Above-Ground and Below-Ground Plant Responses to Fertilization in Two Subarctic Ecosystems

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Above-ground and below-ground plant responses to fertilization in two subarctic ecosystems

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Abstract

Soil nutrient supply is likely to change in the Arctic due to altered process rates associated with climate change. Here, we compare the responses of herbaceous tundra and birch forest understory to fertilization, considering both above- and below-ground responses. We added nitrogen and phosphorus to plots in both vegetation types for three years near Abisko, northern Sweden, and measured the effect on above- and below-ground plant community properties and soil characteristics. Fertilization increased ground-layer shoot mass, the cover of grasses, and tended to enhance total root length below-ground, while it reduced the cover of low statured deciduous dwarf-shrubs. The only statistically significant interaction between vegetation type and fertilization was for grass cover, which increased twofold in forest understory but sixfold in tundra following fertilization. The lack of interactions for other variables suggests that the ground layers in these contrasting vegetation types have similar responses to fertilization. The nutrient-driven increase in grass cover and species-specific differences in productivity and root characters may alter ecosystem dynamics and C cycling in the long-term, but our study indicates that the response of birch forest understory and tundra vegetation may be consistent.

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Introduction

Global changes in climate are expected to have major influences on Arctic ecosystems (Wookey et al., 2009), which are known to be strongly limited by nutrients, particularly nitrogen (N) and phosphorus (P). Many studies have addressed above-ground plant responses to N and P addition (e.g., Chapin et al., 1995; van Wijk et al., 2004; Shaver et al., 2014; Sundqvist et al., 2014; Zamin et al., 2014), revealing increases in density and biomass, shifts in dominant plant functional groups such as increases in deciduous shrubs and grasses, and decreases in lichens and mosses. These above-ground responses to fertilization have been found across both herbaceous and woody vegetation types (Sveinbjornsson et al., 1992; Dormann and Woodin, 2002; Shaver et al., 2014). There is, however, large variation in the way that different Arctic vegetation types respond to altered nutrient supply (van Wijk et al., 2004; Shaver et al., 2014; Sundqvist et al., 2014).

Further, Arctic ecosystems store a large portion of the global carbon (C) pool (Gorham, 1991; Tarnocai et al., 2009), and N and P fertilization leads to a net release of soil C in moist acidic tundra by stimulating decomposition of soil organic matter more than aboveground plant productivity (Mack et al., 2004). Some findings from tundra ecosystems showed increased fine root production in response to fertilization (Nadelhoffer et al., 2002; Mack et al., 2004; Clemmensen and Michelsen, 2006), while others found fertilization resulting in an increase in fine root standing crop but reduced root production (Sullivan et al., 2007). However, despite evidence that plants in high-latitude ecosystems allocate a large proportion of fixed C to roots (Shaver and Billings, 1975; Mokany et al., 2006), little is known about the collective response of above- and below-ground vegetative components to increased nutrient supply. Current knowledge about below-ground responses in tundra comes mostly from grasses, resulting in a pressing need for corresponding information about Arctic woody vegetation, which can also be sensitive to changes in nutrient availability and warming (Iversen et al., 2015).

The functional balance theory predicts that plants shift allocation of resources to maximize uptake of their most limiting resource (Johnson and Thornley, 1987; Cannell and Dewar, 1994). Hence, increasing soil nutrient availability and temperature may often be associated with greater allocation of fixed C to shoots rather than to roots (e.g., Chapin, 1980; Oleksyn et al., 1998; Balogianni et al., 2014). Shifts in plant C allocation in response to nutrient availability and temperature may also affect soil biota associated with plant roots (Wardle et al., 2004). For example, arbuscular mycorrhizal fungi (AMF) respond strongly to certain

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environmental changes and generally decrease with increased fertilization as plants become less nutrient-limited (Treseder, 2004; Johnson et al., 2013). These patterns are, however, not universal. Fertilization of the Arctic shrub *Betula nana* increased the mycelial production of their ectomycorrhizal fungi (ECM) associates (Clemmensen et al., 2006), and knowledge of the distribution and role of mycorrhizal fungi across polar regions in general is still limited (Öpik et al., 2013).

To address this gap in knowledge, we explore above- and below-ground plant responses to increased nutrient supply in both herbaceous and woody vegetation. To acheive this goal, we added N and P to plots in two widespread subarctic ecosystem types—tundra and birch forest understory—at high and low elevations, respectively, and measured above-ground plant biomass and community composition, soil nutrient availability and ecosystem respiration, and root length, root diameter, and hyphal length. In these highly nutrient-limited systems, we hypothesize that with greater soil nutrient supply (i.e., N + P fertilization):

1. Both plant shoot and root growth will increase, but shoot growth will increase more, in line with the functional balance theory.
2. The relative abundance of deciduous shrubs and grasses will increase in response to fertilization.
3. Hyphal growth will decline in response to fertilization.
4. The above- and below-ground plant responses to fertilization will be greatest in the more nutrient-limited tundra compared to in the forest understory.

Testing these hypotheses in two subarctic ecosystems will provide valuable new information about the role of nutrient limitation in governing patterns of plant C allocation across the diverse range of Arctic plant communities under future global changes (Ostle et al., 2009).

Methods

STUDY SITES AND EXPERIMENTAL SET UP

The birch forest site was located near Abisko Scientific Research Station, at 400 m a.s.l., Abisko, Sweden (68°N, 18°E). Vegetation was dominated by the tree species *Betula pubescens* spp. *Czerepanovii* with an understory of the dwarf shrubs *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium vitis-idea,* and the grass *Deschampsia flexuosa*. The tundra site was situated in Gearggevággi valley, 20 km northwest of Abisko, at 700 m a.s.l. Tundra vegetation was dominated by herbaceous species, grasses, and sedges such as *Rumex acetosa*, *Deschampsia flexuosa,* and *Carex bigelowii*. The mean annual air temperature measured at Abisko is 0 °C and mean annual precipitation is 310 mm (1913–2000; Abisko Scientific Research Station), with most precipitation falling in July (51 mm) and the least in April (12 mm) (Kohler et al., 2006).

In July 2010, we set up a fertilization experiment in the understory vegetation in the birch forest and in the tundra. In each vegetation type, we randomly selected 10 circular plots with a diameter of 2 m, separated by >15 m. Half of the plots were randomly chosen to be fertilized annually with N (10 g N m^{-2} yr^{-1} as NH_4NO_3) and P (5 g P m^{-2} yr^{-1} as superphosphate), and half were left unfertilized (control plots). Vegetation in our region is co-limited by N and P (Sundqvist et al., 2014), and we used addition rates comparable to other tundra fertilization experiments (e.g., Chapin et al., 1995; Mack et al., 2004). Plots were fertilized in late June, near the beginning of the growing season, for three consecutive years before commencement of measurements.

VEGETATION AND FUNGAL MEASUREMENTS

In September 2012, we measured ground layer shoot mass (excluding trees) in each plot by clipping all above-ground ground layer vegetation in 10 squares of 10 cm × 10 cm. Samples were pooled for each plot, dried at 60 °C to constant weight, and weighed.

At the start of the experiment we inserted a rhizotron tube in the center of each plot (5 cm diameter, 100 cm long), at an angle of 45° relative to the ground surface. In 2012, we collected images (13 × 18 mm) of the upper tube surface, along the length of each tube, using a minirhizotron camera (Bartz Technology, Carpinteria, California). Images were collected at 78 mm intervals from the first image completely beneath the surface to the bottom of the tube, resulting in nine images per tube. In each image we measured the length, diameter, and color (white: younger roots; brown: older, lignified roots) of all roots using Rootfly software (Clemson College of Engineering and Science). Rhizomes can be enumerated with this method, but we found none. We also recorded the length of fungal hyphae (mm). Total root length and diameter, and hyphal length were determined for each tube. Images were not collected from two of the fertilized forest sites because the tubes could not be located in dense vegetation. Images were not collected from two of the control tundra plots because the tubes had been removed by vandals.

SOIL PROPERTIES

In each plot, we collected three to six soil samples of the top 10 cm of the soil using a polyvinyl chloride (PVC) soil corer (4.5 cm diameter). Soil samples were pooled per plot and kept at 4 °C for 48 h, after which samples were sieved (5 mm) to remove stones and plant roots. We determined soil moisture as weight loss after drying a subsample of each soil sample at 105 °C until constant weight and soil organic matter content (SOM) by loss-on-ignition in a muffle furnace (550 °C for 4 h). Soil pH was measured in a soil:water suspension (6 g fresh soil, 60 mL of deionized water) on a Mettler Toledo pH meter (Instrument Teknik, Sweden) after shaking for 12 h at 150 RPM. For soil nutrient analysis, we extracted 6 g subsamples of fresh soil with 80 mL KCl 1M (2 h, 150 RPM) and analyzed concentrations of NH_4^+, NO_3^-, and PO_4^{3-} in the extract colormetrically using an autoanalyzer (SEAL Analytical, Sweden).

ECOSYSTEM RESPIRATION MEASUREMENTS

In the center of each plot, we recorded ecosystem dark respiration within an opaque chamber (150 cm^3 ground surface area) sealed to the ground, attached to an infrared gas analyzer (PP Systems, EGM-4 and SRC-1 chamber, Hitchin, U.K.). We calculated CO_2 efflux from the linear increase in CO_2 concentration over two minutes within the chamber.

DATA ANALYSIS

Data were analyzed with two-way ANOVAs with vegetation type (V; birch forest understory versus tundra vegetation), fertilization treatment (F; control versus fertilized), and their interaction as fixed factors. We tested the data for homogeneity of variances using a Levene's test and the distribution of the residuals using a Shapiro-Wilk test. Brown root length, hyphal length, soil NH_4^+

concentration, and ecosystem respiration data were transformed with a natural logarithm to obtain normality. We did not include soil NO_3^- concentrations in our analyses because these were only above the detection limit in three of our samples. A one-way ANOVA was used to test for the effect of the fertilization treatment for plant functional groups only common within one vegetation type. For the root data, we omitted one observation from a birch forest understory control plot where root length was more than 17 times higher than the root length in the other four control plots at this site. This did not qualitatively affect the outcome of our analyses. To explore plant community responses to fertilization across sites, we first conducted a detrended correspondence analysis (DCA), which revealed a total inertia >4, indicating a unimodal response (ter Braak and Šmilauer, 2002). The plant community data set was therefore further explored using a correspondence analysis (CA), and the sample scores for the first and second axis of the CA were analyzed for the effect of site and fertilizer treatment, exactly as described above. All univariate analyses were performed in IM SPSS Statistics 22, and all multivariate analyses were performed in Canoco 4.5. We report p-values of ≤0.05 as statistically significant differences, and p-values of ≤0.1 as nonsignificant trends.

Results

ABOVE- AND BELOW-GROUND PLANT RESPONSES

Ground layer shoot mass was significantly greater in fertilized than in unfertilized plots in both forest understory and tundra, but did not differ between the two vegetation types, nor was it responsive to the vegetation type × fertilization interaction (Fig. 1, part a). Plant species richness was greater in tundra than in forest understory, but did not differ between fertilization treatments (Table 1). A full species list with plant functional group and mycorrhizal type is shown in Appendix Table A1. Plant community composition differed significantly between the two vegetation types, as was indicated by the first axis scores from the CA, and tundra vegetation tended to respond more to fertilization than the forest understory along axis 2 (marginally significant vegetation type × fertilization interaction on CA Axis 2 sample scores) (Fig. 2, Table 1). The cover of plant functional types differed between vegetation types and for some types the cover changed with the fertilization treatment (Fig. 3, Appendix Table A2). The cover of grasses was greatest in the tundra compared to the forest understory, and increased in fertilized compared to control plots, and this was particularly pronounced in tundra vegetation. The cover of deciduous shrubs overall declined with fertilization, while pteridophytes were similar across vegetation types and marginally significantly lower in fertilized plots compared to control plots (Table A2). The cover of evergreen shrubs was greatest in forest understory and unresponsive to fertilization. In tundra, the cover of forbs was marginally significantly higher in the fertilized plots compared to the controls, while sedges were unresponsive to fertilization. Shannon's diversity index did not significantly differ between vegetation types or fertilizer treatments.

Fertilizer addition had no significant effect on any below-ground plant variable, although total root length and hyphal length tended to be increased in fertilized plots (Table 1, Fig 1, part b). Brown root length and hyphal length were both greater in forest understory than in tundra, while total root length, white root length, and root diameter did not differ between vegetation types (Table 1).

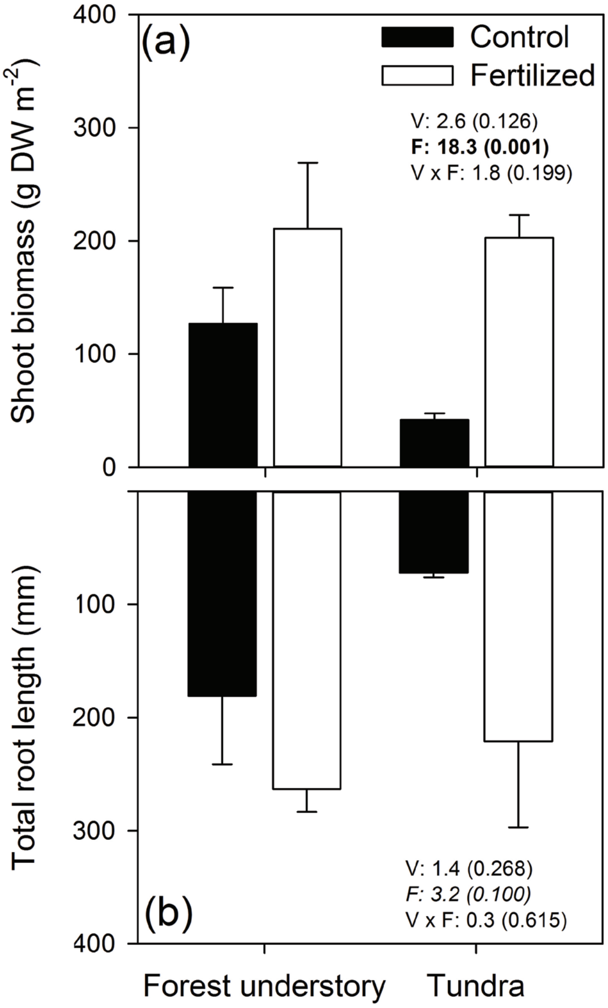

FIGURE 1 (a) Ground layer shoot mass (g dry weight m^{-2}) and (b) total root length (mm) for forest and tundra. ANOVA results are displayed in the figure as *F*-value (*P*-value) for the effect of vegetation type (V), fertilization (F), and their interaction (V × F). For shoot biomass *N* = 3 for fertilized forest understory and *N* = 5 for the other treatments. For total root length *N* = 3 for fertilized forest understory and tundra control, *N* = 4 for control forest understory, and *N* = 5 for fertilized tundra.

SOIL ABIOTIC PROPERTIES AND ECOSYSTEM RESPIRATION

Soil NH_4^+ was greater in fertilized plots, but no other soil abiotic properties responded to fertilization (Appendix Table A3). Concentrations of soil NH_4^+ and PO_4^{-3} were not different between forest understory and tundra. Soil pH was signficantly lower in forest understory than tundra, while soil moisture content was greater in forest understory (Table A3). Ecosystem respiration did not differ between forest understory and tundra, but tended to be greater in fertilized plots (Table A3).

Discussion

Fertilization significantly increased plant biomass and grass cover and decreased the cover of deciduous shrubs above-ground, while there was no significant response of roots, indicating that above-ground plant responses to fertilization were stronger than

TABLE 1

Above- and below-ground plant community properties (mean ± 1 SE) for each of the fertilization treatments (control and fertilized) for birch forest understory (left columns) and tundra (middle columns). The right columns display the statistical results from two-way ANOVAs (*F*-values, with *P*-values in parentheses) testing for the effect of vegetation (forest understory vs. tundra) and fertilization (control vs. fertilization), and their interaction, on vegetation properties. Values in boldface represent statistical significance at $p < 0.05$. Values in italics represent $P < 0.10$. Degrees of freedom for ground layer biomass, species richness, Shannon's H', and the CA-scores are 1, 14. For all root variables, degrees of freedom are 1, 11.

	Birch forest understory		Tundra		ANOVA results		
	Control	Fertilized	Control	Fertilized	Vegetation (V)	Fertilization (F)	V × F
Species richness	7.6 (1.4)	8.3 (0.67)	14.4 (1.4)	17.2 (3.09)	**13.5 (0.002)**	0.7 (0.420)	0.2 (0.635)
Shannon's H	1.2 (0.18)	1.3 (0.11)	1.8 (0.28)	1.5 (0.20)	2.9 (0.109)	0.1 (0.752)	0.4 (0.522)
CA Axis 1 Scores	–0.910 (0.26)	–0.931 (0.33)	1.22 (0.19)	0.564 (0.06)	**69.8 (<0.001)**	2.4 (0.141)	2.1 (0.165)
CA Axis 2 Scores	–0.011 (0.45)	0.222 (0.22)	0.912 (0.62)	–0.723 (0.13)	0.0 (0.981)	2.4 (0.143)	*4.3 (0.058)*
White root length (mm)	154.7 (67.9)	208.4 (29.5)	71.9 (5.2)	195.7 (55.2)	0.7 (0.409)	2.6 (0.139)	0.4 (0.542)
Brown root length (mm)[a]	20.7 (12.7)	54.5 (23.7)	0.0 (0.0)	25.3 (25.3)	**106.4 (0.002)**	1.3 (0.323)	0.9 (0.784)
Hyphal length (mm)[a]	58.94 (50.66)	122.70 (49.41)	0.59 (0.59)	11.11 (4.83)	**13.9 (0.014)**	*4.7 (0.083)*	1.5 (0.271)
Root diameter (mm)	0.26 (0.02)	0.29 (0.01)	0.24 (0.02)	0.26 (0.01)	1.8 (0.202)	1.4 (0.262)	0.1 (0.806)

[a] Data have been ln-transformed before analyse

those below-ground. However, our results also revealed a number of marginally significant trends both for above- and below-ground variables, suggesting that continued fertilization could result in greater shifts in plant community composition and increased root length. Further, our results showed that above- and below-ground plant responses to fertilization were generally similar between forest understory and tundra, suggesting that the effects of nutrient addition on vegetation were generally consistent across these contrasting Arctic ecosystem types.

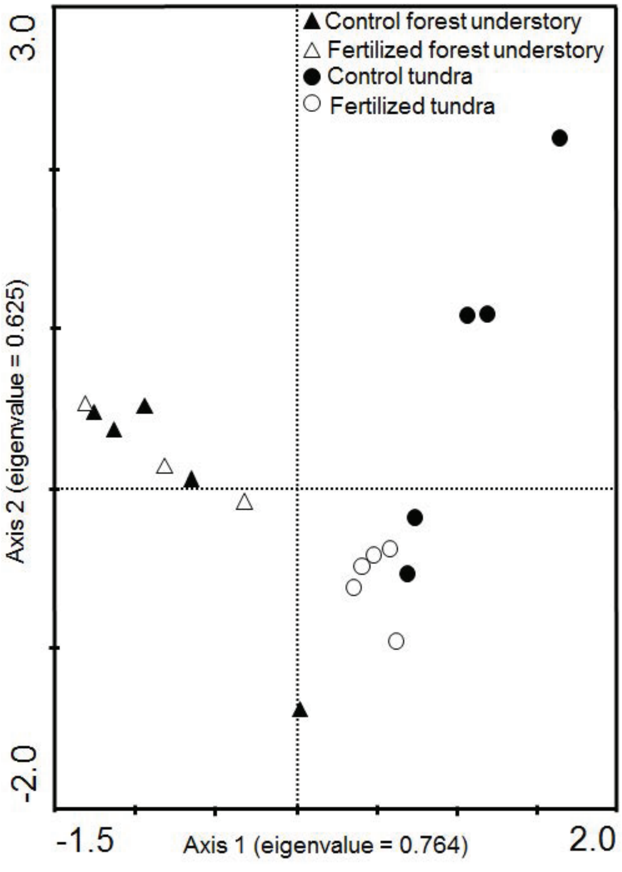

FIGURE 2. Ordination displaying sample scores from a correspondence analysis (CA) of vascular plant cover data from control and fertilized plots in forest understory and tundra. Axis 1 explains 18.4%, and axis 2 explains 15.5% of the variation in the CA. Total inertia = 4.151.

OVERALL RESPONSES TO FERTILIZATION

Our results do not fully support our first hypothesis that fertilization would increase plant resource partitioning above-ground because although shoot mass was significantly greater in fertilized plots, total root length also tended to increase with fertilization. Therefore, our results do not provide strong evidence for the functional balance theory, which predicts that plants would shift C preferably to shoots rather than to roots under increased soil nutrient availability (e.g., Chapin, 1980; Gedroc et al., 1996; Oleksyn et al., 1998; Balogianni et al., 2014), and which has been observed in other studies along natural gradients (Oleksyn et al., 1998; Balogianni et al., 2014). Under conditions where plants allocate more resources above-ground under high nutrient availability, roots may respond to increased nutrient supply by absorbing and translocating more N, rather than by increasing growth (Moar and Wilson, 2006). Although changes in root length in our study may not be directly comparable to changes in root biomass, our findings are broadly consistent with previous work showing increasing above-ground as well as fine root biomass in response to fertilization in the Arctic (Chapin et al., 1995; Nadelhoffer et al., 2002; Mack et al., 2004; Sullivan et al., 2007; Gough et al., 2012). In addition to roots, rhizomes may also respond to changes in nutrient availability (Jónsdóttir and Watson, 1997), but no rhizomes were encountered in our images.

The increase in shoot biomass in response to fertilization was associated with a shift in plant community composition in both vegetation types. Partly in line with our second hypothesis, we found an overall increase in grasses following fertilization, consistent with numerous previous studies (e.g., Parsons et al., 1995; Arens et al., 2008; Gough et al., 2012; Shaver et al., 2014), and

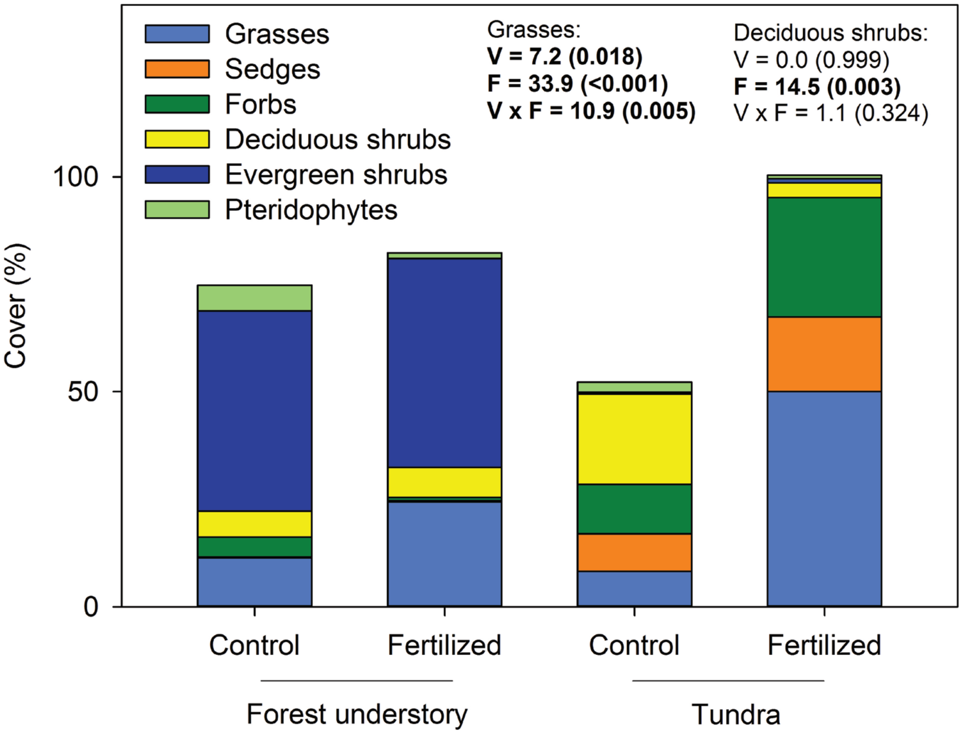

FIGURE 3. Average cover (%) of plant functional groups in control and fertilized plots in forest understory and tundra. ANOVA results are displayed in the figure as *F*-value (*P*-value) for the effect of vegetation type (V), fertilization (F), and their interaction (V × F) on the cover of grass and deciduous shrubs, because these plant functional groups responded significantly to the fertilization treatment. ANOVA results for the other plant functional groups can be found in Appendix Table A1.

this increase was greatest in the tundra. These findings reflect the well-known increase in grasses in nutrient-poor systems undergoing eutrophication (Berendse, 1994). Inconsistent with our prediction, however, we observed a decrease in deciduous shrubs over the course of our experiment. While declines in deciduous shrubs in response to short-term fertilization had been found in other shorter-term studies (Sundqvist et al., 2014), our finding is largely inconsistent with positive responses of deciduous shrubs to more long-term fertilization in the Arctic (Chapin et al., 1995; van Wijk et al., 2004). However, our result does not contradict studies showing positive responses of dwarf-shrubs such as *Betula nana* to fertilization, because the species that declined in response to fertilization in our system were short-statured deciduous dwarf-shrubs, namely *Salix herbacea, Salix polaris*, and *Vaccinium* ssp., which are likely to have become increasingly shaded by increased growth of grasses. This further highlights how generalizations from plant species data classified into plant functional groups should sometimes be made with caution, as species within a functional group may respond very differently to the same environmental factor (Dormann and Woodin, 2002).

Our finding that hyphal length tended to be greater (2–20 times) in fertilized than in unfertilized plots broadly agrees with findings from other subarctic studies revealing increases in fungal biomass and ectomycorrhizal production in response to fertilization (Clemmensen et al., 2006). They could be driven by an increase in the abundance of saprophytes, as has been shown in Alaskan tundra (Deslippe et al., 2011), or by a positive response of root-associated fungi to increased soil nutrient availability, in line with findings of a direct stimulation of ectomycorrhizal mycelial growth in tundra heath vegetation in Abisko, Sweden (Clemmensen et al., 2006). Alternatively, our results could be attributed to plant community responses to fertilization (Clemmensen et al., 2006), whereby the strong increase in grasses resulted in increased arbuscular mycorrizal hyphal length. Further, in a boreal forest ecosystem, ectomycorrhizal fungi have recently been shown to increase N transfer to plants under greater levels of soil nutrient availability (Näsholm et al., 2013). If this is a general pattern, and hence also occurs in tundra ecosystems, fertilization could have stimulated hyphal growth and thereby enhanced the nutrient-acquiring ability of plants. Our data do not allow us to separate out the fungal groups that were most responsive to fertilization, so further studies are required to disentangle the underlying mechanisms driving the observed tendency for a positive response of hyphal length to fertilization in our study system.

We found more differences in plant community characteristics between vegetation types than fertilization treatments. For example, above-ground, forest understory and tundra were significantly different in richness, grass and evergreen shrub cover, and species composition (Table 1, Fig 2). Interestingly, forest understory and tundra were not significantly different in terms of shoot biomass or total root length. Brown root length was significantly greater in forest understory than tundra, suggesting either that roots live longer in forest understory and have more time to undergo lignification, or that roots in forest understory undergo lignification more quickly. Further, hyphal length was 5–10 times greater in forest understory than tundra, reflecting the well-known abundance of mycorrhizal fungi associated with woody vegetation (Steinaker and Wilson, 2008; Öpik et al., 2013).

TUNDRA VERSUS FOREST UNDERSTORY RESPONSES TO FERTILIZATION

The lack of a significant interaction between vegetation type and fertilization on above-ground plant biomass and root length provides no support for our third hypothesis that fertilization would result in an overall greater response in the tundra vegetation compared to the forest understory. Instead, these results suggest that when above- and below-ground components are considered together, plant growth responses to fertilization are relatively similar in forest understory and tundra. This similar above- and below-ground plant response across contrasting vegetation types enhances confidence in predictions of Arctic vegetation responses to increased nutrient availability despite the general paucity of data from many widespread vegetation types in the region (Iversen et al., 2015). With regard to plant community responses, however, above-ground plant functional group responses to fertilization have been shown to differ among tundra vegetation types, as well as among communities adapted to different levels of soil fertility and climatic conditions (van Wijk et al., 2004; Sundqvist et al., 2014). Consistent with such findings, and our fourth prediction, the commonly observed rapid response of grasses to nutrient addition (Parsons et al., 1995; Arens et al., 2008) was stronger in tundra than in forest understory in our study (Fig. 3). This is likely related to overall differences in plant community composition between both vegetation types. Ground layer plant communities in the forest displayed a greater overlap between the fertilized and control plots than in the tundra (Fig. 2). The forest understory vegetation was mostly composed of relatively slow-growing evergreen shrubs (Fig. 3) with a lower capacity to respond to resource shifts than the faster-growing, herbaceous species dominating in the tundra. Further, the greater increase in tundra above-ground biomass following fertilization is also possibly associated with greater light availability. In forest understory, grass growth may be primarily constrained by light availability, which inhibits any fertilization-induced growth increase. Overall, our results suggest that soil nutrient availability itself may not necessarily be as important as the characteristics of the dominant species in a community in predicting plant community responses to fertilization (Sundqvist et al., 2014).

IMPLICATIONS ON THE ALLOCATION AND CYCLING OF C

Our results show that above- and belowground plant biomass responses to fertilization may be similar between different Arctic vegetation types (Tables 1, A2, and A3), which indicates that remotely sensed increases in productivity across Arctic ecosystems (Myneni et al., 1997; Kimball et al., 2007; Bhatt et al., 2010) may also reflect belowground plant responses. Hence, remotely sensed data on plant biomass may be useful to model predictions of whole plant C storage and exchange by Arctic ecosystems under global change (Qian et al., 2010). Further, the observed trends in our study toward increased root biomass, as well as increased soil respiration under fertilization (Fig. 1, part b; Table A3) support predicted ecosystem responses to global change. For example, the alleviation of nutrient limitation and greater below-ground plant C allocation can stimulate breakdown of recalcitrant soil C (Hartley et al., 2012) and may enhance ecosystem respiration and nutrient cycling (Mack et al., 2004).

In summary, fertilization of forest understory and tundra significantly increased grass cover, decreased the cover of deciduous shrubs, and resulted in similar above-ground biomass and below-ground root responses across both vegetation types. These nutrient-driven changes in the cover of plant functional groups and plant biomass may alter ecosystem processes and C cycling in the long term.

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APPENDIX

TABLE A1

A list of all species found in the study system, their functional group and mycorrhizal type, and their occurrence (tundra, birch forest understory, or both).

Species	Plant functional group	Mycorrhizal type	Tundra	Birch forest understory
Agrostis mertensii	grass	—	x	
Alchemilla sp.	forb	AM^{3,7}	x	
Antennaria alpinum	forb	—	x	
Anthoxanthum alpinum	grass	None^{2}	x	
Astragalus alpinus	forb	None^{1}	x	
Oxytropis lapponica	forb	—	x	
Betula pubescens ssp. *czerepanovii*	tree	ECM^{4}		x
Bistorta vivipara	forb	AM + ECM^{5,7}	x	
Calamagrostis lapponica	grass	AM^{1}	x	x
Carex bigelowii	sedge	None^{1,7}	x	x
Carex sp.	sedge	—	x	
Carex vaginatum	sedge	None^{1,7}	x	
Cerastium alpinum	forb	None^{7}	x	
Deschampsia cespitosa	grass	AM^{6}	x	
Deschampsia flexuosa	grass	AM^{7}	x	x
Diaphasiastrum alpinum	pteridophyte	AM + None^{7}	x	
Empetrum hermaphroditum	pteridophyte	ERM^{1}	x	x
Epilobium angustifolium	forb	AM^{7}		x
Equisetum sp.	pteridophyte	None/AM^{2,7}	x	x
Festuca ovina	grass	AM^{7}	x	x
Festuca vivipara	grass	AM^{1,7}	x	
Geranium sylvaticum	forb	None^{2}/AM^{7}		x
Gnaphalium norwegicum	forb	AM^{7}	x	
Hieracium sp.	forb	AM^{7}	x	
Juncus trifidus	sedge	AM^{7}	x	
Juniperus communis	evergreen shrub	AM + ECM^{7}		x
Linnea borealis	evergreen shrub	AM^{7}		x
Luzula wahlengergii	sedge	AM^{1}/None^{2}	x	
Lycopodium annotinum	pteridophyte	None^{1}/AM^{7}	x	x
Melamphyrum pratense	forb	None^{2} (hemiparasitic)		x
Phleum alpinum	grass	AM^{7}	x	
Poa alpina ssp. *vivipara*	grass	AM + None^{2,7}	x	
Poa pratensis ssp. *alpina*	grass	AM + None^{2,7}	x	
Potentilla cranzii	forb	AM^{7}	x	
Pyrola sp.	forb	EEM^{7}	x	
Ranunculus nivalis	forb	—	x	x
Rumex acetosa	forb	None^{2}	x	
Salix herbacea	deciduous shrub	ECM^{1}	x	

TABLE A1

Continued

Species	Plant functional group	Mycorrhizal type	Tundra	Birch forest understory
Salix polaris	deciduous shrub	ECM[1]	x	
Salix sp.	deciduous shrub	ECM[2]	x	
Saussurea alpine	forb	AM[7]	x	
Sibbaldia procumbens	forb	AM[7]	x	
Solidago virgaurea	forb	AM[7]	x	x
Taraxacum sp.	forb	AM[7]	x	
Thalictrum alpinum	forb	—	x	
Trientalis europea	forb	None[2]	x	x
Vaccinium myrtillus	deciduous shrub	ERM[1]	x	x
Vaccinium uliginosum	deciduous shrub	ERM[1]	x	x
Vaccinium vitis-idaea	evergreen shrub	ERM[1]	x	x
Veronica alpine	forb	AM[7]	x	
Viola biflora	forb	—	x	x

[1]Michelsen et al. (1996); [2]Michelsen et al. (1998); [3]Ruotsalainen et al. (2002); [4]Ruotsalainen et al. (2009); [5]Blaalid et al. (2014); [6]Gucwa-Przepióra et al. (2013) ; [7]Wang and Qiu (2006). AM = arbuscular mycorrhiza, ECM = ectomycorrhizal, EEM = ectendomycorrhiza, ERM = ericoid mycorrhiza, None = nonmyorrhiza. Whenever no literature source for mycorrhizal type at plant species level was found, this is indicated by a dash.

TABLE A2

Results from two-way ANOVAs (*F*-values, with *P*-values in parentheses) testing for the effect of vegetation (forest understory vs. tundra) and fertilization (control vs. fertilization), and their interaction, on the % cover of grasses, deciduous and evergreen shrubs, and pteridophytes, and one-way ANOVAs testing for the effect of fertilization on sedges and forbs in tundra. Values in boldface represent statistical significance at $p < 0.05$. Values in italics represent $P < 0.10$. Degrees of freedom for grasses, deciduous and evergreen shrubs, and pteridophytes are 1, 14. For sedges and forbs, degrees of freedom are 1, 8.

% cover	Vegetation type (V)	Fertilization (F)	V × F
Grasses	**7.2 (0.018)**	**33.9 (<0.001)**	**10.9 (0.005)**
Sedges[a,b]	—	0.0 (0.965)	—
Forbs[a]	—	*4.9 (0.058)*	—
Deciduous shrubs[b]	0.0 (0.999)	**14.5 (0.003)**	1.1 (0.324)
Evergreen shrubs	**32.5 (<0.001)**	0.0 (0.874)	0.0 (0.930)
Pteridophytes[c]	1.9 (0.186)	*4.5 (0.051)*	0.0 (0.827)

[a]Analysis performed on tundra plots due to low occurrence in the forest understory (38% and 25% of forbs and sedges, respectively).
[b]Analysis performed on ln-transformed data.
[c]Analysis performed on ln +1-transformed data.

TABLE A3

Means (± 1 SE) for soil properties in forest (left columns) and tundra (middle columns). The right columns display the statistical results from two-way ANOVAs (*F*-values, with *P*-values in parentheses) testing for the effect of site (birch forest vs. tundra) and fertilization (control vs. fertilization), and their interaction on vegetation properties. Values in boldface represent statistical significance at $p < 0.05$. Values in italics represent $P < 0.10$. Degrees of freedom are 1, 12 for soil moisture and respiration; 1, 10 for hyphal length, and 1, 14 for the other variables.

	Forest		Tundra		ANOVA results		
	Control	Fertilized	Control	Fertilized	Vegetation (V)	Fertilization (F)	V × F
NH4$^+$ (mg g^{-1} dry soil)[a]	0.014 (0.006)	0.018 (0.002)	0.009 (0.003)	0.027 (0.007)	0.03 (0.862)	**5.8 (0.030)**	0.23 (0.641)
PO4$^+$ (mg g^{-1} dry soil)[a]	0.012 (0.009)	0.023 (0.009)	<0.000 (<0.000)	0.006 (0.003)	2.8 (0.126)	1.1 (0.318)	0.2 (0.630)
pH	4.75 (0.16)	4.46 (0.06)	5.54 (0.10)	5.48 (0.10)	**50.8 (<0.001)**	1.9 (0.194)	0.9 (0.371)
Soil moisture content (%)	44.3 (9.2)	51.6 (3.3)	25.8 (3.8)	25.8 (2.8)	**15.1 (0.002)**	0.3 (0.610)	0.4 (0.523)
Ecosystem respiration (g CO$_2$ m^2 h^{-1})[a]	0.31 (0.04)	0.47 (0.06)	0.25 (0.03)	0.39 (0.12)	1.8 (0.210)	*3.3 (0.095)*	0.032 (0.861)

[a] Data have been ln-transformed prior to the analysis.

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