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Seasonal changes and vertical distribution of root standing biomass of graminoids and shrubs at a Siberian tundra site

Peng Wang · Liesje Mommer · Jasper van Ruijven · Frank Berendse · Trofim C. Maximov · Monique M. P. D. Heijmans

Abstract

Aims Shrub expansion is common in the tundra biome and has been linked to climate warming. However, the underlying mechanisms are still not fully understood. This study aimed to investigate the seasonal and vertical rooting patterns of different plant functional types, which is important for predicting tundra vegetation dynamics.
Methods We harvested root samples by soil coring and investigated seasonal changes in root biomass and vertical root distribution across a vegetation gradient, focusing on the differences between graminoids and dwarf shrubs, at a northeastern Siberian tundra.
Results Graminoid fine root biomass increased significantly during the growing season, whereas that of shrubs was already high at the beginning and did not change later on. Shrubs had a much shallower rooting pattern than graminoids. Also, shrub roots did not respond to increases in permafrost thawing depth over the growing season, whereas graminoids grew fine roots in deeper, recently thawed soil layers during the growing season.
Conclusions Our results show that shrubs are predominantly shallow-rooted and grow roots earlier than graminoids, which allows shrubs to take advantage of the nutrient pulse after snowmelt in the early growing season. In contrast, the deep-rooted graminoids can access the nutrients in deeper soil and may profit from increasing permafrost thawing depth. The outcome of the competitive interactions between graminoids and shrubs in tundra may depend on the balance between the benefits associated with earlier root growth and deeper root distribution, respectively. The shrub expansion with climate warming observed in recent decades suggests that earlier root growth in the upper soil layer may be more important than increased rooting depth later in the growing season.

Keywords Arctic tundra · Belowground biomass · *Betula nana* · Biomass distribution · *Eriophorum vaginatum* · Rooting pattern

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Introduction

Global annual air temperature is predicted to increase by more than 1.5 °C at the end of this century, and the temperature increase in the Arctic areas is predicted to

be higher than in other regions of the globe (IPCC 2013). Arctic tundra ecosystems have been shown to be strongly affected by climate warming. Due to the increased temperature, the decomposition rate of soil organic matter and release of carbon is accelerated (Belshe et al. 2013; Schuur et al. 2009), and the release of previously frozen soil organic carbon is initiated as permafrost layers thaw (Schuur et al. 2009; Zimov et al. 2006). In addition, increased temperature extends the growing season and improves nutrient availability due to increased permafrost thawing depth (active layer thickness, ALT) (Burn and Kokelj 2009; Hinkel and Nelson 2003) and increased nutrient mineralization at higher soil temperatures (Aerts 2006; Craine et al. 2010). Soil moisture content can change as well, due to the altered balance between thawing and evapotranspiration (Callaghan et al. 2011).

As a result of these environmental changes, aboveground productivity of tundra vegetation has been shown to increase (Epstein et al. 2012; Hill and Henry 2011; Verbyla 2008). Following this increase, vegetation composition is also changing, as shrub expansion at the expense of graminoids and/or cryptogams has been observed in many tundra areas (Callaghan et al. 2011; Myers-Smith et al. 2011a; Myers-Smith et al. 2011b; Tape et al. 2006; Wookey et al. 2009). However, the drivers underlying shrub expansion are still poorly understood. Experimental warming studies suggested that both graminoids and shrubs can increase biomass, cover or canopy height in response to warming treatments (Arft et al. 1999; Elmendorf et al. 2012; Walker et al. 2006), indicating that warming alone does not necessarily increase the competitive advantages of shrubs. All kinds of environmental changes that take place due to climate warming can affect the competitive interactions between the dominant plant functional types (PFTs) in tundra, change vegetation composition, and further influence ecosystem functioning such as carbon and nutrient fluxes (Mack et al. 2004; Shaver and Chapin 1991).

Since the changes that we referred to are primarily experienced by the roots, which constitute 70 % of total plant mass in tundra ecosystems (Poorter et al. 2012), it is important to study the belowground responses of different functional types to understand the responses of tundra vegetation to environmental changes. Roots of different functional types in tundra may differ in morphology, architecture, productivity and life span (Iversen et al. 2015). Here, we focus on dwarf shrubs

and graminoids, the two dominant types of vascular plants in the tundra ecosystem. Graminoids such as *Eriophorum vaginatum* are considered to grow deep roots with a short life span while dwarf shrubs such as *Betula nana* are assumed to have shallow roots with a longer life span (Miller et al. 1982; Shaver and Billings 1975; Shaver and Chapin 1991; Sullivan et al. 2007). Shallow-rooting plants may have a competitive advantage early in the growing season when the deeper soil is still frozen and inaccessible for deep-rooting plants. However, climate warming can lead to increases in ALT (Burn and Kokelj 2009; Hinkel and Nelson 2003), which may favor deep-rooting species later in the growing season. For example, nutrients available at the thaw front of permafrost may benefit plants with deeper roots at the expense of shallow rooting species (Keuper and Dorrepaal 2014; Keuper et al. 2012). However, little is known about the temporal and spatial root responses of shrubs and graminoids to increases in growing season length and ALT. Here, we investigated seasonal changes and vertical distribution of root biomass across a vegetation gradient, focusing on the differences between graminoids and dwarf shrubs. We aimed to answer the following questions:

1) Is belowground biomass development over the growing season different for dwarf shrubs and graminoids?
2) Is the root vertical distribution of these two functional types different and does it change over the growing season?

Materials and methods

Study site

The study site is at the Chokurdakh Scientific Tundra Station (70°49′28″ N, 147°29′23″ E; elevation 11 m a.s.l.) in Kytalyk Wildlife Reserve, which is located in the lowlands of the Indigirka River in northeastern Siberia. The mean annual air temperature at the nearest climate station (Chokurdakh, WMO station code 21,946, 27 km away from the study site) is −13.4 °C (1981–2010), with 10.3 °C as the mean July temperature. Annual precipitation is 196 mm (1981–2010), of which 76 mm falls in the summer (June – August). The study area is the former lake bed of a drained

thermokarst lake, which has a shallow active layer underlain by thick continuous permafrost.

The vegetation surrounding the Chokurdakh Scientific Tundra Station is classified as G4, tussock-sedge, dwarf-shrub, moss tundra, on the Circumpolar Arctic Vegetation Map (Walker et al. 2005). The vegetation in the drained lake bed is a mosaic formed mainly by graminoids, dwarf shrubs, and a mixture of the two (Fig. 1). The dominant graminoid species in this study is the tussock-forming sedge *Eriophorum vaginatum* L, followed by the grasses *Arctagrostis latifolia* (R. Br.) Griseb and *Calamagrostis holmii* Lange. The dominant dwarf shrub is the deciduous shrub *Betula nana* L. Other shrub species include the deciduous shrub *Salix pulchra* Cham, and evergreen shrubs *Vaccinium vitis-idaea* L and *Rhododendron subarcticum* Harmaja. A moss layer with some lichens is present throughout the study area.

Sampling design

In June 2013, 8 blocks were selected in which all three vegetation types, graminoid dominated, dwarf shrub dominated and mixture vegetation, were close to each other. Each block was about 150 m^2 and 40–140 m away from the next block. Within each block we selected one plot in each of the three vegetation types. Vegetation types were determined visually by the relative cover of *B. nana* and *E. vaginatum*. Graminoid vegetation was characterized by cover of *E. vaginatum* exceeding 70 % of total vascular plant cover, whereas in shrub vegetation, the cover of

B. nana was at least 70 %. In mixture plots, cover of both PFTs varied between 30 and 70 % (Fig 1). Plots were squares, with side lengths between 3 and 5 m, and the distances between plots varied between 3 and 10 m. Within these plots, we focused on two plant functional types: graminoids and dwarf shrubs.

In order to investigate seasonal changes in biomass, we sampled twice: once at the beginning of the growing season (28 June – 1 July) approximately two weeks after the surface soil started to thaw (2 cm soil temperature data from VU meteorology data at the study site), and the second one at the end of the growing season (28–30 July) when *B. nana* leaves started to turn red and presumably vegetation biomass reached its peak. For each harvest, two subplots measuring 25 × 25 cm were sampled per plot. These two samples were pooled per plot. In shrub plots, two randomly chosen subplots were harvested, but in graminoid and mixture vegetation plots, one quadrat was located on a randomly selected tussock and one in the inter-tussock area. In order estimate the total amounts of plant mass per plot, we multiplied the measured biomass in the subplots by the relative cover of tussock or inter-tussock area. This was determined using four random point quadrats (0.5 × 0.5 m) in each plot. A pin was lowered at 100 points in each quadrat. For aboveground tussock cover, each pin hitting the actual tussock or *E. vaginatum* leaves expanding from a tussock, was recorded as tussock, and the rest as inter-tussock area. For belowground tussock area, only the pins hitting the actual tussock (from which the roots are assumed to grow directly downwards) were recorded as tussock.
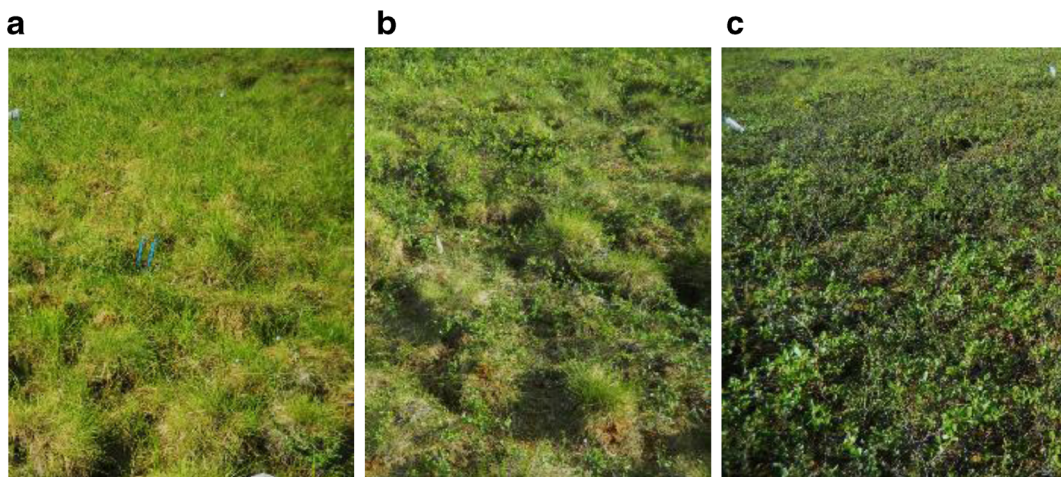
Fig. 1 Pictures of the three vegetation types. Graminoid vegetation (**a**) had a cover of *E. vaginatum* more than 70 %, mixture vegetation (**b**) had covers of both *E. vaginatum* and *B. nana* between 30 and 70 %, and shrub vegetation (**c**) had a cover of *B. nana* more than 70 %

In each subplot, aboveground plant parts were clipped at the moss surface and sorted to different fractions for the different PFTs: leaves for graminoids, and leaves and stems for shrubs. Root biomass was sampled by taking a soil core (8 cm diameter, 30 cm deep) in the center of the subplot. The soil cores were separated into 3 depths: 0–5, 5–15, and 15–30 cm. Early in the growing season, the thawed layer in some plots was still very shallow, and the root corer with 8 cm diameter could not be hammered into the permafrost. In these cases, a smaller corer with 3.2 cm diameter was used instead. Belowground plant parts were sorted out from the soil cores manually by using forceps. To take into account the resulting differences in soil volume between layers, we used the root mass density (g m^{-3}) as a measure of root biomass. Belowground biomass was sorted to different fractions for the different functional types: belowground stems (diameter > 5 mm), coarse roots (1 mm < diameter < 5 mm) and fine roots (diameter < 1 mm) for shrubs, rhizomes (diameter > 1 mm, including leaf bases of *E. vaginatum*) and fine roots (diameter < 1 mm) for graminoids. Belowground stems of shrubs were easily identified to species as they resemble their aboveground part. Roots that were not attached to the belowground stems were identified according to their color and texture (Hobbie and Chapin 1998). Roots of the graminoids were white and smooth while roots of the shrubs were brownish or reddish, with woody texture. The very new roots of *B. nana* were also white or light-colored. However, they were white only in the fore-end part which is normally less than 5 mm long and they were normally finer than the roots of *E. vaginatum* which are about 1 mm in diameter. If the root density was very high, which was usually the case for soil cores from *E. vaginatum* tussocks and cores with high density of very fine evergreen shrub roots, subsamples with a known proportion of the original samples were taken.

All samples were air-dried at the field station before they were transported to Spasskaya Pad Scientific Forest Station, Russia (62°14′ N, 129°37′ E) where they were further dried in an oven at the temperature of 70 °C for at least 24 h. After the samples were transported to the Netherlands, they were dried in an oven at the temperature of 65 °C for 72 h and weighed.

Environmental factors

ALT and soil moisture were measured in each plot at 2 points and 9 points in early and late growing season, respectively. ALT was measured by inserting a metal stick into the soil until it hit the permafrost. Soil moisture was measured at 10 cm soil depth by a Thetaprobe soil moisture sensor (ML3 ThetaKit, Delta-T Devices, UK). Organic layer thickness of each soil core was measured immediately after the soil core was taken. Resin bags were used for measuring exchangeable nutrients in the soil. Each resin bag contained 5 g ion-exchange resin (TMD-8, H+/OH- Form, Type 1, Mixed Bed Resin, 16–50 mesh, Avantor, USA) in a 5 × 5 cm polypropylene bag with a 100 μm mesh size. Before the first harvest 3 resin bags were buried in each plot at the depth of 10 cm. Temperature loggers (iButton DS1922L/DS1921G, Maxim Integrated, USA) were buried at 10 cm depth in 12 plots of 4 blocks. Resin bags and temperature loggers were retrieved after the second sampling. Resin bags were transported back to the Netherlands and extracted overnight in 50 ml 2 M NaCl in 0.1 M HCl. The extracts were brought to neutral pH by the addition of NaOH and analyzed spectrophotometrically for NH_4^+, NO_3^-, PO_4^- and K^+ using an auto-analyzer (Skalar, Breda, The Netherlands).

Data analysis

To test for differences in total aboveground and belowground biomass of the three different vegetation types and their seasonal changes, we used a linear mixed model (lme) with vegetation type, season (early or late), vegetation part (aboveground or belowground) and their interactions as fixed factors, block and plot as random effects in a nested structure (plot within block). The same model was used for the analyses of resource-acquiring leaf and fine root biomass, except that vegetation part was replaced by tissue type (leaf or fine root).

To test for seasonal changes in fine root biomass of the two PFTs in different vegetation types, fine root biomass was analyzed using vegetation type, PFT, season and their interactions as fixed factors, block and plot as random effects in a nested structure.

To test for changes in vertical distribution of fine roots, we used fine root biomass density as a dependent variable to correct for the different soil volume of each layer. Shrubs had few roots in the 3rd layer in our samples, which resulted in a lot of zero values in the data, so that the assumptions of normal distribution and homogeneity of variance were violated. To solve this, we first analyzed fine root biomass density of the upper

two layers using vegetation type, PFT, season, soil layer and their interactions as fixed factors, block and plot as random effects in a nested structure. Then we used a nonparametric method for longitudinal data described by Brunner and Puri (2001) to test for differences in fine root densities in the 3rd layer with plots as the individual subjects on which repeated measurements were taken. In addition, we also used this nonparametric method to analyze the relative biomass in each layer of graminoid and shrub roots to test for seasonal changes in root vertical distribution.

All dependent variables were ln transformed when necessary to achieve normal distribution and homoscedasticity of errors. Analyses were performed with R (version 3.2.1) in RStudio (version 0.98.1091). Linear mixed model analyses were made using package lme4 version 1.1–7 (Bates et al. 2014). P values were obtained through package lmerTest version 2.0–20 (Kuznetsova et al. 2014). Nonparametric analysis was made using nparLD package version 2.1 (Noguchi et al. 2012). Graphics were produced with ggplot2 package version 1.0.0 (Wickham 2009).

Results

Environmental conditions

In the study period, average ALT of all the three vegetation types doubled from 14 cm early in the growing season to 28 cm in the late season (Table 1). ALT in graminoid vegetation was significantly higher than in mixture and shrub vegetation, irrespective of the time of season (Table 1), indicating a larger soil volume available for root development in the graminoid-dominated vegetation type. Temperature at 10 cm soil depth increased over the season but did not differ among the three vegetation types (Table 1). Volumetric soil moisture content was significantly higher in graminoid vegetation than in shrub vegetation (50 % vs 30 %). Over the season, soil moisture content decreased in shrub vegetation, but not in the graminoid and mixed vegetation types (Table 1). The organic layer thickness was approximately 20 cm and did not differ among vegetation types (Table 1). Most soil exchangeable nutrients (NH_4^+, total inorganic N, PO_4^- and K^+) were two times higher in graminoid vegetation than in the other two vegetation types, but the three vegetation types did not

differ in soil nitrate concentration, which amounted to 10 % of the inorganic nitrogen (Table 1).

Community biomass

Community biomass differed significantly among the three vegetation types (Fig. 2, Table 2), both above and below ground. Total (above + below ground) biomass of shrub vegetation was 110 % and 60 % higher than that of graminoid vegetation and mixture vegetation respectively (Fig. 2, Table 2). Biomass was greater belowground than aboveground (Fig. 2). Moreover, the distribution of biomass over above and below ground plant parts differed among the vegetation types (significant vegetation type × part in Table 2; below/above ground ratio in the late season was 4.4 ± 0.3, 3.3 ± 0.3, 2.3 ± 0.2 for graminoid, mixture and shrub vegetation respectively). Both above and below ground community biomass increased significantly over the season in graminoid and mixture vegetation ($F_{1,21} = 56.7$, $P < 0.001$; $F_{1,21} = 10.9$, $P = 0.003$ respectively), but not in shrub vegetation ($F_{1,21} = 1.8$, $P = 0.189$).

As the next step we zoomed in on the actual resource acquiring tissues, i.e. leaves and fine roots. Leaf biomass was not significantly different among the three vegetation types ($F_{2,21} = 0.7$, $P = 0.517$). Fine root biomass was lower in graminoid vegetation than in the other two types, but only in the early growing season ($F_{2,14} = 3.4$, $P = 0.004$ for the early season; $F_{2,21} = 0.4$, $P = 0.182$ for the late season; Fig. 2). Fine root biomass, as well as leaf biomass, increased over the growing season in graminoid and mixture vegetation types vegetation ($F_{1,21} = 71.9$, $P < 0.001$; $F_{1,21} = 12.9$, $P = 0.002$ respectively), but in shrub vegetation no significant changes were found ($F_{1,28} = 3.2$, $P = 0.084$).

Fine roots of PFTs

Fine root biomass density differed between the two PFTs in the first two soil layers, but this effect depended on season, vegetation type and layer (see Table S1). When the two PFTs were analyzed separately, graminoid root density increased significantly over season in the upper two layers of all three vegetation types (Fig. 3, Table 3). Meanwhile, seasonal changes of shrub root density in the upper two layers differed among vegetation types (Fig. 3, Table 3): it increased over season in graminoid vegetation ($F_{1,21} = 5.0$, $P = 0.026$), but there were no significant seasonal

Table 1 Environmental factors in the three vegetation types in early and late growing season. Different letters indicate difference among vegetation types in each season. Data are mean ± SE, $n = 8$ plots except for soil temperature ($n = 4$ plots)

		Graminoid vegetation	Mixture vegetation	Shrub vegetation	Season and vegetation effects
Active layer thickness (cm)	Early	17 ± 0.9^a	14 ± 0.5^b	12 ± 0.5^c	Season *
	Late	34 ± 1.7^a	26 ± 1.1^b	23 ± 0.4^b	Vegetation *
					Season × Veg *
Organic layer thickness (cm)	Early	18 ± 1.6	18 ± 0.7	19 ± 0.9	Season ns
	Late	21 ± 1.4	20 ± 1.4	17 ± 1.0	Vegetation ns
					Season × Veg ns
Soil moisture (% volume)	Early	50 ± 3^a	46 ± 3^{ab}	37 ± 2^b	Season *
	Late	51 ± 5^a	39 ± 5^b	24 ± 1^c	Vegetation *
					Season × Veg ns
Soil temperature (°C)	Early	0.8 ± 0.1^a	0.8 ± 0.2^a	0.7 ± 0.2^a	Season *
	Late	2.8 ± 0.1^a	2.5 ± 0.3^a	2.6 ± 0.2^a	Vegetation ns
					Season × Veg ns
Exchangeable nutrient ($\mu g\ g^{-1}$ resin)	N-NH$_4$	52 ± 6^a	26 ± 4^b	23 ± 4^b	Vegetation *
	N-NO$_3$	3 ± 1	4 ± 1	4 ± 1	Vegetation ns
	Total inorganic N	55 ± 6^a	30 ± 3^b	26 ± 4^b	Vegetation *
	P	5 ± 1^a	3 ± 0.3^b	3 ± 1^b	Vegetation *
	K	124 ± 11^a	90 ± 10^b	50 ± 9^c	Vegetation *

changes in the other two vegetation types ($F_{1,53} = 1.0$, $P = 0.321$). Similar patterns were found in the 3rd layer: graminoid root density increased significantly over the growing season, while shrub root density did not change (Table S2), as it remained at zero or very low values (Fig. 3). The distribution of relative fine root biomass of each PFT over the layers also shows that graminoids

increased relative biomass distribution to deep roots at the expense of shallow roots over the growing season, while the vertical distribution pattern of shrubs did not change much over the growing season (Fig. S2).

The vertical distribution of fine roots also differed between the two PFTs: graminoid root density did not

Fig. 2 Total community biomass of the three vegetation types, subdivided into leaf, aboveground stem, fine root and coarse root (including rhizome and belowground stem), in early and late growing season. Bars indicate mean ± SE ($n = 8$ plots) of each tissue type. Asterisks represent significant seasonal changes ($P < 0.05$). Seasonal change patterns resembled between total aboveground biomass and leaf biomass, total belowground biomass and fine root biomass
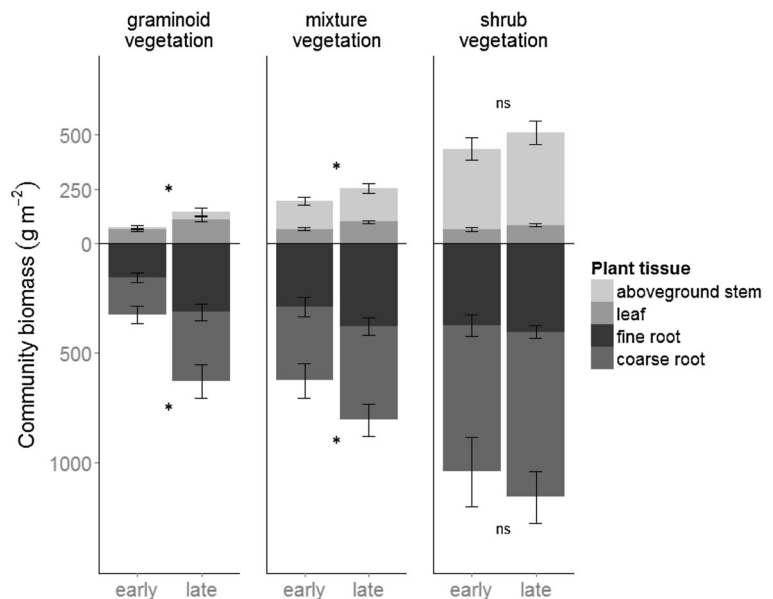
Table 2 Analysis of community biomass (above and below-ground), and acquisitive biomass (leaf and fine root) of the three vegetation typ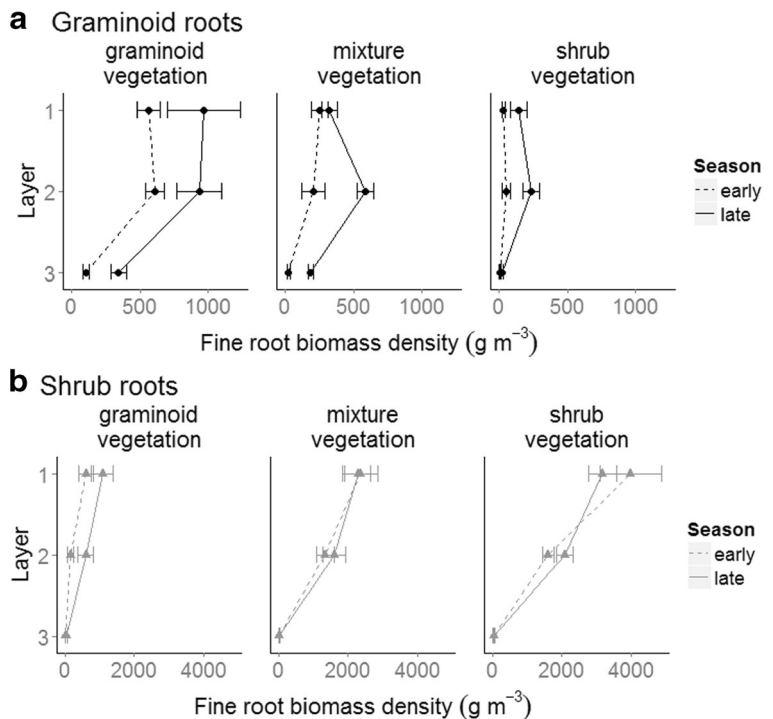es using linear mixed model. Block and plot were taken as random effects in a nested structure. Data were ln transformed. Part refers to aboveground/belowground, tissue refers to leaf/fine root

Variable	Source	Sum of squares	df	F value	P value
Community biomass	Vegetation	9.7	2	66.2	< 0.001 *
	Season	3.2	1	43.6	< 0.001 *
	Part	31.6	1	429.7	< 0.001 *
	Vegetation × season	1.1	2	7.8	0.001 *
	Vegetation × part	1.5	2	10.4	< 0.001 *
	Season × part	< 0.1	1	< 0.1	0.972
	Vegetation × season × part	< 0.1	2	< 0.1	0.961
Leaf and fine root biomass	Vegetation	0.4	2	2.4	0.130
	Season	4.0	1	49.5	< 0.001 *
	Tissue	41.1	1	508.0	< 0.001 *
	Vegetation × season	0.8	2	4.9	0.010 *
	Vegetation × tissue	2.1	2	13.2	< 0.001 *
	Season × tissue	< 0.1	1	< 0.1	0.890
	Vegetation × season × tissue	0.1	2	0.7	0.515

differ between the upper two layers while shrub root density decreased significantly from the 1st to the 2nd layer (Fig. 3, Table 3). Root density in the 3rd layer was lowest for both PFTs (Fig. 3), however, graminoid root density in this deepest layer was significantly higher than shrub root density in all vegetation types except in shrub vegetation where the relative abundance of graminoids was very low ($P < 0.001$, $P < 0.001$, $P = 0.584$ for graminoid, mixture, and shrub vegetation type, respectively; Fig. 3, Table S2).

Fig. 3 Fine root biomass density in different soil layers of the three vegetation types, shown separately for graminoids (**a**) and shrubs (**b**). Layer 1 = 0–5 cm; 2 = 5–15 cm. 3 = 15–30 cm. Note that the scale of the x-axis differs for graminoid and shrub roots. Symbols indicate mean ± SE (n = 8 plots)

Table 3 Analysis of vegetation, season, and layer effects on fine root biomass density in the upper two layers, using linear mixed model for each PFT separately. Block, plot were taken as random effects in a nested structure. Data were ln(x + 1) transformed

Source	df	Graminoid roots			Shrub roots		
		Sum of squares	F value	P value	Sum of squares	F value	P value
Vegetation	2	200.1	52.9	< 0.001 *	35.3	12.8	0.001 *
Season	1	21.6	11.4	0.001 *	6.4	4.6	0.035 *
Layer	1	2.3	1.2	0.278	19.9	14.4	< 0.001 *
Vegetation × season	2	5.9	1.5	0.219	10.8	3.9	0.025 *
Vegetation × layer	2	1.3	0.3	0.708	5.2	1.9	0.157
Season × layer	1	5.4	2.9	0.094	0.9	0.6	0.425
Vegetation × season × layer	2	3.6	0.9	0.392	0.4	0.1	0.865

Discussion

Despite the large differences in community biomass among the three vegetation types, the biomass of the acquisitive organs, i.e., leaves and fine roots, did not differ significantly among the vegetation types in the late growing season. Graminoid fine root biomass increased during the growing season, while shrub fine root biomass did not, suggesting important differences in seasonality of root growth between graminoids and shrubs. Between the early and late sampling date, graminoids increased root growth and distributed relatively more roots in the deepest layer, while shrubs did not change their rooting pattern. Moreover, shrubs grew a larger part of their roots in the shallow layers than the graminoids did. Although shrub root growth was not limited by the available soil volume, as during the late growing season the thawed soil was deeper than 25 cm, still very few shrub roots were found there. Our results suggest important differences both in seasonality and in vertical distribution of root growth between graminoids and shrubs. This finding contributes significantly to our understanding of the mechanisms of shrub expansion in Arctic tundra.

Seasonal changes in fine root biomass

Graminoids and shrubs differed in their aboveground phenology. It was observed in the field that at the time of the first harvest, most of the *B. nana* leaves had already sprouted, while new leaves of the dominant graminoid *E. vaginatum* were still rare. This earlier leaf growth of dwarf shrubs has also been found in other studies (Murray and Miller 1982; Wipf 2010). The seasonal patterns belowground in our study were very similar to the seasonal patterns that we found aboveground, which suggests differences in seasonality of root growth between *E. vaginatum* and *B. nana*. In the mixture vegetation, where graminoids and dwarf shrubs were equally abundant, graminoid fine root biomass increased during the growing season, but shrub fine root biomass did not (Fig. S1). One explanation is that the shrubs already grew most of their fine roots before the early season harvest. It has been shown that *B. glandulosa*, a species similar to *B. nana*, started root growth one week after bud break and achieved maximum root biomass in three weeks (Kummerow et al. 1983). Perhaps, root growth of *B. nana* starts and finishes early in the growing season as well. Only in graminoid-dominated vegetation, fine root biomass of shrubs showed a small increase during the growing season ($F_{1,7} = 5.0$, $P < 0.05$; Fig. S1). We observed that in graminoid vegetation the snowmelt was later than in shrub vegetation (Juszak et al. 2016) and soil temperature at 5 cm depth at the time of snowmelt was lower than in shrub vegetation (unpublished data from another study at the same site). The earlier snowmelt and higher soil temperature in the very early growing season in the shrub-dominated vegetation can also be in favor of the earlier shoot and root growth of the shrubs, which might explain the difference in shrub root growth between the vegetation types.

An alternative explanation for the lack of a season effect in shrub fine root biomass may be that root turnover of shrubs in tundra is very low. As a consequence, root biomass is already high at the start of the growing season and growth is limited, leading to only minor, non-detectable changes in fine root biomass over the growing season. However, at the early season

sampling, we observed in shrub vegetation that many light-colored and water-rich *B. nana* roots, presumably newly-grown roots, were at the interface of thawed soil and still-frozen soil, indicating that in the early growing season shrubs did grow new roots. Therefore, earlier root growth of *B. nana* seems to be a better explanation.

Vertical rooting patterns

Our findings confirm that dwarf shrubs root shallower than graminoids in tundra ecosystems (Miller et al. 1982; Shaver and Billings 1975; Shaver and Cutler 1979). Our results further show that the shallow rooting pattern of shrubs was quite persistent. Even when the active layer was deeper than 25 cm in the late season in all vegetation types (Table 1), there were very few shrub roots in this deeper layer and relative biomass of deep roots did not increase (Fig. 3 and S2). Following our earlier explanation that root growth of shrubs mainly takes place early in the growing season, the persistent shallow root distribution of shrubs is not surprising: as shrubs grow new fine roots early in the growing season, when the active, unfrozen layer is still shallow, their root growth is confined to the upper thawed soil. In contrast, graminoids grow new fine roots later in the growing season and as a consequence, can also access deeper soil layers.

The competitive balance between shrubs
and graminoids

Our results show a clear distinction between shrubs and graminoids: shrubs grow new roots earlier in the growing season, but this is restricted to the upper soil layer, whereas graminoids are able to access deeper soil layers, but only later in the growing season. This suggests that the outcome of the competitive interactions between graminoids and shrubs in tundra depends on the balance between the benefits associated with earlier root growth and deeper root distribution, respectively. Climate warming increases ALT (Burn and Kokelj 2009; Hinkel and Nelson 2003), which can increase plant available nutrients in the deeper soil (Keuper et al. 2012). The deeper root distribution of graminoids would allow them to take advantage over shrubs under warmer conditions (Oulehle et al. 2016). In contrast, the earlier root growth of shrubs enables them to absorb nutrients released from the frozen soil and snowpack in the very early season (Brooks et al. 1998; Sturm et al. 2005; Weih 1998; Weintraub and Schimel 2005), thereby

getting an advantage over graminoids early in the growing season. Moreover, nutrient availability typically is higher in the top of the soil than deeper in the soil (Hobbie and Gough 2002; Jobbágy and Jackson 2001), thus the shallow root distribution could also allow shrubs to take an advantage over graminoids. The observed shrub expansion in tundra ecosystems in recent decades suggests that the ability to grow roots in the top soil early in the growing season is more important than the ability to grow roots in deeper soil layers later in the growing season. However, if climate warming continues in the Arctic, the active layer gets deeper and soil temperature higher, which provides benefits for graminoids because of higher nutrient availability deeper in the soil. Future research explicitly linking vegetation composition and extended growing season and increased ALT is needed to test this hypothesis.

Conclusion

Our results suggest that root growth of graminoids and dwarf shrubs differs both in seasonal timing and in vertical distribution pattern. These patterns are remarkably consistent in the three vegetation types we studied. The current trend of shrub expansion in tundra suggests that shallow root growth early in the growing season is more important for tundra plants than growing roots in deeper soil later in the growing season. If further climate warming leads to increased nutrient release in deeper soil layers, via increased permafrost thawing and nutrient mineralization, graminoids may gain a competitive advantage in the future.

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