson et al., 2003; Guo et al., 2008). We thus compared lifespan for roots born in different seasons (spring, summer and autumn) among the three types of grasslands. We found a consistent pattern for lifespan of roots born in different seasons among the three types of grasslands, i.e. lifespan of roots born in spring was the shortest, while lifespan of roots born in autumn was the longest (Fig. 3). The differences in lifespan of roots initiated in different seasons can be related to their differences in functions. For instance, those roots initiated in spring may mainly involve uptake of water and nutrients, while the roots born in autumn may be mainly used to store nutrients and produce new lateral roots (López et al., 2001). We further observed that lifespan for the roots born in the same season exhibited significant difference among the three types of grasslands. For example, lifespan for the roots initiated in spring of *S. krylovii* and *S. grandis* grasslands was comparable, but it was significantly shorter than lifespan of roots in *S. breviflora* grassland initiated in spring (cf. Fig. 3a). In contrast to the roots born in spring, lifespans of roots born in summer and autumn across the three grasslands exhibited the same patterns, i.e., root lifespan in *S. breviflora* and *S. krylovii* grasslands was longest and shortest, respectively (cf. Fig. 3b and c). These results may suggest that root lifespan in different types of grasslands is mainly determined by lifespan of roots born in summer and autumn. These findings also indicate that lifespan for roots born in the different seasons has different sensitivity to environmental factors. Our previous study found that N addition has different effects on lifespan of roots born in spring, summer and autumn, and can be explained by carbon allocation and the changes in temperature (Bai et al., 2008, 2010, 2012). These observations indicate that the impacts of the different intrinsic and extrinsic factors on the root lifespan born in different seasons are more complex, but the mechanisms underlying the differences in root lifespan across the different seasons remain to be elucidated. Several factors such as soil water contents, temperature, and

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



status of carbohydrates and nutrients in roots may be expected to be involved in determination of the differences in root lifespan (Baddeley and Watson, 2005). Given that a major factor that controls the root lifespan in the three types of grasslands is the contents of soluble sugars in roots, it is conceivable that carbohydrate contents in roots born in different seasons may differ, leading to the different responses of their lifespan in different types of grasslands. In addition, the phenological mechanisms of plant species may also affect the birth and death rates of roots during different seasons. Thus, future studies focusing on how both the intrinsic and extrinsic factors drive the variability in root lifespan across a large range of plant species are warranted.

5 Conclusions

Here, we report, for the first time, that root lifespan differs substantially among the three major types of grasslands within the temperate steppes of Inner Mongolia, such that root lifespan of *Stipa breviflora* > *Stipa grandis* > *Stipa krylovii* grasslands. Root lifespan across the three types of grasslands in the Inner Mongolian temperate steppes displays a similar temporal pattern, i.e. lifespan of the roots born in spring and autumn is shortest and longest, respectively, whereas lifespan of summer-born roots is between that of roots born in spring and autumn. The spatial and temporal differences in root lifespan across the three types of grasslands are mainly determined by contents of soluble sugars in roots of dominant species. The differences in root lifespan across the major types of grasslands and different seasons highlight the necessity to take into account these differences in the prediction of C cycling within grassland ecosystem by the simulating model.

Acknowledgements. We would like to thank G. Wang and Y. Dong for their help in field and laboratory work. This research was supported by the National Natural Science Foundation of China (31370468) and the State Key Basic Research Development Program of China (2013CB956304).

References

- Aerts, R., Bakker, C., and de Caluwe, H.: Root turnover as determinant of the cycling C, N, and P in dry heathland ecosystem, *Biogeochemistry*, 15, 175–190, 1992.
- Anderson, L. J., Comas, L. H., Lakso, A. N., and Eissenstat, D. M.: Multiple risk factors in root survivorship: a 4-year study in Concord grape, *New Phytol.*, 158, 489–501, 2003.
- Baddeley, J. A. and Watson, C. A.: Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*, *Plant Soil*, 276, 15–22, 2005.
- Bai, W. M., Wang, Z. W., Chen, Q. S., Zhang, W. H., and Li, L. H.: Spatial and temporal effects of nitrogen addition on root life span of *Leymus chinensis* in a typical steppe of Inner Mongolia, *Funct. Ecol.*, 22, 583–591, 2008.
- Bai, W. M., Xun, F., Li, Y., Zhang, W. H., and Li, L. H.: Rhizome severing increases root lifespan of *leymus chinensis* in a typical steppe of inner Mongolia, *PLoS ONE*, 5, e12125, doi:10.1371/journal.pone.0012125, 2010.
- Bai, W. M., Xia, J. Y., Wan, S. Q., Zhang, W. H., and Li, L. H.: Day and night warming have different effect on root lifespan, *Biogeosciences*, 9, 375–384, doi:10.5194/bg-9-375-2012, 2012.
- Bai, Y. F., Han, X. G., Wu, J. G., Chen, Z. Z., and Li, L. H.: Ecosystem stability and compensatory effects in the Inner Mongolia grassland, *Nature*, 431, 181–184, 2004.
- Burton, A. J., Pregitzer, K. S., and Hendrick, R. L.: Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests, *Oecologia*, 125, 389–399, 2000.
- Chen, H. Y. H. and Brassard, B. W.: Intrinsic and extrinsic controls of fine root life span, *Crit. Rev. Plant Sci.*, 32, 151–161. 2013.
- Eissenstat, D. M. and Yanai, R. D.: The ecology of root life span, *Adv. Ecol. Res.*, 27, 1–60, 1997.
- Eissenstat, D. M., Wells, C. E., Yanai, R. D., and Whitbeck, J. L.: Building roots in a changing environment: implications for root longevity, *New Phytol.*, 147, 33–42, 2000.
- Guo, D., Mitchell, R. J., Withington, J. M., Fan, P. P., and Hendricks, J. J.: Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a longleaf pine forest: root branch order predominates, *J. Ecol.*, 96, 737–745, 2008.
- Hehdrick, R. L. and Pregitzer, K. S.: Patterns of fine root mortality in two sugar maple forest, *Nature*, 361, 59–61, 1993.

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Iversen, C. M. and O'Brien, S. L.: Reports from the 2009 ESA Annual Meeting, Missing links in the root–soil organic matter continuum, *Ecology*, 91, 54–64, 2010.
- Li, C. L., Hao, X. Y., Zhao, M. L., Han, G. D., and Willms, W. D.: Influence of historic sheep grazing on vegetation and soil properties of a Desert Steppe in Inner Mongolia, *Agr. Ecosyst. Environ.*, 128, 109–116, 2008.
- López, B., Sabate, S., and Gracia, C. A.: Fine-root longevity of *Quercus ilex*, *New Phytol.*, 151, 437–441, 2001.
- Loya, W. M., Johnson, L. C., and Nadelhoffer, K. J.: Seasonal dynamics of leaf- and root-derived C in arctic tundra mesocosms, *Soil Biol. Biochem.*, 36, 655–666, 2004.
- Ma, W. H., Han, M., Lin, X., Ren, Y. L., Wang, Z. H., and Fang, J. Y.: Carbon storage in vegetation of grasslands in inner Mongolia, *J. Arid Land Resour. Environ.*, 20, 192–195, 2006.
- Majdi, H., Pregitzer, K., Moren, A. S., Nylund, J. E., and Agren, G. I.: Measuring fine root turnover in forest ecosystems, *Plant Soil*, 276, 1–8, 2005.
- McCormack, M. L., Adams, T. S., Smithwick, E. A. H., and Eissensat, D. M.: Predicting fine root lifespan from plant functional traits in temperate trees, *New Phytol.*, 195, 823–831, 2012.
- McCormack, M. L., Eissensat, D. M., Prasad, A. M., and Smithwick, E. A. H.: Regional scale patterns of fine root lifespan and turnover under current and future climate, *Glob. Change Biol.*, 19, 1697–1708, 2013.
- McCormack, M. L. and Guo, D. L.: Impacts of environmental factors on fine root lifespan, *Front Plant Sci.*, 5, 1–11, 2014.
- Norby, R. J., Ledford, J., Reilly, C. D., Miller, N. E., and O'Neill, E. G.: Fine-root production dominates response of a deciduous forest to atmospheric CO₂ enrichment, *P. Natl. Acad. Sci. USA*, 101, 9689–9693, 2004.
- Peek, M. S.: Explaining variation in fine root life span, *Prog. Bot.*, 68, 382–398, 2007.
- Ranwala, A. P. and Miller, W. B.: Blackwell Publishing Ltd Analysis of nonstructural carbohydrates in storage organs of 30 ornamental geophytes by high-performance anion-exchange chromatography with pulsed amperometric detection, *New Phytol.*, 180, 421–433, 2008.
- Strand, A. E., Pritchard, S. G., McCormack, M. L., Davis, M. A., and Oren, R.: Irreconcilable differences: fine-root life spans and soil carbon persistence, *Science*, 310, 456–458, 2008.
- Van der Krift, T. A. J. and Berendse, F.: Root life spans of four grass species from habitats differing in nutrient availability, *Funct. Ecol.*, 16, 198–203, 2002.
- Vogt, K. A., Grier, C. C., and Vogt, D. J.: Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests, *Adv. Ecol. Res.*, 15, 303–377, 1986.

Warren, J. M., Hanson, P. J., Iversen, C. M., Kumar, J., Walker, A. P., and Wullschleger, S. D.: Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations, *New Phytol.*, 205, 59–78, 2015.

West, J. B., Espeleta, J. F., and Donovan, L. A.: Root longevity and phenology differences between two co-occurring savanna bunchgrasses with different leaf habits, *Funct. Ecol.*, 17, 20–28, 2003.

Withington, J. M., Reich, P. B., Oleksyn, J., and Eissenstat, D. M.: Comparisons of structure and life span in roots and leaves among temperate trees, *Ecol. Monogr.*, 76, 381–397, 2006.

Yang, H. J., Wu, M. Y., Liu, W. X., Zhang, Z. Zhang, N. L., and Wan, S. Q.: Community structure and composition in response to climate change in a temperate steppe, *Glob. Change Biol.*, 17, 452–465, 2011.

BGD

12, 19999–20023, 2015

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

[Title Page](#)

[Abstract](#) [Introduction](#)

[Conclusions](#) [References](#)

[Tables](#) [Figures](#)

[◀](#) [▶](#)

[◀](#) [▶](#)

[Back](#) [Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 1. Characteristics of soil physical and chemical in 0–10 cm in *Stipa krylovii*, *Stipa grandis* and *Stipa breviflora* grassland in Inner Mongolia temperate steppe. The all data were mean values of six plots with bars as standard errors. Different letters mean significant difference between different grassland types at $P < 0.05$ determined by SAS.

Grassland types	pH	Soil organic matter (g kg^{-1})	Inorganic N concentration (mg kg^{-1})	AP (mg kg^{-1})	AK (mg kg^{-1})	Bulk density (g cm^{-3})	Soil water content (%)
<i>S. krylovii</i>	6.94 ± 0.02 b	43.79 ± 1.45 a	8.69 ± 0.38 a	8.11 ± 0.31 a	200.0 ± 12.31 a	1.22 ± 0.08 a	7.52 ± 0.37 b
<i>S. grandis</i>	7.26 ± 0.14 b	27.89 ± 1.75 b	8.99 ± 0.37 a	5.36 ± 0.42 b	180.9 ± 10.07 a	1.39 ± 0.05 a	12.56 ± 0.30 a
<i>S. breviflora</i>	8.06 ± 0.03 a	21.54 ± 0.78 c	6.12 ± 0.38 b	7.00 ± 0.43 a	162.8 ± 6.86 a	1.38 ± 0.05 a	5.72 ± 0.22 c

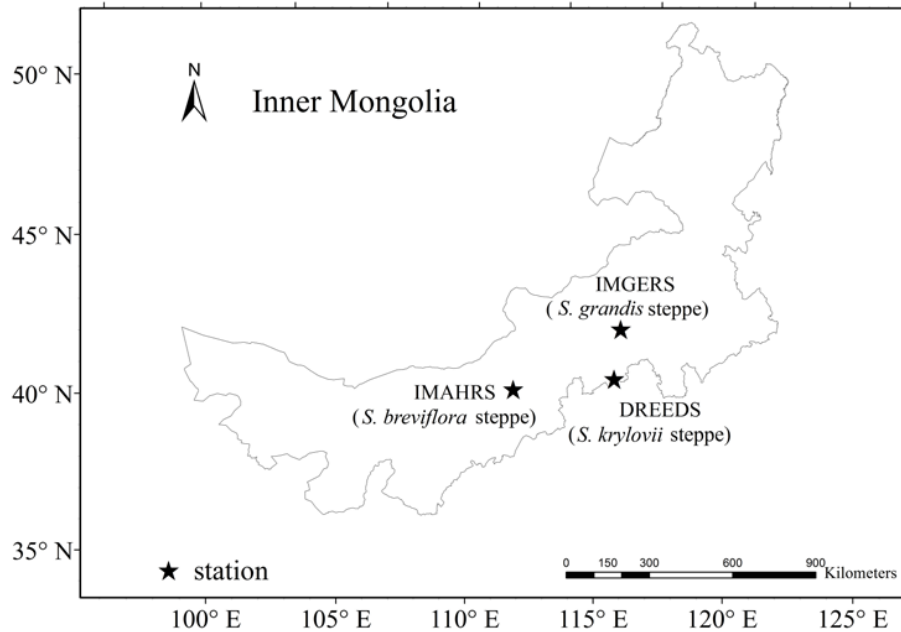


Figure 1. Locations of the Duolun Restoration Ecology Experimentation and Demonstration Station, Institute of Botany, the Chinese Academy of Sciences (DREEDS, 116°17' E, 42°02' N; 1324 m.a.s.l.), the Inner Mongolia Grassland Ecosystem Research Station, the Chinese Academy of Sciences (IMGERS, 116°42' E, 43°38' N; 1100 m.a.s.l.) and the Inner Mongolia Academy of Agriculture and Animal Husbandry Research Station (IMAHRS, 111°53' E, 41°47' N; 1450 m.a.s.l.) in an Inner Mongolia steppe in northern China. The three locations that the root lifespan was determined are representatives of the three types of grasslands within Inner Mongolia steppes.

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

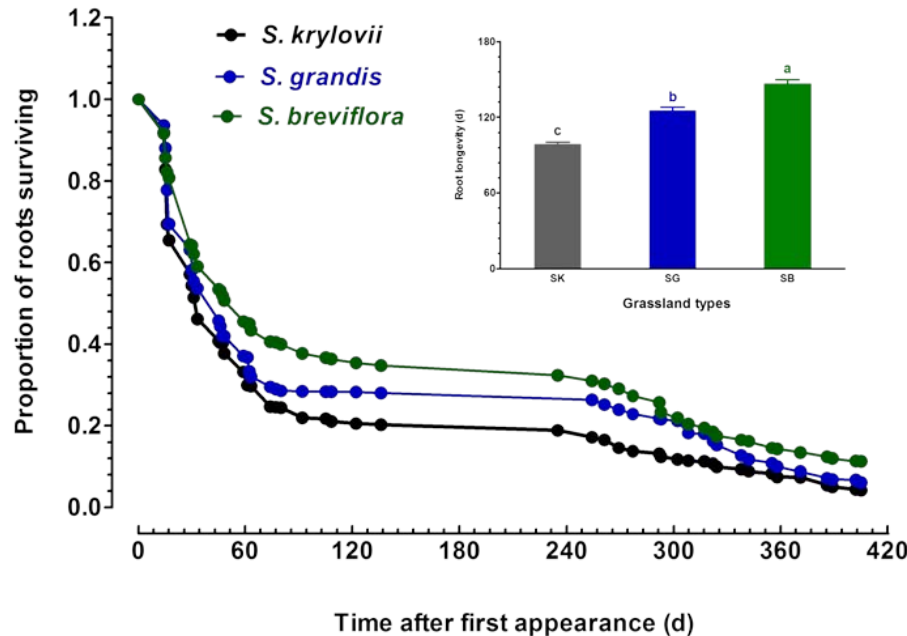


Figure 2. Survival curves and longevity of root under different grassland types at soil depths of 0–30 cm during the growing seasons of 2011 and 2012. Data shown in the figure were based on a total number of 5893 and 4440 and 2974 individual roots for *Stipa krylovii*, *Stipa grandis* and *Stipa breviflora* grassland, respectively. Mean lifespan were generated using the Kaplan–Meier method. Survival differences different grassland types were compared using Log-rank test. Data are means \pm SE of six plots. Different letters above the column mean significant difference between different grassland types at $P < 0.05$ determined by SAS.

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

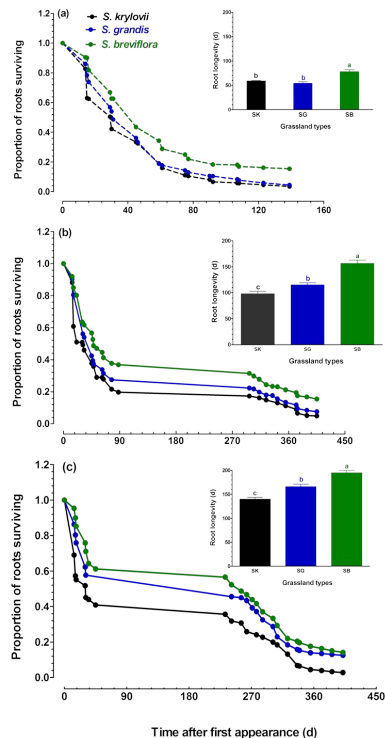


Figure 3. Survival curves and longevity of roots initiated in spring (a), summer (b) and autumn (c) in *Stipa krylovii*, *Stipa grandis* and *Stipa breviflora* grassland at soil depth of 0–30 cm. Data were obtained from total number of 4983, 3939 and 14 385 individual roots initiated in spring, summer and autumn in 2011 and 2012. The Kaplan–Meier method was used to generate the root surviving curves. Survival differences in different grassland types were compared using Log-rank test. Data are means \pm SE of six plots. Different letters above the column mean significant difference between different grassland types at $P < 0.05$ determined by SAS.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)

[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

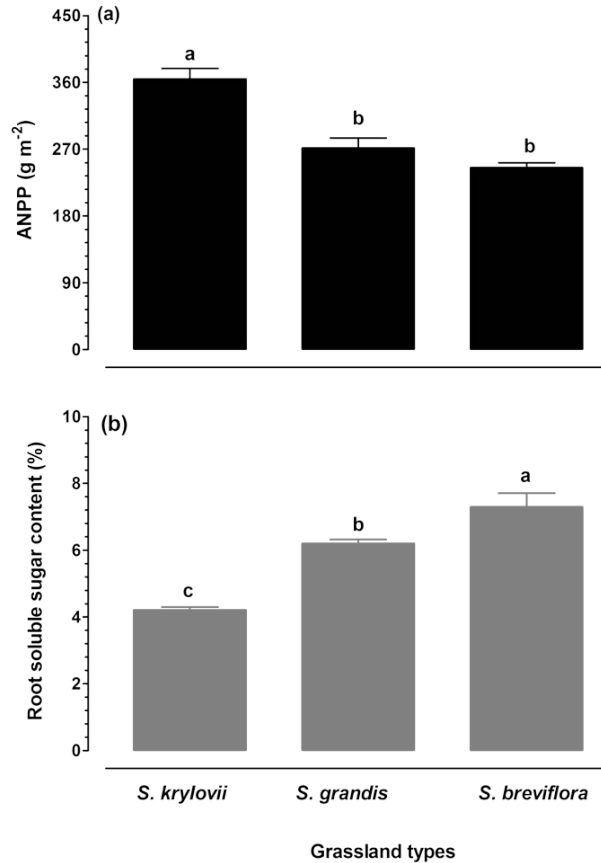



Figure 4. Aboveground net primary production (ANPP, **(a)**) and root soluble sugar content (**(b)**) in *Stipa krylovii*, *Stipa grandis* and *Stipa breviflora* grassland. Data are means \pm SE of six plots. Different letters above the column mean significant difference between different grassland types at $P < 0.05$ determined by SAS.

Spatial and temporal root lifespan of steppe

W.-M. Bai et al.

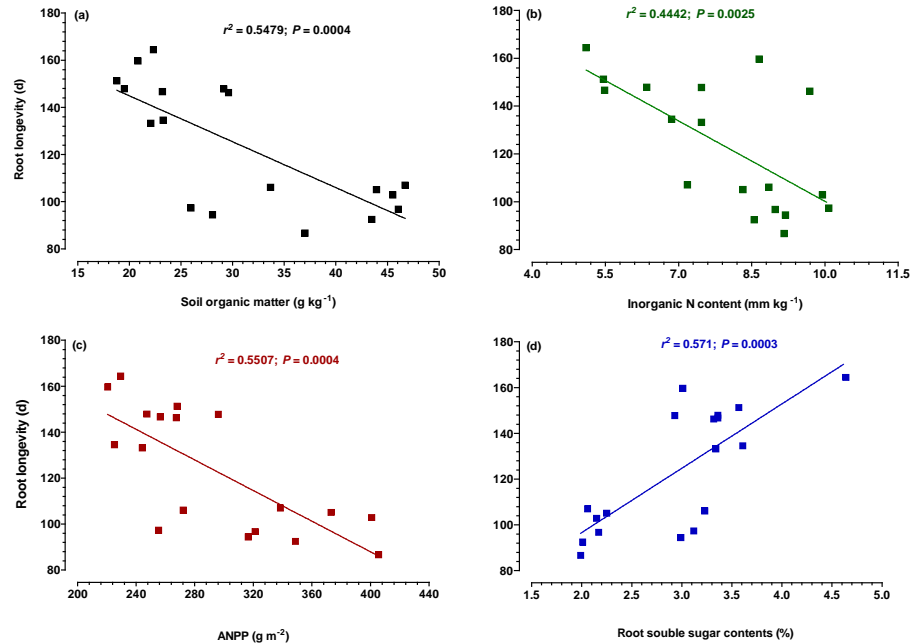


Figure 5. The correlations between root longevity and soil organic matter (SOM, **a**), soil inorganic N concentration (**b**), aboveground net primary production (ANPP, **c**) and contents of root soluble sugars (**d**) in *Stipa krylovii*, *Stipa grandis* and *Stipa breviflora* grassland with data obtained from 18 plots.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

