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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°C 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.

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°C – 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 (Schoor *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, 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. Methods

2.1. Data collection

2.1.1. Community biomass

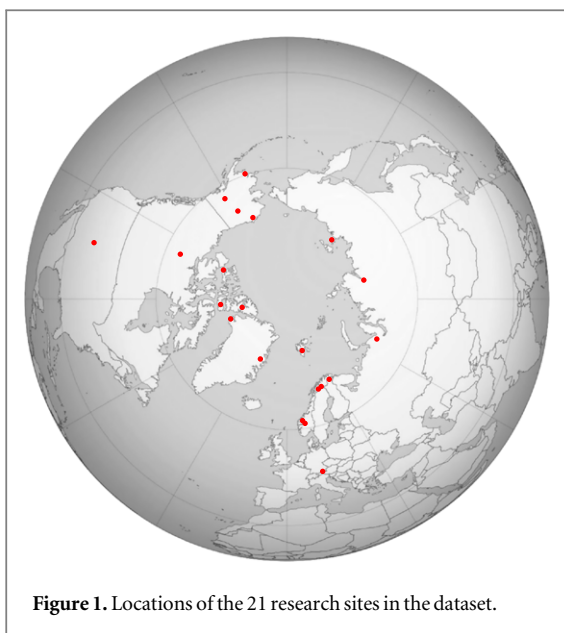
We searched for published journal articles and book chapters with belowground plant biomass data obtained from both experimental and observational studies in both Arctic and alpine tundra. In total 104 cases from 46 studies at 28 research sites were found (supplementary tables A1–A3), with each case 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 (figure 1, supplementary tables A1–A3). 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.

2.1.2. 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.

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* 2012). 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. 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).

3. Results

Total belowground plant biomass was significantly higher than aboveground biomass (853 ± 93 versus $259 \pm 51 \text{ g m}^{-2}$), 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 1). Aboveground biomass clearly increased with MAT (figure 2(a), $F_{1,12.8} = 13.2$, $P = 0.003$), but belowground biomass only tended to increase (figure 2(b), $F_{1,8.3} = 4.2$, $P = 0.072$) 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 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 (figure 2(c), $F_{1,8.2} = 0.26$, $P = 0.625$). Aboveground and belowground biomass had very similar relationships with summer temperature to that they had with MAT (supplementary table A4): aboveground biomass increased significantly with ST ($F_{1,31.3} = 22.2$, $P < 0.001$), but belowground biomass did not show a significant relationship ($F_{1,28.6} = 2.1$, $P = 0.159$).

On average, about 75% of total biomass was belowground and 45% was fine root (belowground fraction

Table 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 *	$R^2_m = 0.52$
	MAT	4.2	1	11.5	0.007 *	$R^2_c = 0.71$
	Vegetation part \times 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	$R^2_m = 0.47$
	MAT	4.0	1	9.4	0.006 *	$R^2_c = 0.55$
	Vegetation part \times MAT	11.5	1	26.9	<0.001 *	
Fine root/aboveground ratio	MAT	4.9	1	8.6	0.029 *	$R^2_m = 0.43$ $R^2_c = 0.70$

0.76 ± 0.02 , fine root fraction 0.47 ± 0.08). The belowground/aboveground ratio tended to decrease with MAT (figure 2(d), table 1), and decreased significantly with ST (supplementary table A4). The fine root/aboveground ratio decreased significantly with MAT and ST (figure 2(e), table 1).

Including the relative abundance of shrubs as a covariate did not change the relationships between biomass and MAT (supplementary table A5). 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 (supplementary table A5). Similar results were found for fine root biomass and fine root/aboveground ratio (supplementary table A5).

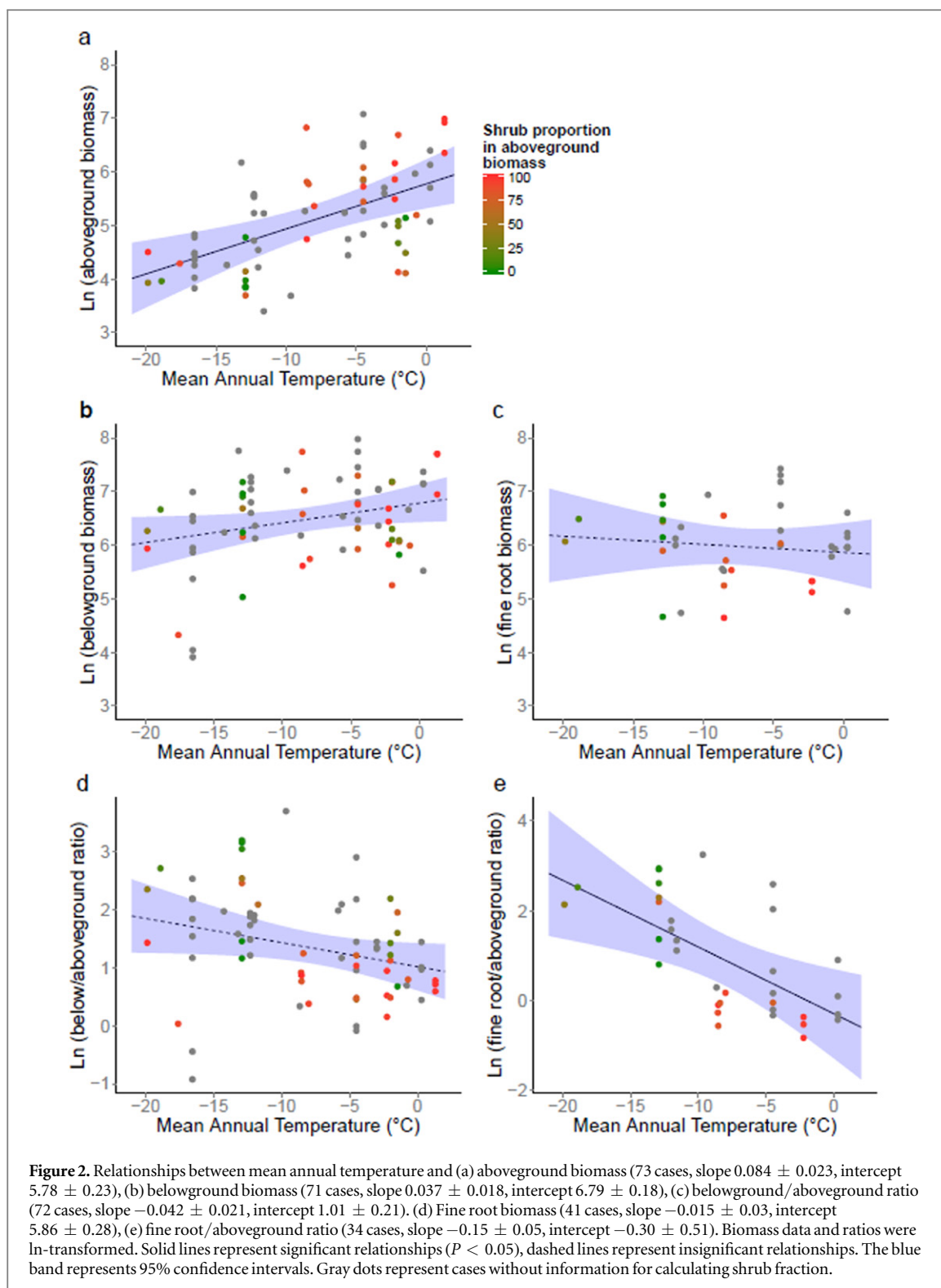
4. Discussion

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 MAT, 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 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 ($\sim 50\%$ 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 (figures 2(d) and (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.

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, 1962b, 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, 1962b). 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* 2003, 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 MAP, 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* 2012, 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.

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, Bassirrad *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 (supplementary table A1). 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.

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.

5. Conclusions

Our meta-analysis of 36 field studies spanning a MAT gradient from -20°C 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.

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