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Experimentally increased nutrient availability at the permafrost thaw front selectively enhances biomass production of deep-rooting subarctic peatland species

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Abstract

Climate warming increases nitrogen (N) mineralization in superficial soil layers (the dominant rooting zone) of subarctic peatlands. Thawing and subsequent mineralization of permafrost increases plant-available N around the thaw-front. Because plant production in these peatlands is N-limited, such changes may substantially affect net primary production and species composition. We aimed to identify the potential impact of increased N-availability due to permafrost thawing on subarctic peatland plant production and species performance, relative to the impact of increased N-availability in superficial organic layers. Therefore, we investigated whether plant roots are present at the thaw-front (45 cm depth) and whether N-uptake (^{15}N-tracer) at the thaw-front occurs during maximum thaw-depth, coinciding with the end of the growing season. Moreover, we performed a unique 3-year *belowground* fertilization experiment with fully factorial combinations of deep- (thaw-front) and shallow-fertilization (10 cm depth) and controls. We found that certain species are present with roots at the thaw-front (*Rubus chamaemorus*) and have the capacity (*R. chamaemorus, Eriophorum vaginatum*) for N-uptake from the thaw-front between autumn and spring when aboveground tissue is largely senescent. In response to 3-year shallow-belowground fertilization (S) both shallow- (*Empetrum hermaphroditum*) and deep-rooting species increased aboveground biomass and N-content, but only deep-rooting species responded positively to enhanced nutrient supply at the thaw-front (D). Moreover, the effects of shallow-fertilization and thaw-front fertilization on aboveground biomass production of the deep-rooting species were similar in magnitude (S: 71%; D: 111% increase compared to control) and additive (S + D: 181% increase). Our results show that plant-available N released from thawing permafrost can form a thus far overlooked additional N-source for deep-rooting subarctic plant species and increase their biomass production beyond the already established impact of warming-driven enhanced shallow N-mineralization. This may result in shifts in plant community composition and may partially counteract the increased carbon losses from thawing permafrost.

KEYWORDS
belowground nitrogen, climate change, *Empetrum hermaphroditum*, fertilization, frozen soil, permafrost thaw, root uptake, *Rubus chamaemorus*

1 | INTRODUCTION

Many of the world's northern peatlands are underlain by permafrost (ground that is at or below the freezing point of water for two or more consecutive years) which is thawing rapidly as a result of climate change (ACIA, 2004, IPCC, 2013). Since about one-third of the terrestrial carbon pool is stored in northern peatlands (Tarnocai et al., 2009), there is a potential for positive feedbacks to climate change (Dorrepaal et al., 2009; Schuur et al., 2015). Thawing and subsequent mineralization of permafrost may release considerable amounts of plant-available nitrogen (N) into subarctic peatlands (up to 0.3 g N m^{-2} year^{-1} in the coming decade) (Keuper et al., 2012). This is consistent with observed increases in N-availability with soil depth in other tundra types (Beermann et al., 2016; Harms & Jones, 2012; Sistla et al., 2013; Wild et al., 2015) and enhanced inorganic N export from permafrost-thaw influenced soils to streams (Frey & McClelland, 2009; Jones, Petrone, Finlay, Hinzman, & Bolton, 2005). This "new" global change-induced N-source at the permafrost thaw front at depth is additional to the predicted and observed increase in N-availability in shallower soil layers due to atmospheric deposition or increased N-mineralization rates by higher air temperatures (Rustad et al., 2001; Weedon et al., 2012). Plant production in northern peatlands is often N-limited (Aerts, Wallen, & Malmer, 1992; Berendse & Jonasson, 1992) and a temperature induced increase in N availability in shallower soil layers stimulates primary production and alters species composition (Chapin et al., 1995; Van Wijk et al., 2004). A release of stored permafrost N due to thawing may likely have similar effects, on the condition that: (1) plants are able to access this new permafrost-thaw induced N-source; (2) the N-limitation is not already relieved by increased decomposition in shallower soil layers; and (3) seasonal asynchrony between deeper nitrogen availability and plant nitrogen demands does not hamper stimulation of primary production.

So far, little is known about the ability of peatland plants to take up nutrients released at the depth of the thaw front. Arctic root ecological research has mostly been associated with long-term ecological research sites with a focus on graminoid and wetland tundra (Iversen et al., 2015). Studies in non-permafrost peatland ecosystems suggest that specific peatland graminoids and forbs are able to extend their roots to deeper soil layers (up to 60 cm soil depth). This applies in particular to the forb *Rubus chamaemorus* (Rapp & Steenberg, 1977) and the sedge *Eriophorum vaginatum* (Wein, 1973), as observed in peatlands of the British Isles. Moreover, in non-peatland permafrost ecosystems, roots of *Eriophorum angustifolium*, *E. vaginatum* and *Arctagrostis latifolia* have been reported to grow at the frozen soil surface while this recedes down the soil profile during the northern summers (Bliss, 1956; Callaghan, Headley, & Lee, 1991) and to resume their growth after having been frozen for several days (Billings, Shaver, & Trent, 1976).

Apart from root presence at the thaw front, asynchrony between the release of nutrients from the permafrost thaw front and the peak of the growing season (Koven, Lawrence, & Riley, 2015;

McConnell et al., 2013) could potentially impair uptake of thawing permafrost nutrients by peatland plants. Yet, most perennial sub-arctic species can store the N in belowground structures such as rhizomes and thick roots (Chapin, Schulze, & Mooney, 1990) and use the stored N in the next growing season. Moreover, the arctic growing season has been shown to continue about 50% longer below-than aboveground (Blume-Werry, Wilson, Kreyling, & Milbau, 2016). Indeed, observations of increased canopy N at an Alaskan graminoid-dominated thermokarst and wet moist tussock tundra sites suggest that increased plant N-uptake from thawing permafrost is possible (Salmon et al., 2016; Schuur, Crummer, Vogel, & Mack, 2007). Hence, although the timing of maximum thaw depth coincides with the end of the plant growing season, this asynchrony does not necessarily need to impair uptake of N from thawing permafrost (Salmon et al., 2016) and might selectively benefit deep-rooting rhizomal species (Iversen et al., 2015). However, none of this has so far been tested in permafrost peatlands.

The depth of the release of plant-available N from thawing permafrost makes this N-source fundamentally different from other climate-change related increases in N-input, which generally affect nutrient availability in the surface layer of the soil only (e.g. increased mineralization as a result of higher temperatures or increased atmospheric N deposition) (Rustad et al., 2001; Weedon et al., 2012). Although species composition is known to be affected by vertical resource partitioning within the shallow rooting zone (0–15 cm) (Berendse, 1982; Casper, Schenk, & Jackson, 2003; McKane et al., 2002), whether vertical nitrogen partitioning in thawing permafrost systems has a similar impact is largely unknown since few studies look at plant-soil interactions at depths >20 cm (Harms & Jones, 2012; but see: Oulehle, Rowe, Myska, Chuman, & Evans, 2016; Sullivan et al., 2007).

Fertilization studies usually apply fertilizer to the soil surface (Haugwitz & Michelsen, 2011; Parsons et al., 1995; Press, Potter, Burke, Callaghan, & Lee, 1998; Shaver et al., 2001), which is a method well-suited to mimic increased N-deposition. But especially in ecosystems such as subarctic peatlands where bryophytes, without rooting systems, are important competitors for nutrients (Marion, Miller, & Black, 1987; Tye et al., 2005), the results from surface-fertilization studies might not be suitable to predict the effects of subsurface increases in N-availability such as warming-induced increased mineralization and/or increased N-input from thawing permafrost. While many studies have been performed on the effects of increased nutrient supply in shallow soil layers, we are not aware of any studies testing for the effects on peatland plant biomass production of shallow versus deep (>20 cm) fertilization nor on the extent to which they rely on deep uptake for their total nutrient budget relative to their nutrient-uptake from shallower soil layers.

In this paper we aim to identify the potential impact of increased N-availability at the permafrost thaw front on subarctic peatland vegetation. We predict that: (1) only particular peatland plant species have roots present at the thaw front of subarctic peatlands (Experiment 1); and that (2) there are species which are able to take up N

at the permafrost thaw front at the end of the growing season (time of maximum permafrost thaw depth) and store N for use early in the next growing season (first leaves in spring) (Experiment 2). Further, we hypothesize that (3) if presented with increased nutrient availability at the permafrost thaw front, only deep-rooting species will increase their aboveground biomass and N-content (Experiment 3) and that (4) these effects can be similar in magnitude to the effects of an equal increase in nutrient availability in shallower layers (Experiment 3). Lastly, we hypothesize that (5) nutrient limitation of plant-growth in subarctic peatlands is strong enough for the effects of increased deep- and shallow-nutrient availability to be additive (Experiment 3).

We tested our hypotheses with three experiments in permafrost peatlands within a nature reserve in Sweden. Hypothesis a was tested by determining plant root biomass in soil cores taken in Peatland I (Experiment 1); hypothesis b was tested with a ^{15}N-tracer study (Experiment 2); and hypotheses c–e were tested with a unique 3-year fully factorial belowground fertilization experiment (Experiment 3).

2 | MATERIALS AND METHODS

2.1 | Site descriptions

All experiments were performed at a non-sloping, *Sphagnum fuscum* (Schimp.) H. Klinggr. dominated ombrotrophic peatland in the Stordalen nature reserve in northernmost Sweden (68°21.428′N, 19°03.181′E, 351 m.a.s.l.). This reserve is the former International Biome Project tundra site and has been described in full detail by Sonesson (1980). The thickness of the peat layer extended below the bottom of the active layer (at 45–50 cm depth). The length of the growing season is 130 days (Karlsson, 1996) and the volume of soil accessible to plant roots increases over the course of the growing season until maximum thaw depth is reached by the end of September. Mean annual rainfall at the sites in the years of the experiments was 287 mm in 2007, 228 mm in 2008 and 190 mm in 2009; with a mean of 235 mm ± 49 SD (Olefeldt & Roulet, 2012). The mean summer (June–August) temperature at the site is 7°C, the mean winter (September–May) temperature is −6°C (meteorological data Abisko Scientific Research Station, http://polar.se/en/abisko-naturvetenskapliga-station). The vegetation type has been classified as dry-growing elevated palsa vegetation by Madsen and Widell (1974).

2.2 | General approach

Firstly, we determined vertical plant root biomass distribution in the active layer down to the thaw front of five plots (Experiment 1). Secondly, we analysed qualitative differences among vascular subarctic peatland species in their capability to take up and store ^{15}N-ammonium injected at the thaw front at the time of maximum thaw depth (coinciding with the end of the growing season) for use at the beginning of the next growing season. To include the full range of species that are potentially able to take up nitrogen from depth, this

^{15}N-tracer study (Experiment 2) included three plots with *R. chamaemorus* L., *Empetrum hermaphroditum* (Hagerup), *Vaccinium uliginosum* L., and *Andromeda polifolia* L. (the dominant species of experiment (1) and three plots that additionally included *Eriophorum vaginatum* L. and *Betula nana* L., two other dominant species of the system. Thirdly, to test whether increased plant-available nutrient supply at the thaw front can affect net aboveground primary production and plant N-content, and to get insight into the relative importance of increased nutrient supply at the thaw front compared to increased nutrient supply in the current (main) rooting zone (5–15 cm) and potential interactions, we performed a 3-year belowground fertilization experiment with full-factorial combinations of deep (thaw front) and shallow fertilization (at 10 cm depth) (Experiment 3). The vegetation of this experiment did not include *E. vaginatum* or *B. nana*.

2.3 | Root presence down to the thaw front (Experiment 1)

Vertical root biomass distribution was determined in five randomly taken cores (measuring 6 × 5 cm, to a depth of 45 cm) which were extracted at the time of maximum thaw depth (second half of September). Upon extraction, each core was divided into four layers of each 10 cm at subsequent depths (5–15 cm; 15–25 cm; 25–35 cm and 35–45 cm, the latter representing the thaw front). All living roots (>0.1 mm) were removed from the *Sphagnum* peat and sorted per species by means of visual estimation of differences in colour, diameter and structure, using entire plant "voucher specimens" of each individual species. The roots were sorted in the lab, oven dried (48 hr, 60°C), weighed and root biomass was expressed as root dry weight per cm^3 soil volume.

2.4 | Winter-storage of ^{15}N-ammonium taken up at the thaw front (Experiment 2)

To test for differences among subarctic peatland species in their capability to take up nitrogen from the thaw front at the time of maximum thaw depth and store it for use in the beginning of the next growing season, a ^{15}N-pulse-labelling at the thaw front was performed. Six peatland plots (of 10 × 10 cm each) were randomly selected from locations that contained an active layer thickness of approximately 45 cm and had a mutual presence of the vascular species *E. hermaphroditum*, *R. chamaemorus*, *V. uliginosum*, *A. polifolia*, (three plots) and additionally *E. vaginatum* and *B. nana* (another three plots). At the time of maximum soil thaw (September 15th, 2008), 28 mg ^{15}N-ammonium chloride (98 atom% ^{15}N, Isotec, Miamisburg, OH, USA) dissolved in 60 ml deionized water, was injected at the thaw front (at 45 cm depth) in triangular grids with sides of 10 cm, using three metal tubes (20 ml per tube) with small openings at the bottom of the tube (See picture, Supporting information Fig. S1). The ^{15}N-ammonium solution was inserted by connecting a syringe to the airtight tubes and forcing the liquid to exit the tube at the bottom under pressure. Six control plots were selected in the proximity of the treatment plots but all plots were at least one metre apart

from each other. At the start of the following growing season (June 12th, 2009), leaf material of all vascular species present within the triangle was collected. The leaves were stored in separate paper bags, oven dried (at 60°C) and ground. As a control analysis we checked if ^{15}N-enrichment had not spread to layers other than the deepest layer (either through vertical redistribution via plant root litter or exudates, capillary rise or methodological contamination), using a cut-off value of 3.75 mg^{15}N gN^{-1}, that is, less than 0.1 mg^{15}N gN^{-1} deviation from control plot values. For this, soil cores were extracted from the centre of every ^{15}N-plot and of four control plots on September 20th, 2009 at the time of maximum thaw, one year after the pulse labelling and three months after sampling of the leaf material. Subsamples were taken at three depths per soil core (15, 30 and 45 cm depth) and roots were removed. Soil samples were then oven dried (48 hr, 70°C) and ground. Atom percentages of ^{15}N of all samples were determined with an elemental analyser (NC2500, ThermoQuest Italia, Rodano, Italy) coupled online to a stable isotope ratio mass spectrometer (Delta^{Plus}, ThermoQuest Finnigan, Bremen, Germany).

2.5 | Three-year full-factorial belowground fertilization experiment (Experiment 3)

To quantitatively assess the relative importance of deep N availability vs. shallow N availability, a full-factorial belowground fertilization experiment was performed with two factors "thaw front (deep)-fertilization treatment" (+ / −) and "current rooting zone (shallow)-fertilization treatment" (+ / −). This thus resulted in four combinations: "shallow-fertilized only" (S), "deep-fertilized only" (D), "shallow- plus deep-fertilized" (SD) and a control treatment (C). Plots of 60 × 60 cm were randomly chosen within an ombrotrophic peatland dominated by E. hermaphroditum and R. chamaemorus (78% and 12% of total biomass respectively), and each experimental treatment was replicated eight times.

In early June 2008, 11.8 g slow release fertilizer grains (NPK 17:3:11, with the 17% N consisting of 8.9% NH$_4$-N and 8.1% NO$_3$-N), equivalent to 8 gN m^{-2} (to be released slowly during the three years after insertion) were added to the shallow-fertilization treatment (S and SD; at 10 cm depth). The grains were inserted through an aluminium tube (diameter 10 mm) in grids of nine points (3 × 3 design with insertion points 20 cm apart, see Supporting Information, Fig. S2). Control plots were equally grid-wise perforated, but did not receive fertilizer. As the deeper soil layers are hard-frozen at the beginning of the growing season, an equal amount of slow release fertilizer was inserted in the same grid of the deep-fertilization treatment (D and SD) at a depth of 45 cm at the time of maximum thaw depth prior to the shallow addition (September 2007). In this way, we synchronized the potential enhanced availability of shallow and deep N into the same growing season.

To verify treatment effects on nutrient availability we tested if the treatment was still measurable two years after the start of the experiment. Plant root simulator (PRS™) soil probes (Western Ag Innovations Inc., Saskatoon, Canada), commercially manufactured ion exchange resins, were inserted in four plots per treatment and at two depths (10–15 cm and 40–45 cm) at the time of maximum thaw depth and recollected one year after. The shallow- and the deep-inserted probes showed higher N-release values at the depths where the fertilizer grains had been inserted but not at other depths (Supporting Information, Fig. S3). There were no interaction effects, showing that our treatments indeed had the intended effect on soil nutrient availability.

Three growing seasons after insertion of the fertilizer, at the peak of the growing season 2010 (July 26th), total aboveground vascular biomass was harvested from two 20 × 20 cm subplots per plot (Supporting Information, Fig. S2) which were combined for further analysis. The samples were divided into leaves of R. chamaemorus, E. hermaphroditum (together 90% of total aboveground biomass) and the remaining species (A. polifolia, V. uliginosum). These remaining species, which were all shallow-rooting, were grouped because of generally low abundance and because none of these remaining species were present in all plots. Leaves were oven dried (48 hr at 60°C), weighed, ground and nitrogen concentrations were determined by dry combustion with a Flash EA1112 elemental analyser (Thermo Scientific, Rodana, Italy).

Additionally, to test whether roots at the thaw front are actively "foraging" when presented with increased nutrient supply, changes in R. chamaemorus root biomass at the thaw front were determined by comparing root biomass in five randomly selected control (C) plots with eight "deep-fertilization only" (D) plots at the time of maximum thaw depth in the last year of the experiment. Due to practical constraints not all treatments and depths were sampled. In every plot one core (of 6 × 5 cm and a depth of 10 cm) was extracted at 35–45 cm. Roots (>0.1 mm) were sorted in the lab, oven dried (48 hr, 60°C), weighed and root biomass was expressed as root dry weight per cm^3 (fresh) soil volume.

2.6 | Statistical analysis

All data were tested for normality and homogeneity of residual variances by visual estimation of residual plots and normal probability plots. Log-transformation improved the homogeneity of residual variances for the ^{15}N labelling data (Experiment 2), as well as for the aboveground biomass, N-content and the root biomass for R. chamaemorus data of the full-factorial belowground fertilization study (Experiment 3).

Due to the high number of zero-values, the ambient root biomass distribution data (Experiment 1) did not render enough power for significance-testing. Therefore, and because we were merely interested in root presence at the thaw front, we chose to present the vertical distribution of mean root biomass and presence-absence data only graphically.

^{15}N-uptake (the difference between ^{15}N mg gDW^{-1} in leaves from treatment plots and from control plots) by plant leaves in the ^{15}N-labelling experiment (Experiment 2) were analysed with a linear mixed effects model (lme) with fixed factor "species" (A. polifolia, B. nana, V. uliginosum, E. hermaphroditum and R. chamaemorus) and

random factors "plot" and "plot in site", the latter factor signifying we had two clusters of plots within this experiment. The difference among species was subsequently analysed by multiple comparison of the means (Tukey contrasts) and confidence intervals.

Aboveground biomass and N-content of the two dominant species (*R. chamaemorus*, *E. hermaphroditum*) in the full-factorial belowground fertilization study (Experiment 3) were analysed with *lme* with "species" (*R. chamaemorus*, *E. hermaphroditum*), "shallow-fertilization" (+ / −) and "deep-fertilization" (+ / −) as fixed factors and plot as random factor. We performed the analyses on aboveground biomass and N-content data in the full-factorial belowground fertilization experiment on the two key species only (*R. chamaemorus* and *E. hermaphroditum*, together 90% of total biomass) because of many near-zero values in the "rest-group". Differences in root biomass at the thaw front in control plots vs. deep-fertilization plots were analysed with a *lme* model with fixed factor "treatment" (shallow fertilization/S; deep fertilization/D) and random factor "plot".

The statistical analyses were performed using R statistical software (R Core Team, 2010) using the nlme and mulcomp packages.

3 | RESULTS

3.1 | Roots at the thaw front (Experiment 1)

We found strong interspecific differences in vertical root distribution patterns among *R. chamaemorus*, *E. hermaphroditum* and *A. polifolia*. Only roots of *R. chamaemorus* were present at the thaw front (Figure 1). Root biomass of *R. chamaemorus* was relatively evenly distributed over the soil profile, with an average root biomass of 0.8 ± 0.1 (*SE*) gDW cm^{-3} (*n* = 5) in the deepest layer. Roots of the
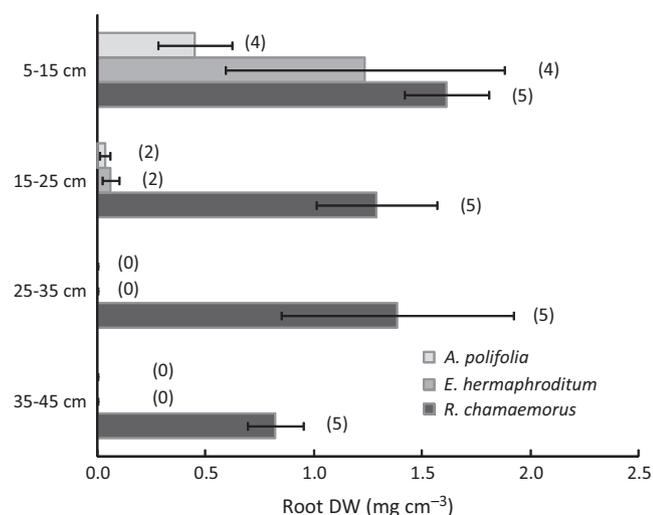
other species were largely confined to the upper soil layer (up to 15 cm depth) and were scarcely (at 15–25 cm) or not at all (below 25 cm) found at greater depth (Figure 1). Thus the bulk of root biomass of *A. polifolia* or *E. hermaphroditum* occurred at 5–15 cm soil depth, with a steep vertical decrease in root biomass (e.g. for *Empetrum* 1.5 gDW cm^{-3} at 5–15 cm and only 0.15 gDW cm^{-3} at 15–25 cm) (Figure 1).

3.2 | Winter-storage of ^{15}N-ammonium taken up at the thaw front (Experiment 2)

Rubus chamaemorus, *E. hermaphroditum*, *A. polifolia*, *Eriophorum vaginatum*, *B. nana* and *Vaccinium uliginosum* differed in their mean ^{15}N uptake at the thaw front at the time of maximum thaw depth until the beginning of the following growing season ("species" *p* < .0001). Tukey's multiple comparison and confidence intervals showed that the significant differences among species were due to the significantly higher ^{15}N-uptake by *R. chamaemorus* and *E. vaginatum* compared to each of the other species. None of the shallower-rooting species took up the labelled nitrogen (Figure 2). A control analysis for the three plots without *E. vaginatum* and *B. nana* yielded highly similar results (supporting information Table SI 1). Because in some plots vertical redistribution of the ^{15}N-label was measured when the soil was sufficiently thawed to be sampled, that is, three months after the (spring-time) leaf-sampling, an additional analysis was performed with exclusively the five plots where this was not observed. This analysis showed the same pattern ("species" *p* = .0005) with both the deep-rooting species *R. chamaemorus* and *E. vaginatum*, significantly different from the other species.
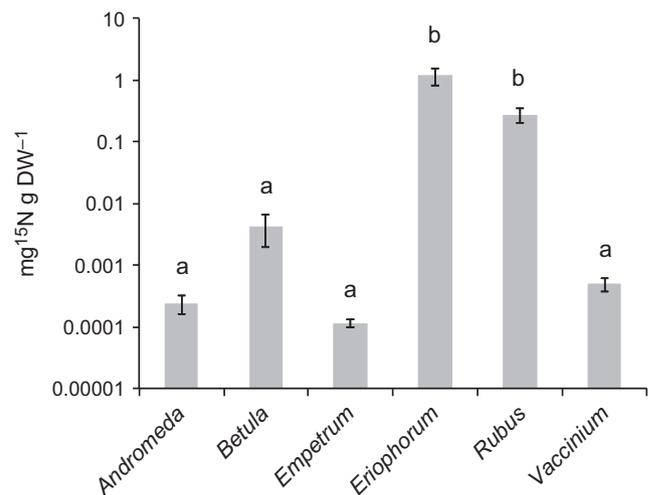

FIGURE 1 Mean (±*SE*) root dry weight for three subarctic peatland species at increasing soil depths, down to the thaw front, at the time of maximum thaw depth (experiment 1). Five cores were sampled; the number of cores in which roots were present is indicated in parentheses

FIGURE 2 ^{15}N-uptake from the thaw front by subarctic peatland species (experiment 2). The ^{15}N-label was inserted at the thaw front at end of the growing season (September 15th) and leaves were harvested the following spring (June 12th). Data are means ± *SE* expressed on a logarithmic scale and *n* = 6 for all species except *Eriophorum vaginatum* (*n* = 3) and *Betula nana* (*n* = 3). Different letters indicate significant differences according to a Tukey's posthoc test following a linear mixed effect model with species as fixed factor, and plot and "plot in site" as random factors

3.3 | Full-factorial belowground fertilization experiment: aboveground biomass and N-content (Experiment 3)

Deep-fertilization caused significantly different responses of the two dominant species in both mean biomass and N-content (significant "deep-fertilization × species" interaction, Table 1). Only the deep-rooting *R. chamaemorus* showed higher biomass and N content in response to fertilization at the thaw front, whereas this was not the case for the shallow-rooting *E. hermaphroditum* (Figure 3). In contrast, shallow fertilization had the same positive effect on biomass and N-content of both species (i.e. no "shallow-fertilization" × "species" interaction, Table 1). Similar results were obtained when including the biomass data of the "other species" as a third level in the within-subject factor (within-subject factor "species" $F = 107.8$, $p < .001$; "shallow-fertilization × species" $F = 1.3$, $P = ns$; "deep-fertilization × species" $F = 4.0$, $p < .05$). Moreover, for all analyses, there was no interaction between the treatment effects: thus, the effects of the shallow- and deep-fertilization on mean aboveground biomass and N-content were additive (Figure 3, Table 1).

3.4 | Root biomass at the thaw front in response to increased nutrient supply

Root biomass of *R. chamaemorus* increased up to 100% at the thaw front in the deep-fertilized plots compared to the control plots (1.6 ± 0.8 (*SD*) mg cm^{-3} in the deep-fertilized plots vs. 0.8 ± 0.3 (*SD*) mg cm^{-3} in the control plots), a difference which was significant despite high variation in root biomass ("treatment" $p = .042$).

4 | DISCUSSION

Thawing permafrost is often characterized as one of the main climate change-induced threats to northern peatlands (ACIA, 2004). It has

TABLE 1 Results of a linear mixed effects model for the effects of shallow-fertilization, deep-fertilization and species (*Rubus chamaemorus* vs. *Empetrum hermaphroditum*) as fixed factor and plot as random factor on aboveground biomass and N-content of two subarctic peatland key-species (*R. chamaemorus* and *E. hermaphroditum*)

Source	Aboveground biomass (g m^{-2}) F-value	N-content (gN m^{-2}) F-value
Species (*Rubus*, *Empetrum*)	352.3***	10.7**
Shallow-fertilization	13.1***	4.9*
Deep-fertilization	15.5***	20.6***
Species × shallow-fertilization	2.6	0.5
Species × deep-fertilization	17.5***	13.4**
Shallow- × deep-fertilization	1.8	2.2
Species × shallow- x deep-fertilization	0.8	0.1

Data were log-transformed and had 28 degrees of freedom, *depicts $p \leq .05$; **$p \leq .01$ and ***$p \leq .001$.
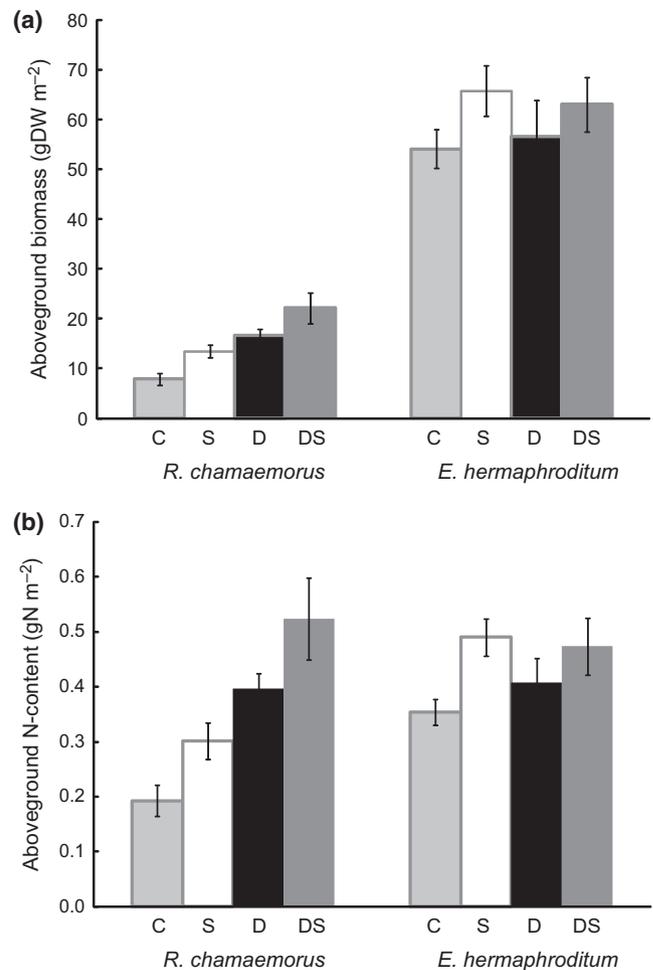
FIGURE 3 Mean ($\pm SE$) aboveground biomass (a) and canopy N-content (b) of the two key species *Rubus chamaemorus* (12% of total biomass) and *Empetrum hermaphroditum* (78% of total biomass) in control (C), shallow-fertilized (S), deep-fertilized (D) and shallow-plus deep-fertilized (SD) plots of the full-factorial belowground fertilization experiment ($n = 8$, experiment 3, see Table 1 for statistical results)

been shown that permanently frozen soils of subarctic permafrost peatlands contain substantial amounts of plant-available N (Keuper et al., 2012), which may be released upon thawing. Changes in nutrient availability due to climate change are likely to influence the vegetation composition and biomass of subarctic peatlands as these ecosystems are usually strongly N-limited (Dormann & Woodin, 2002; Limpens et al., 2011). Here, we show for the first time that particular vascular peatland plants are, indeed, able to utilize N at the permafrost thaw front to increase their biomass and N content.

4.1 | Roots at the thaw front: present and actively taking up nutrients

We found large differences in rooting depth among species in our permafrost peatland, similar to findings in other tundra systems (Iversen et al., 2015; Oulehle et al., 2016). Only one of our species present, *Rubus chamaemorus*, had roots at the thaw front (hypothesis a;

Figure 1). These findings are consistent with earlier observations of deep-rooting *R. chamaemorus* in non-permafrost peatlands (Rapp & Steenberg, 1977) and demonstrate that indeed only certain species have roots at the thaw front. Moreover, our labelling study (Experiment 2) showed that nutrients can be taken up both by *R. chamaemorus* and *Eriophorum vaginatum* (known from literature to be present at the thaw front; Bliss, 1956; Callaghan et al., 1991) at the end of the growing season and used in aboveground plant material the following spring (Figure 2). These species are thus most likely capable of storing nutrients that are acquired late in the growing season in rhizomes (Chapin et al., 1990; Taylor, 1971), ready for quick use in early spring of the next growing season. Moreover, the impacts of shallow- and deep-fertilization on aboveground biomass of deep-rooting *R. chamaemorus* were remarkably similar in magnitude (with a 71% increase compared to control in the shallow-fertilization treatment; 111% increase in response to the deep-fertilization, Experiment 3, Figure 3), despite the fact that the timing of maximum thaw depth coincides with the end of the growing season (hypothesis c, Figure 3). Such uptake-capacity late in the season, when aboveground tissue is largely senescent, is critical for plant species to benefit from nitrogen released from thawing permafrost, given that the largest extent of unfrozen deeper layers is obtained at the end of the growing season. Our findings for permafrost peatlands corroborate recent findings in tussock tundra (Salmon et al., 2016) and show that tundra vegetation can take up, store and use nitrogen released from thawing permafrost. Together, these results contradict the current assumption (Koven et al., 2015) that nitrogen released from thawing permafrost will not affect biomass production due seasonal asynchrony between deeper nitrogen availability and plant nitrogen demand, at least in this ecosystem with a relatively shallow thaw front.

4.2 | Differential competition for nutrients at the thaw front

As hypothesized, both deep- and shallow-rooting species were responsive to the shallow belowground fertilization. This is consistent with the strong effects of experimentally increased nutrient supply studies in shallow soil layers, usually with fertilizer applied to the soil surface (Aerts, van Logtestijn, & Karlsson, 2006; Haugwitz & Michelsen, 2011; Parsons et al., 1995; Press et al., 1998; Shaver et al., 2001). However, our results also suggest that fertilizer applied deep-belowground affects a different combination of species, due to differences in vertical root distribution (Figures 1 and 2), potentially in combination with the absence of nutrient uptake by the moss layer that occurs in the case of superficial fertilization. Our results for the permafrost-peatland system are consistent with observations in high-Arctic tundra (Oulehle et al., 2016) and seem to indicate that spatial niche differentiation, that is, niche differentiation between different soil layers (Berendse, 1982; Casper et al., 2003; McKane et al., 2002), is more important in tundra ecosystems than in other systems (de Kroon et al., 2012).

The different resource partitioning by increased nutrient supply at the permafrost thaw front is also likely to be an important driver

of other discrepancies between our results and two other fertilization studies: Firstly, a long-term surface-only fertilization of acidic tussock tundra led to a replacement of deep-rooting *E. vaginatum* by shallow-rooting *B. nana* (Sullivan et al., 2007). In our experiment, the additional N-uptake at the thaw front clearly provided the deep-rooting *R. chamaemorus* with a competitive advantage as it significantly increased its aboveground biomass and N-content in the belowground fertilization experiment after three years of treatment (Figure 3; Table 1). A second example is the difference in results between a surface-only fertilization experiment performed on non-permafrost bogs with a similarly low nutrient status in northern Norway, where instead of being favoured by the fertilization, *R. chamaemorus* growth was suppressed by the "vigorous response shown by the dwarf shrubs" (Østgård, 1964, as cited by: Taylor, 1971).

Although nutrient utilization in shallow layers (0–15 cm depth), is largely determined by species-specific plant traits related to their competitive ability for nutrient uptake such as nutrient absorption capacity, specific root length and root allocation (Iversen et al., 2015; Lambers, Stuart Chapin, & Pons, 1998), competition for the uptake of nutrients released from thawing permafrost takes the importance of these last two traits to a different level: in areas with thawing permafrost, community responses will first and foremost depend on whether and which specific species can reach this "new" deep N source. Hence, increased nutrient supply at the thaw front, in combination with strong spatial niche differentiation caused by differential vertical rooting patterns (species x deep-fertilization interaction, $p < .001$, Table 1), may lead in the long term to a species composition shift in favour of deep-rooting species in these nutrient-limited ecosystems.

4.3 | Additive effects of increased shallow- and thaw-front-nutrient supply

There was no interaction between effects of the shallow-fertilization and the deep-fertilization treatments on aboveground biomass; the effects were additive (hypothesis d; Figure 3a,b; Table 1). Hence, shallow fertilization did not dampen uptake from the thaw front, in contrast to what has been suggested by Koven et al. (2015). Our results indicate that nutrient limitation in these peatlands is sufficiently strong that nutrient saturation is not reached, at least not until other nutrients such as phosphorus become limiting (Aerts, Wallen, Malmer, & de Caluwe, 2001). This is corroborated by the fact that above- and belowground allocation of *R. chamaemorus* did not change, suggesting that no change in limiting factors had occurred.

The amount of nutrients applied in this experiment was relatively large (an initial supply of 8 gN m^{-2}) compared to the amount that might be released from thawing permafrost of subarctic peatlands (up to 0.3 g N m^{-2} year^{-1} in the coming decade) (Keuper et al., 2012), or to the estimated increase in nutrient supply in shallower layers (e.g. climate-warming in the range of 0.3–6.0°C would induce an estimated "46% increase in the 0.8 g N m^{-2} year^{-1}" net N mineralization in northern peatland ecosystems) (Rosswall & Granhall, 1980). Hence, it seems likely that the effects of natural amounts of shallow and deep increased N-supply in northern peatlands will also be additive.

4.4 | Potential longer-term effects

So far, observational records on species composition shifts upon thawing permafrost exist only for two systems with well documented multi-decadal thaw-histories (Alaska: Schuur et al., 2007; our study area: Malmer, Johansson, Olsrud, & Christensen, 2005). These records show mixed results: in Alaska, a shift from graminoid-dominated tundra to shrub-dominated tundra was observed since 1980 (Schuur et al., 2007) and comparison of permafrost thaw slump sites in the Mackenzie delta in Canada with surrounding undisturbed dwarf shrub tundra showed an increase in mosses and herbaceous species (Lantz, Kokelj, Gergel, & Henryz, 2009). In contrast, in a subarctic permafrost peatland site in subarctic Sweden, 30 years of vegetation observations revealed that dwarf-shrub-dominated hummock sites recede and give way to sites dominated by graminoids (Malmer et al., 2005) as the thaw, and collapse, of ice-rich permafrost permafrost results in subsidence (thermokarst) and an increase in wetness. This is consistent with results of experimental permafrost thaw situations in both Sweden and Alaska where strong increases in cover of *E. vaginatum* are observed (Johansson, Callaghan, Akerman, Jackowicz-Korczynsky, & Christensen, 2009; Johansson et al., 2013; Natali, Schuur, & Rubin, 2012; Wahren, Walker, & Bret-Harte, 2005). This illustrates that long-term vegetation responses to thawing permafrost are not only due to changes in nutrient availability, but also to multiple related factors such as co-occurring changes in hydrology or soil temperature. As such factors were not included in our experimental design, we do not address these related factors in depth, but instead confine this discussion to potential medium- to long-term responses to permafrost-thaw-induced changes in nutrient availability.

Long-term plant-responses to permafrost-thaw-induced increases in nutrient availability can be affected by several factors. Firstly, vertical transport of nitrogen via root and leaf litter of deep-rooting species from the thaw front to shallower layers may occur. Thus, permafrost-N can, in the longer term, become a new N-source also for shallower-rooting species, which might utilize this N after it has been redistributed through the soil layers. Secondly, microbial biomass is a strong sink for nutrients in arctic soils (Jonasson, Michelsen, Schmidt, Nielsen, & Callaghan, 1996) and the competitive strength of the microbial community could increase in response to increased N-supply. However, within the scope of our full-factorial belowground fertilization study (Experiment 3) the large increases in vascular plant biomass in response to fertilization at the thaw front were not matched by similar increases in mean microbial biomass N. Instead, microbial biomass was not affected by the deep-fertilization treatment and only slightly by the shallow fertilization treatment, although this was only tested in the last year of the experiment (Supporting Information, Fig. S4). This suggests that the microbial community benefits less than the vegetation from the additional deep N-source. This may increase the discrepancy between vegetation responses to climate-change-induced shallow- versus deep increases in N-supply in the longer-term. Thirdly, longer-term plant responses may differ from the results of this study due to changes in vertical root biomass distribution in response to increased deep

nutrient supply (Hodge, 2004). In this experiment, root biomass at the thaw front tended to increase (up to 100%, $p = .042$) in response to thaw-front fertilization, which is consistent with plant "foraging" as described by Callaghan et al. (1991) and McNickle, St Clair, and Cahill (2009). The observed altered root biomass distribution in response to three years of experiment suggests that, in the longer-term, the effects on plant productivity of increased nutrient supply at the thaw front may aggravate due to increased root biomass and thus uptake capacity at the thaw front. Effects of increasing root presence and an associated increase in input of low-molecular-weight carbon compounds at depth via roots (root litter, root exudates) (Jones, 1998) on belowground carbon storage can either be an increased storage of soil organic matter (SOM) in these layers (Bjork, Majdi, Klemedtsson, Lewis-Jonsson, & Molau, 2007), or the opposite: increased decomposition of old, recalcitrant SOM (Hartley et al., 2012; Hicks Pries, Schuur, & Crummer, 2013; Perveen et al., 2014; Wild et al., 2014). Overall, although plant responses to thawing permafrost in subarctic peatlands are affected by multiple factors, the experimental results presented in this study suggest that, in the longer term, a release of nutrients from thawing permafrost could accelerate N-cycling in these nutrient-deprived ecosystems.

In conclusion, we have shown for the first time that nitrogen released from thawing peatland permafrost can be taken up by deep-rooting plant species and can result in increased biomass production of these species. This plant-available N from thawing permafrost can, in functional terms, be considered "new" N input. The effect of a deep, belowground release of nutrients on subarctic peatland vegetation is fundamentally different from the effect of a shallow increase in nutrient availability: In the longer term, this climate change-induced new N source may lead to an accelerated N cycle and changes in species composition of subarctic peatlands, as well as interacting effects with C cycling (e.g. fluxes of carbon dioxide and/or methane).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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