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Abstract

In tundra ecosystems, global warming is expected to accelerate litter decomposition and to lead to shifts in vegetation composition. To understand these shifts, it is important to understand the interactions between global warming, vegetation composition, litter quality and decomposition in the tundra. In addition, it is important to consider root litter since roots are the major part of plant biomass in the tundra. In order to increase our understanding of decomposition, and root decomposition in particular, we performed a litter transplant experiment in northeastern Siberia, in which we measured mass loss for leaf and root litter (live and dead material) of the two dominant plant species, graminoid *Eriophorum vaginatum* and shrub *Betula nana*, in three vegetation types (*E. vaginatum* or *B. nana* dominated and mixed vegetation) during the growing season.

Our results show that although leaf decomposition did not differ between the two species, root decomposition showed significant differences. Mass loss of live roots was higher for *E. vaginatum* than for *B. nana*, but mass loss of *E. vaginatum* dead roots was lowest. In addition, we found evidence for home-field advantage in litter decomposition: litter of a plant decomposed faster in vegetation where it was dominant. Mass loss rates of the litter types were significantly correlated with phosphorus content, rather than nitrogen content. This indicates that phosphorus limits decomposition in this tundra site.

The low decomposition rate of *B. nana* live roots compared to *E. vaginatum* live roots suggests that the acceleration of decomposition in the Arctic may be partly counteracted by the expected expansion of shrubs. However, 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, *Betula nana*, *Eriophorum vaginatum*, home-field advantage, leaf litter, root litter

1. Introduction

Arctic soils are an important global carbon reservoir, as half of the terrestrial belowground organic carbon pool is sequestered in the northern circumpolar soil (Tarnocai et al., 2009).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 has been estimated that decomposition of plant litter accounts for half of the terrestrial carbon release into the atmosphere (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, strongly limiting decomposition of plant litter. However, due to climate change, temperature has already increased by about 1 ºC in the last century and is predicted to further increase by 2 – 8 ºC this century (IPCC, 2013; Jones et al., 2012). Consequently, Arctic tundra soils will be warmer, permafrost will thaw and decomposition of organic carbon will be accelerated (Cornelissen et al., 2007; Davidson and Janssens, 2006; 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 high nutrients and low lignin content decays faster than litter with low nutrients and high lignin content (Freschet et al., 2012; Zhang et al., 2008). In most studies, nitrogen appears to be the most important nutrient limiting decomposition, but phosphorus content has also been found to be related to decomposition (Cornwell et al., 2008; Enriquez et al., 1993). Litter decomposition can differ substantially between plant species or plant functional types (PFTs) within the same ecosystem. In the tundra, the main PFTs are dwarf shrubs and graminoids. Generally, it is thought that shrub litter is less decomposable than graminoid litter, as the former has a higher lignin concentration (Cornelissen et al., 2007; Hobbie, 1996; Zhang et al., 2008).

Decomposition rates may also differ between different plant tissues of the same species. For example, root litter generally decays slower than leaf litter (Birouste et al., 2011; Bryant et al., 1998;

Fujii and Takeda, 2010; Ma et al., 2016; Robinson et al., 1997; Thormann et al., 2001). In Arctic tundra, up to 70% of plant biomass is allocated belowground (Iversen et al., 2015; Poorter et al., 2012; Wang et al., 2016a). This high fraction suggests that root litter is a major source of carbon input and root litter decomposition is likely to be an important component of the carbon cycle in this ecosystem. However, detailed information about differences in root litter decomposition rates among species or PFTs in the field is scarce. Hobbie (1996) and Robinson et al. (1999) showed that root and/or leaf litters of graminoid species decomposed faster than those of shrub species, but these experiments were performed under controlled conditions.

Understanding the differences in decomposition rates between PFTs is particularly relevant in the Arctic as both recent observations and experimental researches show that climate warming affects the distribution and abundance of the different PFTs (Elmendorf et al., 2012; Hill and Henry, 2011; Tape et al., 2006). Shrub expansion has been observed in many tundra ecosystems (Callaghan et al., 2011; Myers-Smith et al., 2011a; Myers-Smith et al., 2011b; Tape et al., 2006; Wookey et al., 2009). Such changes in plant distribution and abundance will likely lead to differences in the quantity and quality of litter input into the soil, which may affect decomposition rates and thus carbon cycling (Aerts, 2006; Berendse et al., 1989; Berendse et al., 1987; Cornelissen et al., 2007).

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., 2015a). Home-field advantage effects on decomposition have been observed worldwide (Ayres et al., 2009; Veen et al., 2015a), but have rarely been studied in tundra ecosystems. One study we know determined home-field advantage in a sub-arctic tundra ecosystem but found no support for it (Veen et al., 2015b).

Here, we determined the decomposition rates of leaf and root litter for the two dominant species, representing the main PFTs in Siberian tundra, and tested for home-field advantage effects. We performed a litter transplant experiment, in which leaf and root litters of both the graminoid

Eriophorum vaginatum L. and the deciduous shrub *Betula nana* L. were incubated for five weeks during the growing season in three different vegetation types: *E. vaginatum*-dominated, *B. nana*-dominated, and mixed vegetation. We hypothesized that:

1. The decomposition rate of root litter is lower than that of leaves,
2. The decomposition rate of *E. vaginatum* litter is lower than that of *B. nana*,
3. Differences in decomposition rates between litter types and species are related to litter quality,
4. Litter of a species decomposes faster in its own vegetation (i.e. home-field advantage occurs).

2. Material and methods

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, 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 (20 – 45 cm) active layer (the soil layer that thaws in the summer) 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: vegetation dominated by the tussock-forming sedge *E. vaginatum* (> 70% cover); vegetation dominated by the deciduous shrub *B. nana* (> 70% cover) and a mixed vegetation of both species (Wang et al., 2016b). Other co-existing species with minor abundances include the grasses *Arctagrostis latifolia* (R. Br.) Griseb and *Calamagrostis holmii* Lange, the sedge *Carex aquatilis* Wahlenberg, the deciduous shrub *Salix pulchra* Cham, the evergreen shrubs *Vaccinium vitis-idaea* L and *Rhododendron subarcticum*

119 Harmaja. A moss layer with some lichen species is present throughout the study area (Blok et al.,
120 2010).

121

122 *2.2. Experimental design*

123 We focused on the two dominant plant species from different PFTs, the graminoid *E. vaginatum*
124 and the deciduous shrub *B. nana*. For *E. vaginatum* it was possible to collect dead roots as its roots are
125 mostly annual (Chapin, 1974; Sullivan et al., 2007; but see Iversen et al., 2015) and white-colored
126 when alive, and become black after senescence. Roots of E. vaginatum grow from the base of the tiller
127 and are unbranched with a uniform diameter of ~ 1 mm along the length, so all E. vaginatum roots
128 were considered fine roots. In addition, B. nana roots are usually ectomycorrizal while E. vaginatum
129 roots are non-mycorrhizal (Iversen et al., 2015). We also included senesced leaves of *E. vaginatum*
130 (referred to as dead leaves here) to compare the decomposition leaf and root litter of this species. It
131 was impossible to collect shrub root litter (*B. nana* dead roots) from the soil, because roots are not
132 likely to shed discretely like leaves, but rather gradually lose functions and become colonized by
133 decomposers as they age (Hobbie et al., 2010). Hence, for *B. nana* we only could collect live fine roots
134 (< 1 mm in diameter) (referred to as live roots in the text). To reliably compare root and leaf
135 decomposition for *B. nana*, we also included leaves that were alive at the time of sampling (e.g. green;
136 referred to as live leaves here). To reliably compare decomposition of the two species, we also
137 included live leaves and live roots of *E. vaginatum*, and dead leaves of *B. nana*. In total we included
138 seven litter types in this experiment: live and dead leaves of *E. vaginatum* and *B. nana*, live and dead
139 roots of the *E. vaginatum*, and live roots of *B. nana*.

140 Due to logistic constraints, the litters were collected in different years and dried differently (see
141 Table S1 for an overview). Three litter (live leaves of *E. vaginatum* and *B. nana*, and live roots of *B.*
142 *nana*) were collected in July 2013 from the 8 blocks where the litter bags would be buried in (see
143 below). *E. vaginatum* live leaves were collected in the *E. vaginatum* dominated vegetation, and *B.*
144 *nana* live leaves and live roots were collected in *B. nana* dominated vegetation. Live leaves of the two
145 species were collected by clipping leaves from leaf bases of *E. vaginatum* and *B. nana* shoots. Live

146 fine roots of *B. nana* were collected by taking soil cores from the *B. nana* dominated vegetation and
147 picking out roots manually with forceps (Wang et al., 2016b). As mentioned above, *B. nana* roots are
148 not likely to shed discretely, so it is possible that the roots from *B. nana* classified as 'alive' contained
149 some dead roots. However, when collecting *B. nana* roots, roots that were darker in color and easily
150 torn apart were excluded. Thus, dead roots should only account for a very minor part of the samples.
151 The samples collected in 2013 were oven dried at 65 ºC for 72 h after collection and stored in dry
152 conditions until the start of the decomposition experiment.

153 The other four litter types (live leaves, dead leaves and dead roots of *E. vaginatum*, and dead leaves
154 of *B. nana*) were collected in July 2015 at a location close to the experimental plots. Dead leaves of
155 the two species were collected from the ground underneath the *E. vaginatum* dominated or *B. nana*
156 dominated vegetation, respectively. As dead leaves of *B. nana* on the soil surface were probably
157 recently shed, we collected dead *E. vaginatum* leaves that were still standing up-right (assuming that
158 older dead leaves would be lying close to the ground) to minimize the age difference of the two
159 species' leaf litter we collected. Live and dead roots of *E. vaginatum* were collected in the center of
160 tussocks formed by *E. vaginatum*. Roots of *E. vaginatum* were either white (live) or black (dead), non-
161 woody, unbranched, and densely clustered underneath the tussock. The samples collected in July 2015
162 were air-dried around 10 ºC for 24 hours prior to filling the litter bags.

163 These differences in collection time and processing could potentially affect our results. To take this
164 into account, we focused on pairwise comparisons of litter collected in the same year (e.g. dead leaves
165 of *B. nana* and *E. vaginatum*) as much as possible. In the discussion, we will critically evaluate the
166 potentially confounding effects of differences in collection time and processing on our conclusions.

167 *E. vaginatum* leaves and roots, both live and dead, were cut to pieces of 3 – 5 cm long to fit in the
168 litter bags. Samples of each litter type were mixed and then carefully placed into litterbags, which
169 were 10×10 cm made from nylon mesh with a 0.5 mm mesh size (Top Zeven B.V., the Netherlands).
170 Each litter bag contained one type of litter with approximately 0.4 g dry weight. We recorded the
171 initial weight of each sample before putting it to a litter bag. To close the litter bags, they were folded
172 and staple-sealed with stainless steel staples.

Litter bags were buried in the three vegetation types. The three vegetation types differ in abiotic factors, with *E. vaginatum* vegetation higher in soil moisture (volumetric moisture content 51%, 39%, 24% in the late growing season, for *E. vaginatum*, mixture, and *B. nana* vegetation respectively) and exchangeable nutrients (total inorganic N 55, 30, 26 μg g^{-1} resin, available P 5, 3, 3 μg g^{-1} resin, K 124, 90, 50 μg g^{-1} resin, for *E. vaginatum*, mixture, and *B. nana* vegetation respectively; see Wang et al., 2016b). 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 being buried into the soil, the litter bags were moderately moisturized for 10 minutes. A spade was used to cut a gap in the soil with a 45˚ angle to the moss surface, and then one litter bag was placed at a depth of 5 cm from the moss surface to the upper edge of the litter bag.

After 38 days, on 13 August 2015, the litter bags were harvested. After the litter bags were gently removed from the soil, organic matter and soil on the surface of the litter bags was carefully brushed off. The litter bags were stored in paper envelopes 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. To determine the water content of each litter type in the initial weight, additional six samples of each litter type (four samples for *B. nana* live roots, see section 2.3), with known initial weight at the time of filling the litter bags, were oven-dried and weighed at Wageningen University, the Netherlands, and then average water contents were calculated. Initial weights were corrected for their water content when calculating mass loss.

2.3. Litter quality

To determine the relationship between decomposition and litter quality, the chemical composition of the seven litter types was determined. For each litter type, six samples (four for *B. nana* live roots due to a limited amount of samples) were taken to measure the initial tissue moisture content (see

section 2.2) and litter quality. Three samples of each litter type were then used to analyze the initial carbon, nitrogen, and phosphorus concentration. The other three samples (one sample for *B. nana* live 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 and P concentrations were measured in separate samples, lignin:N and lignin:P ratios were calculated using mean values of lignin and N and P concentrations in each litter type.

2.4. Calculations and statistical analysis

Mass loss data of the tissue types which we had for both species, i.e., live leaves, live roots, and dead leaves of the two species, were used to test HFA. Home-field advantage (HFA) was calculated following the method described in Ayres et al. (2009):

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

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

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*. HFAIs were calculated separately for live and dead leaf, and live root litter for each block in the field. The formula 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 formula only tests for the presence of a general 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.

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 plant material was not fully balanced (because we did not include *B. nana* dead roots), we tested live and dead plant material separately. In the model for live leaves and roots, vegetation type, species and tissue type (leaf, root) were included as fixed effects. In the model for dead leaves and roots, vegetation type and litter type (*E. vaginatum* leaf, *E. vaginatum* root, *B. nana* 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 significance difference (LSD) method was used for post hoc tests when an effect was significant in one of the models.

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.

Litter quality was compared among the seven litter types using a model with litter type as fixed factor, block and plot as random factors with nested structure for each chemical characteristic. To determine relationships between litter quality and litter mass loss, linear regression models were fitted to the average mass loss of each litter type, using important chemical characteristics, including nitrogen, phosphorus, lignin concentration, and C:N, C:P, lignin:N, lignin:P ratios as predictors. We also calculated the AIC (Akaike information criterion) values and Akaike weight of each model to evaluate which chemical characteristics best explained mass loss. The lowest AIC indicates the most preferable among a set of models based on the goodness of fit and the number of parameters (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).

3. Results

3.1. Mass loss of leaf and root litter and home-field advantage

When focusing on live leaves and roots, differences in mass loss between the two species depended on tissue type (roots vs. leaves; significant interaction of species × tissue; Table 1). Leaves of the two species showed a similar mass loss ($F_{1,42}$ = 0.7, P = 0.424), but mass loss of *E. vaginatum* live roots

was significantly higher than that of *B. nana* live roots ($F_{1,21}$ = 747, P < 0.001; Fig. 1a). Vegetation type effects on mass loss significantly differed between the two species (significant interaction of species × vegetation; Table 1): live leaves and roots of *E. vaginatum* had similar mass losses in the three types of vegetation ($F_{2,30}$ = 0.4, P = 0.657), whereas live roots (but not leaves) of *B. nana* had significantly larger mass losses in *B. nana* vegetation than in *E. vaginatum* vegetation ($F_{2,21}$ = 4.2, P = 0.03; Fig. 1a).

Table 1

Effects of vegetation, species and tissue (leaf/root) on live litter mass loss.

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

When focusing on dead leaves and roots, decomposition of different litter types was significantly different (Table 2): mass loss of *B. nana* and *E. vaginatum* leaves was similar, but both were significantly higher than *E. vaginatum* roots (P = 0.002 and P < 0.001 respectively; Fig. 1b). Similar to live plant tissues, vegetation type effects on mass loss depended on species (significant interaction of litter type × vegetation; Table 2). Dead roots of *E. vaginatum* decayed significantly faster in *E. vaginatum* vegetation than in *B. nana* vegetation ($F_{2,30}$ = 5.1, P = 0.013), while live roots and dead leaves of *B. nana* had significantly larger mass loss in *B. nana* vegetation than in *E. vaginatum* vegetation ($F_{2,21}$ = 4.5, P = 0.023). As indicated by these significant interactions between vegetation type and species, we found a clear home-field advantage for our litter types. This effect was significantly greater than zero for live roots and dead leaves (see Fig. S1).

Table 2

Effects of vegetation and dead litter type (*E. vaginatum* and *B. nana* leaves, *E. vaginatum* 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 *

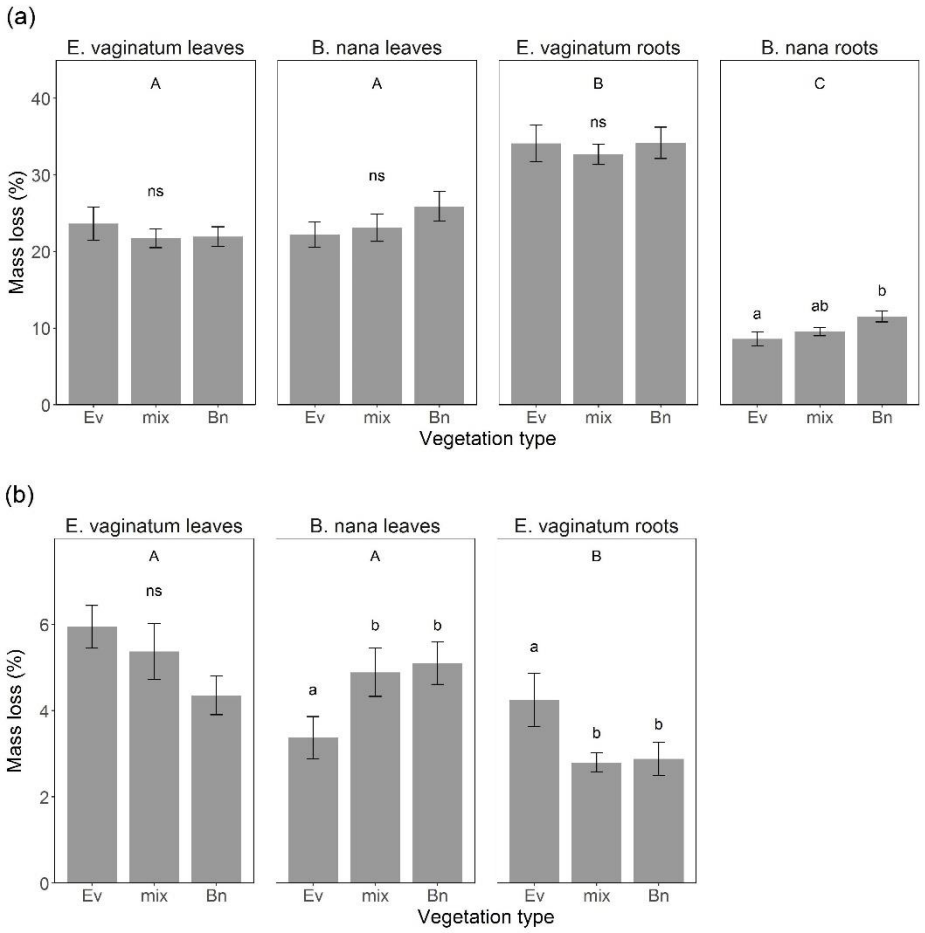


Fig. 1. Mass loss of live (a) and dead (b) litter types in the three vegetation types: *E. vaginatum* (Ev), mixed (mix) and *B. nana* (Bn). Bars are means ± SE, n = 8. Scales of y-axes in (a) and (b) are different as mass loss of dead litter was much smaller. Capital letters represent significant ($P < 0.05$) pairwise differences in mass loss between litter types for live and dead litter respectively; lowercase letters represent significant ($P < 0.05$) pairwise differences in mass loss between vegetation types within litter types.

3.2. Relations between mass loss and litter quality

The seven litter types differed significantly in nitrogen, phosphorus and lignin content and related ratios (Table 3). In general, *B. nana* litter was characterized by higher lignin concentrations than litter of *E. vaginatum.* Not surprisingly, dead plant material showed lower nitrogen and phosphorus concentrations than live plant material, but dead roots and leaves of *E. vaginatum* had particularly low nitrogen and phosphorus contents (Table 3). Across all litter types, nitrogen content differed up to 5 fold (between *B. nana* live leaves and *E. vaginatum* dead roots), whereas phosphorus content differed up to 17 fold (between *B. nana* live leaves and *E. vaginatum* dead leaves; Table 3).

The average mass loss of a litter type was significantly related to litter characteristics involving phosphorus. Mass loss significantly increased with increasing P concentration, and decreased with the C:P and lignin:P ratios (Fig. 2). Mass loss also significantly decreased, albeit weaker, with the lignin:N ratio. No significant relationships between mass loss and nitrogen concentration, C:N and lignin concentration were found (Fig. 2). Model comparisons revealed that phosphorus concentration and lignin:P were the best predictors for mass loss of the different litters in the tundra (Table S2).

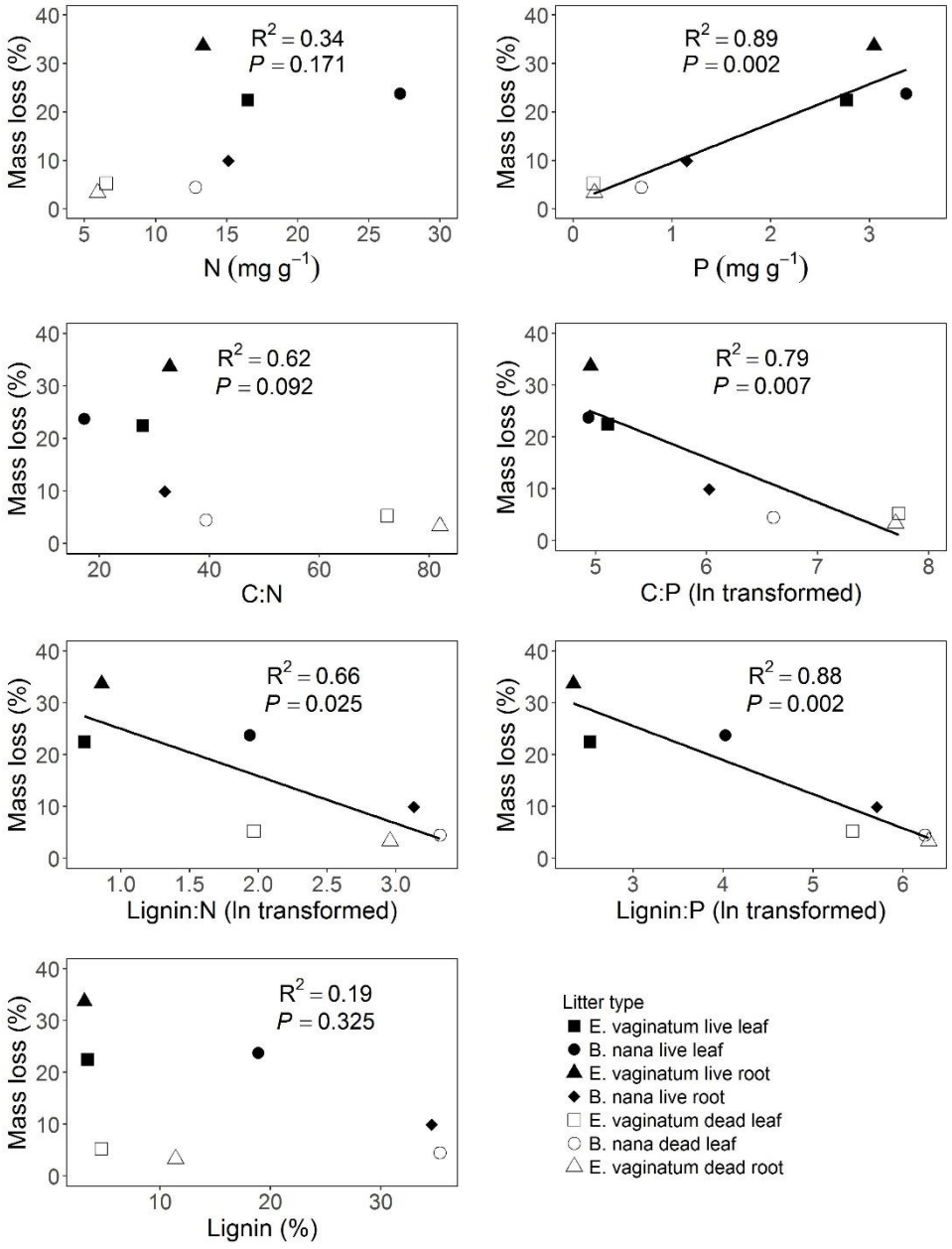
Table 3

Initial chemical characteristics of the different litter types. Different letters indicate differences between litter types using Tukey HSD post hoc method. N= 3 except for lignin concentration in *B. nana* 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	*E. vaginatum* live leaves	*E. vaginatum* dead leaves	*B. nana* live leaves	*B. nana* dead leaves	*E. vaginatum* live roots	*E. vaginatum* dead roots	*B. nana* live roots
C (%)	45.9 ± 0.2^{ab}	45.7 ± 0.2^{ab}	47.0 ± 2.6^{ab}	50.2 ± 0.3^{a}	43.2 ± 0.1^{b}	46.8 ± 0.2^{ab}	47.4 ± 1.0^{ab}
Lignin (%)	3.4 ± 0.02^{d}	4.7 ± 0.1^{d}	18.9 ± 0.5^{b}	35.3 ± 0.2^{a}	3.2 ± 0.3^{d}	11.4 ± 0.8^{c}	34.6
N (mg g^{-1})	16.5 ± 0.6^{b}	6.5 ± 0.8^{c}	27.2 ± 1.6^{a}	12.8 ± 0.5^{b}	13.3 ± 1.0^{b}	5.9 ± 0.9^{c}	15.1 ± 1.4^{b}

P (mg g^{-1})	2.77 ± 0.04^{c}	0.20 ± 0.02^{f}	3.37 ± 0.01^{a}	0.69 ± 0.04^{e}	3.05 ± 0.03^{b}	0.21 ± 0.01^{f}	1.15 ± 0.04^{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 ± 1.0^{b}	72.4 ± 9.4^{a}	17.3 ± 0.4^{c}	39.4 ± 1.8^{b}	32.8 ± 2.7^{b}	82.0 ± 10.9^{a}	31.9 ± 3.5^{b}
C:P	166 ± 2^{d}	2277 ± 181^{a}	139 ± 8^{d}	735 ± 44^{b}	142 ± 1^{d}	2212 ± 132^{a}	413 ± 18^{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

305



306

307 **Fig. 2.** Relationships between mass loss of the seven litter types and their initial chemical
308 characteristics. Relationships between mass loss and litter quality were particularly strong for P-related
309 characteristics (right column). Symbols show average mass loss (n = 24) and chemical characteristic
310 values (n = 1 for lignin content of *B. nana* dead roots and lignin:N, lignin:P; n = 3 for other
311 characteristics; see Table 3).

4. Discussion

The decomposition of root litter was different between the two species, in contrast to the decomposition of leaf litter. The differences in mass loss rate among the litter types were significantly correlated to phosphorus content, not to nitrogen content. In addition, we found evidence for home-field advantage in litter decomposition: litter of the two species decomposed faster in vegetation in which they were dominant. As root litter constitutes a considerable fraction of the organic matter input in this system (Freschet et al., 2013), the difference in root decomposition rates between the two dominant species at the research site suggests that changes in carbon dynamics with vegetation shifts in tundra ecosystems will largely depend on root decomposition.

4.1. Decomposition of leaves and roots of the two species

The decomposition of leaf litter did not differ between the two species. This was true for both dead and live leaves. However, the decomposition of live roots was significantly different between the two species, although we cannot exclude a potential small effect of the inclusion of some *B. nana* dead roots in the 'live' root samples, which might have led to an overestimation of the difference between the decomposition of *E. vaginatum* and *B. nana* roots. These results only partly confirm our hypotheses that root decomposition is slower than leaf decomposition and that the decomposition of *B. nana* litter is slower than that of *E. vaginatum* litter, and they suggest that we need to consider the differences between tissue types and species or PFTs, as PFTs are a reasonable classification of major plant species in the tundra (Chapin et al., 1996), at the same time.

Shrub litter is generally thought to be less decomposable than graminoid litter, as the former has a higher lignin concentration and C:N ratio (Cornelissen et al., 2007; Hobbie, 1996; Zhang et al., 2008). In our study, this is only the case for root litter, as leaf litter of the two species exhibited similar mass loss rates. *B. nana* leaves had higher nitrogen and phosphorus concentrations than *E. vaginatum* leaves, however, the former also had higher lignin concentration, which could offset the positive effects of higher nutrient concentrations on the litter decomposition.

Mass loss of live roots of the two species showed large difference. *B. nana* fine roots in our samples are mainly first- and second-order roots, which fact could make the actual decomposition of the whole root system a bit higher, as some studies found that lowest order roots decay slower that higher order roots (Fan and Guo, 2010; Goebel et al., 2011). However, the lower turnover rates of higher order roots (McCormack et al., 2015) make it unlikely to offset or reverse this difference we found. Therefore, we suggest that root decomposition in the tundra can differ between shrubs and graminoids, at least in the early stage of decomposition for the two dominant species. However, in the later stages of decomposition the differences may change, as the decomposition of *E. vaginatum* dead roots decreased drastically. Our results emphasize that it is important to consider root litter separately from leaf litter when comparing different species or PFTs, even when the decomposition of leaf litter does not show differences.

Many studies have shown that root litter is less decomposable than leaf litter as roots contain more chemically recalcitrant substances (Freschet et al., 2012; Freschet et al., 2013; Gorissen and Cotrufo, 2000; Ma et al., 2016). In our study this is only partly true, as *E. vaginatum* live leaves were decomposed slower than its live roots. However, the dead leaves of the *E. vaginatum* decomposed faster than its dead roots. This discrepancy between live and dead plant material when comparing leaf and root decomposition illustrates that live roots may not necessarily be a good predictor of dead root decomposition, particularly for *E. vaginatum* roots, and that conclusions about decomposition based on live tissues 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).

Litter quality (e.g., nitrogen and lignin concentration, C:N ratio) is one of the most important factors in decomposition from grassland to forest ecosystems (Cornwell et al., 2008; Freschet et al., 2012; Zhang et al., 2008). It is well known that nutrient concentrations, particularly nitrogen, are among 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 litter decomposition, suggesting that at least the early phases of

365 decomposition are phosphorus-limited. This finding is consistent with another study (Beermann et al.,
366 2014) which suggested that at the research site nitrogen mineralization and fixation by bacteria are
367 limited by phosphorus availability. On the other hand, according to Koerselman and Meuleman
368 (1996), an N:P ratio below 14 indicates nitrogen limitation for plant growth. The low N:P ratio of
369 green leaves in our study (6.0 – 8.1; Table 3) suggests that plant growth was limited by nitrogen
370 availability. The explanation for the limitation of microbial growth and plants growth by different
371 elements could be that the accessibility to phosphorus is different for them. While microbes in the
372 shallow soil are limited by phosphorus, graminoids can exploit the deep soil, where larger amounts of
373 phosphorus are available (Beermann et al., 2014; Chapin et al., 1978). Shrubs can depend on
374 mycorrhizal fungi to absorb phosphorus from the deep soil (Bolan, 1991; Landeweert et al., 2001).
375 Efficient phosphorus resorption by plants from senescing plant parts could be another explanation of
376 the phosphorus limitation of microbes. However, we could not examine this hypothesis with our data
377 as the dead leaves/roots were not freshly senesced and we do not know to what extent the massive
378 differences in phosphorus concentration and N:P can be attributed to plant resorption and microbial
379 mobilization, respectively.

380

381 *4.2. Home-field advantage effects on decomposition*

382 Decomposition of both species tended to be faster in the vegetation in which they were dominant,
383 i.e. in their 'own' vegetation, suggesting home-field advantage effects in our study. Home-field
384 advantage was significant for *B. nana* (for roots and dead leaves) and *E. vaginatum* (dead leaves), even
385 though there are big differences in decomposability between these litter types. In fact, in our study the
386 site effects are stronger for dead than for live tissue (i.e. stronger for tissues with lower
387 decomposability; see Fig S1), consistent with the idea that litter with low decomposability requires
388 more specialized decomposers (Ayres et al., 2009; Milcu and Manning, 2011). However, in a subarctic
389 tundra in northern Sweden, Veen et al. (2015b) found no significant home-field advantage in the
390 decomposition of leaf litter. The reason could be that in their experiment they used a mixture of litters

391 from different plant species, therefore the HFA effect at the species level, as shown in our study, could
392 be masked by the community level measurement.

393 The *E. vaginatum* and *B. nana* vegetation in our study differ in abiotic factors. *E. vaginatum*
394 vegetation is wetter and more nutrient-rich than the *B. nana* vegetation (Nauta et al., 2015; Wang et
395 al., 2016b). However, the lack of overall vegetation effects on mass loss suggests that abiotic factors
396 are not decisive in our experiment. Instead, the different environmental conditions may have shaped
397 different microbial communities, that also determine the home-field advantage effects in litter
398 decomposition (Wallenstein et al., 2007).

399

400 *4.3. Influences of the collection years and drying of litter*

401 As mentioned in the methods, there were differences in litter collection and processing between
402 live and dead plant material. All live materials, except *E. vaginatum* live roots, were collected in 2013,
403 dried at 65°C and stored until the decomposition experiment, whereas all dead materials were
404 collected in 2015 and air-dried. *E. vaginatum* live roots were collected in 2015, together with the
405 collection of dead materials, and air-dried. This could potentially affect our results, but we avoided
406 this problem by drawing conclusions based on comparisons of litter types collected in the same year
407 (i.e., with the same drying process). The only exception are the live roots. *E. vaginatum live* roots were
408 collected in 2015, whereas those of *B. nana* were collected in 2013. This could potentially affect our
409 first conclusion that root decomposition differs between *E. vaginatum* and *B. nana*. To check this, we
410 compared the initial P and N concentrations in *E. vaginatum* live roots of both years (a small amount
411 of *E. vaginatum* live roots was also collected in 2013 and dried at 65°C in another experiment at the
412 same site), and found no significant differences between years for P (2.97 $\pm$ 0.04 vs 3.05 $\pm$ 0.03
413 mg/g, $P = 0.85$), and a marginally significant difference for N (17.0 $\pm$ 1.6 vs 13.3 $\pm$ 1.0 mg/g, $P =$
414 0.09). Given these small differences, it is unlikely that the large (3-fold) difference in mass loss we
415 report for *B. nana* and *E. vaginatum* roots (Fig. 1) is affected by differences in year of collection or
416 drying.

Across all seven litter types, P concentration was the main driver of differences in decomposition (Fig. 2). However, as can also be seen in this figure, the three dead litters collected in 2015 (except *E. vaginatum* live root) did show lower mass loss than the ones collected in 2013, suggesting that the P concentration effect could also be driven by year of litter collection. We checked this by comparing our litter quality model to one that explains mass loss by year of collection. The results show that year did not have a significant effect on decomposition ($F_{1,5} = 0.55$, $P = 0.49$), which is not surprising given that litters collected in 2015 included both *E. vaginatum* live roots and three dead materials and thus the variance of mass loss was large. In addition, when comparing the AIC values of both models it was clear that litter quality (P and lignin:P) performed better (AIC = −20.3 and −19.9, respectively) than the year model (AIC = −5.8). Thus, although we cannot completely rule out that year of collection affected mass loss, it is more likely that decomposition is indeed driven by litter quality. This is supported by the lack of difference in P content between *E. vaginatum* live roots collected in 2013 and 2015, as explained above.

4.4. Implications for carbon dynamics in the tundra

There is major concern that tundra ecosystems might shift from a carbon sink to a carbon source with warmer climates (Belshe et al., 2013; Oechel et al., 1993; Webb et al., 2016). A warmer climate will increase primary productivity of tundra vegetation and thus increase carbon uptake by the ecosystem (Epstein et al., 2012; Hill and Henry, 2011; Verbyla, 2008). On the other hand, higher temperatures also accelerate decomposition and thus increase carbon emission from the soil (Davidson and Janssens, 2006; Hobbie, 1996). The balance between these two changes will determine whether tundra ecosystems will continue to act as a carbon sink or will shift to a carbon source. These changes in carbon dynamics can be modified by shifts in tundra vegetation composition due to 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 tissues, our study does not provide evidence for vegetation induced changes in decomposition rates, as the decomposability of leaf litter did not differ between the two species. However, root litter decomposition was lower for *B. nana* than for *E. vaginatum*, at least in the early stage. Also, it is known that root turnover rates of shrubs are lower than that of graminoids in the tundra (Mack et al., 2004; Shaver and Chapin, 1991; Sullivan et al., 2007). When extrapolating this finding, it would suggest that shrub expansion with increasing temperatures could reduce decomposition and increase carbon storage. However, it may be important to consider that graminoids roots typically grow deeper than shrubs (Miller et al., 1982; Shaver and Chapin, 1991; Wang et al., 2016b). As deeper soil layers will be colder, decomposition of graminoid roots may be slower than observed in litter bag studies in the upper soil layer. This is illustrated by the observation that yedoma (windblown dust, deposited during the glacial age) permafrost contains almost intact graminoid roots (Zimov et al., 2006). To accurately predict the long-term effects of vegetation shifts on decomposition and the carbon balance, detailed knowledge of the temporal dynamics in root turnover and decomposition at different soil depths in relation to soil temperature are needed.

5. Conclusion

Our study shows that although leaf litter decomposition did not differ between the two dominant species, root litter decomposition was significantly higher for the graminoid *E. vaginatum* than for the shrub *B. nana*. The differences we found in decomposability could be mainly attributed to litter traits related to phosphorus. In addition, home-field advantage effects were found, which may lead to temporary reductions in litter decomposition when vegetation shifts occur. Our results indicate that root decomposition can be an important driver of changes in carbon dynamics when vegetation shifts and consequently plant litter changes in the tundra. The large difference between the mass loss of the live and dead plant materials, particularly between the live and dead *E. vaginatum* roots, suggests that only looking at the initial phase of decomposition does not give a clear indication of decomposition rate over time.

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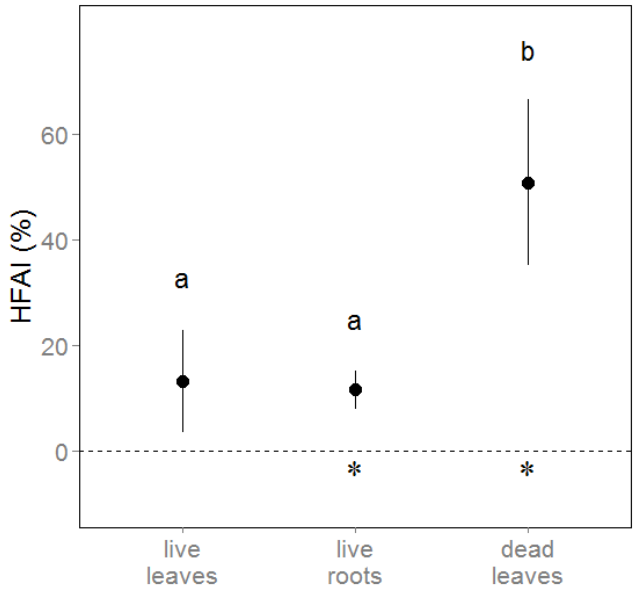
678 **Supplementary materials**

679



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681 Fig. S1. Home-field advantage index (HFAI) of litter from different tissue types. Letters above error
682 bars indicate significant difference between groups. Asterisks show that HFAI was significantly
683 different from zero for live root and dead leaf litter. Dotted line represents zero level of HFAI.
684 Symbols with error bars show mean ± SE, n = 8 blocks.

685

686 Table S1. Overview of the collection and preparation of samples used in this experiment

	Litter type	Time of collection	Location of collection	Drying method	Drying time
Live materials	*E. vaginatum* live leaves	July 2013	*E. vaginatum* dominated vegetation	65 ºC ove n dried	72 h
	B. nana live leaves	July 2013	*B. nana* dominated vegetation	65 ºC oven dried	72 h
	B. nana live roots	July 2013	*B. nana* dominated vegetation	65 ºC oven dried	72 h
	E. vaginatum live roots	July 2015	Nearby *E. vaginatum* dominated vegetation	~ 10 ºC air dried	24 h
Dead materials	*E. vaginatum* dead leaves	July 2015	Nearby *E. vaginatum* dominated vegetation	~ 10 ºC air dried	24 h
	E. vaginatum dead roots	July 2015	Nearby *E. vaginatum* dominated vegetation	~ 10 ºC air dried	24 h
	B. nana dead leaves	July 2015	Nearby *B. nana* dominated vegetation	~ 10 ºC air dried	24 h

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688

689 Table S2. Comparison of the regression models of mass loss and chemical characteristics using AIC
690 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

691