Roots in the tundra

Relations between climate warming and root biomass and implications for vegetation change and carbon dynamics

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General introduction

1.1 Climate warming in the Arctic

The global mean surface air temperature increased by 0.85 °C over the period 1880 to 2012, with an expected further increase of more than 1.5 °C by the end of 21st century (IPCC 2013). In the Arctic, greater rates of temperature increase have been observed for recent decades (ACIA 2005). This is also known as Arctic amplification, which can be attributed to less emitted blackbody radiation per unit warming in high latitudes and the increase in surface absorption of solar radiation when snow and ice retreat (Screen and Simmonds 2010, Serreze and Barry 2011, Pithan and Mauritsen 2014). It is predicted that surface air temperature in the Arctic will increase twice as rapid as the global average at the end of this century (Fig. 1.1).

The warming climate may cause the permafrost to thaw (Lawrence et al. 2008, Park et al. 2016), making the organic matter, that has been stored in the permafrost for thousands of years, available for microbial decomposition (Schuur et al. 2009, Romanovsky et al. 2010). This is expected to enhance the carbon release from Arctic soil (Schuur et al. 2015). On the other hand, a warmer climate can increase the growing season length (Schwartz et al. 2006, Høye et al. 2007) and soil nutrient availability (Mikan et al. 2002, Aerts 2006), thereby increasing primary productivity and carbon storage in tundra vegetation (Epstein et al. 2012, Forkel et al. 2016). The net carbon exchange of tundra ecosystems will depend on the balance between increased carbon release from the soil and increased carbon uptake by the vegetation. For example, Belshe et al. (2013) showed that with higher temperatures, net carbon uptake during summers increased, while net carbon emission during winters also increased, making tundra ecosystems net carbon sources on the annual basis across a temperature gradient from –16 to 0 °C.

Tundra vegetation can be sorted into various vegetation types according to the percentages of different vascular plants (forbs, sedges, grasses, deciduous shrubs, evergreen shrubs), bryophytes and lichens (Wielgolaski 1972). Due to climate warming, vegetation composition in Arctic tundra is also changing. The most dramatic change is the shrub expansion across Arctic tundra, which has been observed by the use of satellite imagery and/or aerial photographs (Callaghan et al. 2011, Myers-Smith et al. 2011b). However, it remains unclear what is (are) the most important cause(s). Growth of both shrubs and graminoids is limited by low temperatures in the Arctic, and meta-analyses of experimental warming studies have suggested that both of them can respond positively to warming in terms of biomass, cover or canopy height (Arft et al. 1999, Walker et al. 2006, Elmendorf et al. 2012), indicating that warming alone does not necessarily increase the competitive advantage of shrubs.

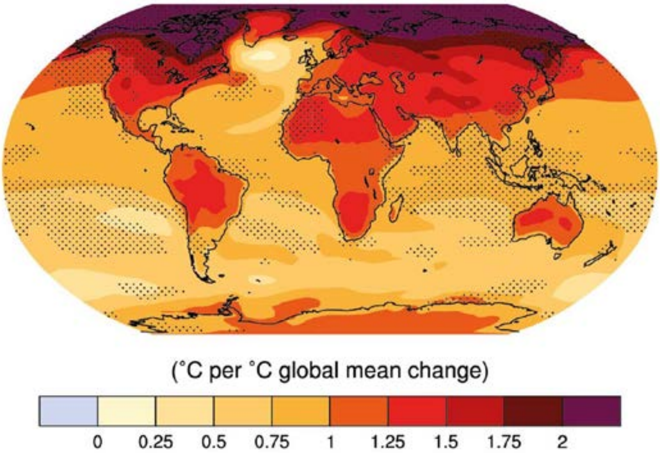

Fig 1.1 Predicted relative climate change rate of the globe 2081 – 2100 derived from transient simulations from the Coupled Model Intercomparison Project Phase 5 (CMIP5) ensembles (IPCC 2013). Temperature increase in the Arctic is twice as large as the global average.

Multiple abiotic factors can influence plant growth in tundra. Some dendrochronological studies suggested a high correlation between shrub growth and summer temperatures (Forbes et al. 2010, Blok et al. 2011). However, some experimental studies suggested that the indirect temperature effects on soil nutrient availability are more important for plant growth in tundra compared to direct temperature effects (Hobbie and Chapin, 1998; Shaver et al., 1998). Moreover, other factors such as soil pH and precipitation were also found important (Walker et al. 2003a, Blok et al. 2011). In addition to temperature, precipitation is also expected to increase in the Arctic (IPCC 2013, Bintanja and Selten 2014). The changes in precipitation and soil moisture, particularly the latter which is more site specific because of local topography and evapotranspiration/precipitation ratio, can interact with temperature to impact tundra ecosystems (Callaghan et al. 2011, Myers-Smith et al. 2015).

Apart from abiotic factors, biotic factors can also influence tundra vegetation. Herbivory has been found to be able to inhibit shrub expansion (Olofsson et al. 2009, Naito and Cairns 2011). In addition, trampling and faecal inputs from herbivores can play a role in determining tundra vegetation (Wal 2006). Predators also have an indirect effect on tundra vegetation by controlling herbivore populations (Hambäck et al. 2004).

There are much less studies on vegetation changes in Siberian tundra than in other tundra areas. Frost and Epstein (2014) showed that shrub and tree cover increased in 9 out of 11 ecotones in northern Siberia; however, these increases were more related to disturbance regimes rather than temperature. Siberian tundra needs to be more studied as it occupies a very large part of the tundra biome.

1.2 Plant roots in tundra ecosystems

In general belowground parts account for 70% of total vascular plant biomass in tundra vegetation (Poorter et al. 2012), although plant functional types can differ in their belowground to aboveground biomass ratios (Iversen et al. 2015). Fine roots are the parts that are directly involved in the nutrient uptake of plants, which can largely influence the competitive relationship between tundra plant species since tundra ecosystems are greatly limited by nutrient availability (Chapin 1987, Chapin et al. 1995). In addition, the senesced roots are important contributors to soil organic matter (Loya et al. 2002, Loya et al. 2004, Freschet et al. 2013). Therefore, it is of particular importance to incorporate root responses of tundra vegetation in order to fully understand the effects of climate warming on tundra ecosystems.

However, it is not yet well studied how climate warming can affect the belowground parts, particularly the roots, of tundra vegetation, as most studies focused on the aboveground parts (Arft et al. 1999, Walker et al. 2006, Elmendorf et al. 2012). Only a few studies investigated warming effects on tundra belowground biomass through manipulated warming experiments, and they yielded inconsistent results. Some studies found that belowground biomass was increased by manipulated warming (Sistla et al. 2013, Zamin et al. 2014), while other studies found no significant effects (Björk et al. 2007, DeMarco et al. 2014) or even negative effects of warming on belowground biomass (Gough and Hobbie 2003, Björk et al. 2007).

Differences in vegetation composition may partly explain the mixed results found for belowground responses to warming treatments. Plant species or functional types differ greatly in their root traits such as morphology, turnover, rooting depth and plasticity in response to environmental changes, all of which can influence their belowground responses to warmer climates (Bardgett et al. 2014, Iversen et al. 2015). For example, in a fertilization experiment, fine root biomass increased while root production decreased, because fertilization changed the vegetation from graminoid-dominated to shrub-dominated and the shrub had a lower root turnover rate (Sullivan et al. 2007). Therefore, it is important to take into account the differences in vegetation composition to fully understand warming effects on tundra belowground.

1.3 Influences on carbon dynamics

As roots account for a major part of plant carbon pool in the tundra, warming effects on roots can largely influence the carbon dynamics of tundra ecosystems through biomass allocation, carbon storage and turnover of roots. In addition, because shrubs have higher primary productivity and carbon storage capacity than graminoids (Johnson and Tieszen 1976, Shaver and Chapin 1991), shrub expansion with climate warming can further change the carbon dynamics of tundra ecosystems. For example, shrubs have a large proportion of biomass stored in woody stems, which have very low turnover and decomposition rates (Hobbie 1996, Cornelissen et al. 2007), and thus shrub expansion can increase the carbon storage in the vegetation. Moreover, through its lower albedo (Sturm et al. 2005a, Juszak et al. 2016), winter warming and summer shading effects on soils (Sturm et al. 2005b, Blok et al. 2010), increased shrub cover can influence the surface energy exchange between the atmosphere, vegetation and soil, which will further change permafrost conditions.

One of the important processes in carbon cycling is the litter decomposition which results in carbon emission into the atmosphere. In tundra ecosystems the decomposition of root litter is particularly important, which, however, is understudied. On the one hand, higher temperatures can accelerate root decomposition (Hobbie 1996). On the other hand, vegetation changes caused by climate warming can also change the quality of root litter and thus have complex influences on decomposition. With shrub expansion, more shrub root litter is anticipated to enter the system and the decomposition processes. However, it is still unclear whether and to what extent root litter of shrubs and graminoids differ in their decomposability, which is essential for our understanding of climate warming effects on carbon dynamics of tundra ecosystems.

1.4 Research aims

With the research described in this thesis I aimed to improve our understanding of the effects of climate warming on root biomass and its vertical distribution in tundra vegetation, and their potential effects on tundra vegetation change and carbon cycling in the scenario of climate warming. In this thesis I focus on two species that are dominant at the site and many other tundra sites: *Eriophorum vaginatum* L and *Betula nana* L (Fig. 1.2).

Fig. 1.2 Leaves and roots of *Eriophorum vaginatum* (a, b) and *Betula nana* (c, d)

Also known as cotton grass, *E. vaginatum* is a rhizomatous perennial sedge which has leaves with two years life span and annual roots that grow deep in the soil (Wein 1973). *B. nana* is a deciduous dwarf shrub which has annual leaves and grows roots shallower in the soil and can be colonized by ectomycorrhizal fungi (De Groot et al. 1997).

I try to answer the following questions in this thesis:

1) Does the belowground biomass of tundra vegetation increase with temperature, as the aboveground biomass does, and is the relationship affected by shrub abundance?

2) Do the fine root biomass and its temporal and spatial rooting patterns differ between shrub- and graminoid-dominated tundra vegetation types, as a result of different rooting patterns of graminoids and shrubs?

3) Can the different rooting patterns of different plant functional groups affect their competitive relationships when climate warming increases thawing depth and nutrient availability?

4) Does the root decomposition differ between graminoids and shrubs? Will vegetation change affect decomposition in tundra ecosystems?

1.5 Outline of the thesis

The aims are accomplished through synthesis of results from literature (chapter 2) as well as field investigation and experiments (chapter 3 – 5). The research site of the field investigation and experiments is Chokurdakh Scientific Tundra Station which is situated in the Kytalyk Nature Reserve, Sakha Republic, Russia (Fig. 1.3).

In chapter 2 the relationships between temperature and different plant biomass pools, particularly belowground pools and biomass allocation between above and belowground, are explored through synthesizing published data on the belowground biomass of tundra vegetation across the tundra biome spanning a mean annual temperature gradient from –20 to 0 °C. With this space-for-time approach the effects of future climate warming effects on tundra belowground can be extrapolated. Also the effects of vegetation composition on these temperature relationships are examined in this chapter.

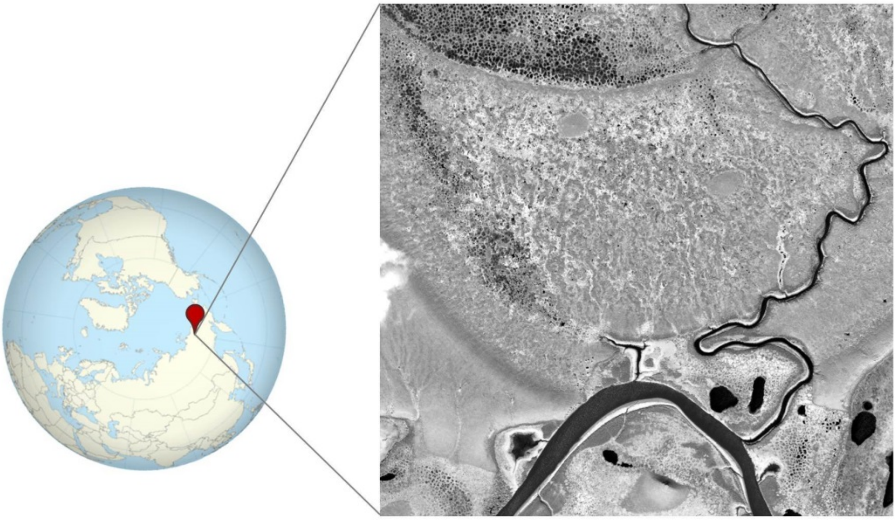

Fig. 1.3 Location and satellite image of the Chokurdakh Scientific Tundra Station in northeastern Siberia. The study area is the former lake bed of a drained thermokarst lake, which has a shallow active layer underlain by continuous permafrost. The vegetation surrounding the Chokurdakh Scientific Tundra Station is classified as G4, tussock-sedge, dwarf-shrub, moss tundra, on the Circumpolar Arctic Vegetation Map (Walker et al. 2005).

Chapter 3 shows the differences in belowground and fine root biomass among graminoid-dominated, shrub-dominated vegetation and mixture vegetation at the research site, and the differences in the seasonal changes and vertical distribution of root biomass of the two dominant plant functional types. The roles of spatio-temporal rooting patterns in relation to shrub expansion are discussed.

In chapter 4 above and belowground responses, particularly the responses of vertical root distribution, of different plant functional types to nutrient changes at different soil depths is further investigated. The role of vertical root distribution in the competition between tundra plants is discussed and the implications for future plant competitive relationships under different scenarios are given.

Chapter 5 describes the differences in the decomposition rates of leaf and root litter from the shrub *B. nana* and the graminoid *E. vaginatum*, and shows the home-field advantage in the decomposition at the research site. The results have implications for the effects of vegetation change on carbon dynamics of tundra ecosystems.

Finally, in chapter 6 I synthesize the results of chapter 2 – 5 and discuss the implications for the relationship between climate warming and tundra vegetation change as well as their effects on the carbon dynamics of tundra ecosystems. Also knowledge gaps that need future researches for a better understanding of climate warming effects on tundra ecosystems are discussed.

2

Belowground plant biomass allocation in tundra ecosystems and its relationship with temperature

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Abstract

Climate warming is known to increase the aboveground productivity of tundra ecosystems. Recently, belowground biomass is receiving more attention, but the effects of climate warming on belowground productivity remain unclear. Enhanced understanding of the belowground component of the tundra is important in the context of climate warming, since most carbon is sequestered belowground in these ecosystems. In this study we synthesized published tundra belowground biomass data from 36 field studies spanning a mean annual temperature (MAT) gradient from −20 to 0 °C across the tundra biome, and determined the relationships between different plant biomass pools and MAT. Our results show that the plant community biomass – temperature relationships are significantly different between above and belowground. Aboveground biomass clearly increased with MAT, whereas total belowground biomass and fine root biomass did not show a significant increase over the broad MAT gradient. Our results suggest that biomass allocation of tundra vegetation shifts towards aboveground in warmer conditions, which could impact on the carbon cycling in tundra ecosystems through altered litter input and distribution in the soil, as well as possible changes in root turnover.

Key words: tundra vegetation, belowground biomass, biomass allocation, climate change, root biomass, root:shoot ratio

2.1 Introduction

The global climate has been warming in the past half century and is predicted to continue warming beyond this century (IPCC 2013). In the Arctic areas where tundra ecosystems occur, climate warming is expected to be more severe than in other areas of the world. An increase in average annual air temperature of 2 to 8 °C at the end of this century has been predicted in different future scenarios (IPCC 2013). Climate warming is associated with large changes in Arctic tundra ecosystems, including permafrost thawing (Romanovsky et al. 2010), accelerated decomposition and carbon (C) release (Schuur et al. 2009, Craine et al. 2010), expansion of deciduous shrubs (Tape et al. 2006, Frost and Epstein 2014) and increased aboveground productivity. A number of studies using either remote sensing or field observations in tundra revealed that aboveground primary productivity had increased with climate warming in tundra (Verbyla 2008, Hudson and Henry 2009, Hill and Henry 2011, Epstein et al. 2012).

The relationships between climate warming and aboveground productivity in tundra are reasonably well established, but we have limited understanding of belowground responses of tundra vegetation to climate change (Iversen et al. 2015). In tundra vegetation, belowground biomass is much larger than aboveground biomass (Shaver and Chapin 1991, Mokany et al. 2006). On average about 70% of the vascular plant biomass in tundra ecosystems is belowground (Poorter et al. 2012), thus a small fraction of change in plant belowground biomass can have large effects on ecosystem carbon stock. Since warmer temperatures will affect water and nutrient availability (Hobbie and Chapin 1998, Shaver et al. 1998, Hodkinson et al. 1999), it is also important to focus on fine root biomass, being the component of belowground plant biomass active in water and nutrient uptake – at least compared to the belowground stems and rhizomes.

Ten available warming experiments in tundra ecosystems examining belowground plant responses yielded contrasting results. Two studies showed significant positive effects of manipulated warming on total belowground plant biomass (Zamin et al. 2014) or rhizome biomass (Sistla et al. 2013), and one study showed positive effects of warming on root production (Sullivan et al. 2008). The other seven studies did not show significant warming effects on total belowground or fine root biomass. Out of these seven studies, two studies even reported a trend of decrease in belowground (Björk et al. 2007) or rhizome biomass (Gough and Hobbie 2003) in response to warming.

Both theoretical and empirical researches suggest that with temperature rise, relative biomass allocation to belowground plant parts may decrease (Bloom et al. 1985, Mokany et al. 2006, Reich et al. 2014). In line with this prediction, three studies indeed showed a decrease in the belowground/aboveground ratio with experimental warming in tundra (Hollister and Flaherty 2010, DeMarco et al. 2014, Zamin et al. 2014), but one study showed the opposite (Hobbie and Chapin 1998). Currently there is no clear pattern of how warming effects influence biomass allocation patterns of tundra vegetation. Understanding plant biomass allocation in response to climate warming is crucial in order to be able to predict ecosystem C storage and flux (Ise et al. 2010). Changes in plant biomass allocation due to climate change can impact the carbon storage in tundra ecosystems, as altered input of root material into the tundra soil may alter the large soil organic carbon pools (Hobbie 1996, Zimov et al. 2006, De Deyn et al. 2008).

Different plant functional types (i.e. shrubs and graminoids) differ in traits regarding productivity, biomass allocation and root distribution as well as in their plasticity in response to warming (Bret-Harte et al. 2001, Van Wijk et al. 2003, Björk et al. 2007, Sullivan et al. 2008). A meta-analysis study showed that aboveground responses of graminoids and shrubs to warming are different and depend on ambient temperature (Elmendorf et al. 2012): positive effects of warming on shrub growth increased with ambient temperature and, while positive effects of warming on graminoid growth decreased with ambient temperature. This study suggested that it is necessary to take vegetation composition and ambient temperature into account when studying warming effects on tundra vegetation, as many studies have reported shrub expansion at the expense of the graminoids (Tape et al. 2006, Myers-Smith et al. 2011a, Myers-Smith et al. 2011b, Frost and Epstein 2014).

Here, we aimed to elucidate the relationships of aboveground and belowground biomass with ambient temperature, using data from 36 field studies over the temperature gradient across the tundra biome. Specifically, our hypotheses were: 1) above and belowground biomass respond differently to increasing temperatures, and 2) belowground biomass allocation decreases with temperature.

2.2 Methods

2.2.1 Data collection

2.2.1.1 Community biomass

We searched for published journal articles and book chapters with belowground plant biomass data obtained from both experimental and observational studies in both Arctic and alpine tundra. In total104 cases from 46 studies at 28 research sites were found (Tables A2.1–A2.3), with each case representing a replicated sampling of a plant community type in a study. Among these studies 29 were from field observations from undisturbed sites and 17 from field experiments with warming or fertilization treatments. It is important to note that from the field experiments, only the control plots were included in the analyses. Studies were included if they met the following criteria to reduce the variation introduced by varying sampling methods:

1) Samples included both rhizomes (belowground stems) and fine roots.

2) Samples excluded dead roots or at least were within the normal biomass range, as in some studies belowground biomass was extremely high because of the inclusion of dead roots. It should be noted that it is difficult to distinguish live and dead roots, particularly for shrubs, which has probably increased the variation in belowground biomass data.

3) The community aboveground biomass was at least 20 g m^{-2}. This was done to exclude extreme conditions, e.g. polar deserts with sparse vegetation.

4) The sampling depth was at least 10 cm for shrub-dominated vegetation and at least 20 cm for vegetation in which graminoids were abundant. We differentiated because in tundra, shrubs generally have a shallower root distribution than graminoids .

After evaluation based on these criteria, 81 cases from 36 studies at 21 sites remained in our dataset (Fig. 2.1, Tables A2.1–A2.3). From these papers we collected data for aboveground biomass, total root biomass (belowground stem + rhizome + root) and/or fine root biomass (if available). From these data belowground/aboveground ratio and fine root/aboveground ratio were calculated by dividing the belowground biomass and fine root biomass by the aboveground biomass. We further calculated relative shrub abundance for each case, which is the proportion of shrub biomass in the aboveground biomass, if the aboveground biomass of different plant functional groups was distinguished.

2.2.1.2 Climate data

Mean annual air temperature (MAT) as well as summer temperature (ST, average temperature of June, July and August) from or near the research sites were obtained using the ‘Climate Explorer’ of the Royal Netherlands Meteorological Institute (KNMI), which is based on the Global Historical Climatology Network (GHCN Monthly) database. For some sites the climate data were obtained from another dataset: the Toolik Field Station Environmental Data Center was used for the Toolik site, the Zackenberg GIS Data for the Zackenberg site, and the National Water & Climate Center of the United States Department of Agriculture for the Eagle Summit site. In the analysis we used MAT averaged over the 20 years preceding the year in which the sampling of a specific study was carried out.

Fig. 2.1 Locations of the 21 research sites in the dataset

Initially, we also planned to include mean annual precipitation (MAP) data, as precipitation may also affect plant productivity (Blok et al. 2011, Keuper et al. 2012a). However, MAP was not homogeneously distributed in the dataset. Alpine tundra sites had at least 400 – 500 mm higher MAP than other sites, which made the model highly unbalanced, and the outcome greatly affected by the cases with high precipitation. These problems did not occur with MAT. In addition, MAP and MAT were clearly correlated (R^2 = 0.57, $P < 0.001$), making it difficult to disentangle the effects of MAP and MAT. Therefore, we decided to omit MAP from the analyses and focus on MAT only.

2.2.2 Data analysis

We used linear mixed models to explore the relationship between site temperature (MAT) and aboveground biomass, belowground biomass, belowground/aboveground ratio, fine root biomass, and fine root/aboveground ratio. To take into account that our dataset contains sites with multiple measurements, which were made in different years or at different locations within the site, we included site, study and case as random factors in a nested structure. To compare the aboveground and belowground responses, we ran two models. One included total aboveground and belowground biomass, and the other total aboveground biomass and fine root biomass. In these models, MAT was included as a covariate, and vegetation part (aboveground or belowground) as a fixed factor. The interaction between MAT and vegetation part was also included. For below/above and fine root/aboveground ratio, the same model as above, but without vegetation part, was used. Data were ln-transformed to achieve normal distribution and homoscedasticity of errors. To check if summer temperature had the same relationships with vegetation biomass and below/above ratio, we ran the same models for summer temperature as well.

To investigate the potential effect of shifts in vegetation composition with temperature on the temperature-biomass relationships, we included the shrub abundance as a covariate in each of the models described above. We first checked if shrub proportion was dependent on MAT, but this was not the case ($F_{1,9.7} = 0.6$, $P = 0.459$). Unfortunately, data of the relative abundance of the different plant functional types was not available for each study. Consequently, this analysis was limited to 35 cases from 18 studies at 12 sites.

Analyses were performed with R (version 3.1.3) in RStudio (version 0.98.1091). Linear mixed model analyses were made using package lme4 version 1.1-7 (Kuznetsova et al. 2014); *P* values were obtained through package lmerTest version 2.0-20 (Bartoń 2014); R^2 values were calculated using package MuMIn version 1.10.5 as described by Nakagawa and Schielzeth (2013).

2.3 Results

Total belowground plant biomass was significantly higher than aboveground biomass (853 ± 93 vs. 259 ± 51 g m^{-2}), resulting in an average belowground/aboveground biomass ratio of 3.7 ± 0.9. Biomass of tundra vegetation increased with MAT, but this MAT effect significantly differed between aboveground and belowground biomass (Table 2.1). Aboveground biomass clearly increased with MAT (Fig. 2.2a; $F_{1,12.8} = 13.2$, $P = 0.003$), but belowground biomass only tended to increase (Fig. 2.2b; $F_{1,8.3} = 4.2$, $P = 0.072$) and the increases were smaller than that in aboveground biomass.

Similar patterns were found when analyzing the subset for fine root biomass. Aboveground biomass and fine root biomass did not differ significantly, but their relationships with MAT did (Table 2.1). Aboveground biomass again increased with MAT ($F_{1,7.2} = 15.7$, $P = 0.005$), whereas fine root biomass did not increase with MAT (Fig. 2.2c; $F_{1,8.2} = 0.26$, $P = 0.625$). Aboveground and belowground biomass had very similar relationships with summer temperature to that they had with MAT (Table A2.4): aboveground biomass increased significantly with ST ($F_{1,31.3} = 22.2$, $P < 0.001$), but belowground biomass did not show a significant relationship ($F_{1,28.6} = 2.1$, $P = 0.159$).

Table 2.1 Summary of analyses of MAT effects on community biomass and differences between vegetation or tissue part (aboveground/belowground or aboveground/fine root), and MAT effects on belowground/aboveground ratio and fine root/aboveground ratio, using linear mixed models. Biomass data and ratios were ln-transformed. R^2_m (Marginal R^2) describes the proportion of variance explained by the fixed factors alone. R^2_c (conditional R^2) describes the proportion of variance explained by both the fixed and random factors.

Total community biomass (data from 34 studies)

Variable	Fixed factor	Sum of squares	df	*F* value	*P* value	R^2
Community biomass	Vegetation part	13.7	1	37.6	< 0.001 *	$R^2_m = 0.52$ $R^2_c = 0.71$
	MAT	4.2	1	11.5	0.007 *	
	Vegetation part × MAT	3.0	1	8.3	0.005 *	
Belowground/ aboveground ratio	MAT	2.4	1	3.9	0.073	$R^2_m = 0.08$ $R^2_c = 0.24$

Aboveground and fine root biomass (data from 18 studies)

Variable	Fixed factor	Sum of squares	df	*F* value	*P* value	R^2
Aboveground and fine root biomass	Vegetation part	0.4	1	1.0	0.319	$R^2_m = 0.47$ $R^2_c = 0.55$
	MAT	4.0	1	9.4	0.006 *	
	Vegetation part × MAT	11.5	1	26.9	< 0.001 *	
Fine root/ aboveground ratio	MAT	4.9	1	8.6	0.029 *	$R^2_m = 0.43$ $R^2_c = 0.70$

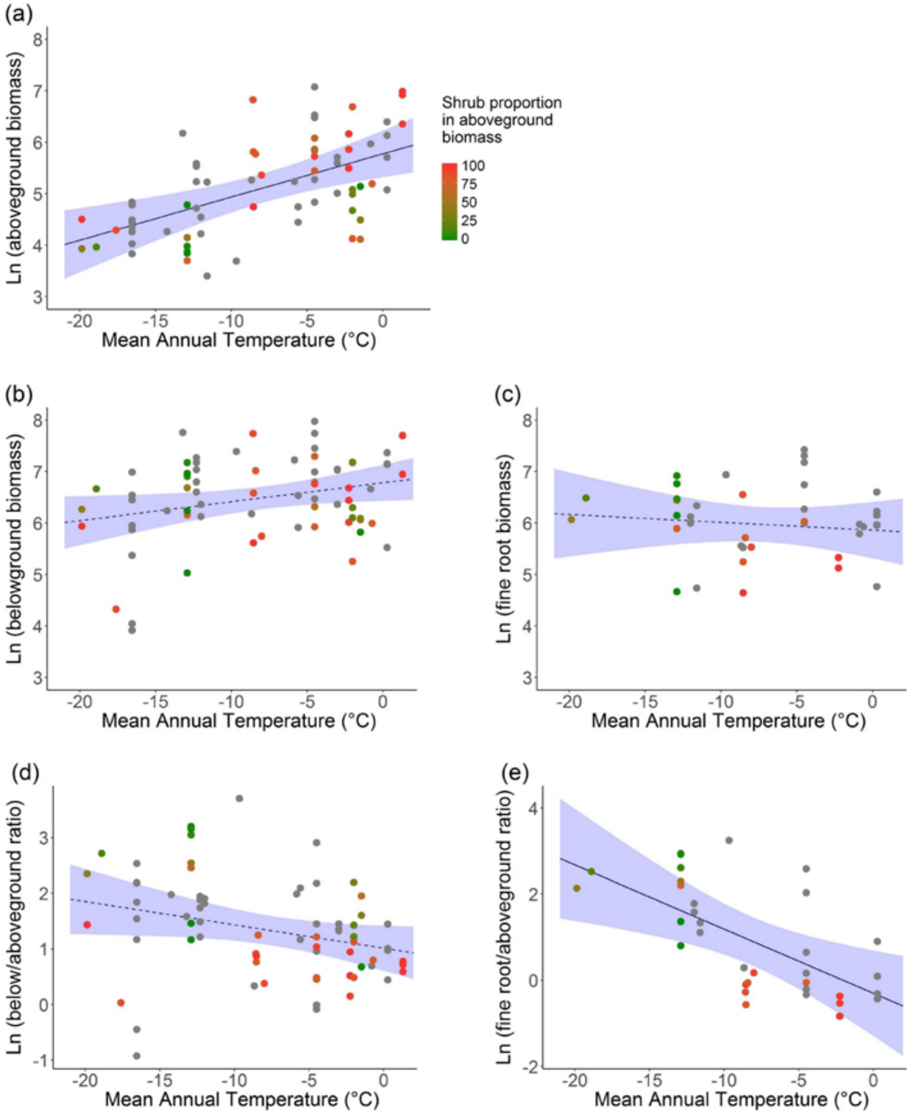

Fig. 2.2 Relationships between mean annual temperature and (a) aboveground biomass (73 cases, slope 0.084 ± 0.023, intercept 5.78 ± 0.23), (b) belowground biomass (71 cases, slope 0.037 ± 0.018, intercept 6.79 ± 0.18), (c) belowground/aboveground ratio (72 cases, slope −0.042 ± 0.021, intercept 1.01 ± 0.21). (d) fine root biomass (41 cases, slope −0.015 ± 0.03, intercept 5.86 ± 0.28), (e) fine root/aboveground ratio (34 cases, slope −0.15 ± 0.05, intercept −0.30 ± 0.51). Biomass data and ratios were ln-transformed. Solid lines represent significant relationships (*P* < 0.05), dashed lines represent insignificant relationships. The blue band represents 95% confidence intervals. Gray dots represent cases without information for calculating shrub fraction.

On average, about 75% of total biomass was belowground and 45% was fine root (belowground fraction 0.76 ± 0.02, fine root fraction 0.47 ± 0.08). The belowground/aboveground ratio tended to decrease with MAT (Fig. 2.2d, Table 2.1), and decreased significantly with ST (Table A2.4). The fine root/aboveground ratio decreased significantly with MAT and ST (Fig. 2.2e, Table 2.1).

Including the relative abundance of shrubs as a covariate did not change the relationships between biomass and MAT (Table A2.5). Despite the smaller dataset, the interaction between MAT and vegetation part remained significant ($F_{1,31} = 6.8$, $P = 0.014$). Aboveground biomass still increased with MAT ($F_{1,16.9} = 8.02$, $P = 0.02$), while belowground biomass did not ($F_{1,31} = 5.39$, $P = 0.26$). Consequently, the negative relationship between belowground/aboveground ratio and MAT was significant (Table A2.5). Similar results were found for fine root biomass and fine root/aboveground ratio (Table A2.5).

2.4 Discussion

Our results show that belowground parts account for three quarters of total vascular plant biomass in the tundra ecosystems, which highlights the importance of understanding belowground responses of tundra vegetation to climate warming. Our analysis suggests that the biomass – temperature relationship of tundra vegetation differs between the aboveground and belowground parts, which may lead to reduced allocation belowground with climate warming. Aboveground biomass of tundra ecosystems increased significantly with local mean annual temperature, which is consistent with other studies (Hudson and Henry 2009, Hill and Henry 2011, Epstein et al. 2012). The average increase was approximately 20 $g \cdot m^{-2}$ per degree Celsius. In contrast, belowground biomass did not significantly increase over a MAT gradient of more than 20 °C. This difference in the temperature relationships between aboveground and belowground biomass appeared quite robust, as it remained significant in the subset of cases for which shrub abundance was known (~50% of the data). Variation in root biomass is considered to be relatively large due to methodological issues such as distinguishing live from dead roots. In our dataset, different criteria were used to define fine roots: a diameter smaller than 0.25 mm, 1 mm, or 2 mm, respectively in different studies (e.g., Miller et al. 1982, Sloan et al. 2013, DeMarco et al. 2014), or not defined (e.g., Hobbie and Chapin 1998, Hill and Henry 2011). Nevertheless, the results for this subset of the data were very similar (Fig. 2.2d–e). To us, this suggests that methodological issues are not likely to explain the lack of a response of belowground biomass to temperature. Rather, our results suggest increased biomass allocation to aboveground parts.

2.4.1 Possible environmental influences

The different biomass – temperature relationships for aboveground and belowground of tundra vegetation may be explained by changes in different environmental factors. First, an initial increase in productivity in response to warming may have increased aboveground competition for light, thereby increasing allocation to aboveground plants parts (Brouwer 1962a, b, Niklas 1994). Second, plant biomass allocation also depends on nutrient availability in the soil. Plant productivity in tundra is nutrient-limited (Chapin 1987, Chapin et al. 1995, Gough et al. 2012, DeMarco et al. 2014). This would limit the allocation to aboveground plant parts, and lead to increased allocation to fine root biomass to acquire more nutrients (Brouwer 1962a, b). Our result of a reduced proportion of belowground biomass with increasing temperature suggests that either, nutrient availability is not strongly limiting plant growth, or that nutrient availability increased with increasing temperatures. Indeed, it has been suggested that higher air temperatures lead to higher soil temperatures (Marion et al. 1997, Schmidt et al. 1999), enhancing organic matter decomposition and nutrient mineralization (Nadelhoffer et al. 1991, Hobbie 1996, Schmidt et al. 1999). However, soil temperature can also be influenced by the insulation effect of plant canopies and soil organic layer (Walker et al. 2003b, Buttler et al. 2015, Myers-Smith et al. 2015), which may reduce the root responses to increased air temperature. In our dataset only seven studies measured the soil temperatures in the investigated plots and they differed in the duration and depth of the measurement. Therefore we cannot confirm whether soil temperature increased with MAT in our dataset.

A third factor that may affect plant productivity is water availability. We could not reliably test for effects of mean annual precipitation, but the actual soil moisture content, which also depends on micro-topography, is probably more relevant. Soil moisture is known to influence tundra productivity and can also affect the responses of tundra plants to warming. Several studies have shown that aboveground biomass is affected by precipitation or soil moisture (Fisk et al. 1998, Blok et al. 2011, Keuper et al. 2012a, Myers-Smith et al. 2015), but few studies have investigated moisture effects on belowground biomass. Unfortunately, the number of studies that measured soil moisture content in our dataset was too low to take soil moisture into account in our analyses.

2.4.2 The role of vegetation composition

Shrubs are very important in tundra ecosystems as they can influence permafrost thaw (Blok et al. 2010, Nauta et al. 2015), carbon and nutrient cycling (Myers-Smith et al. 2011b, Cahoon et al. 2012), and they are also important food resources for some herbivores (Chapin et al. 1986, Olofsson et al. 2009). Deciduous shrubs have been found to expand in tundra areas (Tape et al. 2006, Callaghan et al. 2011, Myers-Smith et al. 2011b, Frost and Epstein 2014) and their expansion may be greater in relatively warm and moist areas (Elmendorf et al. 2012). This can affect responses of tundra vegetation to climate warming as shrubs differ in phenology, tissue structure and biomass allocation patterns from other growth forms such as sedges and grasses (Chapin et al. 1996, Iversen et al. 2015). However, in our dataset shrub abundance did not have a significant effect on the relationship between MAT and biomass or allocation. Still, we cannot rule out that belowground plant responses to MAT were obscured by shifts in abundance of co-occurring plant species or functional types. For example, in a warming experiment, belowground biomass of *Carex bigelowii* and *Betula nana* increased by 135% and 53% respectively, but belowground biomass of *Eriophorum vaginatum* decreased by 74%, resulting in a minor change in total belowground biomass at the community level (Hobbie and Chapin 1998). However, species-specific responses to warming in terms of belowground biomass are poorly known. Most of the available information comes from individuals grown in pots and from the graminoid *E. vaginatum* (e.g., Kummerow et al. 1980, Ellis and Kummerow 1982, Bassirirad et al. 1996), which may be difficult to extrapolate to field conditions. In addition, belowground responses to climate warming can also differ among different community types. In the manipulated warming experiments, plant communities in a moist acidic tussock tundra and in an erect dwarf shrub tundra increased their belowground biomass in response to warming (Sistla et al. 2013, Zamin et al. 2014), while other communities did not show significant responses in belowground biomass (Table A2.1). In an experiment which was at a site with a mosaic microtopography of hummocks and hollows, root production of the plant community in the hummocks did not change in response, while that in the hollows increased significantly to the manipulated warming (Sullivan et al. 2008). Distinguishing the responses to warming for different plant species and/or functional types in different plant communities, both aboveground and belowground, will be crucial to fully understand the consequences of changes in vegetation composition in future global warming scenarios.

2.4.3 Implications for C cycling in tundra

Increased aboveground biomass allocation is often accompanied by an increase in the biomass fraction of leaves (Mokany et al. 2006, Reich et al. 2014), thereby increasing leaf litter input to the soil, especially for graminoids which lack woody stems for C storage. In general, leaf litter is decomposed faster than root litter (Hobbie 1996, Thormann et al. 2001). In addition, leaf litter is mostly decomposed at the soil surface, where the summer temperature is much higher than deeper in the tundra soil. As a consequence, leaf litter may not contribute that much to long-term carbon sequestration in the tundra soil, while root litter that is deposited deeper in the soil close to the permafrost may form a substantial part of the soil organic matter pool (Zimov et al. 2006). Greater allocation to leaves than to roots may thus result in a lower C storage in tundra ecosystems than one might expect on the basis of unchanged allocation pattern.

In our study, we focused on standing belowground or root biomass. This is a pool, constituting a balance between root production and root losses due to mortality (Gill and Jackson 2000, Sullivan et al. 2007). A few studies have investigated warming effects on root production in tundra and showed that, at least for graminoids, root production increased in warmer conditions (Chapin 1974, Kummerow et al. 1980, Sullivan and Welker 2005, Sullivan et al. 2008, Xue et al. 2015). If root production increases with temperature while root biomass does not, as we found in this study, this implies that root turnover in tundra also increases with climate warming. Therefore, C cycling in tundra ecosystems might be accelerated by climate warming, especially in areas which are dominated by graminoids. However, studies of warming effects on tundra root production and mortality are still scarce, especially for shrubs and shrub dominated vegetation. To fully understand the relationships between tundra belowground biomass and temperature, future studies of root production, mortality, and assimilated C allocation of different plant functional types in response to climate warming are clearly needed.

2.5 Conclusions

Our meta-analysis of 36 field studies spanning a MAT gradient from −20 to 0 °C across the tundra biome shows that with increasing temperatures, total belowground biomass and fine root biomass does not increase significantly, while aboveground biomass clearly increases. Together, this leads to a shift in biomass allocation to aboveground biomass with climate warming, which may influence carbon cycling in tundra ecosystems. Future research should focus on the effects of temperature on root production and root losses, which ultimately determine root biomass. To incorporate shifts in vegetation composition that are known to occur with increasing temperatures, detailed knowledge of the responses of different plant functional types is crucial.

2.6 Acknowledgements

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2.7 Appendices

Appendix 2.1 List of papers containing data of belowground biomass and/or root production in tundra

Aleksandrova. 1969. Aerial and underground mass of plants in the polar desert on Alexandra Island (Franz Josef Land) (in Russian). Problemy Botaniki 11.

Bardgett RD, van der Wal R, Jónsdóttir IS, Quirk H, Dutton S. 2007. Temporal variability in plant and soil nitrogen pools in a high-Arctic ecosystem. Soil Biology and Biochemistry 39: 2129-2137.

Björk RG, Majdi H, Klemedtsson L, Lewis-Jonsson L, Molau U. 2007. Long-term warming effects on root morphology, root mass distribution, and microbial activity in two dry tundra plant communities in northern Sweden. New Phytologist 176: 862-873.

Bliss L. 1966. Plant productivity in alpine microenvironments on Mt. Washington, New Hampshire. Ecological Monographs 36: 125-155.

Bliss LC. 1975. Devon Island, Canada. Rosswall T, Heal OW editors. Structure and Function of Tundra Ecosystems. Stockholm: Swedish Natural Science Research Council, p17-60.

Bliss LC, Svoboda J. 1984. Plant communities and plant production in the western Queen Elizabeth Islands. Ecography 7: 325-344.

Campioli M, Michelsen A, Demey A, Vermeulen A, Samson R, Lemeur R. 2009. Net primary production and carbon stocks for subarctic mesic–dry tundras with contrasting microtopography, altitude, and dominant species. Ecosystems 12: 760-776.

Christensen TR, Michelsen A, Jonasson S, Schmidt IK. 1997. Carbon dioxide and methane exchange of a subarctic heath in response to climate change related environmental manipulations. Oikos: 34-44.

DeMarco J, Mack MC, Bret-Harte MS, Burton M, Shaver GR. 2014. Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. Ecosphere 5: art72.

Dennis JG. 1977. Distribution patterns of belowground standing crop in arctic tundra at Barrow, Alaska. Arctic and Alpine Research: 113-127.

Dennis JG, Johnson PL. 1970. Shoot and rhizome-root standing crops of tundra vegetation at Barrow, Alaska. Arctic and Alpine Research: 253-266.

Fisk MC, Schmidt SK, Seastedt TR. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. Ecology 79: 2253-2266.

Gough L, Hobbie SE. 2003. Responses of moist non-acidic arctic tundra to altered environment: productivity, biomass, and species richness. Oikos 103: 204-216.

Gough L, Moore JC, Shaver GR, Simpson RT, Johnson DR. 2012. Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. Ecology 93: 1683-1694.

Gross MF, Hardisky MA, Doolittle JA, Klemas V. 1990. Relationships among depth to frozen soil, soil wetness, and vegetation type and biomass in tundra near Bethel, Alaska, USA. Arctic and Alpine Research: 275-282.

Henry GHR, Svoboda J, Freedman B. 1990. Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. Canadian Journal of Botany 68: 2660-2667.

Hill GB, Henry GHR. 2011. Responses of High Arctic wet sedge tundra to climate warming since 1980. Global Change Biology 17: 276-287.

Hobbie SE, Chapin FS, III. 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO2 flux to experimental warming. Ecology 79: 1526-1544.

Hollister RD, Flaherty KJ. 2010. Above- and below-ground plant biomass response to experimental warming in northern Alaska. Applied Vegetation Science 13: 378-387.

Joabsson A, Christensen TR. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Global Change Biology 7: 919-932.

Jonasson S. 1982. Organic matter and phytomass on three north Swedish tundra sites, and some connections with adjacent tundra areas. Ecography 5: 367-375.

Jones H, Gore A. 1981. A simulation approach to primary production. Tundra ecosystems: a comparative analysis. Cambridge University Press, Cambridge: 239-256.

Larcher W, Cernusca A, Schmidt L, Grabherr G, Nötzel E, Smeets N. 1975. Mt. Patscherkofel, Austria. Rosswall T, Heal OW editors. Structure and Function of Tundra Ecosystems. Stockholm: Swedish Natural Science Research Council, p125-139.

Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin FS, III. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature 431: 440-443.

Miller PC, Mangan R, Kummerow J. 1982. Vertical distribution of organic matter in eight vegetation types near Eagle Summit, Alaska. Ecography 5: 117-124.

Muc M. 1977. Ecology and primary production of sedge-moss meadow communities, Truelove Lowland. Bliss LC editor. Truelove Lowland, Devon Island, Canada. Edmonton Alberta: The University of Alberta Press.

Nadelhoffer KJ, Johnson L, Laundre J, Giblin AE, Shaver GR. 2002. Fine root production and nutrient content in wet and moist arctic tundras as influenced by chronic fertilization. Plant and Soil 242: 107-113.

Nams MLN, Freedman B. 1987. Phenology and resource allocation in a high arctic evergreen dwarf shrub, Cassiope tetragona. Ecography 10: 128-136.

Norin BN, Ignatenko IV. 1975. Ary-Mas, USSr. Rosswall T, Heal OW editors. Structure and Function of Tundra Ecosystems. Stockholm: Swedish Natural Science Research Council, p183-191.

Olsrud M, Christensen TR. 2004. Carbon cycling in subarctic tundra; seasonal variation in ecosystem partitioning based on in situ 14C pulse-labelling. Soil

Biology and Biochemistry 36: 245-253.

Østbye E, Berg A, Blehr O, Espeland M, Gaare E, hagen A, hesjedal D, Haagvar S, Kjelvik S, Lien L, Mysterud I, Sandhaug A, Skar HJ, Skartveit A, Skre O, Skogland T, Solhøy T, Stenseth NC, Wielgolaski FE. 1975. Hardangervidda, Norway. Rosswall T, Heal OW editors. Structure and Function of Tundra Ecosystems. Stockholm: Swedish Natural Science Research Council, p193-223.

Rosswall T, Heal OW. 1975. Structure and function of tundra ecosystems. Stockholm: Swedish Natural Sience Research Council. 450p.

Shaver GR, Cutler JC. 1979. The Vertical Distribution of Live Vascular Phytomass in Cottongrass Tussock Tundra. Arctic and Alpine Research 11: 335-342.

Sistla SA, Moore JC, Simpson RT, Gough L, Shaver GR, Schimel JP. 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497: 615-618.

Sloan VL, Fletcher BJ, Press MC, Williams M, Phoenix GK. 2013. Leaf and fine root carbon stocks and turnover are coupled across Arctic ecosystems. Global Change Biology 19: 3668-3676.

Stoner WA, Miller P, Miller PC. 1982. Seasonal dynamics and standing crops of biomass and nutrients in a subarctic tundra vegetation. Ecography 5: 172-179.

Sullivan P, Arens ST, Chimner R, Welker J. 2008. Temperature and Microtopography Interact to Control Carbon Cycling in a High Arctic Fen. Ecosystems 11: 61-76.

Sullivan P, Sommerkorn M, Rueth H, Nadelhoffer K, Shaver G, Welker J. 2007. Climate and species affect fine root production with long-term fertilization in acidic tussock tundra near Toolik Lake, Alaska. Oecologia 153: 643-652.

Sullivan PF, Welker JM. 2005. Warming chambers stimulate early season growth of an arctic sedge: results of a minirhizotron field study. Oecologia 142: 616-626.

Svoboda J. 1977. Ecology and primary production of raised beach communities, Truelove Lowland. Bliss LC editor. Truelove Lowland, Devon Island, Canada. Edmonton, Alberta: The University of Alberta Press.

Tikhomirov B, Shamurin V, Aleksandrova V. 1981. Phytomass and primary production of tundra communities, USSR. Tundra ecosystems: a comparative analysis. Cambridge University Press, Cambridge: 227-238.

Van Wijk MT, Williams M, Gough L, Hobbie SE, Shaver GR. 2003. Luxury consumption of soil nutrients: a possible competitive strategy in above-ground and below-ground biomass allocation and root morphology for slow-growing arctic vegetation? Journal of Ecology 91: 664-676.

Webber PJ. 1978. Spatial and temporal variation of the vegetation and its production, Barrow, Alaska. Tieszen LL editor. Vegetation and production ecology of an Alaskan arctic tundra. New York: Springer, p37-112.

Wein RW, Bliss LC. 1974. Primary production in arctic cottongrass tussock tundra communities. Arctic and Alpine Research: 261-274.

Zamin TJ, Bret-Harte MS, Grogan P. 2014. Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low arctic tundra. Journal of Ecology 102: 749-766.

Table A2.1 Warming experiments with measurements of belowground biomass or root production in tundra ecosystems. Data are average values for control or treatment plots. Only values of the control treatment were included in the analysis. MAT, mean annual air temperature; ST, summer temperature; MAP, mean annual precipitation.

Reference	Treatment	Above-ground biomass (g/m^{2})	Shrub fraction of above-ground biomass	Root biomass (g/m^{2})	Rhizome biomass (g/m^{2})	Total below-ground biomass (g/m^{2})	Below /above ratio	Root produc-tion (g/m^{2}yr)	MAT (˚C)	ST (˚C)	MAP (mm)	Site
Björk et al., 2007	Control					290^{a}			0.0	10.4	334	Latnjavagge, Sweden (68°21′N, 18°30′E)
	>10 yrs OTCs					261^{a}						
	Control					536^{a}			0.0	10.4	334	
	>10 yrs OTCs					580^{a}						
Christensen et al., 1997	Control			375^{b}					−0.6	9.7	320	Abisko, Sweden (68'20'N, 20 51'E)
	7 yrs OTCs			450^{b}								
DeMarco et al., 2014	Control	920^{b}	0.88	700^{b}	1600^{b}	2300^{b}	2.45		−8.6	9.4	295	Toolik Lake (68°38′ N, 149°38′ W)
	18 yrs greenhouse	1660^{b,}*		950^{b}	1400^{b}	2350^{b}	1.44					
Gough and Hobbie, 2003	Control	190			233				−9.5	10.2	320	Toolik Lake (68˚38'N, 149˚34'W)
	4 yrs greenhouses	189			221							
Hobbie and Chapin, 1998	Control	321	0.81	303	814	1117	3.55		−8.4	9.9	233	Toolik Lake (68˚38'N, 149˚34'W)
	4 summers greenhouses	327	0.84	416	799	1214	3.76					
Hollister and Flaherty, 2010	Control	135	0.62			1089^{c}	8.09		−11.7	3.5	104	Barrow, Alaska (71˚18'N, 156˚40'W)
	3-4 yrs OTCs	173	0.58			1286^{c}	7.33					

Table A2.1 (Continued)

Sistla et al., 2013	Control	370			438				−8.6	9.3	284	Toolik Lake (68˚37'N, 149˚36'W)
	14 yrs greenhouses	721*			712*							
Sullivan and Welk, 2005	Control			746				119	−8.6	9.3	284	Toolik Lake (68˚37'N, 149˚36'W)
	1 yr OTCs							191				
Sullivan et al., 2008	Control	30		114				23	−11.6	3.5	122	Pituffik, Greenland (76˚33'N, 68˚30' W)
	3 yrs OTCs							100 [b],*				
	Control	186		565				110	−11.6	3.5	122	
	3 yrs OTCs							105[b]				
Zamin et al., 2014	Control	213	0.92	253	59	312	1.44		−8.0	11	250	Daring Lake, Canada (64° 52' N, 111°33' W)
	8 yrs greenhouses	370*	0.96	431	86	517*	1.38					

[a] Dead roots were not distinguished. [b] Values were estimated value from graphics in corresponding article. [c] Sampling depth was 10 cm

* Significantly different from control ($P < 0.05$)

Table A2.2 Fertilization experiments with measurements of belowground biomass or root production in tundra ecosystems. Data are average values for control or treatment plots. Only values of the control treatment were included in the analysis. MAT, mean annual air temperature; ST, summer temperature; MAP, mean annual precipitation.

Reference	Duration	Above-ground biomass (g/m^2)	Shrub fraction of above-ground biomass	Rhizome biomass (g/m^2)	Root biomass (g/m^2)	Total below-ground biomass (g/m^2)	Below /above ratio	Root produc-tion (g/m^{2}yr)	MAT (˚C)	ST (˚C)	MAP (mm)	Site
Christensen et al., 1997	Control				375^a				−0.6			Abisko, Sweden (68°20'N, 20°51'E)
	7 yrs				475^a							
DeMarco et al., 2014	Control	920^a	0.88		700^a	2300^a	2.45		−8.6			Toolik Lake (68°38′ N, 149°38′ W)
	18 yrs	1830^{a,}*			800^a	2600^a	1.44					
Dennis, 1977	Control	68			402	457	6.69		−12.0			Barrow, Alaska (71˚20'N, 156˚39'W)
	4 yrs	102			648*	867*	8.09					
Gough and Hobbie, 2003	Control	190		233					−9.5			Toolik Lake (68˚38'N, 149˚43'W)
	4 yrs	353		234								
Gough et al., 2012	Control	335^a	1		190	720	2.13		−8.5			Toolik Lake (68.2° N, 149.6° W)
	11yrs	645 ^{a,}*	0.71		230	745	1.17					
	Control	115^a	0.82		104	274	2.33		−8.5			
	11 yrs	140^a	0.70		119	214	1.50					
Mack et al., 2004	Control				300^{a,b}							Toolik lake (68˚38'N, 149˚34'W)
	20 yrs				240^{a,b}							

Table A2.2 (Continued)

Nadelhoffer et al., 2002	Control					56	−8.5	Toolik Lake (68˚38'N, 149˚43'W)
	7 yrs					67		
	Control					75	−8.5	
	7 yrs					85		
Sullivan et al., 2007	Control		250			74^{a}	−8.5	Toolik lake (68˚38'N, 149˚34'W)
	7 yrs		375			$45^{a,*}$		
	15 yrs		490*			$12^{a,*}$		
Van Wijk et al., 2003	Control	194	259	483	2.45		−8.7	Toolik Lake (68°38′N, 149°36′W)
	4 yrs	240	552	760	3.17			

[a] Values were estimated from graphics in corresponding article. [b] The unit was g C m^{-2}.

* Significantly different from control ($P < 0.05$)

Table A2.3 Field studies that included belowground biomass or root production measurements in tundra ecosystems. MAT = mean annual air temperature, ST = summer temperature, MAP = mean annual precipitation.

Reference	Above-ground biomass (g/m^2)	Shrub fraction of above-ground biomass	Root biomass (g/m^2)	Total below-ground biomass (g/m^2)	Below /above ratio	Root produc-tion (g/m^2yr)	MAT (˚C)	ST (˚C)	MAP (mm)	Site
Aleksandrova, 1958 from Tikhomirov et al., 1981	71			511	7.33		−14.2	1.6	112	Bolshoy Lyakhovsky Island, Russia (73.4°N, 141.5°E)
Aleksandrova, 1969	6			29	4.88		−14.3	−0.4	265	Alexandra Land Island, Russia (80.63°N 46.58°E)
Bardgett et al., 2007	85			690	8.09		−5.6	4.7	452	Longyearbyen, Svalbard (78°13′N, 15°33′E)
	115			370	3.17		−5.6	4.7	452	
Bliss, 1966				542[a]			−3.4	8.4	1662	Mt. Washington, USA (44°16′N, 71°18′W, elevation 1850m)
Bliss, 1975	126			50	0.39	5	−16.6	2.0	134	Devon Island, Canada (75°33'N, 84°40'W)
	89			57	0.64	3	−16.6	2.0	134	
	46			215	4.56	29	−16.6	2.0	134	
	86			1085	13.29	104	−16.6	2.0	134	
	78			691	9.00	130	−16.6	2.0	134	
	56			353	6.14	59	−16.6	2.0	134	

Table A2.3 (Continued)

Bliss and Svoboda, 1984	73	0.91		76	1.04	13	−17.6	1.2	62	Sverdrup Basin, Canada (75°N, 110°W)
	4	0		17	4.26	4	−19.2	0.5	127	Ellef Ringnes Island, Canada (78°37′N, 101°56′W)
	13	0		88	6.69	13	−19.2	0.5	127	
	4	0		519	99.00	4	−19.2	0.5	127	
	4	0		11	2.70	4	−19.2	0.5	127	
	3	0		8	2.70	2	−19.2	0.5	127	King Christian Island, Canada (77°45′N, 102°00′W)
	5	0		23	4.56	5	−19.2	0.5	127	
	13	0		21	1.63	7	−17.6	1.2	62	Rea Point, Melville Island, Canada (75.36°N, 105.73°W)
Campioli et al., 2009	600[b]		1582	1720[b]	2.85		0.3	10.6	304	Abisko, Sweden (68°21′N, 18°49′E)
	460[b]		1260	1280[b]	2.85		0.3	10.6	304	
	300[b]		1272	1300[b]	4.26		0.3	10.6	304	
	160[b]		250	260[b]	1.63		0.3	10.6	304	
	20[b]		162	170[b]	8.09		0.3	10.6	304	
Dennis, 1977	94		456	579	0.00	176	−12.0	2.5	104	Barrow, Alaska (71˚20'N, 156˚39'W)
Dennis and Johnson, 1970	253[b]			1435	5.67		−12.3	2.5	104	Barrow, Alaska (71˚20'N, 156˚39'W)
	258[b]			1140	4.56		−12.3	2.5	104	
	187[b]			1305	6.69		−12.3	2.5	104	
	112[b]			735	6.69		−12.3	2.5	104	
	266[b]			895	3.35		−12.3	2.5	104	
Fisk et al., 1998	150[b]			580[b]	3.76	198	−3.0	5.6	900	Niwot Ridge, USA (40˚03' N,105˚35' W, elevation 3500m)
	270[b]			1150[b]	4.26	230	−3.0	5.6	900	
	300[b]			1130[b]	3.76	364	−3.0	5.6	900	

Table A2.3 (Continued)

Gross et al., 1990	89	0.34		441	4.88		−1.5	11.6	372	Bethel, Alaska (60°45'N, 161°44'W)
	171	0		337	1.94		−1.5	11.6	372	
	61	0.71		430	7.33		−1.5	11.6	372	
Henry et al., 1990	51	0.40	432	526	10.11	100	−19.9	3.3	64	Alexandra Fiord, Canada (78˚53'N, 75˚55'W)
Hill and Henry 2011	53	0.13	656[b]	784[b]	15.67		−18.9	3.9	78	Alexandra Fiord, Canada (78˚53'N, 75˚55'W)
Jonasson, 1982	243	0.98	168	626	2.33		−2.3	11.4	443	Lake Torneträsk, Sweden (68°30′N, 20°15′E)
	474	0.99	206	798	1.70		−2.3	11.4	443	
	351	0.95	206	409	1.17		−2.3	11.4	443	
Joabsson and Christensen, 2001	40		1030[b]	1620[b]	49.00		−9.7	3.7	224	Zackenberg, Greenland (74˚30'N, 21˚00' W)
Larcher et al., 1975	1013	0.99		2206	2.23		1.3	8.3	951	Mt. Patscherkofel, Austria (47°13'N, 11°20'E, elevation 1980m)
	1084	0.99		2213	2.03		1.3	8.3	951	
	574	0.98		1039	1.78		1.3	8.3	951	
Miller et al., 1982	342		402	892	2.57		−4.5	9.4	1729	Eagle Summit, Alaska (65°26'N, 145°30'W)
	437	0.75	416	1471	3.35		−4.5	9.4	1729	
	651		529	645	1.00		−4.5	9.4	1729	
	1183		848	1087	0.92		−4.5	9.4	1729	
	684		1311	2909	4.26		−4.5	9.4	1729	
	195		1488	1724	9.00		−4.5	9.4	1729	
	126		1677	2302	19.00		−4.5	9.4	1729	
Muc, 1977	71			633	9.00	94[b]	−16.6	2.0	134	Truelove Lowland, Devon Island (75°08'N, 87°51'W)

Table A2.3 (Continued)

Nams and Freedman, 1987	90	0.99		379	4.26		−19.9	3.3	64	Alexandra Fiord, Canada (78˚53'N, 75˚55'W)
Norin and Ignatenko, 1975	480			2340	4.88		−13.2	5.5	243	Ary-Mas, Russia (72.40°N, 101.84°E)
Olsrud and Chistensen, 2004	390			780	2.00		−0.8	11.0	300	Stordalen (Abisko), Sweden (68°21'N, 19°00'E)
Østbye et al., 1975	804	0.87		1305	1.63	290	−2.0	6.1	1006	Hardangervidda, Norway (60°18'N, 7°41'E, elevation 1230m)
	62	0.87		191	3.00	100	−2.0	6.1	1006	
	147	0.28		1316	9.00	410	−2.0	6.1	1006	
	161	0.22		545	3.35	245	−2.0	6.1	1006	
Rosswall et al., 1975	180			400	2.23	24	−0.7	10.7	300[b]	Stordalen (Abisko), Sweden (68°22'N, 19°03'E)
Shamurin, 1970 from Tikhomirov et al., 1981	188			1370	7.33		−5.8	9.7	565	Vorkuta area, Russia (67°30′N, 64°02′E)
Shaver and Cutler, 1979	351	0.62		554	1.56		−4.5	9.4	1729	Eagle Summit, Alaska (65°26'N, 145°30'W)
Sloan et al., 2013			385			55	0.3	10.6	328	Abisko, Sweden (68.35°N, 18.82°E)
			385			44	0.3	10.6	328	
			468			45	0.3	10.6	328	
			393			43	−0.9	11.4	444	Kevo, Finland (69°45′N, 27°01′E)
			326			62	−0.9	11.4	444	
Stoner et al., 1982	231	0.78		374	1.63		−4.5	9.4	1729	Eagle Summit, Alaska (65°26'N, 145°30'W)

Table A2.3 (Continued)

Svoboda, 1977	119			384	3.17	26	−16.6	2.0	134	Truelove Lowland, Devon Island
Webber, 1978	40	0.77	363	471	11.50		−12.9	2.4	131	Barrow, Alaska (71˚20'N, 156˚39'W)
	63	0.49	626	801	13.29		−12.9	2.4	131	
	47	0.05	645	996	19.00		−12.9	2.4	131	
	53	0.02	1008	1305	24.00		−12.9	2.4	131	
	47	0	866	1055	24.00		−12.9	2.4	131	
	119	0	466	512	4.26		−12.9	2.4	131	
	48	0.01	106	153	3.17		−12.9	2.4	131	
	19	0.28	399	571	32.33		−12.9	2.4	131	
Wein and Bliss, 1974	66			2372[a]	32.33		−9.93	11.1	221	Dempster, USA (64°45'N, 138°21'W, elevation 1100m)
	169			6684[a]	49.00		−4.5	14.1	1729	Eagle Summit, Alaska (65°26'N, 145°30'W, elevation 730m)
Wielgolaski and Kjelvik, 1973 from Jones and Gore, 1981	107	0.20		445	4.26		−2.0	6.1	1006	Hardangervidda, Norway

[a] Dead tissues were not distinguished. [b] Values were obtained from graphics in the article.

Table A2.4 Summary of analyses of summer temperature (ST) effects on community biomass and differences between vegetation part (above-/belowground or aboveground/fine root), and ST effects on belowground/aboveground ratio and fine root/aboveground ratio.

Total community biomass (data from 34 studies)						
Variable	Fixed factor	Sum of squares	df	F value	P value	R^2
Community biomass	Vegetation part	36.6	1	109.1	< 0.001 *	$R^2_m = 0.53$ $R^2_c = 0.73$
	ST	4.1	1	12.1	0.001 *	
	Vegetation part × ST	4.8	1	14.4	< 0.001 *	
Belowground/ aboveground ratio	ST	5.8	1	9.5	0.014 *	$R^2_m = 0.16$ $R^2_c = 0.24$

Aboveground and fine root biomass (data from 18 studies)						
Variable	Fixed factor	Sum of squares	df	F value	P value	R^2
Aboveground and fine root biomass	Vegetation part	27.8	1	94.7	< 0.001 *	$R^2_m = 0.55$ $R^2_c = 0.69$
	ST	2.7	1	9.3	0.008 *	
	Vegetation part × ST	16.1	1	54.7	< 0.001 *	
Fine root/ aboveground ratio	ST	21.5	1	36.7	0.004 *	$R^2_m = 0.61$ $R^2_c = 0.64$

Table A2.5 Summary of analyses of vegetation part, MAT and shrub fraction effects on community biomass, and MAT, shrub fraction effects on below/aboveground ratio, fine root biomass and root/above ratio. Biomass data and ratios were ln-transformed.

Total community biomass (data from 20 studies)					
Variable	Source	Sum of squares[a]	df	F value	*P* value
Community biomass	MAT	0.5	1	2.7	0.120
	Shrub abundance	< 0.1	1	0.3	0.619
	Vegetation part	2.5	1	12.4	0.001*
	MAT × shrub abundance	< 0.1	1	< 0.1	0.956
	MAT × vegetation part	1.3	1	6.8	0.014*
	Shrub abundance × vegetation part	0.4	1	1.8	0.185
	Vegetation part × shrub abundance × MAT	0.5	1	2.3	0.138
Belowground/ aboveground ratio	MAT	2.7	1	6.9	0.013*
	Shrub abundance	0.7	1	1.8	0.188
	Shrub abundance × MAT	0.9	1	2.4	0.135
Aboveground and fine root biomass (data from 9 studies)					
Fine root biomass	MAT	0.3	1	0.9	0.389
	Shrub abundance	0.1	1	0.3	0.607
	Vegetation part	8.2	1	29.7	< 0.001*
	MAT × shrub abundance	0.1	1	0.3	0.612
	MAT × Tissue part	10.9	1	39.5	< 0.001*
	Shrub abundance × tissue part	1.5	1	5.4	0.035*
	MAT × shrub abundance × tissue part	0.1	1	0.2	0.669
Fine root/ aboveground ratio	MAT	5.4	1	13.9	0.033*
	Shrub abundance	0.2	1	0.5	0.509
	Shrub abundance × MAT	< 0.1	1	< 0.1	0.860

[a] Type III sum of squares was used in the analysis of total biomass and belowground/aboveground ratio. In the subset of fine root biomass data, shrub abundance and MAT were positively correlated, so we used Type I sum of squares and first considered MAT effect and then shrub abundance effect.

3

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

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Abstract

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. 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. 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. 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

3.1 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 (Schuur et al. 2009, Belshe et al. 2013), and the release of previously frozen soil organic carbon is initiated as permafrost layers thaw (Zimov et al. 2006, Schuur et al. 2009). In addition, increased temperature extends the growing season and improves nutrient availability due to increased permafrost thawing depth (active layer thickness, ALT) (Hinkel and Nelson 2003, Burn and Kokelj 2009) 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 (Verbyla 2008, Hill and Henry 2011, Epstein et al. 2012). 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 (Tape et al. 2006, Wookey et al. 2009, Callaghan et al. 2011, Myers-Smith et al. 2011a, Myers-Smith et al. 2011b). 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, Walker et al. 2006, Elmendorf et al. 2012), indicating that warming alone does not necessarily increase the competitive advantage 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 (Shaver and Chapin 1991, Mack et al. 2004).

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 (Shaver and Billings 1975, Miller et al. 1982, 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 (Hinkel and Nelson 2003, Burn and Kokelj 2009), 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 et al. 2012b, Keuper et al. 2014). 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?

3.2 Materials and methods

3.2.1 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 21946, 27 km away from the study site) is −13.4 ºC (1981 – 2010), with 10.3 ºC 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. 3.1). 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.

3.2.2 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. 3.1). 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 x 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.

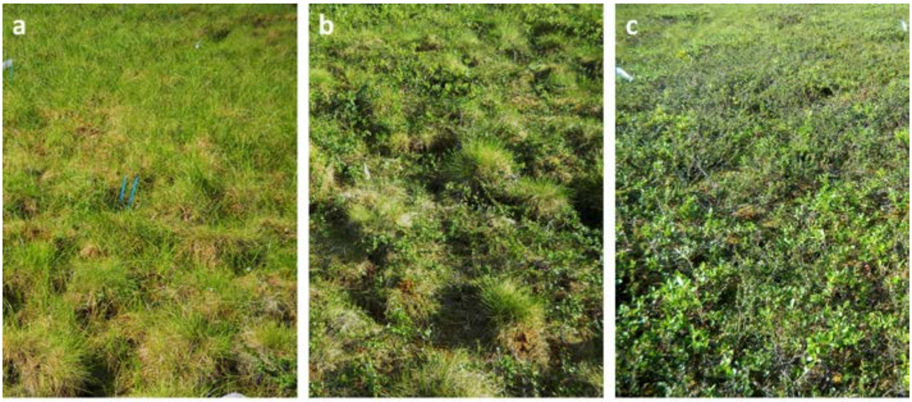


Fig. 3.1 Pictures of the three vegetation types. Graminoid vegetation (a) had a cover of *E. vaginatum* more than 70%; in mixture vegetation (b) the cover of *E. vaginatum* or *B. nana* was between 30 and 70%; shrub vegetation (c) had a cover of *B. nana* more than 70%.

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 ºC for at least 24 hours. After the samples were transported to the Netherlands, they were dried in an oven at the temperature of 65 ºC for 72 hours and weighed.

3.2.3 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^{3-} and K^+ using an auto-analyzer (Skalar, Breda, The Netherlands).

3.2.4 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).

3.3 Results

3.3.1 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 3.1). ALT in the graminoid vegetation was significantly higher than in the mixture and shrub vegetation, irrespective of the time of season (Table 3.1), indicating a larger soil volume available for root development in the graminoid vegetation type. Soil temperature at 10 cm depth increased over the season but did not differ among the three vegetation types (Table 3.1).

Table 3.1 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 * Vegetation * Season × Veg *
	Late	34 ± 1.7^{a}	26 ± 1.1^{b}	23 ± 0.4^{b}	
Organic layer thickness (cm)	Early	18 ± 1.6	18 ± 0.7	19 ± 0.9	Season ^{ns} Vegetation ^{ns} Season × Veg ^{ns}
	Late	21 ± 1.4	20 ± 1.4	17 ± 1.0	
Soil moisture (% volume)	Early	50 ± 3^{a}	46 ± 3^{ab}	37 ± 2^{b}	Season * Vegetation * Season × Veg ^{ns}
	Late	51 ± 5^{a}	39 ± 5^{b}	24 ± 1^{c}	
Soil temperature (˚C)	Early	0.8 ± 0.1^{a}	0.8 ± 0.2^{a}	0.7 ± 0.2^{a}	Season * Vegetation ^{ns} Season × Veg ^{ns}
	Late	2.8 ± 0.1^{a}	2.5 ± 0.3^{a}	2.6 ± 0.2^{a}	
Exchangeable nutrient (μg g^{-1}resin)	$N\text{-}NH_4$	52 ± 6^{a}	26 ± 4^{b}	23 ± 4^{b}	Vegetation *
	$N\text{-}NO_3$	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 *

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 3.1). The organic layer thickness was approximately 20 cm and did not differ among vegetation types (Table 3.1). Most soil exchangeable nutrients (NH_4^+, total inorganic N, PO_4^{3-} 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 3.1).

3.3.2 Community biomass

Community biomass differed significantly among the three vegetation types (Fig. 3.2, Table 3.2), 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. 3.2, Table 3.2).

Biomass was greater belowground than aboveground (Fig. 3.2). Moreover, the distribution of biomass over above and below ground plant parts differed among the vegetation types (significant vegetation type × part in Table 3.2; 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. 3.2). Fine root biomass, as well as leaf biomass, increased over the growing season in graminoid and mixture 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).

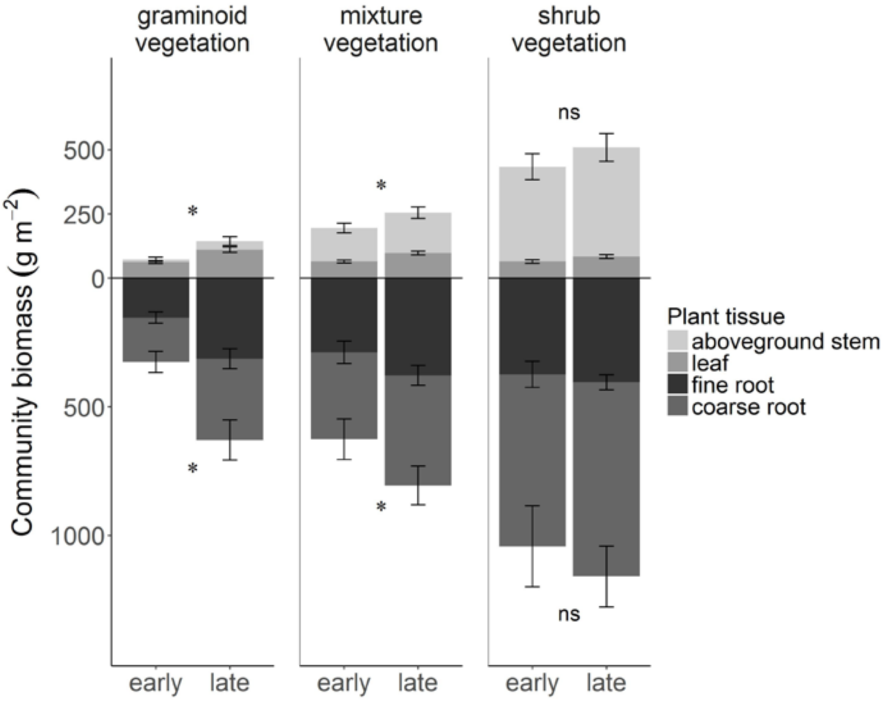


Fig. 3.2 Total community biomass of the three vegetation types, subdivided into leaf, aboveground stem, fine root and coarse root (including rhizome and belowground stem), in early and late growing season. Bars indicate mean ± SE (n = 8 plots) of each tissue type. Asterisks represent significant seasonal changes (P < 0.05). Seasonal change patterns resembled between total aboveground biomass and leaf biomass, total belowground biomass and fine root biomass.

Table 3.2 Analysis of community biomass (above and belowground), and acquisitive biomass (leaf and fine root) of the three vegetation types 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.

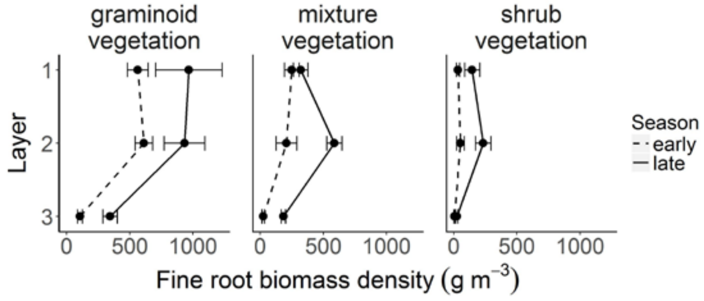
Variable	Source	Sum of squares	df	*F* value	*P* value
Community biomass	Vegetation	9.7	2	66.2	< 0.001*
	Season	3.2	1	43.6	< 0.001*
	Part	31.6	1	429.7	< 0.001*
	Vegetation × season	1.1	2	7.8	0.001*
	Vegetation × part	1.5	2	10.4	< 0.001*
	Season × part	< 0.1	1	< 0.1	0.972
	Vegetation × season × part	< 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

3.3.3 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 A3.1). 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. 3.3, Table 3.3). Meanwhile, seasonal changes of shrub root density in the upper two layers differed among vegetation types (Fig. 3.3, Table 3.3): it increased over season in graminoid vegetation ($F_{1,21} = 5.0$, $P = 0.026$), but there were no significant seasonal 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 A3.2), as it remained at zero or very low values (Fig. 3.3).

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. A3.2).

a) graminoid roots



b) shrub roots

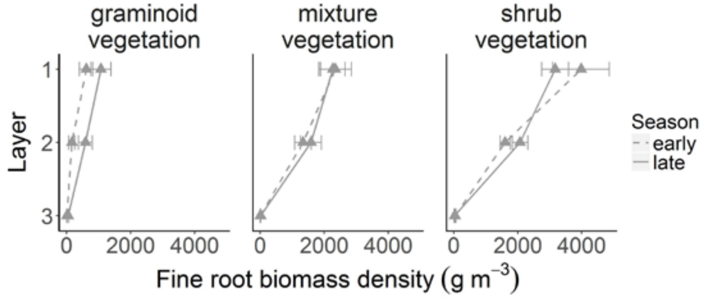


Fig. 3.3 Fine root biomass density in different soil layers of the three vegetation types, shown separately for graminoids (a) and shrubs (b). Layer 1 = 0 – 5 cm; 2 = 5 – 15 cm. 3 = 15 – 30 cm. Note that the scale of the x-axis differs for graminoid and shrub roots. Symbols indicate mean ± SE (n = 8 plots).

Table 3.3 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

The vertical distribution of fine roots also differed between the two PFTs: graminoid root density did not differ between the upper two layers while shrub root density decreased significantly from the 1st to the 2nd layer (Fig. 3.3, Table 3.3). Root density in the 3rd layer was lowest for both PFTs (Fig. 3.3), 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. 3.3, Table A3.2).

3.4 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.

3.4.1 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. A3.1). 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. A3.1). 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.

3.4.2 Vertical rooting patterns

Our findings confirm that dwarf shrubs root shallower than graminoids in tundra ecosystems (Shaver and Billings 1975, Shaver and Cutler 1979, Miller et al. 1982). 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 3.1), there were very few shrub roots in this deeper layer and relative biomass of deep roots did not increase (Fig. 3.3 and A3.2). 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.

3.4.3 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 (Hinkel and Nelson 2003, Burn and Kokelj 2009), which can increase plant available nutrients in the deeper soil (Keuper et al. 2012b). 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, Weih 1998, Sturm et al. 2005b, 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 (Jobbágy and Jackson 2001, Hobbie and Gough 2002), 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.

3.5 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.

3.6 Acknowledgements

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3.7 Appendices

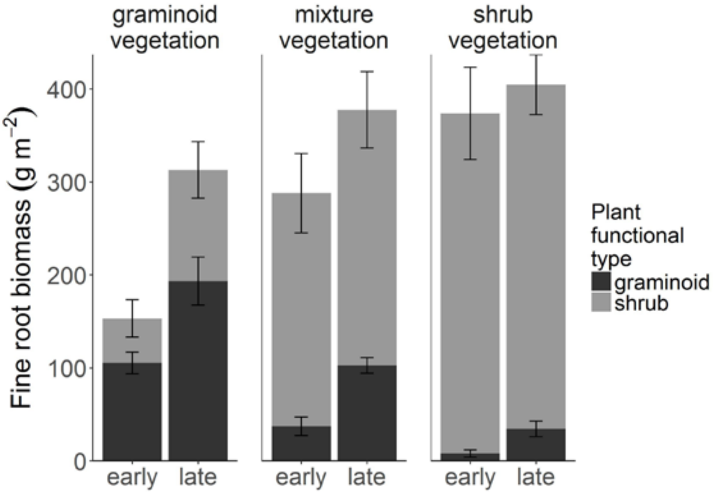

Fig. A3.1 Fine root biomass of graminoids and shrubs in each vegetation type. Error bars indicate ± SE. Graminoid fine root biomass increased over season in all three vegetation types, but shrub fine roots did not change significantly over season

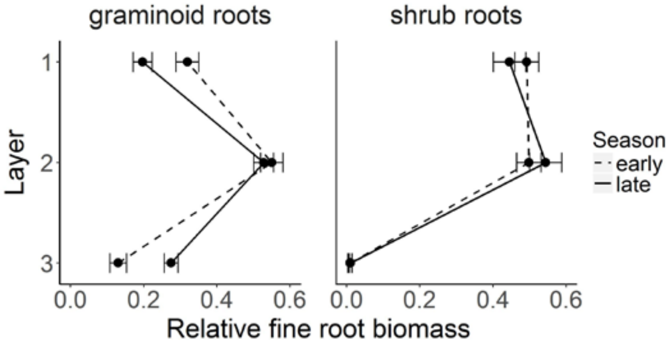

Fig. A3.2 Relative fine root biomass (proportion of total fine root biomass) distribution of each PFT over the three soil layers in the early and late growing season. Data of graminoid roots in shrub vegetation and data of shrub roots in graminoid vegetation were excluded as graminoids and shrubs were low in abundance in shrub vegetation and graminoid vegetation respectively and had large variation. For graminoid roots relative biomass distribution changed significantly over the growing season (P < 0.001 for layer × season interaction): it decreased in 1st layer (P = 0.001) while increased in the 3rd (P < 0.001). For shrub roots the distribution pattern did not change significantly over the growing season (P = 0.390 for layer × season interaction)

Table A3.1 Analysis of vegetation, season, PFT and layer effects on fine root biomass density in the upper two layers using linear mixed model. Block, plot were taken as random effects in a nested structure. Data were ln(x+1) transformed

Source	df	Sum of squares	*F* value	*P* value
Vegetation	2	12.9	3.8	0.040*
Season	1	25.7	15.0	< 0.001*
PFT	1	39.8	23.2	< 0.001*
Layer	1	4.4	2.5	0.113
Vegetation × season	2	2.1	0.6	0.547
Vegetation × PFT	2	125.7	36.7	< 0.001*
Season × PFT	1	2.3	1.3	0.252
Vegetation × layer	2	4.8	1.4	0.248
Season × layer	1	5.3	3.1	0.080
PFT × layer	1	17.8	10.4	0.002*
Vegetation × season × PFT	2	14.6	4.2	0.016*
Vegetation × season × layer	2	1.3	0.4	0.690
Vegetation × PFT × layer	2	1.7	0.5	0.605
Season × PFT × layer	1	1.0	0.6	0.455
Vegetation × season × PFT × layer	2	2.7	0.8	0.456

Table A3.2 Nonparametric analysis of vegetation, PFT and season effects on fine root biomass density in the 3rd layer (15 – 30 cm)

Source	df	ANOVA-Type statistic	*P* value
Vegetation	2.0	10.4	< 0.001*
PFT	1.0	39.5	< 0.001*
Season	1.0	27.5	< 0.001*
Vegetation × PFT	1.8	15.0	< 0.001*
Season × PFT	1.0	5.9	0.015*
Vegetation × season	1.9	1.2	0.299
Vegetation × PFT × season	1.6	0.5	0.567

4

Above and belowground responses of tundra vegetation to soil thawing and fertilization

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Abstract

Climate warming is faster in the Arctic than the global average. Nutrient availability in tundra soil can be increased by climate warming through accelerated mineralization in the upper organic layer, while increased thawing of permafrost due to climate warming releases nutrients locked up in previously frozen soil layers, both of which may initiate vegetation shifts. As vegetation plays a key role in ecosystem carbon dynamics, it is important to understand the effects of these two processes on tundra vegetation.

We manipulated soil thawing depth and nutrient availability in a full-factorial field experiment to investigate their effects on above and belowground responses of four plant functional types (grasses, sedges, deciduous shrubs and evergreen shrubs). At a Northeast-Siberian tundra site, thawing depth was increased by heating cables at ~15 cm depth, whereas nutrient availability was increased by slow-release fertilizer at ~5 cm depth. This is the first study to our knowledge specifically investigating the effects increased thawing depth in tundra ecosystems.

We found that the four plant functional types responded differently to the increased thawing depth and fertilization. Thawing increased the aboveground biomass of sedges, the plant functional type with the highest deep root proportion in our study, but did not affect biomass of the other plant functional types. In contrast, fertilization increased aboveground biomass of the two dwarf shrub functional types, both of which had very shallow root systems. Fertilization also increased above and belowground biomass of grasses. Grasses had the highest plasticity in terms of vertical root distribution, as they shifted root distribution in different soil layers in response to both soil thawing and fertilization.

Our results show that increased thawing depth can only benefit deep-rooted sedges, while increased nutrient availability in the upper soil layers can benefit shallow-rooted shrubs as well as deep-rooted grasses, with the latter shifting root distribution to the shallower soil. Our results suggest that grasses have the highest root plasticity, which enables them to be more competitive in rapidly changing environmental conditions. We conclude that root allocation strategies are key to understanding vegetation responses to climate-induced increases in nutrient availability in arctic tundra.

Keywords: active layer thickness, Arctic tundra, climate warming, competition, nutrient availability, permafrost thawing, plant functional types, root biomass, vertical root distribution, vegetation composition

4.1 Introduction

Global temperatures have increased by 0.7 °C since the 1900s (IPCC 2013). This trend will continue this century with an increase of 1.5 degrees or more, particularly in the Arctic (IPCC 2013). Arctic warming has already resulted in large scale thawing of permafrost (Romanovsky et al. 2010), accelerating decomposition of organic matter (Aerts 2006), releasing carbon and nutrients (Schuur et al. 2009, Belshe et al. 2013). Tundra vegetation is responding by increasing aboveground productivity (Verbyla 2008, Hill and Henry 2011, Epstein et al. 2012), and shifting species composition (Tape et al. 2006, Wookey et al. 2009, Callaghan et al. 2011, Myers-Smith et al. 2011b). Since vegetation characteristics can have decisive impacts on greenhouse gas emissions (Cahoon et al. 2012, Nauta et al. 2015) and the energy balance of the earth surface (Blok et al. 2010, Myers-Smith et al. 2011b), the crucial question is whether such shifts in plant species composition will decelerate or accelerate Arctic warming. One of the key factors influencing the competitive balance between plant species is their capacity to monopolize the newly available resources.

Due to the low temperatures and short growing season, microbial decomposition and nutrient mineralization are very slow, making the tundra ecosystem highly nutrient-limited (Chapin 1987, Chapin et al. 1995). Climate warming can influence nutrient availability in tundra soils along different pathways. With climate warming, the depth of active layer which is frozen during the winter and thaws in the growing season is prone to increase (Hinkel and Nelson 2003, Burn and Kokelj 2009, Park et al. 2016). Increased thawing depth can release nutrients that were previously locked up in the frozen soil, thus increasing nutrient availability in the deep soil (Frey and McClelland 2009, Keuper et al. 2012b). On the other hand, microbial activity can be stimulated by climate warming (Mikan et al. 2002). As a result, nutrient availability in the shallow soil is expected to increase due to accelerated microbial decomposition and mineralization of organic matter in the shallow soil (Aerts 2006, Craine et al. 2010). Fertilization experiments in tundra ecosystems have hitherto focused on the effects of increased nutrient availability in the top soil layers showing that both shrubs and graminoids, particularly grasses, benefit from the increased nutrient availability (Dormann and Woodin 2002, Gough and Hobbie 2003, Gough et al. 2012, Zamin et al. 2014). However, to our knowledge no study explored the effects of increased nutrient availability in deeper soil layers as a result of increased thawing depth.

Since fine roots are the plant parts that absorb soil nutrients, the responses of fine root mass will likely determine which species can take advantage of the expected increase in nutrient availability. Shallow-rooting dwarf shrubs such as *Betula nana* L. and *Vaccinium vitis-idaea* L. are likely to monopolize nutrients released in the top soil whereas deep-rooting species such as grass *Calamagrostis holmii* Lange and sedge *Eriophorum vaginatum* L. are likely to forage on nutrients at the deeper thawfront (Keuper et al. 2014, Oulehle et al. 2016). In addition, plants that have short-lived roots can better adapt the placement of their roots to changes in nutrient availability than plants that have long-lived roots (Eissenstat et al. 2000), which probably gives them a competitive advantage in changing environments. Until now, it remains unresolved however to what extent aboveground vegetation responses can be traced back to belowground root foraging strategies.

To improve our understanding of climate warming effects on tundra plants and vegetation composition, we investigated the effects of increases in permafrost thawing depth and nutrient availability in the shallow soil on above and belowground responses of tundra plants. Specifically, our hypotheses were:

1) Increased thawing depth will benefit deep-rooting species such as grasses

and sedges, as they can actively forage at the deeper thaw front;

2) Increased nutrient availability in the shallow soil will benefit shallow-rooting species such as dwarf shrubs, as they already have a well-established root system in the top soil;

3) Aboveground responses of plant species to increased thawing depth or nutrient availability are linked to belowground shifts in vertical rooting patterns.

To test these hypotheses we carried out a field experiment in which the thawing depth and nutrient availability was manipulated from 2010 to 2014 at a Siberian tundra site.

4.2 Materials and methods

4.2.1 Study site

We performed our research at the long-term research facility in the Kytalyk Nature reserve (70º49’N, 147º29’E) which is 28 km Northwest of the town of Chokurdakh (Yakutia, Russian Federation), 150 km south of the Arctic Ocean. The mean annual air temperature is −13.4 ºC (1981 – 2010), with a mean July temperature of 10.3 ºC. Annual precipitation at the nearest climate station (Chokurdakh, WMO station code 21946, 27 km away from the study site) is 196 mm (1981 – 2010), of which 76 mm falls in the summer (June – August).

The study area is located in the lowlands of Indigirka River and underlain by thick continuous permafrost with a shallow active layer. The circumpolar Arctic Vegetation Map (Walker et al., 2005) classifies the vegetation of the research area as tussock-sedge tundra, dominated by *E. vaginatum* and dwarf shrubs, with high moss cover (G4). The experiment is located on the top of a 20 – 30 m elevated ridge that surrounds part of a drained thaw lake. This ridge is probably a remaining Pleistocene river terrace surface (Van der Molen et al., 2007). The 200 – 300 m wide ridge is covered by a relatively homogeneous moist tussock tundra vegetation with *E. vaginatum* as the dominant graminoid species and abundant dwarf shrubs such as *B. nana*, *Salix pulchra* Cham., *Rhododendron tomentosum* Harmaja and *V. vitis-idaea.* Throughout the ridge a moss layer with some lichens is present below the vascular plants. On the ridge, frost boils without any vegetation cover are sparsely distributed. Soils are classified as Gelisol and consist of an organic layer on top of silty clay parent deposits. The organic layer varies in thickness from a few cm up to 25 cm.

4.2.2 Experimental setup

We established 20 plots of 1.5 by 1.5 m in 2010. The plots were clustered in 5 blocks containing 4 plots each. Plot selection was based on vegetation composition: we made sure each plot contained species of 5 plant functional types (grasses, sedges, deciduous shrubs, evergreen shrubs and moss or lichen). Within each block we randomly assigned 4 treatments, comprising 2 levels of fertilization: fertilized and unfertilized; and 2 levels of thawing: thawing treatment with heating cable, control treatment with cable but without heating (Fig. 4.1a).

The thawing treatment was realized by heating cables buried in the soil and connected to solar panels. The heating cables were inserted into the soil at a depth of about 15 cm below surface in July 2010. The horizontal spacing between the cable lines was 20 cm. The cables were inserted into the soil from excavated trenches at two opposing sides of the plots to minimize disturbance of root and microbial activity within the plots. The total length of the cable for a single plot was 15 m and the total resistance was 15 Ohm. In the thawing plots, the heating cables were connected to two parallel connected solar panels of 85 Watt each on July 3, 2011, which is one year after the cable installation. No battery was included in the circuit, so the solar energy mainly enlarged the natural ground heat flux and allowed for diurnal and seasonal variation in solar intensity. The two solar panels had an angle of 60° to each other in order to capture sunlight during 20 hours per day. The fertilization treatment was realized by inserting slow-release fertilizer tablets (Osmocote Exact Tablet 3-4M, Scotts International BV, Waardenburg, The Netherlands) into the soil at 5 cm below soil surface in early July 2011. The fertilization treatment was repeated in early July 2013. Fertilizer was added within a 1.75 × 1.75 m area for each plot, making sure plants at the plot edge with roots beyond the plot border also completely experience the fertilization treatment. Within the 1.75 × 1.75 m area, 68 tablets of 5 g fertilizer were inserted in a pattern of 25 cm spacing between each pair of neighbouring tablets. We added 5.6 g N m^{-2} yr^{-1}, 1.4 g P m^{-2} yr^{-1} and 3.7 g K m^{-2} yr^{-1}, but as we do not know exactly how fast the nutrients were released from the slow-release fertilizer tablets, the actual nutrient release rates could have been lower.

4.2.3 Measurements

4.2.3.1 Environmental factors

The thawing depth and soil moisture were measured 2 – 4 times during the growing season from 2010 to 2014 at five points in each plot. Thawing depth was measured by inserting a metal stick into the soil until hitting the frozen soil. Soil moisture was measured at 10 cm soil depth using a Thetaprobe soil moisture sensor (ML3 ThetaKit, Delta-T Devices, UK).

Soil temperature was measured continuously in each plot at depths of 0, 5, 15 and 25 cm below the soil surface from 8th August 2010 to 30th July 2014. Temperature was recorded automatically every 3 hours using temperature loggers (iButton DS1922L/DS1921G, Maxim Integrated, USA).

Soil nutrient availability was assessed by measuring soil exchangeable nutrient concentrations in each plot at depths of 5 and 25 cm below the soil surface using resin bags. 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. The bags were first inserted in 2010 and replaced by new ones at the beginning of August each year until 2014. Resin bags were 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^{3-} and K^+ using an auto-analyzer (Skalar, Breda, The Netherlands).

4.2.3.2 Plant abundance

The abundance of each plant species in each plot was recorded in the 50 × 50 cm plot center (Fig. 4.1b) in 2010, before installing the heating cables, and in 2013, at the end of the third growing season of treatments, by taking point intercept measurements on a grid of 11 by 11 points spaced 5 cm apart. The 121 grid points were used to determine species abundances. To determine species presence at each point in the grid, a thin rod was lowered from above the point to the ground and each plant species it touched on its descent to the ground was recorded. A species, e.g. *B. nana*, could be hit multiple times at one point. The total number of hits for each species in a plot is taken as the indicator of the abundance of that species in that plot.

4.2.3.3 Biomass

Aboveground and belowground plant biomass was harvested on 1 – 15 August 2014. In each plot, two 25 × 25 cm subplots were sampled (Fig.

4.1b). In each subplot, aboveground plant parts were clipped flush with the moss surface and sorted into different fractions for the four PFTs: leaves for grasses and sedges, leaves and stems for deciduous and evergreen shrubs.

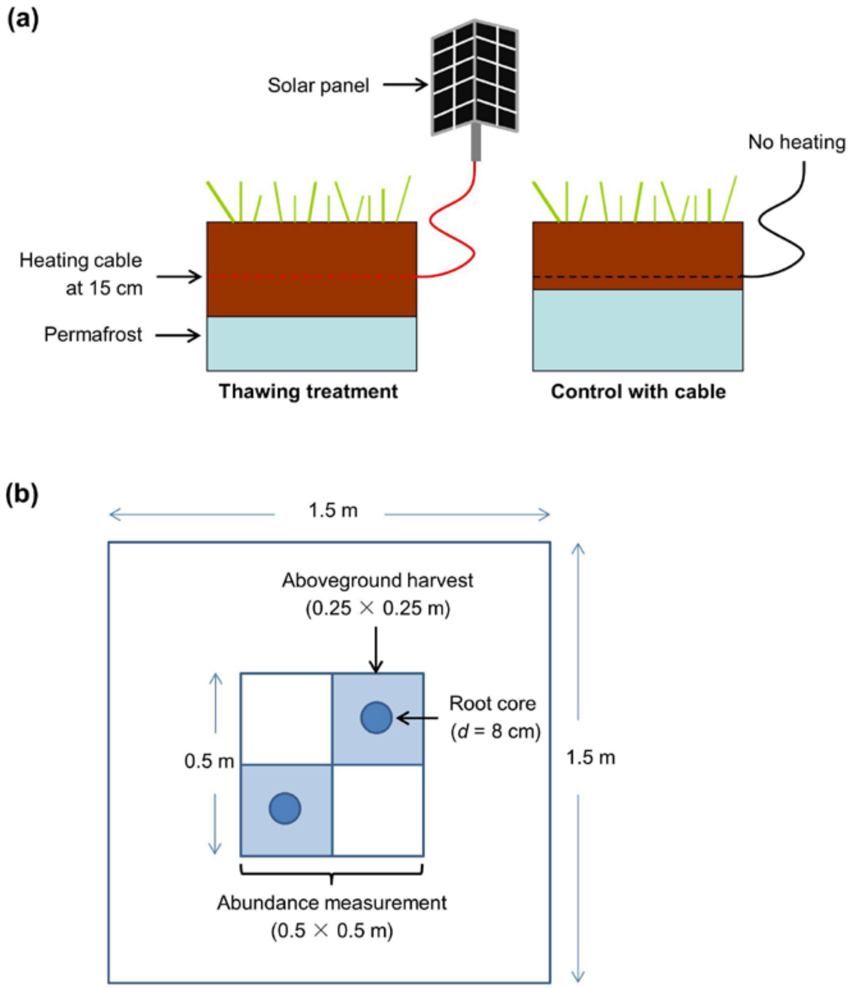

Fig. 4.1 Diagrams showing the setup of the thawing and control treatments (a) and the location of point-quadrat measurements and harvests of above and belowground biomass (b).

Root biomass was sampled by taking a soil core (8 cm diameter) in the center of each subplot. Organic layer thickness was measured for each soil core. The soil cores were separated into 4 layers: 0 – 5 cm as the first layer, 5 – 15 cm as the second layer, 15 – 30 cm as the third layer, and 30 – thawing depth as the fourth layer. To take into account the differences in soil volume between layers, we used the biomass density (g m^{-3}) when comparing the rooting patterns over layers. Belowground biomass was sorted into different fractions for the four PFTs: belowground stems (diameter > 5 mm), coarse roots (1 mm < diameter < 5 mm) and fine roots (diameter < 1 mm) for deciduous and evergreen shrubs; rhizomes (diameter > 1 mm, including stem bases of *E. vaginatum*) and fine roots (diameter < 1 mm) for grasses and sedges. Belowground stems of shrubs were easily identified to species as they resemble their aboveground parts. Roots that were not attached to the belowground stems or rhizomes were identified according to their colour and texture (Hobbie and Chapin 1998). *Arctagrostis latifolia* (R. Br.) Griseb. and *C. holmii* roots are white and smooth, and with a light yellow colour for older roots. *E. vaginatum* roots are also white and smooth, but unbranched, which differs from grass roots. *Carex bigelowii* Torr. ex Schwein. roots are tan coloured, with a pubescent texture. The roots deciduous shrubs are reddish to brown coloured, with woody structure and usually can be recognized by the colonization of ectomycorrhizal fungi. The roots of evergreen shrubs are also reddish to brown coloured but much finer than the roots of deciduous shrubs.

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 dried in an oven at the temperature of 70 ºC for at least 24 hours. After the samples were transported to the Netherlands, they were further dried in an oven at the temperature of 65 ºC for 72 hours and weighed.

4.2.4 Analysis

We used linear mixed effects models (LMM) with thawing treatment, fertilization treatment as fixed factors, block and plot as random effects in a nested structure (plot within block) to test for treatment effects on the environmental factors, including soil temperature at different depths, thawing depth, soil moisture and soil exchangeable nutrients (nitrogen and phosphorus).

We also used the same linear mixed effects models as above to test for changes in the abundance of different PFTs from 2010 to 2013 (differences in hits between 2010 and 2013) and differences in the aboveground biomass, belowground biomass, and fine root biomass of vascular plants in the four different treatments.

To test for differences in the vertical distribution of fine roots of different PFTs and treatment effects, we calculated mean root depth of each PFT in each treatment:

$$\text{mean root depth} = \frac{\sum (b_i \times D_i)}{\sum b_i}$$

where b_i is the biomass of layer i, D_i is the depth of the middle of layer i. For the fourth layer, the depth was calculated as the middle from 30 cm to the depth beyond which no roots were found any more. Then a linear mixed effects model same as above was used. To further investigate changes in mean root depth, we analysed the proportion of root biomass in each layer separately for each PFT, using linear mixed effects models with thawing and fertilization as fixed factors, block as random effect.

The differences in the abundance change, aboveground biomass, belowground biomass, and fine root biomass of vascular plants of the whole plot community were also tested, using linear mixed effects models with thawing and fertilization as fixed factors, block as random effect. Least significant difference (LSD) method was used for post hoc tests when an effect was significant in one of the above models.

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 calculated using package *lmerTest* version 2.0-20 (Kuznetsova et al. 2014).

4.3 Results

4.3.1 Environmental factors

Thawing significantly warmed the deeper soil layers (15 and 25 cm), and increased average thawing depth in July by 7 cm (Fig. A4.1). Thawing did not affect soil exchangeable nutrient concentrations significantly (Fig. A4.1), although the exchangeable phosphorus concentration at 25 cm depth tended to be increased by thawing ($F_{1,12} = 3.56$, $P = 0.083$). Fertilization cooled all soil layers by 0.6 – 0.9 °C, reduced thawing depth in July by 4 cm, and increased soil exchangeable nutrient concentrations in the shallow soil layer (5 cm) four (nitrogen) to five (phosphorus) times (Fig. A4.1). Neither thawing nor fertilization affected soil moisture significantly (Fig. A4.1, Table A4.1). In the control plots exchangeable nitrogen was higher at 5 cm depth than at 25 cm depth ($P = 0.028$), but exchangeable phosphorus did not differ between the two depths ($P = 0.732$; Fig. A4.1).

4.3.2 Aboveground plant responses

Thawing increased community plant abundance ($F_{1,12} = 4.9$, $P = 0.047$), although each PFT individually did not respond significantly (Table 4.1 and

4.2; Fig. A4.2, Table A4,2). Thawing did not affect community aboveground biomass ($F_{1,12}$ = 0.1, P = 0.809; Fig. A4.3) but did significantly increase sedge aboveground biomass (Fig. 4.2a; Table 4.1 and 4.2). The other PFTs did not respond to the thawing treatment (Table 4.2). In contrast, fertilization increased community aboveground biomass by 60% ($F_{1,12}$ = 15.9, P = 0.002; Fig. A4.3). For each PFT, fertilization increased the aboveground biomass and/or abundance, except for sedges (Fig. 4.2a, Fig. A4.2; Table 4.2). The biomass increase was strongest for grass leaves (Fig. 4.2a). Mosses and lichens decreased with fertilization as vascular plants increased (Fig. A4.2).

4.3.3 Belowground plant responses

Community belowground biomass was about three times as high as aboveground biomass ($F_{1,28}$ = 15.7, P < 0.001; Fig. A4.3). The four PFTs differed significantly in belowground biomass, fine root biomass and mean root depth (Table 4.1). Sedges had lower total belowground biomass than deciduous and evergreen shrubs, while grasses had higher fine root biomass than other PFTs (Fig. 4.2b). The mean root depth of different PFTs followed the order: grass/sedge > deciduous shrub > evergreen shrub (Fig. 4.3).

Thawing did not affect belowground biomass and fine root biomass of either the community (Fig. A4.3) or individual PFT (Fig. 4.2b; Table 4.1 and 4.2). Thawing significantly increased community mean root depth ($F_{1,12}$ = 5.9, P = 0.031), although it did not significantly affect mean root depth of any individual PFT (Table 4.2). However, grasses did tend to shift their root distribution to deeper soil layers in response to thawing: thawing marginally decreased the proportion of grass roots in the second layer and significantly increased that in the third layer (Fig. 4.3a; $F_{1,16}$ = 3.1, P = 0.098; $F_{1,16}$ = 5.1, P = 0.038 respectively). The other PFTs did not show any significant responses to thawing in their vertical root distribution (Fig. 4.3a).

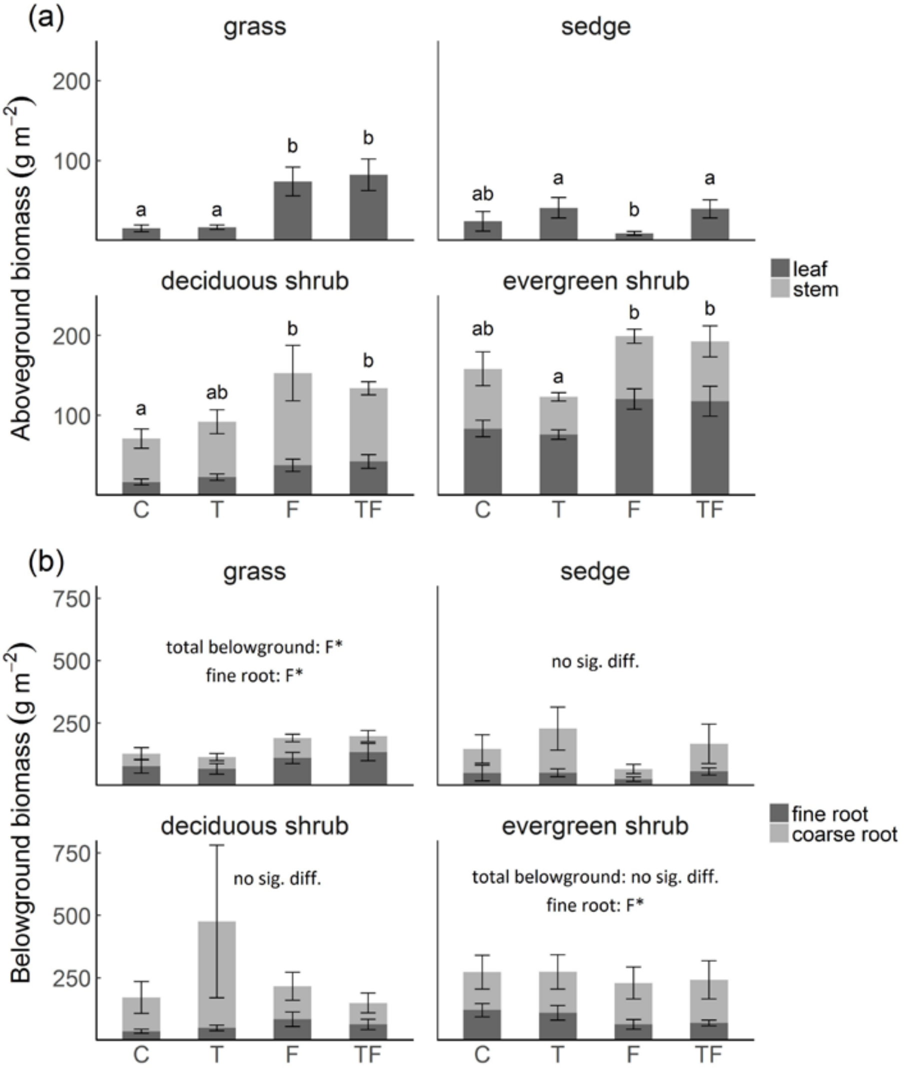

Fig. 4.2 Aboveground (a) and belowground (b) biomass of each vascular PFT separated by tissue types. C, control; T, thawing treatment; F, fertilization treatment; TF, combination of thawing and fertilization treatment. Belowground stems and rhizomes were included in the coarse root category. Letters above the bars in Fig. 4.2a represent pairwise statistical differences in total aboveground biomass. Total belowground biomass did not show significant pairwise differences among treatments while there were overall fertilization effects.

Table 4.1 Analysis of PFT differences in and treatment effects on aboveground biomass, belowground biomass, fine root biomass and mean root depth. Biomass data were ln(x+1) transformed.

Source	df	Abundance change 2010 – 2013		Aboveground biomass		Belowground biomass		Fine root biomass		Mean root depth	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Thawing	1	6.3	0.028 *	6.6	0.012 *	0.9	0.345	0.6	0.529	2.2	0.146
Fertilization	1	11.0	0.006 *	21.5	< 0.001 *	< 0.1	0.883	3.3	0.072 **·**	5.3	0.025 *
PFT	3	8.5	< 0.001 *	67.5	< 0.001 *	4.0	0.012 *	11.0	< 0.001 *	98.4	< 0.001 *
Thawing × fertilization	1	0.1	0.769	0.3	0.603	< 0.1	0.900	0.9	0.393	1.8	0.188
Thawing × PFT	3	0.3	0.828	4.5	0.007 *	0.2	0.862	0.5	0.826	0.4	0.723
Fertilization × PFT	3	0.7	0.528	10.6	< 0.001 *	0.8	0.510	2.5	0.068 **·**	3.1	0.035 *
Thawing × fertilization × PFT	3	3.0	0.040 *	1.0	0.389	0.4	0.722	0.4	0.881	0.4	0.782

· 0.05 < *P* < 0.10; * *P* < 0.05

Table 4.2 Analysis of treatment effects on abundance change, aboveground biomass, belowground biomass, fine root biomass and mean root depth of each functional type separately. Biomass data were ln(x+1) transformed.

PFT	Source	df	Abundance change 2010 – 2013		Aboveground biomass		Belowground biomass		Fine root biomass		Mean root depth	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Grass	Thawing	1	2.8	0.119	0.5	0.477	0.0	0.888	< 0.1	0.958	2.9	0.107
	Fertilization	1	13.7	0.003 *	46.1	< 0.001*	4.9	0.046*	5.2	0.042*	11.4	0.004*
	Thawing × Fertilization	1	0.1	0.712	< 0.1	0.965	0.0	0.880	0.2	0.670	2.1	0.169
Sedge	Thawing	1	3.8	0.074 ·	16.3	0.002*	0.6	0.456	0.7	0.429	0.07	0.799
	Fertilization	1	0.7	0.410	1.5	0.239	0.1	0.802	0.2	0.699	0.6	0.437
	Thawing × Fertilization	1	4.0	0.069 ·	2.3	0.152	0.1	0.712	0.9	0.359	0.4	0.550
Deciduous shrub	Thawing	1	1.6	0.235	0.4	0.533	0.7	0.410	< 0.1	0.942	1.5	0.250
	Fertilization	1	8.7	0.012 *	6.8	0.019*	0.8	0.385	1.2	0.292	2.3	0.157
	Thawing × Fertilization	1	0.1	0.791	0.6	0.452	1.4	0.254	0.6	0.458	0.02	0.872
Evergreen shrub	Thawing	1	1.5	0.246	0.6	0.447	0.1	0.761	< 0.1	0.914	0.04	0.837
	Fertilization	1	2.2	0.162	4.8	0.049*	0.5	0.504	5.2	0.041*	9.7	0.007*
	Thawing × Fertilization	1	2.3	0.152	0.1	0.767	0.2	0.680	0.6	0.471	0.3	0.578

· $0.05 < P < 0.10$; * $P < 0.05$

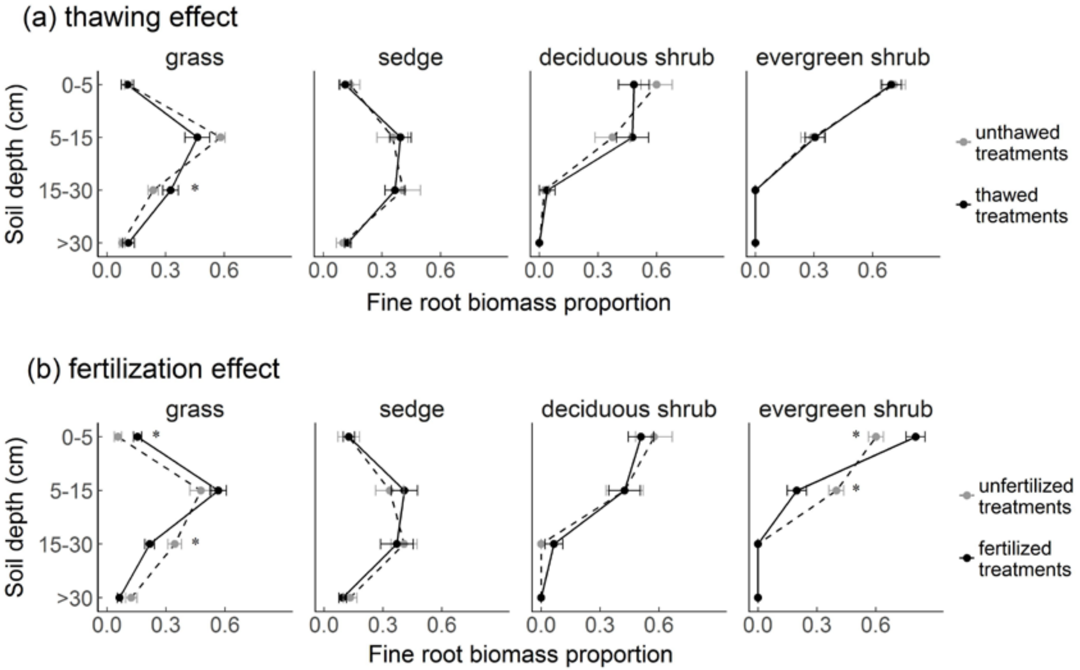

Fig. 4.3 Proportional distribution of fine root biomass over the four soil layers for each PFT in a) the thawed and unthawed treatments and b) the unfertilized and fertilized treatments. Thawing effects and fertilization effects are illustrated separately as there is no significant effect of the interaction between the two treatments on the proportional biomass distribution. Unthawed treatments include control treatment and fertilization treatment, thawed treatments include thawing treatment and thawing×fertilization treatment; unfertilized treatments include control treatment and thawing treatment, fertilized treatments include fertilization and thawing×fertilization treatment. Error bars represent ± SE (n = 10 plots). Asterisks indicate significant differences.

Fertilization did not affect belowground biomass and mean root depth at the community level, but did affect them at PFT level: fertilization significantly increased fine root biomass of grasses but decreased that of evergreen shrubs (Table 4.2). Fertilization also decreased the mean root depth of grasses and evergreen shrubs by 4 and 1.5 cm respectively (Table 4.2). When zooming in to specific layers, grasses increased their root proportion in the first layer and decreased that in the third layer (Fig. 4.3b; $F_{1,12} = 16.0$, $P = 0.002$; $F_{1,16} = 10.3$, $P = 0.005$ respectively), while evergreen shrubs increased their root proportion in the first layer and decreased that in the second layer (Fig. 4.3b; $F_{1,16} = 9.7$, $P = 0.007$).

4.4 Discussion

Our results show that aboveground responses of tundra vegetation to thawing and fertilization depend on functional type and are related to their vertical root distribution. Increased thawing depth benefited the deep-rooted sedges in their aboveground biomass, and tended to increase the root distribution of grasses in deeper soil. Fertilization promoted aboveground biomass of the shallow-rooted dwarf shrubs and the flexible-rooted grasses. Overall, our results suggest that deep-rooted sedges may benefit from increased thawing depth and shallow-rooted species can benefit from increased nutrient contents in the upper soil. The competitive relationship between the two rooting strategies will depend on the balance between the nutrient changes in the shallow and deep soil, while the flexible-rooted grasses may benefit in rapidly changing conditions.

4.4.1 Environmental changes caused by the treatments

Thawing depth was increased without influencing soil temperatures in the upper organic soil layer, enabling us to examine the effects of increased thawing depth without the confounding effects of shallow soil environmental changes for the first time in tundra studies. Thawing depth was also increased in previous field experiments using either open-top chamber (OTC) to increase air and soil temperatures or snow-fences to increase snow depth in the experimental plots (e.g., Wahren et al. 2005, Björk et al. 2007, Natali et al. 2012, Zamin et al. 2014). OTC treatments usually only increased the air temperature in the chamber and did not influence thawing depth much or not at all (Sullivan and Welker 2005, Natali et al. 2012). Snow fence treatments have opposing effects on thawing depth depending on the soil thermal conditions and snowmelt time (Hinkel and Hurd 2006, Leffler et al. 2016), also it adds a thicker protective layer against frost damage in winter, which benefits taller plants and increases spring water flow (Wahren et al. 2005, Wipf 2010), making it difficult to isolate soil thawing effects on vegetation.

In our study, thawing did not influence nutrient availability significantly. Probably the nutrient content of the newly thawed mineral soil layers was rather small, and although the average soil temperature in the deeper layers was increased by 0.7 degree, they were still low compared to the temperatures of the shallow soil, thereby limiting mineralization of soil organic matter.

In contrast to the thawing treatment, fertilization decreased soil temperature and thawing depth, probably through increased shading by vascular plants (Chapin et al. 1995), as suggested by a significant correlation between total aboveground biomass and average June – July soil temperature of all depths ($P = 0.037$, $R^2 = 0.29$, n = 15 plots with temperature records). This shading effect on thawing depth illustrates a negative feedback between plant productivity and soil temperature, which can mitigate changes resulting from climate warming.

4.4.2 Plant responses in biomass

Soil thawing had minor effects on plant biomass in our experiment, which might be due to the fact that nutrient availability in the soil was not influenced much by the thawing treatment, as nutrient availability is an important limiting factor for plant growth in tundra ecosystems (Chapin et al. 1995, Chapin et al. 1996). However, the deep-rooted sedges, which had the highest root proportion beyond 15 cm ($F_{1,18} = 4.5$, $P = 0.048$), did benefit a little from the thawing treatment. As the phosphorus concentration in the deep soil showed a marginally significant increase, it suggests that sedges might have profited from the slightly more available nutrients deeper in the soil. Thawing may also have mitigated the competition between sedges and other plants in the surface soil layer, as suggested by the fact that in the fertilization treatment sedge aboveground biomass was significantly lower than in other treatments, while thawing enabled sedges to have more biomass in fertilized plots.

In our study, the response to fertilization was strongest in grasses and deciduous shrubs, with evergreen shrubs taking a third position. Sedges did not respond to fertilization, which might be due to the intensified competition in the shallow soil where most roots of the other PFTs were. Also in other studies grasses were very responsive to fertilization (Dormann and Woodin 2002), as well as deciduous shrubs (Shaver and Chapin 1986, Gough and Hobbie 2003). However, responses of sedges and evergreen shrubs to fertilization were quite mixed in previous studies. Positive, negative, and neutral responses were observed in different studies/sites (Shaver and Chapin 1986, Grellmann 2002, Gough et al. 2012, Zamin et al. 2014), which suggests that the limiting factor for the growth of sedges and evergreen shrubs differs from site to site, such as nutrient, soil moisture, and/or snow depth in winter (Shaver and Chapin 1986). It is well known that increased nutrient availability results in reduced plant root:shoot ratio

(Brouwer 1962b, Chapin 1980), which is also the case in our experiment (Table A4.3).

We also found that fertilization effects on fine root biomass of grasses and evergreen shrubs were opposite: fertilization increased fine root biomass of grasses while it decreased that of evergreen shrubs. The increases in fine root biomass of grasses can help grasses to absorb more nutrients and thus increase their aboveground biomass. However, evergreen shrubs also increased their aboveground biomass in response to fertilization despite the decreases in fine root biomass. This discrepancy might be explained by the fact that the evergreen shrub species in our plots can be colonized by ericoid mycorrhizal fungi which form mutualistic symbionts with and provide nutrients to their host plants (Iversen et al. 2015). Clemmensen et al. (2006) showed that the abundance of ectomycorrhizal fungi at a heath tundra site was increased by fertilization while fine root biomass was not affected. We observed that deciduous shrubs had more ectomycorrhizal roots in fertilization plots, although we did not quantify the colonization rates. Therefore we assume that in our study both evergreen and deciduous dwarf shrubs responded to fertilization through increased mycorrhizal symbiosis instead of root growth itself.

4.4.3 Vertical root distribution

To our knowledge this study is the first to show changes in vertical root distribution in response to environmental changes in tundra ecosystems. Thawing increased community mean root depth, suggesting that with climate warming and permafrost thawing, tundra vegetation can exploit the previously frozen soil and thus affect the carbon dynamics there. Although each PFT individually did not show significant response to thawing in mean root depth, grasses did show a trend of increasing deep root proportion, indicating that when permafrost thaws and more nutrients are available in the deeper soil, grasses have the potential to grow roots deeper, where dwarf shrubs have hardly any roots.

Fertilization shifted root distribution of grasses and evergreen shrubs to shallower soil layers. However, the shifts were caused by opposite changes in root biomass of the two plant functional types: root biomass density of grasses increased in the upper 15 cm (Fig. A4.4; $F_{1,16} = 14.4$, $P = 0.002$; $F_{1,16} = 3.8$, $P = 0.07$; for the 0 – 5 cm and 5 – 15 cm respectively), while root biomass density of evergreen shrubs decreased in the 5 – 15 cm layer (Fig. A4.4; $F_{1,16} = 6.2$, $P = 0.024$), suggesting competitive advantage for the grasses over the evergreen shrubs. The shift in rooting pattern of grasses could enable them to make better use of available nutrients in the soil probably explains their strong increase in abundance and aboveground biomass due to fertilization, whereas the fine roots of evergreen shrubs might have been driven out of the 5 – 15 cm layer by the grass roots, where nutrient availability was probably the highest as the fertilizer tablets were inserted into the soil at ca. 5 cm depth. The shift of root distribution of grasses towards the depth of newly available nutrients, both in the fertilization and thawing treatment, suggests their high plasticity for reacting quickly to changed nutrient conditions.

4.4.4 Implication for plant competitive relationships in the warmer future

Our results suggest that responses of tundra vegetation to climate warming will depend on the balance between thawing depth and nutrient availability in the shallow soil. For example, the top soil layers are where fresh litter is deposited and the temperatures are more influenced by the increases of air temperature (Jobbágy and Jackson 2000, Jobbágy and Jackson 2001, Tarnocai et al. 2009), which means that the decomposition in the top soil is likely to be accelerated more than in the deeper soil. In this case, mineralization of soil organic matter increases more in the top soil than in the deeper soil with climate warming, and thus dwarf shrubs will gain more advantages through their shallow roots. However, warming can also dry up the top soil (Hinzman et al. 2005, Smith et al. 2005), thereby limiting nutrient mineralization rates in the top layer (Aerts 2006, Hicks Pries et al. 2013), decreasing the advantage of the shallow-rooted dwarf shrubs. Instead, the deep-rooted sedges and/or the plastic grasses, can ‘escape’ the dried-out top soil and forage the thaw front instead (Keuper et al. 2012b, Oulehle et al. 2016), perhaps even leading to graminoid dominance.

Another study found that *A. latifolia,* which was the dominant grass species in our study, responded rapidly to disturbances and changing soil conditions (Jorgenson et al. 2015). Our results suggest that grasses have the highest root plasticity among the four PFTs in terms of vertical root distribution, as they actively responded to both thawing and fertilization. This plasticity enable grasses to better deal with the changes in both deep and shallow nutrients as consequences of climate warming in tundra ecosystems, and may give grasses advantages over other plants if climate warming results in more erratic nutrient distributions in the future.

4.5 Conclusions

We show that increased thawing depth had modest effects, and only affected aboveground biomass of sedges which had the deepest root distribution, while fertilization strongly increased aboveground biomass of the shallow-rooted shrubs as well as grasses, which were more plastic than other plant functional types in terms of vertical root distribution. Increased thawing depth and increased nutrient availability in the upper soil have different effects on plants that differ in rooting depths and plasticity, which might have important consequences for further successional trajectories. The high root plasticity of grasses enables them to gain advantage over dwarf shrubs and sedges in the competition for soil nutrients if climate warming leads to more erratic environmental conditions.

4.6 Acknowledgement

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4.7 Appendices

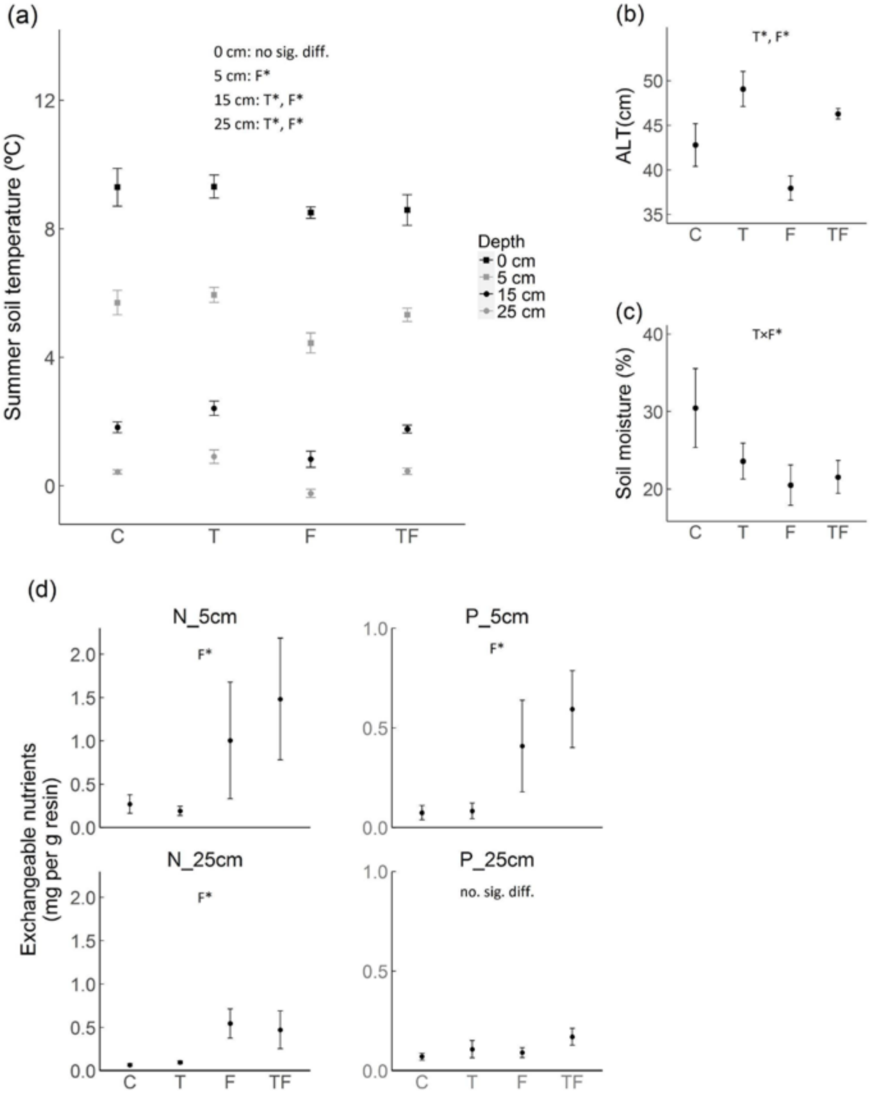

Fig. A4.1 Treatment effects on a) June – July soil temperature at four depths, b) average active layer thickness (thawing depth) in July, c) volumetric soil moisture and d) soil exchangeable N and P in 2014. C, control; T, thawing treatment; F, fertilization treatment; TF, combination of thawing and fertilization treatment. Error bars represent ± SE (n = 5). Fertilization effect on 0 cm temperature was marginally significant (*P* = 0.088). Soil moisture was higher in control treatment than in other treatments, but this difference existed already at the beginning of the experiment (Table A4.1). When considering initial differences, treatments did not significantly affect soil moisture.

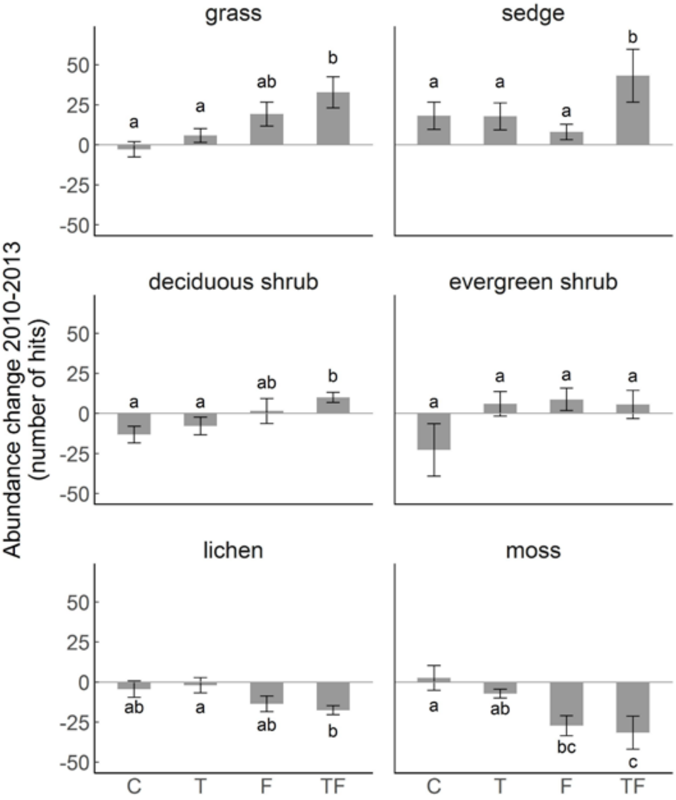

Fig. A4.2 Changes in abundances from 2010 (pre-treatment year) to 2013 of different PFTs. C, control; T, thawing treatment; F, fertilization treatment; TF, combination of thawing and fertilization treatment. Error bars represent ± SE (n = 5). Letters above the bars represent pairwise statistical differences. There were no significant differences among the treatments in the abundances of the plant functional types in 2010. Abundance changes of lichen and moss were analyzed separately from the four vascular PFTs which were analyzed as mentioned in the Materals and methods.

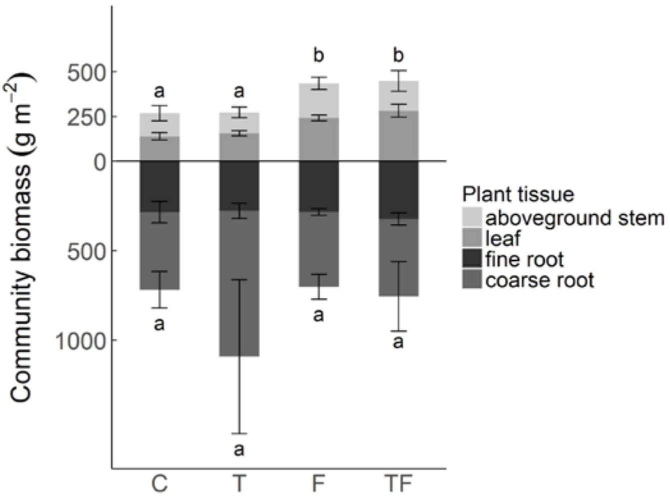

Fig. A4.3 Aboveground and belowground plant community biomass separated by tissue types. Belowground stems and rhizomes are included in the coarse root category. C, control; T, thawing treatment; F, fertilization treatment; TF, combination of thawing and fertilization treatment. Error bars represent ± SE (n = 5). Letters above the bars represent pairwise statistical differences. Patterns resembled between total aboveground biomass and leaf biomass, total belowground biomass and fine root biomass.

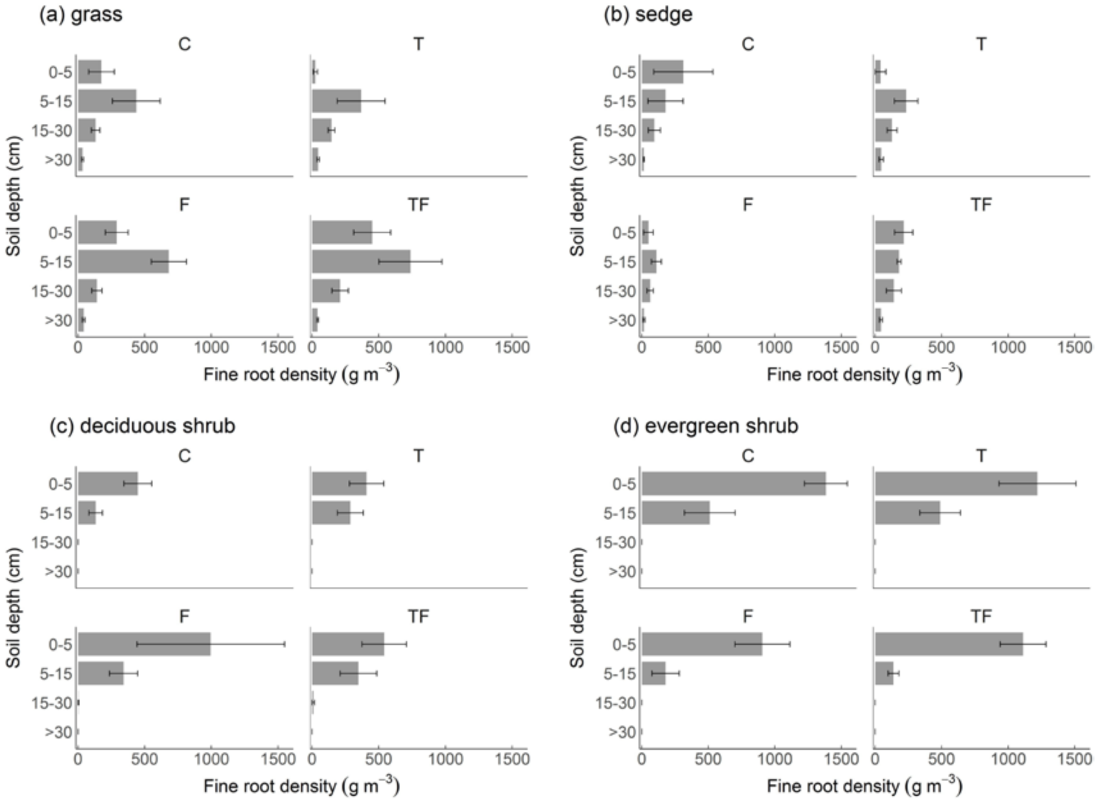

Fig. A4.4 Fine root biomass density of each functional type in different soil layers. Deciduous shrubs did not have any roots in the fourth layer, evergreen shrubs did not have any roots in the third and fourth layers.

Table A4.1 Environmental factors in each treatment. Soil moisture in 2010 in unfertilized-unthawed treatment was already higher than that in other treatments. Root growing degree days is the number of days during 10 August 2013 – 29 July 2014 when daily average temperature was above zero. Values show mean ± SE.

		Unthawed	Thawed	Treatment effects
2010 ALT (cm)	Unfertilized	43 ± 2	40 ± 3	Thawing ^{ns} Fertilization ^{ns} Thawing×fertilization ^{ns}
	Fertilized	42 ± 2	41 ± 3	
Organic layer thickness (cm)	Unfertilized	12 ± 1	10 ± 1	Thawing ^{ns} Fertilization ^{ns} Thawing×fertilization ^{ns}
	Fertilized	13 ± 2	13 ± 2	
2010 Soil moisture (% volume)	Unfertilized	26 ± 3.1	20 ± 1.2	Thawing ^{ns} Fertilization ^{ns} Thawing×fertilization .
	Fertilized	20 ± 0.6	22 ± 1.4	
Shallow inorganic K (mg g^{-1}resin)	Unfertilized	0.7 ± 0.2	1.0 ± 0.6	Thawing ^{ns} Fertilization * Thawing×fertilization ^{ns}
	Fertilized	1.6 ± 0.4	3.2 ± 1.0	
Deep inorganic K (mg g^{-1}resin)	Unfertilized	0.3 ± 0.1	0.3 ± 0.1	Thawing ^{ns} Fertilization ^{ns} Thawing×fertilization ^{ns}
	Fertilized	0.4 ± 0.1	0.6 ± 0.3	
0 cm growing degree days (> 0 °C)	Unfertilized	98 ± 1	96 ± 2	Thawing ^{ns} Fertilization * Thawing×fertilization ^{ns}
	Fertilized	95 ± 1	95 ± 1	
5 cm growing degree days (> 0 °C)	Unfertilized	93 ± 3	102 ± 6	Thawing * Fertilization * Thawing×fertilization ^{ns}
	Fertilized	84 ± 0.3	94 ± 6	
15 cm growing degree days (> 0 °C)	Unfertilized	82 ± 3	99 ± 1	Thawing * Fertilization ^{ns} Thawing×fertilization ^{ns}
	Fertilized	81 ± 4	99 ± 1	
25 cm growing degree days (> 0 °C)	Unfertilized	70 ± 5	105 ± 5	Thawing * Fertilization ^{ns} Thawing×fertilization ^{ns}
	Fertilized	70 ± 8	95 ± 5	

Table A4.2 Abundance (number of hits in point-quadrat) of each PFT in 2010 and 2013. Values show mean ± SE.

PFT	Year	C	T	F	TF
Grass	2010	16 ± 9	5 ± 2	7 ± 3	5 ± 2
	2013	13 ± 7	11 ± 4	26 ± 12	38 ± 12
Sedge	2010	5 ± 3	12 ± 4	12 ± 2	14 ± 3
	2013	23 ± 8	30 ± 10	20 ± 7	57 ± 20
Deciduous shrub	2010	34 ± 9	30 ± 7	31 ± 6	29 ± 6
	2013	21 ± 5	22 ± 7	33 ± 6	39 ± 6
Evergreen shrub	2010	86 ± 18	63 ± 9	70 ± 9	66 ± 5
	2013	63 ± 10	69 ± 4	79 ± 10	72 ± 11
Lichen	2010	42 ± 11	40 ± 10	32 ± 9	31 ± 6
	2013	37 ± 14	26 ± 12	30 ± 10	13 ± 3
Moss	2010	49 ± 5	60 ± 11	56 ± 11	59 ± 5
	2013	52 ± 10	33 ± 9	49 ± 8	28 ± 11

Table A4.3 Analysis of treatment effects on root:shoot ratios. Data were ln transformed.

Source	df	Belowground : aboveground		Fine root : leaf	
		F value	*P* value	*F* value	*P* value
Thawing	1	< 0.1	0.958	1.4	0.242
Fertilization	1	10.3	0.002*	11.0	0.001 *
PFT	3	10.9	< 0.001*	9.6	< 0.001 *
Thawing × fertilization	1	0.8	0.365	< 0.1	0.961
Thawing × PFT	3	0.4	0.736	0.4	0.720
Fertilization × PFT	3	1.5	0.218	3.2	0.030 *
Thawing × fertilization × PFT	3	0.5	0.697	0.3	0.817

Table A4.4 Treatment effects on fine root biomass density of each functional type in each layer. For deciduous and evergreen shrubs only the upper two layers were included in the analysis since shrub roots were very rare in the third layers and no shrub roots were found in the fourth layer. Data were ln transformed.

PFT	Source	df	*F* value	*P* value
Grass	Thawing	1	0.6	0.437
	Fertilization	1	14.8	0.002 *
	Layer	3	20.4	< 0.001 *
	Thawing × fertilization	1	2.3	0.155
	Thawing × layer	3	1.6	0.206
	Fertilization × layer	3	9.3	< 0.001 *
	Thawing × fertilization × layer	3	2.5	0.071 ·
Sedge	Thawing	1	1.7	0.221
	Fertilization	1	0.5	0.512
	Layer	3	5.0	0.004 *
	Thawing × fertilization	1	2.9	0.116
	Thawing × layer	3	0.3	0.818
	Fertilization × layer	3	0.8	0.487
	Thawing × fertilization × layer	3	3.2	0.033 *
Deciduous shrub	Thawing	1	0.1	0.763
	Fertilization	1	0.9	0.358
	Layer	2	8.5	0.010 *
	Thawing × fertilization	1	< 0.1	0.874
	Thawing × layer	2	0.6	0.438
	Fertilization × layer	2	0.2	0.652
	Thawing × fertilization × layer	2	< 0.1	0.989
Evergreen shrub	Thawing	1	< 0.1	0.893
	Fertilization	1	6.0	0.026 *
	Layer	2	31.4	< 0.001 *
	Thawing × fertilization	1	0.1	0.716
	Thawing × layer	2	< 0.1	0.896
	Fertilization × layer	2	5.9	0.027 *
	Thawing × fertilization × layer	2	< 0.1	0.848

· 0.05 < *P* < 0.10; * *P* < 0.05

5

Decomposition in the tundra: Leaf and root litter mass loss rates in shrub and graminoid vegetation

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Abstract

Litter decomposition is an important component of ecosystem carbon dynamics. With climate warming, decomposition often accelerates in tundra ecosystems. However, the observed shrub expansion in tundra can also affect litter decomposition through changes in litter quality which is associated with vegetation composition. Most studies so far have mainly focused on aboveground litter input. In tundra ecosystems, however, roots account for a major part of plant biomass and, consequently, root litter input may actually be larger than leaf litter input. Carbon sequestration in tundra soils depends on the decomposability of root litter. However, in contrast to leaf litter decomposition, root decomposition generally is understudied.

In order to increase our understanding of root decomposition in the Arctic, as well as the potential consequences of large-scale vegetation shifts, we performed a litter transplant experiment in which we measured decomposition rates of leaf and root litter of the two dominant plant functional types (shrub and graminoid) in three vegetation types in a northeastern Siberian tundra.

Our results show that root decomposition can be different from leaf decomposition. While the mass loss of leaf litter did not differ between the two plant functional types, the decay of shrub roots was much slower than that of living graminoid roots. We found evidence for home-field advantage effects when we compared decomposition rates in the different vegetation types. The observed differences in mass loss rate among the litter types could to a great extent be attributed to differences in phosphorus concentration, indicating that phosphorus limits microbial activity in this tundra site.

The low decomposition rate of shrub root litter compared to graminoid root litter suggests that soil carbon sequestration is larger in shrub vegetation than in graminoid vegetation. However, decomposition of graminoid root litter may be limited by cold soil temperatures, as graminoid roots are located closer to the permafrost than shrub roots. More information on litter input rates and direct effects of climate change on decomposition rates are needed to accurately predict the effects of climate change on carbon dynamics in tundra ecosystems.

Keywords: Arctic tundra, mass loss, deciduous shrub, graminoid, home-field advantage; litter quality

5.1 Introduction

The Arctic soils are an important carbon reservoir, as half of the terrestrial belowground organic carbon pool is sequestered in the northern circumpolar soil (Tarnocai et al. 2009), which is two times as large as the global atmospheric carbon pool (Houghton 2007). One of the key processes in the global carbon cycle is the decomposition of organic plant litter (Bonan et al. 2013, Wieder et al. 2013). It was estimated that the decomposition of plant litter accounts for half of the terrestrial carbon release into the atmosphere, and that 4 Pg carbon originating from plant litter is stored in the soil per year (Houghton 2007). Therefore, changes in decomposition rates will greatly affect the soil carbon stocks of the Arctic ecosystems.

Important abiotic factors controlling decomposition rates include soil moisture, temperature and nutrient availability (Swift et al. 1979). In the Arctic, temperature arguably is the most important driver of decomposition (Hobbie 1996, Robinson 2002), as the soil is frozen for most of the year, preventing decomposition. However, due to climate change, Arctic temperature has already increased by about 1 ºC in the last century and is predicted to further increase with 2 – 8 ºC this century (Jones et al. 2012, IPCC 2013). As a result, Arctic tundra soils will be warmer, permafrost will thaw faster and decomposition of organic carbon will be accelerated (Davidson and Janssens 2006, Cornelissen et al. 2007, Schuur et al. 2009). Ultimately, the Arctic tundra may shift from a net carbon sink to a net carbon source (Belshe et al. 2013, Webb et al. 2016).

In addition to abiotic factors, litter quality is an important driver of decomposition (Cornwell et al. 2008). In general, plant litter with a high nitrogen and low lignin content decays faster than litter with low nutrient and high lignin content (Zhang et al. 2008, Freschet et al. 2012). In most studies, nitrogen appears to be the most important limiting nutrient, but phosphorus content has also been found to be important and positively correlated to decomposability (Enriquez et al. 1993, Cornwell et al. 2008). Litter quality can differ substantially between plant species within the same ecosystem. In tundra, the main plant functional types (PFTs) are dwarf shrub and graminoid. These two PFTs may differ in nutrient concentrations of their litter and consequently in decomposition rates (Berendse et al. 1989, Hobbie 1996, Aerts 2006).

Decomposition rates may also differ between different tissues. For example, root litter generally decays slower than leaf litter (Thormann et al. 2001, Fujii and Takeda 2010, Birouste et al. 2011, Ma et al. 2016). In Arctic tundra, up to 70% of plant biomass is allocated belowground (Poorter et al. 2012). Although there is little knowledge of biomass turnover rates of these tissues in tundra ecosystems, the high root biomass suggests that root litter is a major source of carbon input in this ecosystem. Consequently, root litter decomposition may be an important component of the carbon dynamics. However, detailed information about differences in root litter decomposition rates among species or PFTs in the field is scarce. Bryant et al. (1998) investigated leaf and root litter decomposition in an alpine tundra and found that root litter was decomposed slower than leaf litter, but they did not link this to PFTs. Another study found that leaf and root litter of two graminoid species were decomposed faster than those of three shrub species, but this experiment was performed in microcosms under controlled conditions (Hobbie 1996). Detailed knowledge of decomposition rates of leaf and root litter of shrubs and graminoids in Siberian tundra is lacking.

Understanding the differences in decomposition rates between PFTs in the Arctic is important because evidence is accumulating that climate warming affects the distribution and abundance of these PFTs (Tape et al. 2006, Hill and Henry 2011, Elmendorf et al. 2012). Shrub expansion has been observed across the tundra biome (Tape et al. 2006, Wookey et al. 2009, Callaghan et al. 2011, Myers-Smith et al. 2011a, Myers-Smith et al. 2011b). These changes in plant species composition will likely lead to differences in the quantity and quality of litter input to the soil, which may affect decomposition rates and thus carbon dynamics (Berendse et al. 1987, Berendse et al. 1989).

Moreover, there are feedbacks among vegetation type and decomposition rates (Ward et al. 2015). Decomposition of plant litter can be up to 70% faster in the species' own habitat compared to a different environment, a phenomenon referred to as "home-field advantage" (Gholz et al. 2000, Strickland et al. 2009, Veen et al. 2015). Home-field advantage effects on decomposition have been observed worldwide (Ayres et al. 2009, Veen et al. 2015), but it is not known whether such effects also exist in tundra ecosystems.

Here, we determined the decomposition rates of leaf and root litter for the two dominant PFTs in Siberian tundra, and tested for home-field advantage effects. We performed a litter transplant experiment, in which leaf and root litter of both PFTs (the deciduous shrub *Betula nana* L. and the graminoid *Eriophorum vaginatum* L.) was incubated in three different vegetation types: shrub-dominated, graminoid-dominated and mixed vegetation. We hypothesized that:

1) The decomposition of shrub litter is slower than that of graminoid litter;

2) Root decomposition is slower than leaf decomposition;

3) Litter of a PFT is decomposed faster in its 'home' vegetation; i.e. home-field advantage in decomposition exists in tundra.

5.2 Material and methods

5.2.1 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 Indigirka River in northeastern Siberia, Russia. The mean annual air temperature at the nearest climate station (Chokurdakh, WMO station code 21946, 27 km away from the study site) is −13.4 ºC (1981 – 2010), with 10.3 ºC as the mean July temperature. Annual precipitation is 196 mm (1981 – 2010), of which on average 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 (Blok et al. 2010, Nauta et al. 2015).

The vegetation surrounding the Chokurdakh Scientific Tundra Station is classified as G4, consisting of tussock-sedges (i.e. graminoids), dwarf-shrubs and moss on the Circumpolar Arctic Vegetation Map (Walker et al. 2005). In the lake bed we distinguished 3 vegetation types: graminoid vegetation dominated by the tussock-forming sedge *Eriophorum vaginatum* L (> 70% cover); shrub vegetation dominated by the deciduous shrub *Betula nana* L (> 70% cover) and a mixed vegetation of both species. Other co-existing species with minor abundances include grasses *Arctagrostis latifolia* (R. Br.) Griseb and *Calamagrostis holmii* Lange, sedge *Carex aquatilis* Wahlenberg, deciduous shrub *Salix pulchra* Cham, evergreen shrubs *Vaccinium vitis-idaea* L and *Rhododendron subarcticum* Harmaja. A moss layer with some lichen species is present throughout the study area (Blok et al. 2010).

5.2.2 Experimental design

We focused on the two dominant plant species, the graminoid *E. vaginatum* and the deciduous shrub *B. nana*. We intended to include both live and dead samples of leaves and roots of the graminoid and shrub. However, as most other root decomposition studies, it was difficult to collect dead shrub roots from the soil. It has been suggested that roots are not likely to shed discretely like leaves, but rather they gradually lose functions and become colonized by decomposers as they age, making it impossible to collect freshly senesced root litter (Hobbie et al. 2010). So we did not include dead shrub roots in this experiment. However, it is possible to collect the dead roots of *E. vaginatum* as its roots are annual and white-colored when alive, and become black after senescence. Thus, seven litter types were included in this experiment. They were: live and dead leaves of graminoids and shrubs, live and dead roots of graminoids, and live roots of shrubs.

Litter of *E. vaginatum* was collected in the graminoid-dominated vegetation, and litter of *B. nana* was collected in the shrub-dominated vegetation. Live leaves of the two species were collected in July of 2013 by clipping leaves from *B. nana* shoots and *E. vaginatum* leaf bases, and dried and stored in dry condition. Dead leaves of the two species were collected in July of 2015 from the ground underneath shrub vegetation or graminoid vegetation, respectively.

Soil cores were taken and roots were collected manually with forceps from the cores. Roots of the two species could be distinguished as roots of *B. nana* had a reddish to brown color, woody structure and were usually colonized by ecto-mycorrhizal fungi, whereas roots of *E. vaginatum* were either white (live) or black (dead), non-woody, unbranched, and densely clustered underneath the tussock (Fig. 1.2). Live fine roots (< 1 mm) of *B. nana* were collected and dried in July 2013 and stored in dry condition. As mentioned above, shrub roots are not likely to shed discretely, so it is possible that the shrub live root samples contained some dead roots. However, when collecting *B. nana* roots, strong efforts were made to distinguish live and dead roots, as live roots were reddish to brown with white newly-grown root tips or mycorrhizal fungi colonization, while dead roots were darker in color and easily torn apart. Thus dead roots should only account for a very minor part of the samples. Live and dead roots of *E. vaginatum* were collected in July 2015. Leaf and root litter that was collected in 2015 was air-dried for 24 hours prior to filling the litter bags.

Plant materials were carefully placed into litter bags, which were 10 × 10 cm made from nylon mesh with a 0.5 mm mesh size (Top Zeven B.V., the Netherlands). Each litterbag contained one type of litter with approximately 0.4 g dry weight. We recorded the exact initial weight of each sample. Initial weights were corrected for their water content using the water contents of additional samples which were dried at 60 ºC one month later in Wageningen University, the Netherlands (see section 5.2.3). To close the litterbags, they were folded and staple-sealed with stainless steel staples.

Litter bags were buried in the three vegetation types: graminoid vegetation dominated by *E. vaginatum*, shrub vegetation dominated by *B. nana* and mixture vegetation co-dominated by the two species. The three vegetation types differ in abiotic factors, with graminoid vegetation higher in soil moisture and exchangeable nutrients (Chapter 3). In the study area, eight blocks were selected in which all three vegetation types were close to each other (3 – 10 m distance). Each block was 40 – 140 m away from the next block. In each of the 24 plots, seven litter bags (representing the different litter types) were buried. In total, we buried 168 litter bags (7 litter types × 8 blocks × 3 vegetation types) on 6 July 2015. Before buried into the soil, they were moderately moisturized for 10 minutes. A spade was used to cut a gap in the soil with a 45˚ angle to the soil surface, and then one litterbag was placed at the depth of 5 cm.

After 38 days, on 13 August 2015, the litterbags were harvested. After the litterbags were gently removed from the soil, organic matter and soil on the surface of the litterbags was carefully brushed off. The litterbags were stored in paper envelops and air-dried in the field, then they were transported to the

Netherlands, where they were oven-dried at 60 ºC for at least 48 hours and weighed. Mass loss was calculated as the difference between the initial dry weight and the final dry weight, divided by the initial dry weight.

5.2.3 Litter quality

Six additional initial samples of each litter type (four samples for shrub fine roots because of limited amount) were used to estimate the initial moisture content (see section 5.2.2). After the determination of initial water content, litter quality of each litter type was analyzed. Three samples of each litter type were used to analyze the initial carbon, nitrogen, phosphorus concentration, and the other three samples (only one sample for shrub fine roots) were used for lignin analysis. Carbon and nitrogen concentrations were determined with an elemental analyzer (Fisons EA 1108 CHN-O). Phosphorus concentration was determined with a segmented flow analyzer (SKALAR SAN Plus System, Breda, The Netherlands) after digestion with H_2SO_4-salicylic acid-H_2O_2 and selenium (Novozamsky et al. 1983). Acid detergent lignin was determined with Ankom 220 Fiber Analyzer (Ankom Technology, USA). C:N, C:P, lignin:N, lignin:P ratios were calculated. Because lignin and N/P concentrations were measured in separate samples, lignin:N and lignin:P ratios were calculated using mean values of lignin and N/P concentrations in each litter type.

5.2.4 Statistical analysis

We used linear mixed effects models (LMM) to take into account that mass loss of samples in the same plot or block are not fully independent. As the experimental design in terms of litter species and dead vs live litter was not fully balanced (because we did not include dead shrub roots), we tested live and dead litter separately. In the model for live litter, vegetation type, PFT and tissue type (leaf, root) were included as fixed effects. In the model for dead litter, vegetation type and litter type (graminoid leaf, graminoid root, shrub leaf) were included as fixed effects. In both models block and plot were included as random effects with a nested structure (plot within block). Mass loss data were ln transformed. Least significant difference (LSD) method was used for post hoc tests when an effect was significant in one of the models.

Litter quality were compared among the seven litter types using a model with litter type as fixed effect, block and plot as random effects with a nested structure for each chemical characteristics. To investigate effects of litter quality on litter mass loss, we used linear models to test for the relationships between the average mass loss of each litter type and chemical characteristics, including nitrogen, phosphorus, lignin concentration, and C:N, C:P, lignin:N, lignin:P ratios. We also calculated the AIC (Akaike information criterion) values and Akaike weight of each model to evaluate which chemical characteristics best explained mass loss. A lower AIC value indicates a better model (Burnham and Anderson 2004), and an Akaike weight is the probability that a model is the actual best model among a set of models (Wagenmakers and Farrell 2004).

5.3 Results

5.3.1 Mass loss of different litter types and vegetation effects

For live litter, differences in mass loss between the two PFTs depended on tissue type (significant interaction of PFT × tissue; Table 5.1). Mass loss of *E. vaginatum* roots was significantly higher than that of *B. nana* roots ($F_{1,21} = 747$, $P < 0.001$; Fig. 5.1a). Leaves of the two PFTs showed a similar mass loss ($F_{1,42} = 0.7$, $P = 0.424$). Vegetation effects on mass loss significantly differed between the two PFTs (significant interaction of PFT × vegetation; Table 5.1): leaf and root litter of *E. vaginatum* had similar mass losses in the three types of vegetation ($F_{2,30}$ = 0.4, P = 0.657), whereas root (but not leaf) litter of *B. nana* had significantly larger mass losses in shrub vegetation than in graminoid vegetation (P = 0.02; Fig. 5.1a).

Table 5.1 Effects of vegetation type, PFT and tissue type (leaf/root) on live litter mass loss

Source	df	*F* value	*P* value
Vegetation	2	1.4	0.259
PFT	1	264.3	< 0.001 *
Tissue	1	40.9	< 0.001 *
Vegetation × PFT	2	4.2	0.019 *
Vegetation × tissue	2	0.8	0.441
PFT × tissue	1	310.4	< 0.001 *
Vegetation × PFT × tissue	2	0.2	0.829

For dead litter, decomposition of different litter types was significantly different (Table 5.2): mass loss of *B. nana* and *E. vaginatum* leaves were significantly higher than *E. vaginatum* roots (P = 0.002 and P < 0.001 respectively; Fig. 5.1b). Similar to live plant tissues, vegetation effects on mass loss of dead plant tissues depended on the PFT (significant interaction of litter type × vegetation; Table 5.2). Dead roots of *E. vaginatum* decayed significantly faster in graminoid vegetation than in shrub vegetation ($F_{2,30}$ = 5.1, P = 0.013), while dead leaves of *B. nana* had significantly larger mass loss in shrub vegetation than in graminoid vegetation ($F_{2,21}$ = 4.5, P = 0.023).

The significant interactions between vegetation and PFT/litter type for live/dead litter show a clear home-field advantage (Table 5.1 and 5.2). Dead graminoid roots decayed significantly faster in graminoid-dominated vegetation, while live roots and dead leaves of shrubs decomposed faster in shrub-dominated vegetation (Fig. 5.1, see also Fig. A5.1).

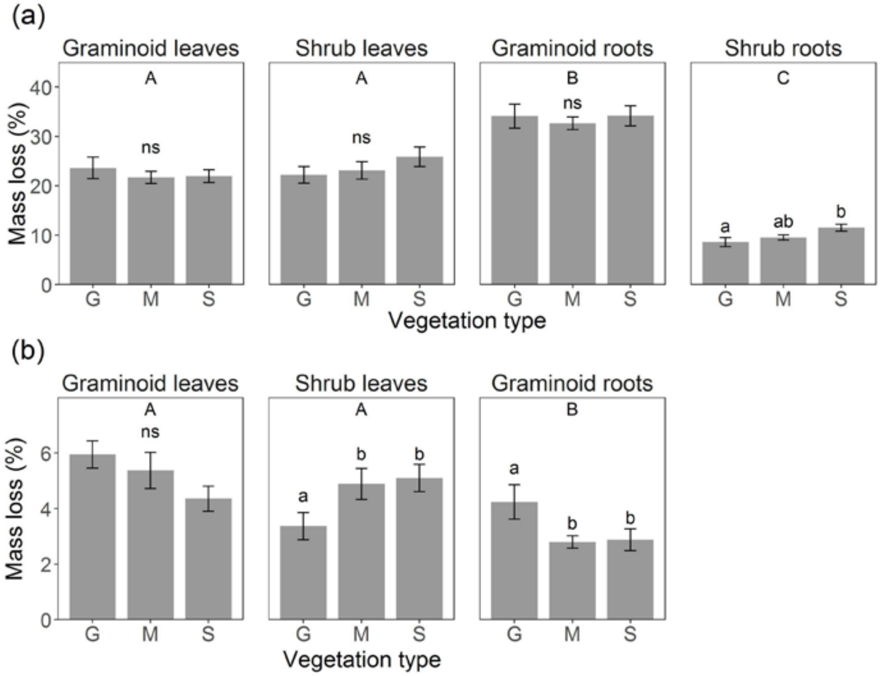

Fig. 5.1 Mass loss of live (a) and dead (b) litter types in three vegetation types: graminoid (G), mixed (M) and shrub (S). Bars are means ± SE, n = 8. Scales of y-axes in (a) and (b) are different as mass loss of dead litter was much smaller. Capital letters represent pairwise differences in mass loss between litter types for live and dead litter respectively; lowercase letters represent pairwise differences in the mass loss of each litter type between vegetation types.

Table 5.2 Effects of vegetation type and dead litter type (shrub and graminoid leaves, graminoid roots) on mass loss

Source	df	*F* value	*P* value
Vegetation	2	0.4	0.697
Litter type	2	12.4	< 0.001 *
Vegetation × litter type	4	4.2	0.005 *

5.3.2 Litter quality

The seven litter types differed significantly in nitrogen, phosphorus and lignin concentrations and related ratios (Table 5.3). In general, shrub litter had higher lignin concentrations than graminoid litter. Not surprisingly, dead litter types showed lower nitrogen and phosphorus concentrations than live litter types, but dead roots and leaves of *E. vaginatum* had particularly low nitrogen and phosphorus concentrations (Table 5.3). Nitrogen concentration differed up to 4.6 fold (between live shrub leaves and dead graminoid roots), whereas phosphorus concentration differed up to 16.9 fold (between live shrub leaves and dead graminoid leaves; see Table 5.3).

The average mass loss of a litter type was closely related to litter characteristics related to phosphorus. Mass loss strongly increased with P concentration, and decreased with N:P and lignin:P ratios (Fig. 5.2). Mass loss also decreased, albeit less clearly, with the lignin:N ratio. No significant relationships between mass loss and nitrogen concentration, C:N ratio and lignin concentration were found (Fig. 5.2). Model comparison revealed that phosphorus concentration and lignin:P ratio were the best predictors for mass loss (Table A5.1).

5.4 Discussion

In contrast to the decomposition of leaf litter, which did not differ between graminoids and shrubs, the decomposition of root litter can be different between the two PFTs. On average, live root litter decomposition was 3 times greater for graminoid roots compared to shrub roots. The possible inclusion of some dead shrub roots in the shrub root samples, might have led to an overestimation of the real difference between the decomposition of graminoid and shrub roots, but our results still highlight the necessity of distinguishing the decomposition of leaf litter and root litter.

Table 5.3 Chemical characteristics of different litter types. Different letters indicate differences between litter types using Tukey HSD post hoc method. N= 3 except for lignin concentration in shrub roots. Lignin:N and lignin:P were calculated with mean values of lignin and N/P concentration as they were from separate samples

Chemical characteristics	Graminoid live leaves	Graminoid dead leaves	Shrub live leaves	Shrub dead leaves	Graminoid live roots	Graminoid dead roots	Shrub live roots
C (%)	45.9 ± 0.2^{ab}	45.7 ± 0.3^{ab}	47.0 ± 3.2^{ab}	50.2 ± 0.4^{a}	43.2 ± 0.2^{b}	46.8 ± 0.2^{ab}	47.4 ± 1.2^{ab}
Lignin (%)	3.4 ± 0.02^{d}	4.7 ± 0.2^{d}	18.9 ± 0.6^{b}	35.3 ± 0.2^{a}	3.2 ± 0.3^{d}	11.4 ± 0.9^{c}	34.6
N (mg g^{-1})	16.5 ± 0.7^{b}	6.5 ± 1.0^{c}	27.2 ± 2.0^{a}	12.8 ± 0.6^{b}	13.3 ± 1.2^{b}	5.9 ± 1.0^{c}	15.1 ± 1.7^{b}
P (mg g^{-1})	2.77 ± 0.05^{c}	0.20 ± 0.02^{f}	3.37 ± 0.01^{a}	0.69 ± 0.05^{e}	3.05 ± 0.03^{b}	0.21 ± 0.02^{f}	1.15 ± 0.05^{d}
N:P	6.0 ± 0.3^{a}	32.0 ± 2.7^{d}	8.1 ± 0.5^{a}	18.8 ± 1.8^{bc}	4.4 ± 0.4^{a}	28.2 ± 4.7^{cd}	13.2 ± 1.2^{ab}
C:N	27.9 ± 1.2^{b}	72.4 ± 11.6^{a}	17.3 ± 0.5^{c}	39.4 ± 2.3^{b}	32.8 ± 3.3^{b}	82.0 ± 13.3^{a}	31.9 ± 4.3^{b}
C:P	166 ± 2^{d}	2277 ± 222^{a}	139 ± 9^{d}	735 ± 53^{b}	142 ± 1^{d}	2212 ± 161^{a}	413 ± 22^{c}
Lignin:N	2.1	7.2	7.0	27.6	2.4	19.2	22.9
Lignin:P	12.5	229.7	56.1	513.5	10.4	535.9	301.1

As root litter constitutes a considerable fraction of organic matter input in this system (Freschet et al. 2013), the difference in root decomposition rates between the two PFTs suggest that vegetation composition is an important factor in the carbon dynamics of tundra ecosystems. This is particularly relevant because climate warming has been shown to induce shifts in vegetation composition (Callaghan et al. 2011, Myers-Smith et al. 2011b). In addition, we provide the first evidence for home-field advantage in litter decomposition in Arctic tundra and we also show that litter phosphorus concentrations are the main driver of mass loss at our study site, indicating phosphorus is the main nutrient limiting microbial activity in this area.

5.4.1 Decomposition of leaves and roots of PFTs

The decomposition of leaf litter did not differ between the two PFTs. This was true for both dead and live leaves. However, decomposition of root litter might differ between the two PFTs, although we have to take into account the uncertainty due to the possible inclusion of dead roots in the shrub root samples. These results only partly confirm our first and second hypothesis and they suggest that we need to consider the differences between tissue types and PFTs at the same time.

Shrub litter is generally thought to be less decomposable than graminoid litter, as the former has a higher lignin concentration (Hobbie 1996, Cornelissen et al. 2007, Zhang et al. 2008). In our study, this is only the case for root litter, as leaf litter of the two PFTs exhibited similar mass loss rates. The difference in the decomposition of live roots between the two PFTs suggests that root decomposition in tundra can differ between shrubs and graminoids, at least in the early stage. These results emphasize that it is important to consider root litter separately from leaf litter when comparing PFTs, even if the decomposition of leaf litter does not show differences.

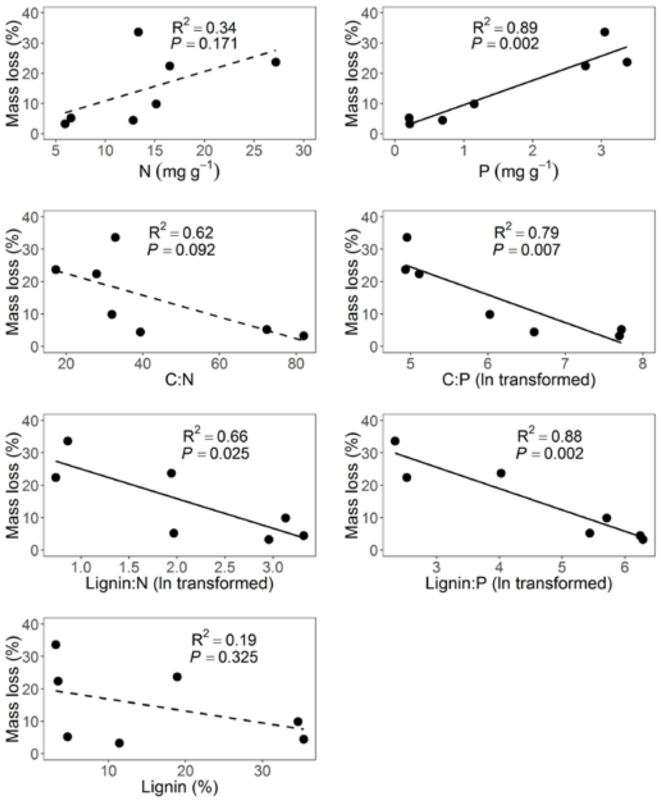

Fig. 5.2 Relationships between mass loss of the seven litter types and their chemical characteristics. Solid lines represent significant relationships while dashed lines represent insignificant relationships. Relationships between mass loss and litter quality were particularly strong for P-related characteristics (right column). Symbols show average mass loss (n = 24) and chemical characteristic (n = 1 for lignin content of shrub dead roots and lignin:N, lignin:P; n = 3 for other characteristics; see Table 5.3) values.

Many studies showed that leaf litter is more decomposable than root litter as roots contain more chemically recalcitrant substances (Gorissen and Cotrufo 2000, Freschet et al. 2012, Freschet et al. 2013, Ma et al. 2016). In our study this is only partly true, as live graminoid leaves were decomposed slower that its live roots. However, dead graminoid leaves were decomposed faster than its dead roots. It illustrates that conclusions about decomposition based on live litter of different plants should be treated with caution, especially if species differ in characteristics such as nutrient resorption efficiency (Scheffer and Aerts 2000, Snyder and Rejmánková 2015). Since root death is hard to determine (Eissenstat and Yanai 1997), the advantage of using live roots is that they better represent roots that have not yet started to decay (Hobbie et al. 2010). It may be more realistic to use live roots for long-term decomposition experiments, as live roots become real litter in the course of the experiments.

5.4.2 Effects of vegetation and litter quality on decomposition

Decomposition of both PFTs tended to be faster in the vegetation in which they were dominant. This led to significant home-field advantage effects in our study. We found these effects for roots and dead leaves shrubs and for dead graminoid leaves, even though there are big differences in decomposability between these litter types. In fact, in our study the site effects are more significant for dead than for live materials, confirming the hypothesis that litter with low decomposability requires more specialized decomposers (Ayres et al. 2009, Milcu and Manning 2011). The graminoid and shrub vegetation in our study differ in abiotic factors, as the former is wetter and more nutrient-rich (Chapter 3). However, the lack of overall vegetation effects on decomposition suggests that the environmental factors are not decisive in this experiment. Instead, the different environmental conditions may help to shape different microbial communities that are acclimated to decompose the litter of the dominant species of each vegetation type, resulting in home-field advantage effects in litter decomposition (Wallenstein et al. 2007). It has to be noted that all the litterbags were buried at 5 cm in this experiment. Since graminoids grow roots deeper than shrubs at the study site (Chapter 3), a large part of graminoid roots are decomposed in the deeper soil at lower temperatures. Therefore our results do not mean that overall root decomposition is slower in shrub vegetation, as the natural root decomposition occurs at different soil depths between the two vegetation types.

Litter quality (e.g., nitrogen and lignin concentrations, C:N ratio) is one of the most important factors in decomposition from grassland to forest ecosystems (Cornwell et al. 2008, Zhang et al. 2008, Freschet et al. 2012). It is well known that nitrogen and phosphorus are the best predictors during the early stage of decomposition, while lignin is the best predictor during later stages (Berg and McClaugherty 2014). In our study, traits related to phosphorus content were identified as the main drivers of early litter decomposition, suggesting that the early phases of decomposition are phosphorus-limited. This finding agrees with another study at the same site (Beermann et al. 2014), which suggested that mineralization is limited by phosphorus. However, the relatively low N:P ratios of live plant samples in our study (7.9 ± 1.1; Table 5.3) suggest that for plants nitrogen is likely more limiting, as Koerselman and Meuleman (1996) suggested that a N:P ratio lower than 14 indicates nitrogen limitation for plant growth. The explanation for the limitation of microbial growth and plants growth by different elements could be that the accessibility to phosphorus is different between microbes and plants. While microbes in the shallow soil are limited by phosphorus, graminoids can exploit the deep soil, where larger amounts of bioavailable phosphorus are available (Chapin et al. 1978, Beermann et al. 2014). Shrubs can depend on mycorrhizal fungi to absorb phosphorus from the deep soil (Bolan 1991, Landeweert et al. 2001).

5.4.3 Implications for carbon dynamics in tundra

For a long time there has been concern that tundra ecosystems might shift from a carbon sink to a carbon source with warmer climates (Oechel et al. 1993, Belshe et al. 2013, Webb et al. 2016). A warmer climate increases primary productivity of tundra vegetation and thus increases carbon uptake by the ecosystem (Verbyla 2008, Hill and Henry 2011, Epstein et al. 2012). On the other hand, higher temperatures also accelerate decomposition and thus increase carbon emission from the soil (Hobbie 1996, Davidson and Janssens 2006). The balance between the two changes will determine whether tundra ecosystems will be a carbon sink or source. The two changes can also be affected by vegetation shifts induced by climate warming. The home-field advantage in litter decomposition in our study suggests that litter decomposition rates may be temporarily reduced when vegetation shifts occur. However, whether this reduction in decomposition due to home-field advantage can at least temporarily offset the increase in decomposition due to climate warming needs further investigation.

Shifts in vegetation composition also affect decomposition via changes in litter quality (Cornelissen et al. 2007). Focusing on the aboveground part of the ecosystem, our study provides little evidence for such effects, as the decomposability of leaf litter did not differ between the two PFTs in our study. However, root litter decomposition could be lower for shrubs, at least in the early stage. This means that shrub expansion with increasing temperatures could reduce decomposition and increase carbon storage. However, the latter also depends on litter input. Estimates for root litter input of different PFTs are scarce, but the available data suggest that root turnover rates of shrubs are lower in tundra (Shaver and Chapin 1991, Mack et al. 2004, Sullivan et al. 2007). This could at least partly counteract the effects of shrub expansion on soil carbon storage. Moreover, graminoids grow roots deeper than shrubs (Miller et al. 1982, Shaver and Chapin 1991), and thus part of the graminoid roots are decomposed at lower temperatures, which can make the decomposition of graminoid roots even slower than shrub roots.

The finding of almost intact graminoid roots in yedoma (windblown dust, deposited during the glacial age) permafrost also suggests that graminoid roots can be decomposed very slowly in the deep soil (Zimov et al. 2006). So far the effects of vegetation shifts on decomposition and the carbon balance remain unresolved.

5.5 Conclusion

Our study shows that it is important to consider root decomposition to understand carbon dynamics in tundra ecosystems. Although leaf litter decomposition did not differ between PFTs, root litter decomposition showed important differences. Differences in litter decomposability could be mainly attributed to traits related to phosphorus. In addition, we show that home-field advantage effects may lead to a temporary reduction in litter decomposition when vegetation shifts occur. Accurate determination of the balance between litter input and decomposition for different PFTs in a changing climate would enhance our understanding of potential climate – vegetation feedbacks and its consequences for carbon cycling.

5.6 Acknowledgements

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5.7 Appendices

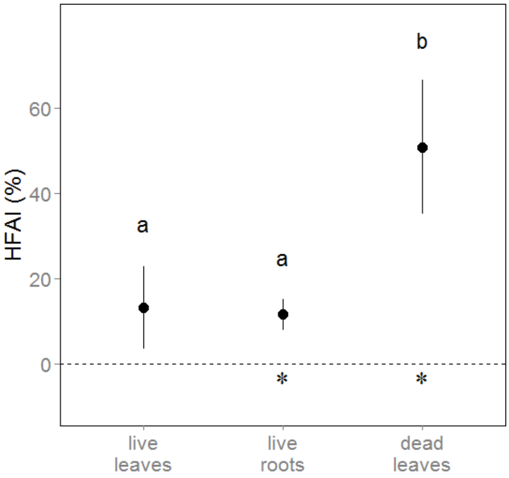

Fig. A5.1 Home-field advantage index (HFAI) of litter from different tissue types. Letters above error bars indicate pairwise differences between litter types. Dotted line represents zero level of HFAI. Asterisks indicate HFAIs that are significantly different from zero. Symbols with error bars show mean ± SE, n = 8 blocks. HFAIs were calculated following the method described in Ayres et al. (2009):

$$A_{RMLa} = \frac{A_a}{A_a + B_a} \times 100$$

$$\mathrm{HFAI} = \left[\frac{A_{RMLa} + B_{RMLb}}{2} / \frac{A_{RMLb} + B_{RMLa}}{2}\right] \times 100 - 100$$

in which A_{RMLa} is the relative mass loss of species *A* at site *a*, A_a and B_a are the percent mass loss of species *A* and *B* at site *a*. This formulation controls for inherent habitat differences in decomposition, i.e., in one habitat the decomposition of most litter may be faster than in other habitats. Note that this formulation only tests for the presence of HFA at the site and it does not quantify the HFA for an individual species. To calculate the HFA for individual species requires three or more reciprocally transplanted species (Ayres et al. 2009), which is beyond the scope of this study. Mass loss data in shrub vegetation and graminoid vegetation were used to calculate the HFAIs within each block. HFAIs for live and dead leaf, and live roots were determined separately. To test if the HFAI for each litter type is significantly larger than zero and if it differed significantly between tissue types, we ran a linear mixed model with litter type as fixed effect and block as random effect.

Table A5.1 Comparison of the regression models of mass loss and chemical characteristics using AIC values and Akaike weights

Model parameter	Log-likelihood	AIC	ΔAIC	Akaike weight
N	6.95	−7.91	12.38	0.001
P	13.15	−20.29	0.00	0.479
Lignin	6.26	−6.52	13.77	0.001
C:N	7.69	−9.38	10.91	0.002
C:P (ln transformed)	11.68	−17.36	2.93	0.111
Lignin:N (ln transformed)	9.31	−12.63	7.66	0.010
Lignin:P (ln transformed)	12.95	−19.91	0.38	0.396

6

Synthesis

Global climate has been warming rapidly for the last half century, and the Arctic warms about twice as fast as the global average (ACIA 2005, IPCC 2013), which has large impacts on Arctic tundra ecosystems. Climate warming increases the thaw depth of permafrost in the summer (Hinkel and Nelson 2003, Romanovsky et al. 2010, Park et al. 2016), which accelerates the release of the carbon that is stored in the permafrost, and triggers a positive feedback with climate warming (Schuur et al. 2015). Moreover, climate warming lengthens the growing season in the Arctic (Schwartz et al. 2006, Høye et al. 2007), stimulates the aboveground primary productivity of Arctic tundra (Verbyla 2008, Forbes et al. 2010, Epstein et al. 2012), and changes vegetation composition with deciduous shrubs being observed to expand across the tundra biome (Stow et al. 2004, Tape et al. 2006, Frost and Epstein 2014).

Although the aboveground productivity of tundra vegetation has been found to increase with climate warming, the responses of the belowground parts are largely unknown. In tundra vegetation the majority of vascular plant biomass is belowground (Poorter et al. 2012, Iversen et al. 2015). Roots play a critical role in plant competition, particularly in tundra where nutrients often limit plant growth (Chapin 1987, Chapin et al. 1995). Different plant functional types (PFTs) differ greatly in their root traits such as rooting depth and traits related to morphology (Mack et al. 2004, Iversen et al. 2015), litter input and quality (Hobbie 1996, Gill and Jackson 2000, Silver and Miya 2001). Therefore, changes in vegetation composition and plant biomass allocation with climate warming can have large impacts on ecosystem functioning and plant-soil-atmosphere feedbacks. In this thesis I investigated the climate warming effects on the belowground biomass of tundra vegetation, as well as the role roots can play in the vegetation shifts caused by warmer climates.

We performed both an analysis of published data and three field studies. We synthesized published data on belowground vascular plant biomass across the tundra biome, and compared the biomass – temperature relationships for the aboveground and belowground of tundra vegetation. We did a field investigation to compare the seasonal changes in root biomass and vertical root distribution of different PFTs in different tundra vegetation types. In a thawing and fertilization experiment we investigated the role of vertical root distribution in the responses of tundra plants to environmental changes. Furthermore, we compared the decomposition rates of leaves and roots of graminoids and shrubs in different tundra vegetation types.

As a first step, we analyzed the relationship between annual air temperature and reported above and belowground biomass of tundra plant communities across different tundra locations, spanning a gradient of −20 to 0 °C in mean annual air temperature (Chapter 2). We found a clear positive relationship between the temperature and aboveground biomass. This was not the case for belowground biomass. The biomass – temperature relationship differed significantly between above and belowground biomass. It is possible that the lack of community-level belowground biomass responses to temperature might obscure contrasting species- or PFT-level responses. In the limited number of tundra root studies, one study showed that the increases of *Carex bigelowii* and *Betula nana* root biomass in response to experimental warming were offset by the decrease of *Eriophorum vaginatum* root biomass, resulting in a minor change in total belowground biomass at the community level (Hobbie and Chapin 1998). It highlights the importance of distinguishing the responses of different PFTs in future studies. Even if climate warming has minor community-level effects on belowground biomass, different PFT-level responses also matter as their roots differ in their ecosystem functions such as turnover and decomposability.

In order to improve our understanding of PFT-level differences in root biomass and rooting patterns, we investigated the seasonal changes in root biomass and vertical root distribution patterns of shrubs and graminoids in graminoid-dominated, shrub-dominated and mixture vegetation types at a Siberian tundra site (Chapter 3). We found that although total belowground biomass differed significantly, fine root biomass was similar among the three vegetation types in the late growing season. However, graminoids and shrubs showed different spatio-temporal rooting patterns. Shrubs grow roots in the very early growing season and exploit mainly the shallow soil, while graminoids continue to grow roots later in the growing season, and exploit the deeper soil layers. The separate niches of graminoids and shrubs in both time and space can promote their coexistence (Berendse 1981, McKane et al. 2002). It also suggests that changes in the spatio-temporal distribution of nutrients with climate warming can shift the competitive relationships between graminoids and shrubs.

Through a 4-year soil thawing and fertilization experiment, we examined the effects of increased thawing depth and nutrient availability in the top soil on the aboveground and belowground biomass of various PFTs and the role that vertical root distribution plays in plant responses (Chapter 4). We show that shallow-rooted plants (deciduous and evergreen shrubs) benefited from the increased nutrient availability in the top soil, while only deep-rooted plants (sedges) benefited from increased thawing depth. The deep-rooted grasses had the highest plasticity in terms of vertical root distribution in response to thawing and fertilization, which helped them also to benefit from the increased nutrient availability in the top soil, and may help them be more competitive in a more erratic climate scenario. These results confirm that different rooting strategies of PFTs play an important role in plant competition and vegetation shifts in tundra.

Shrub expansion may become more widespread in tundra ecosystems as long as nutrient availability increases mainly in the top soil. The effects of shrub expansion on carbon dynamics in tundra ecosystems also depend on the differences in the decomposition rates of graminoid and shrub litter, particularly root litter, which is still largely unknown so far. We performed a plant litter transplant experiment to compare the decomposition of roots and leaves of *E. vaginatum* and *B. nana* in different vegetation types. The results show that despite the similarities in leaf decomposability, the decomposition rate of roots may differ between the two species in the early stage, which was driven by phosphorus concentration of litter (Chapter 5). We also find evidence of home-field advantage in plant litter decomposition in Arctic tundra.

Based on the results of this thesis, below I provide an overview of how vegetation composition can change in a future warmer climate and how carbon dynamics can be influenced by climate warming and vegetation shifts, as well as the knowledge gaps that need future studies.

6.1 Vegetation shifts in a warmer future

Shrub expansion has been observed across the tundra biome (Callaghan et al. 2011, Myers-Smith et al. 2011b), which is hypothesized to result from climate warming. However, the exact mechanisms behind shrub expansion are still unclear. Multiple factors, such as temperature, precipitation, nutrient availability, length of growing season, and their interactions, can influence plant growth and competition (Hobbie and Chapin 1998, Shaver et al. 1998, Walker et al. 2003a, Forbes et al. 2010, Blok et al. 2011). Based on the finding of Chapter 3 of this thesis, shrubs differ from graminoids both in the period and duration of root growth and in vertical root distribution. Shrubs grow roots in the very early growing season and are shallow-rooted, while graminoids grow roots for a longer period during the growing season and are deep-rooted. Probably shrubs can get advantages from the early and shallow root growth when snowmelt and soil thaw begin and release nutrients to the top soil. However, the future competitive relationship between shrubs and graminoids may depend on the balance between the benefits they can get from increased nutrient availability in the top soil and in the deeper soil, respectively (Chapter 4).

Warmer climates can facilitate litter decomposition, which will probably be more significant in the top soil where organic matter content is higher (Tarnocai et al. 2009, Baughman et al. 2015) and temperature increases probably are larger than deeper in the soil. In this case shrubs can benefit more than graminoids from the increased nutrient availability in the top soil through their shallow root systems. The recent widespread shrub expansion in tundra ecosystems suggests that this is the most likely vegetation shift in most tundra areas at least in the near future.

However, when organic matter content is high in the deep soil, nutrient availability in the deeper soil can also be increased substantially in warmer climates, which will favor deep-rooted graminoids. It has been shown that increased thawing depth can increase nutrient availability in the deep soil and that deep-rooted graminoids can take up these newly available nutrients (Keuper et al. 2012b, Oulehle et al. 2016). In addition, warmer but dry climates may dry up the top soil (Hinzman et al. 2005, Smith et al. 2005), which can inhibit microbial decomposition (Aerts 2006, Hicks Pries et al. 2013), and thus decrease the nutrient availability in the top soil. Under such conditions shrubs will be less competitive while graminoids can still absorb the nutrients in the deeper soil and become more competitive.

Another important factor that can influence plant competitive relationships is soil moisture, as graminoids and shrubs generally differ in their preferred soil moisture condition. Graminoids such as *E. vaginatum* prefer wet conditions while shrubs such as *B. nana* prefer moist, but well-drained soils (Wein 1973, De Groot et al. 1997). It is predicted that precipitation will increase with climate warming (IPCC 2013), however, soil moisture depends not only on precipitation, but also on the thawing of the ice in the permafrost, evapotranspiration and microtopography, which could make the vegetation responses more spatially heterogeneous. If ice-rich permafrost thaws with climate warming, increasing the soil water content, the vegetation will become more graminoid-dominated (Blok et al. 2010, Nauta et al. 2015). However, if the melt water is drained, for example in discontinuous permafrost zones (Frost and Epstein 2014), climate warming can also reduce soil moisture as evapotranspiration increases, which will make shrubs able to establish and dominate the site.

In conclusion, this thesis highlights the importance of spatio-temporal nutrient distribution in the soil for tundra vegetation shifts in a warmer future, as graminoids and shrubs differ in their root seasonal development and vertical distribution. In the meanwhile, changes in soil moisture also need to be taken into account to better predict possible vegetation shifts.

6.2 Influences of climate warming and shrub expansion on carbon dynamics

With climate warming, tundra might shift from a net carbon sink to a net carbon source (Oechel et al. 1993, Belshe et al. 2013, Webb et al. 2016). Warming climates can influence both carbon uptake by the vegetation and carbon release from the soil. Warmer climates can increase plant primary productivity, and hence carbon uptake of tundra vegetation (Verbyla 2008, Hill and Henry 2011, Epstein et al. 2012). On the other hand, warmer climates can also accelerate the decomposition of soil organic matter and thus increase carbon emission from the soil (Hobbie 1996, Davidson and Janssens 2006). The balance between the warming effects on productivity and decomposition will determine the carbon balance of tundra ecosystems in the future. Moreover, vegetation change induced by climate warming can also influence carbon dynamics through shifts in carbon assimilation capacity and litter input and quality, which can have both positive and negative feedbacks on climate warming effects on carbon dynamics in tundra ecosystems (Fig. 6.1 and Fig. 6.2).

6.2.1 Climate warming effects on carbon dynamics

Climate warming increases total aboveground biomass as well as leaf biomass of tundra vegetation (Chapter 2), which has also been shown by remote sensing studies and experimental warming experiments (Arft et al. 1999, Walker et al. 2006, Verbyla 2008, Epstein et al. 2012), suggesting that carbon storage in the aboveground parts of tundra vegetation increases with climate warming. On the one hand, increased leaf biomass can increase carbon uptake of tundra vegetation through more photosynthesis. On the other hand, it can be assumed that increased leaf biomass also increases leaf litter input to the soil surface, particularly leaf litter of deciduous shrubs, which has greater decomposability than evergreen leaves (Cornwell et al. 2008). Therefore, carbon emission from the decomposition of leaf litter will also increase with climate warming through both higher temperature and increased leaf litter input.

Total belowground and fine root biomass may not increase much with climate warming as our results suggest (Chapter 2). Therefore carbon storage in belowground biomass may not change. Carbon emission from root litter decomposition depends on root litter input, which further depends on root turnover rate. However, root turnover is still largely unknown for tundra plants. Some studies investigated warming effects on root production of tundra graminoids, and showed that warming increased graminoid root production (Sullivan and Welker 2005, Sullivan et al. 2008). This suggests that root turnover in tundra is likely to be accelerated by climate warming, at least for graminoids. According to studies of other ecosystems, shrub root turnover might increase with higher temperatures (Gill and Jackson 2000, Kitajima et al. 2010). But knowledge of shrub root production and turnover in tundra is still lacking, making it difficult to estimate root litter inputs and the impacts of warming effects.

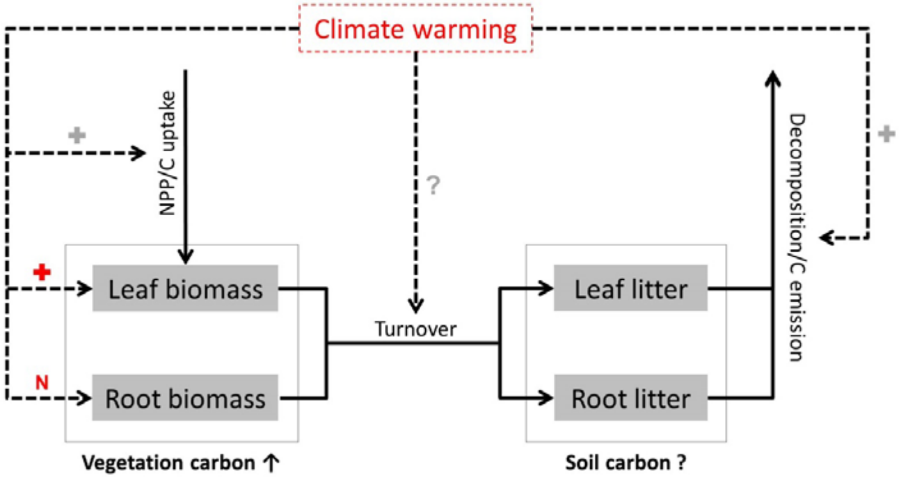

Fig. 6.1 Schematic diagram of climate warming effects on carbon dynamics in tundra ecosystems. Plus signs represent positive effects, minus signs represent negative effects, N represents neutral effects, and question marks represent unclear effects. Signs with red color indicate the finding of this thesis; signs with grey color indicate effects assumed from literature.

If permafrost thaw does not increase nutrient availability much, climate warming may only have minor effects on plant root biomass and vertical root distribution (Chapter 4). However, permafrost itself contains a huge amount of organic carbon that has accumulated for thousands of years, which will be mobilized by climate warming and emitted from the soil (Zimov et al. 2006, Schuur et al. 2009).

Therefore, climate warming will probably accelerate carbon cycling in tundra ecosystems through increased carbon uptake of plants and increased carbon emission from litter decomposition and thawing permafrost. However, the net effect of climate warming on these two fluxes still needs to be determined.

6.2.2 Effects of shrub expansion on carbon dynamics

In addition to directly influencing tundra carbon dynamics, climate warming can also indirectly influence carbon dynamics through induced vegetation change in tundra ecosystems (Cornelissen et al. 2007, Knapp et al. 2008). If recently observed shrub expansion continues in tundra ecosystems, carbon dynamics will be further affected.

For the aboveground, as shrub vegetation has similar leaf biomass as graminoid vegetation (Chapter 3), shrub expansion and the replacement of graminoids may not increase leaf litter input. But this is based on the assumption that leaf turnover rates are the same for shrubs and graminoids. *E. vaginatum*, the graminoid species that this thesis focuses on, has an average life span of two years (Wein 1973), which is longer than the deciduous shrub leaves. This also implies that leaf production (carbon uptake) is higher in deciduous shrubs than in graminoids with perennial leaves. Since shrub expansion is mostly observed for deciduous shrubs such as *B. nana*, shrub expansion can increase leaf production and litter input if it happens in an area dominated by graminoids with perennial leaves. Increased leaf litter input will possibly increase carbon emission through the decomposition of the extra leaf litter, as the decomposition rate of leaves is similar between graminoid and shrub (Chapter 5), which was also found by some other studies (Thormann et al. 2001, Quested et al. 2003, Hobbie and Gough 2004, Moore et al. 2007). Although some other studies suggested that shrub leaves can decay slower than graminoid leaves (Hobbie 1996, Cornelissen et al. 2007), our results implies that, at least at our research site, if shrub expands and replaces graminoids, carbon emission from leaf decomposition will increase.

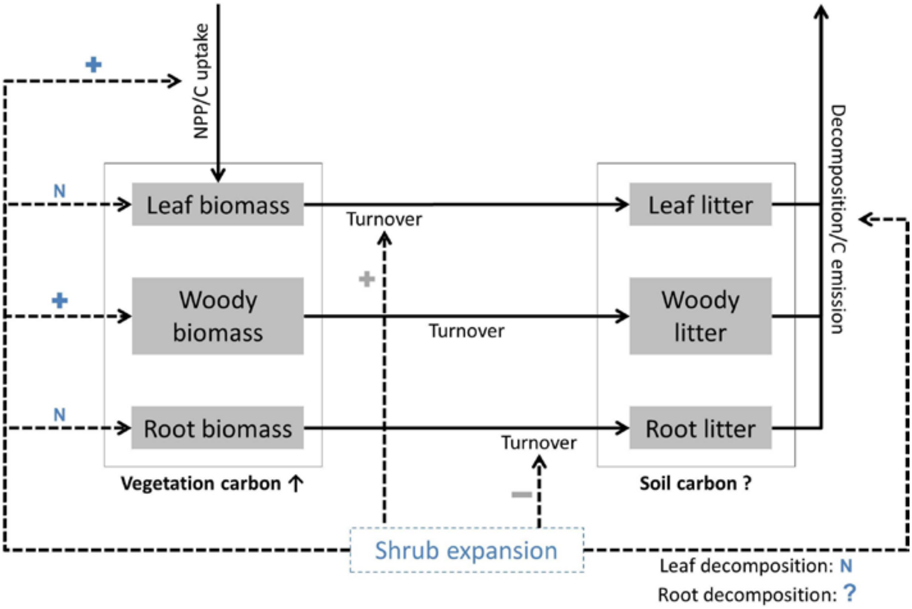

Fig. 6.2 Schematic diagram of shrub expansion effects on carbon dynamics in tundra ecosystems. Plus signs represent positive effects, minus signs represent negative effects, Ns represent neutral effects, and question marks represent unclear effects. Signs with blue color indicate the finding of this thesis; signs with grey color indicate effects assumed from literature.

For the belowground, shrub expansion is not likely to increase fine root biomass since it is similar between the graminoid-dominated vegetation and shrub-dominated vegetation (Chapter 3). However, root litter input also depends on root turnover rate. Although studies on root turnover rates of tundra shrubs are lacking, root turnover of shrubs possibly is slower than that of graminoids (Shaver and Chapin 1991, Mack et al. 2004, Sullivan et al.

2007), particularly when compared to *E. vaginatum*, which has an annual root system (Wein 1973). Therefore, root litter input can also be reduced by shrub expansion, thereby limiting the carbon emission from root decomposition, which is just opposite to what happens aboveground. Shrub root litter may be less decomposable than graminoid root litter (Chapter 5). A possible consequence is that an increasing proportion of shrub root biomass may slow down root decomposition through less litter input and lower decomposability, thereby reducing carbon emission. However, since shrubs grow roots shallower than graminoids (Chapter 3–4), overall shrub roots are decomposed in the shallower soil at higher temperatures, which can offset the effects of the possible lower decomposability and turnover rates of shrub roots. Moreover, the difference in long-term root decomposition between graminoids and shrubs is not clear yet.

Despite that leaf and fine root biomass is not likely to increase with shrub expansion, a large portion of shrub biomass lies in the woody stems and coarse roots (Chapter 3–4), with very low turnover and decomposability (Hobbie 1996, Cornelissen et al. 2007). Therefore shrub expansion can increase the carbon stock by storing carbon in shrub stems and coarse roots. One study showed that 20 years experimental warming increased plant biomass and woody dominance but did not change soil carbon storage, resulting in a net increase in ecosystem carbon storage (Sistla et al. 2013). Whether this can be extrapolated to larger scales needs further studies.

6.3 Future research needs

Although our results suggest that tundra vegetation may not respond much to climate warming in total belowground biomass, species or plant functional type specific responses can be different. We have shown that fine root biomass did not differ much between the different tundra vegetation types at the research site, but the spatio-temporal rooting patterns of PFTs did differ. This implies that they have different abilities to use the increased nutrient availability and soil thaw depth. However, we are still far from drawing a general picture of how the roots of different PFTs in tundra will respond to climate or experimental warming when they grow together, which highlights the necessity to distinguish different PFTs in future root studies in tundra.

We have also shown that plant competitive relationships depended on the relative changes in nutrient availability in the top soil and in the deeper soil. In addition to nutrient availability, soil moisture is another very important factor that determines root growth. Furthermore, soil moisture can affect microbial activities and thus affect nutrient availability, thereby influencing plant competition. There are not many studies about the moisture effects on vegetation shifts in tundra yet. Since climate warming induces permafrost thaw and shifts in precipitation and evapotranspiration regimes, soil moisture condition are expected to change significantly. Therefore it is urgently needed for future tundra studies to take soil moisture into account.

We found that there may be important differences in root decomposition of different PFTs. The possible changes in the species composition of root biomass with climate warming can influence tundra carbon dynamics through shifted decomposability of root litter. However, so far we know little about root production, root turnover and root litter decomposition in tundra ecosystems, particularly for shrubs, which are expanding across the tundra biome. As roots account for a large part of plant standing biomass and litter input into the soil in tundra ecosystems, it is essential to acquire more knowledge on these subjects for a better understanding of climate warming effects on the carbon balance of tundra ecosystems.

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Summary

Global climate has been warming up for the last decades and it will continue in this century. The Arctic is the part of the globe that warms fastest and is more sensitive to climate warming. Aboveground productivity of Arctic tundra has been shown to increase in response to warmer climates. However, belowground responses of tundra vegetation are still unclear. As the major part of plant biomass in tundra lies belowground, it is pivotal to investigate changes in the belowground parts of tundra vegetation for our understanding of climate warming effects on tundra ecosystems.

To get a general idea of how belowground plant biomass may change in a warmer climate, we synthesized published data on the belowground biomass of tundra vegetation across a broad gradient of mean annual air temperature from −20 to 0 °C. We found that aboveground biomass of tundra biomass indeed increases with mean annual temperature as well as summer air temperature, while belowground biomass did not show a significant relationship with temperature. The increases in the aboveground biomass were significantly larger than belowground biomass, resulting in reduced below/above ratios at higher temperatures. The shifted biomass allocation with temperature can influence the carbon dynamics of tundra ecosystems. Future tundra studies need to focus more on the species or functional type composition of belowground biomass and species or functional type specific belowground responses to climate warming.

To determine the seasonal changes and vertical distribution of root biomass of different plant functional types, we sampled roots at a Siberian tundra site in the early and late growing season, from vegetation types dominated by graminoids and shrubs respectively. We distinguished the roots of graminoids and shrubs, and found that shrub roots grew earlier and

shallower than graminoid roots, which enables shrubs to gain advantage over graminoids at the early growing season when nutrient pulses occur during snowmelt and soil thaw. The deeper roots of graminoids can help them to be more competitive if climate warming induces more nutrient release in the deeper soil.

In a soil thawing and fertilization experiment, we further investigated the effects of increased thawing depth and nutrient supply in the upper soil, which can be the consequences of climate warming, on root biomass and its vertical distribution. In this study we distinguished between the roots of grasses, sedges, deciduous shrubs and evergreen shrubs. The study was done in a moist tussock tundra site with similar abundance of the different plant functional types. We found that only sedges benefited from the increased thawing depth, probably through their deepest root distribution among the four functional types, while the shrubs, which were shallower-rooted, benefited from the increased nutrient availability in the upper soil. The deep-rooted grasses had the highest plasticity in vertical root distribution, which enabled them also to benefit greatly from the fertilization. Our results show that tundra plants with different rooting strategies can show different responses to climate warming dependent on the relative warming impacts on the nutrient supply in shallow and deeper soil layers. This insight can help to predict future tundra vegetation dynamics.

The carbon balance of tundra ecosystems also depends on the decomposition of plant litter, particularly the root litter, which may account for a larger part of annual litter input than leaf litter in tundra ecosystems. Vegetation shifts also change litter quality which ultimately influences carbon dynamics. To investigate the differences in the decomposition of leaves and roots of graminoids and shrubs, we performed a litter transplant experiment. We found that although the decomposability of leaf litter did not differ between the graminoid and shrub, root decomposability might be lower for the shrub.

However, this cannot be extrapolated to the overall decomposition in different vegetation types, as these different plant communities differ in rooting depths. We also found evidence of home-field advantage in the decomposition in Arctic tundra, and we show that the early stage of litter decomposition at our research site could be driven by the phosphorus concentration of the litter. To get a full understanding of the carbon balance of tundra ecosystems, much more efforts are needed to quantify litter input and decomposition.

In this thesis we show that belowground parts, which account for a major part of plant biomass in tundra, can show a different response to climate warming from aboveground parts. Belowground responses to climate warming can have crucial impacts on the competitive balance between tundra plants, and consequently result in vegetation shifts in tundra. Such shifts in species composition can have large effects on carbon dynamics through altered input and decomposability of plant litter, particularly root litter.

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About the author

Peng Wang was born on 5th October 1986 in Cangshan, a small town in Sichuan province, China, where he spent his childhood and attended primary school and junior middle school. After living in his hometown for fifteen years, he attended senior middle school in Mianyang, Sichuan, which is one hundred kilometers away. From 2005 he studied biology in Beijing Normal University and got his Bachelor degree. Then at the same university he studied ecology and got his Master degree in 2012. For his MSc thesis he studied root responses to nutrient heterogeneity of two tree species in competition. He afterwards started his PhD study in Wageningen University, the Netherlands and continued his research on roots, but in a cold region. After extensive searching and reading of literature about roots in tundra ecosystems, three summer visits to northeastern Siberia, and intensive data-analyzing and article-writing, he accomplished this thesis in 2016.

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