Received: 9 March 2018 | Accepted: 9 August 2018

DOI: 10.1111/1365-2745.13062

RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

Below-ground plant traits influence tundra plant acquisition of newly thawed permafrost nitrogen

Rebecca E. Hewitt[1] | D. Lee Taylor[2] | Hélène Genet[3] | A. David McGuire[3] | Michelle C. Mack[1]

[1]Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona

[2]Department of Biology, University of New Mexico, Albuquerque, New Mexico

[3]Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska

Correspondence
Rebecca. E. Hewitt
Email: rebecca.hewitt@nau.edu

Funding information
Division of Polar Programs, Grant/Award Number: 1504312

Handling Editor: Pierre Mariotte

Abstract

1. The release of permafrost-derived nitrogen (N) has the potential to fertilize tundra vegetation, which in turn may stimulate productivity and thus offset carbon (C) losses from thawing permafrost. Below-ground plant traits may mediate ecosystem response to permafrost thaw and associated feedbacks to the atmosphere by differentially conferring access to deep, newly thawed permafrost N. Yet, identifying roots and quantifying root N uptake from deep, cold soils in complex plant communities has proved challenging to date.
2. We investigated plant acquisition of experimentally added ^{15}N isotope tracer applied at the permafrost boundary in graminoid- and shrub-dominated tundra at Eight Mile Lake, Alaska, when the thaw front was close to its maximum depth, simulating the release of newly thawed permafrost N. We used molecular tools to verify species and estimate biomass, nitrogen, and isotope pools.
3. Root biomass depth distributions follow an asymptotic relationship with depth, typical of other ecosystems. Few species had roots occurring close to the thaw front. *Rubus chamaemorus*, a short-statured non-mycorrhizal forb, and *Carex bigelowii*, a sedge, consistently had the deepest roots. Twenty-four hours after isotope addition, we observed that deep-rooted, non-mycorrhizal species had the highest ^{15}N enrichment values in their fine root tissue indicating that they access deep N late in the growing season when the thaw front is deepest. Deep-rooted plants are therefore able to immediately take up newly thawed permafrost-derived N. During the following growing season, herbaceous, non-mycorrhizal plants allocated tracer above-ground before woody, mycorrhizal plants. Ectomycorrhizal deciduous and ericoid mycorrhizal evergreen shrubs, by contrast, did not have immediate access to the deep N tracer and assimilated it into new foliar tissue gradually over the following growing season.
4. *Synthesis*. Graminoids and forbs that have immediate access to deep N represent a modest C sink compared to C emissions from thawing permafrost. However, the effects of deep N fertilization on shrubs over longer time-scales may stimulate productivity and account for a more considerable N and C sink, thus constraining the permafrost C-climate feedback.

KEYWORDS
Alaska, isotope ^{15}N, moist acidic tundra, mycorrhizae, roots, shrub expansion

1 | INTRODUCTION

The role of vegetation in constraining the permafrost carbon (C)-climate feedback is a major source of uncertainty in predicting regional C balance under future scenarios of warming in the Arctic. Thawing of permafrost soils results in microbial decomposition of soil organic matter that had previously been cryogenically protected for decades to millennia (Romanovsky, Smith, & Christiansen, 2010; Schuur et al., 2009). Permafrost thaw results in the release of greenhouse gases, CO_2 and CH_4, which are expected to amplify anthropogenic warming; this process has been identified as one of the strongest positive feedbacks to a warming climate at high latitudes (Koven et al., 2011; Schuur et al., 2008, 2015). Along with the release of C from permafrost soils, newly thawed permafrost releases nitrogen (N) (Keuper et al., 2012; Mack et al., 2010; Mu et al., 2015), a primary limiting nutrient for tundra productivity (Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995; Shaver & Chapin, 1991; Zamin & Grogan, 2012). If plants can acquire N from this source, then plant productivity may be stimulated and offset C losses from these ecosystems.

Tundra plant growth, competitive interactions, and allocation patterns are highly responsive to nutrient availability, and particularly N, in both graminoid and shrub tundra vegetation communities (Chapin & Shaver, 1985; DeMarco, Mack, Bret-Harte, Burton, & Shaver, 2014; Shaver & Chapin, 1980; Shaver et al., 2001; Shaver, Chapin, & Gartner, 1986; Van Wijk, Williams, Gough, Hobbie, & Shaver, 2003). Furthermore, there is a marked shift in the dominance of plant functional types from graminoid- to shrub-dominated tundra and an associated increase in productivity with the experimental addition of nutrients to tundra ecosystems (Mack, Schuur, Bret-Harte, Shaver, & Chapin, 2004; Shaver et al., 2001). Warmer climate conditions may also ameliorate nutrient constraints on plant growth. Experimental warming results in increased productivity and compositional shifts that mirror the effects of experimental fertilization, presumably due to increased soil resources associated with warming (Chapin et al., 1995; Hobbie, 1996; Sistla et al., 2013; Weintraub & Schimel, 2003). These experimental observations match patterns observed across the Arctic, where directional warming has resulted in shrub expansion and dominance in formerly tussock-dominated tundra (Elmendorf et al., 2012; Myers-Smith et al., 2011; Tape, Sturm, & Racine, 2006).

Nitrogen stored in upper permafrost or transition layer soils is a deep nutrient source that is potentially accessible to tundra plants upon thaw. Tundra plants root in a seasonally dynamic environment where the active layer, or portion of the soil that thaws over the growing season, deepens with the progression of the warm months of the growing season (Schuur et al., 2008).The accumulation of dissolved organic N, dissolved inorganic N, and other ions at the thaw boundary, or transition layer (Shur, Hinkel, & Nelson, 2005), from seasonal, vertical leaching through the active layer yields a rich layer of concentrated nutrients at depth (Finger et al., 2016; Kokelj & Burn, 2003). With directional climate change, the thawing of the transition layer and upper permafrost results in a release of N that is 2–15 times greater than the quantity of N available in active layer soils (Keuper et al., 2012; Mack et al., 2010). For every cm of thawed permafrost, 1.8–3.0 g N m^2 is released, with the upper estimate meeting annual plant demand (Shaver & Chapin, 1991).

When soil resource availability is at steady state, plant acquisition of soil resources is generally thought to be controlled by nutrient supply (Tilman, 1984). Yet, when resource availability changes, the importance of variability in below-ground plant traits for plant nutrient uptake may become more pronounced (Aerts & Chapin, 1999; Chapin, 2003). The rich but deep source of N from thawing transition layer soils and upper permafrost may be within the reach of tundra root systems, but plant access to this resource is uncertain due to limited data on rooting traits and function late in the growing season when the active layer is deepest and permafrost is most likely to thaw.

Rooting traits, such as rooting depth, biomass, and mycorrhizal type, have the potential to modulate ecosystem response to thawing permafrost by controlling access to permafrost-derived N as these soils thaw, thereby influencing both N and C sink strength of tundra vegetation at the ecosystem scale. Moist acidic tundra (MAT) is composed of plants with contrasting root architecture and mycorrhizal types that may affect their ability to access deep, permafrost-derived N. For example, the dominant graminoids, *Eriophorum vaginatum* and *Carex bigelowii*, have putatively deep maximum rooting depths, are non-mycorrhizal (NM) (Bliss, 1956; Callaghan, Headley, & Lee, 1991), and therefore may access deep N through close proximity of rooting systems to a deep N source. *Betula nana*, a dominant dwarf deciduous shrub, has moderately shallow roots and hosts ectomycorrhizae (ECM), which could substantially extend its foraging depth. In contrast, ericoid shrubs have relatively shallow roots colonized by ericoid mycorrhizae (ERM) that provide limited extension of the root surface (Brundrett, 2009; Iversen et al., 2015 and citations therein). Very little is known about depth profiles of mycobionts across the full active layer of tundra soils (but see Penton et al., 2013) and descriptions of fungal distributions by tundra soil horizon are often at coarse taxonomic resolutions (Wallenstein, McMahon, & Schimel, 2007) that make inferences of ecological function challenging. Given the limited resolution of fungal depth profiles in conjunction with the well-known physiological differences in mycelial characteristics, associated potential nutrient capture, and carbon costs based on mycorrhizal type (ECM, ERM), we include the mycorrhizal type of each plant species (Cripps & Eddington, 2005) as a root trait as a first step towards addressing the potential mycorrhizal role in deep N access. Below-ground traits and their potential

impacts on ecosystem C and N sink strength must be considered within the context of shifting plant composition across tussock- and shrub-dominated tundra in order to infer relative impacts on local and regional elemental cycling. To date, this has proved challenging because it is difficult to collect and accurately identify roots from deep, cold soils near the permafrost table in complex plant communities. As such, studies addressing plant access to permafrost N have been limited to harvests of simplified communities, single plants, or mesocosms with reliance on morphotyped root identification without additional verification or foliar sampling as a proxy for root access (Keuper et al., 2017, 2012; Zhu, Iversen, Riley, Slette, & Vander Stel, 2016).

We investigated whether plants have the ability to access deep N by quantifying species-specific rooting depth profiles in concert with acquisition of a ^{15}N tracer applied at the permafrost boundary at Eight Mile Lake (EML) in the warm, southerly end of the Arctic tundra and permafrost distribution in Alaska (Schuur, Crummer, Vogel, & Mack, 2007). Understanding this process at the southern boundary of the permafrost zone will improve our ability to predict plant access and uptake in colder portions of the permafrost region as the climate continues to warm. Because graminoid- and shrub-dominated tundra represent two points on the continuum of expected vegetation transitions in response to climate change, we stratified our sampling across these two communities. Our study provides important insights into how below-ground plant traits will influence ecosystem N and C sink strength with increased nutrient availability as permafrost soils thaw. Our research addresses the following questions:

1. How do below-ground properties and species rooting traits vary between tussock and shrub tundra, and among species?
2. Do rooting traits and responsiveness to changes in thaw depth influence immediate uptake of N from the permafrost boundary, storage, and subsequent allocation to above-ground foliar tissue the following growing season?
3. How does knowledge of the plant species that access N from the permafrost boundary inform our conceptual model for the role of vegetation in modulating the permafrost C-climate feedback?

2 | MATERIALS AND METHODS

2.1 | Eight Mile Lake study site

The experiment was conducted in the northern foothills of the Alaska Range in subarctic tundra near EML, Alaska (63°52'42N, 149°15'12W), north of Denali National Park. The effects of warming on permafrost characteristics and vulnerability, vegetation, and ecosystem carbon balance are well studied in the EML watershed (Mauritz et al., 2017; Natali et al., 2011; Natali, Schuur, & Rubin, 2012; Schuur et al., 2007). We conducted our research in the relatively undisturbed region of a permafrost thaw gradient adjacent to areas of more degraded permafrost (Schuur et al., 2007). The soils are Gelisols with an average organic horizon thickness of 45–65 cm, below which mineral soils are composed of glacial till and loess underlain by permafrost (Vogel, Schuur, Trucco, & Lee, 2009). The average active layer thickness is 43–89 cm (Hutchings, Bracho, & Schuur, 2017). This site is in the discontinuous permafrost zone, although entirely underlain by relatively warm permafrost (–1.0°C) within 1 m of the surface and thus vulnerable to thaw (Osterkamp & Romanovsky, 1999).

The vegetation is classified as MAT with a dominant cover of a tussock forming sedge (*E. vaginatum*, ~22% of total biomass) along with another abundant sedge (*C. bigelowii*, ~5% of total biomass), evergreen (*Andromeda polifolia*, *Rhododendron tomentosum*, *Vaccinium vitis-idaea*, *Empetrum nigrum*, ~18%) and deciduous (*Vaccinium uliginosum*, ~14%, *B. nana*, ~7%) shrubs, forbs (*Rubus chamaemorus*, ~3%), mosses (*Sphagnum* spp. and feather mosses, ~18%), and lichens (~13%) that occur in the inter-tussock space (Schuur et al., 2007). Within this tussock-dominated vegetation matrix, there are shrub-dominated communities with a *B. nana* canopy and a feather moss (mainly *Hylocomium splendens* and *Pleurozium schreberi*) understorey.

2.2 | Site selection of tussock- and shrub-dominated tundra

Within the MAT at EML, the tundra is a mosaic of graminoid- and shrub- dominated communities (Belshe, Schuur, & Grosse, 2013; Viereck, Dyrness, Batten, & Wenzlick, 1992). In July 2015, we surveyed the EML site for representative patches (>1 m^2) of tussock (<25% cover as shrubs) and shrub tundra (25%–75% cover by shrubs) each at least 10 m apart. From 25 potential tussock plots, we randomly selected five representative plots, and from 25 potential shrub plots, we selected another five plots for our experimental isotope addition.

2.3 | Isotope tracer addition

To investigate the ability of tundra plants to access deep, permafrost-derived N, we applied a ^{15}N isotope tracer at the thaw boundary. We timed the addition of our isotope tracer to coincide with seasonal maximum thaw and before plant senescence. In early September 2015, the onset of senescence of the deciduous and graminoid species had started and thaw depth was at 97% of the 12-year average (average thaw depth for September 63.4 cm ± 0.45 *SE* from 2004 to 2015; Hutchings et al., 2017) compared to the mean thaw depth measured in our 10 plots 61.2 ± 4.8 *SE* in 2015). We labelled ten (tussock = 5, shrub = 5) 1-m^2 plots with 98 atom % ammonium chloride (Sigma Aldrich, St. Louis, MO, USA) applied at the boundary between the active layer and the permafrost table to achieve common label addition of 250 mg of ^{15}N m^2 matching estimates of N form and pool size of newly thawed, upper permafrost soils (Keuper et al., 2012; Salmon et al., 2018). Additions were made at nine injection points within a 25 cm buffer inside the 1-m^2 plot by

inserting a frost probe, recording active layer thickness, and then inserting a sheathed stainless steel needle into the hole created by the frost probe. When the needle hit the permafrost table, the sheath was retracted uncovering pinholes at the tip on the needle. A syringe was connected to the far end of the needle, the tracer was injected (25 mls per injection), the needle was then retracted into the sheath, and the whole injection system was retracted from the soil. The sheath ensured that labelling occurred only at maximum thaw depth by preventing tracer from bleeding through the soil profile as the needle was retracted. Our tracer addition provided a simulation of both the hot moment and hot spot of newly thawed permafrost N in our plots; yet, it is uncertain whether the 25 cm spacing of the injection points resulted in a well-mixed supply of tracer at depth. Twenty-four hours after application of the isotopically labelled tracer, we harvested above- and below-ground vegetation to measure immediate uptake.

2.4 | Above-ground and below-ground vegetation harvest and processing

To determine immediate the tracer uptake, we sampled a 400-cm^2 (40 × 10 cm) subplot in each 1 m^2 experimentally labelled plot that included the above-ground vegetation and the soil below to a standard depth of 20 cm so as to include below-ground stems, that is, rhizomes. Sampling in the tussock tundra plots encompassed both tussock and inter-tussock space. Vegetation was sorted into species pools and then further separated by tissue type (new/old foliar, stem, and reproductive). Each species × tissue pool was dried at 60°C for 48 hr, weighed, and ground for isotope analysis on an Elemental Analysis-Isotope Ratio Mass Spectrometer (IRMS, Delta Advantage, Thermo Fisher Scientific, Waltham, MA, USA) coupled to an Elemental Combustion Analyzer (Costech ECS4010, Valencia, CA, USA), located at Northern Arizona University.

We harvested organic soil as a monolith (10 × 10 cm) that was on average 20 cm deep below the surface of the vegetation. Below the monolith, we cored deep organic and mineral soils (7 cm diameter core) until we hit ice at the permafrost boundary. The soil samples were separated by 10 cm depth increments with the exception of the top 0–5 cm. We measured the dimensions for each soil depth increment to determine volume of each sample. Samples were stored at 4°C and processed within 5 days of harvest.

2.5 | Root sampling and identification

Live roots and rhizomes were removed from each depth increment by hand, separated by size class (>2 mm or <2 mm), and then by species morphotype based on colour, texture, and branching pattern. Using microscopy (10–40×), we further sorted species morphotype samples and removed dead roots. From this cleaned sample, we measured the wet weight accounting for a subsample of fine roots used for RFLP-based molecular verification of the root species identity (Appendix S1). The majority of fine root identities were successfully verified with molecular tools (Appendix S1); however, in a few cases, identities were unresolved due to unsuccessful PCR. In these cases, identity was informed by microscopy and accuracy estimates of similar samples (Appendix S1). The wet weight of the remainder of the sample was measured, dried at 60°C for 48 hr, and reweighed to obtain the dry weight. We analysed a subsample of the dried root sample for percent C and N and recovery of the isotope tracer using IRMS as described above. We used the molecular verification to correct root species identity, biomass, and tissue atom percent enrichment for the majority of fine root samples (Appendix S1).

2.6 | Foliar enrichment one growing season after isotope addition

To determine which plant species had access to the deep N throughout the growing season following the isotope addition (May to August 2016), we harvested new foliar material from seven species in each plot (*E. vaginatum*, *C. bigelowii*, *R. tomentosum*, *V. vitis-idaea*, *V. uliginosum*, *B. nana*, and *R. chamaemorus*) at five time points (first leaf out in early and late May and then monthly). Early season foliar isotope concentrations provide a confirmation of late-season uptake and storage from the previous year, while changes in foliar concentration over the growing season may indicate redistribution of tracer or allocation of deep N as foliar sink strength changes over the growing season. Leaves were dried at 60°C for 48 hr, ground, and run for IRMS analysis following the procedure described above.

2.7 | ^{15}N calculations

To derive atom percent enrichment of plant material, we first calculated mean natural abundance values for each species and tissue type. These values were based on a natural abundance harvest that took place prior to the labelling experiment in July 2015 in three tussock plots and three shrubs plots and supplemented by foliar isotope values reported from our research site (Rodenhizer & Schuur, 2017). In cases where we did not have a species-specific value for each tissue type, we used the mean value for the species or tissue grouping that appeared most appropriate.

We calculated the ^{15}N enrichment (atom%^{15}N) of a sample as (atom%$^{15}N_{measured}$ − atom%$^{15}N_{natural\ abundance}$). The tracer pool (^{15}N g) recovered was calculated as (atom%$^{15}N_{measured}$ − atom%$^{15}N_{natural\ abundance}$) × total N pool size (g). The percent tracer added that was recovered was calculated as the tracer pool (^{15}N g)/tracer added (^{15}N g) × 100.

2.8 | Statistical analyses

We used linear mixed effects models with vegetation community (tussock and shrub) as a fixed factor and plot as a random factor to test for differences in soil properties (organic layer thickness and average thaw depth) using the nlme package (Pinheiro, Bates, DebRoy, & Sarkar, 2017). Average plot thaw depth was calculated as the mean of the nine thaw depths measured at each injection site in each plot. We used a similar model structure with the addition of plant species

as a fixed factor to test for differences in maximum rooting depth, maximum root: thaw depth ratio, and biomass of below-ground size classes. We also tested whether maximum rooting depth was related to the fixed factors maximum September thaw depth and species with plot as a random factor to test for rooting plasticity in response to thaw.

We used a random forest regression tree approach to assess both (a) the relative importance of species traits (species, plant functional type (PFT), or mycorrhizal type) in explaining variation in maximum root: thaw depth ratio and (b) the relative importance of rooting traits such as depth, fine root biomass, species identity, PFT, or mycorrhizal type in explaining atom percent enrichment of fine root material using the randomForest package (Liaw & Wiener, 2015).

The response variables accounting for tracer recovery (percent tracer recovered and species sink strength – the proportion of the tracer pool recovered in relation to the fine root biomass pool) were transformed with the Aligned Rank Transformation using the package ARTool (Kay & Wobbrock, 2016) and evaluated with a nonparametric mixed effects model with vegetation community and species as fixed factors and plot as a random factor. The relationship between mean atom percent enrichment in fine root material to the mean root: thaw depth ratio for each species was evaluated using a nonparametric regression in the mblm package (Komsta, 2013). Foliar atom percent enrichment throughout the growing season after isotope addition was tested with a mixed effects model with date of sampling, plant species, and vegetation community as fixed factors and plot as a random factor.

Data were transformed to meet assumptions of normality and homoscedasticity when necessary. For all the models, interaction terms were tested, but dropped from the final model if the interaction was not significant. We used the lsmeans package (Lenth, 2016) to conduct post hoc Bonferroni-corrected pairwise comparisons. We used the r statistical package 3.3.2 (R Core Team, 2016) for all analyses (Appendix S2).

3 | RESULTS

3.1 | Below-ground properties in tussock and shrub tundra

3.1.1 | Soil properties

Tussock-dominated plots were thawed more deeply than shrub-dominated plots at the time of our isotope addition ($F = 27.43$, $p < 0.0001$, Table 1). Average thaw depth per plot calculated from measurements at the nine injection sites in each plot ranged from 62 to 83 cm deep in tussock tundra plots and 46–55 cm in shrub tundra plots. Organic soil thickness did not vary between tussock and shrub plots ($F = 0.72$, $p = 0.42$, Table 1). Notably, however, the variability in organic soil thickness was higher in tussock plots ranging from 31 to 65 cm, while organic horizons in shrub-dominated plots were remarkably similar ranging from 40 to 47 cm deep.

TABLE 1 Soil and vegetation characteristics for tussock and shrub tundra at Eight Mile Lake, Alaska. Values represent plot means (tussock $n = 5$, shrub $n = 5$) with (*SE*). Above-ground biomass and tracer recovery excludes rhizomes. Below-ground biomass includes coarse and fine roots and rhizomes. Tracer recovered accounts for isotope uptake 24 hr after tracer addition

Variable	Tussock	Shrub
Avg. organic soil depth (cm)	39.8 (6.46)	43.2 (1.16)
Avg. thaw depth (cm)	69.57 (3.59)	49.2 (2.82)
Total above-ground biomass (g m^2)	717.0 (272.00)	943.40 (124.66)
Total below-ground biomass (g m^2)	1,187.80 (374.40)	2,021.57 (340.86)
Avg. max rooting depth (cm)	74.6 (6.88)	48.0 (1.84)
Avg. % tracer recovered		
Above-ground	0.11 (0.06)	0.10 (0.03)
Below-ground	4.53 (2.51)	2.32 (1.38)

3.1.2 | Accuracy of root identification

Our ability to identify species and PFTs with morphological characteristics alone was highest for graminoid species and deciduous shrubs in comparison to ericoid shrubs and forbs (Table S1). For example, in tussock tundra, our ability to accurately identify *E. vaginatum* was 100%, and *B. nana* was 96%, while 31% of the time we accurately identified *R. chamaemorus*. Unexpectedly, we found two species of forbs, *P. frigidus* and *P. bistorta*, and an ericoid dwarf shrub, *A. polifolia*, in our DNA-based rooting profiles that we did not observe above-ground and which are rare at EML. For many of the dominant species, we were fairly successful at identifying roots by morphological features. However, verification with molecular methods was imperative for correctly identifying species that occurred at depth and those that had the greatest access to deep N (Table S1). For all subsequent analyses, we used the molecular-corrected data.

3.1.3 | Root biomass

Biomass of the structural components of the below-ground pool (rhizomes and coarse roots) varied by plant species ($F = 22.12$, $p < 0.0001$), but not by vegetation community alone ($F = 4.52$, $p = 0.07$, Table S2a). Pairwise comparisons of species indicated that ericoid rhizome and coarse root biomass was higher than *R. chamaemorus* (t-ratio = −7.08, $p < 0.01$), *E. vaginatum* (t-ratio = −7.05, $p < 0.01$), *C. bigelowii* (t-ratio = −3.62, $p = 0.01$), and *B. nana* (t-ratio = −4.19, $p < 0.01$), which makes sense given the widespread occurrence of ericoid plants throughout both vegetation communities and minimal *B. nana* in our tussock plots. Similarly we saw overall greater *C. bigelowii* biomass than *R. chamaemorus* (t-ratio = −3.46, $p = 0.02$) and *E. vaginatum* (t-ratio = −3.43, $p = 0.02$).

TABLE 2 Rooting characteristics for plant species observed in tussock and shrub tundra communities. Maximum rooting depth and thaw depth of fine root material was measured in cm. Fine root biomass was quantified as g m^2. Values reported as means (*SE*)

Family	Species	PFT	Tussock tundra max rooting depth	Shrub tundra max rooting depth	Tussock tundra max root: thaw depth	Shrub tundra max root: thaw depth	Tussock tundra fine root biomass	Shrub tundra fine root biomass
Rosaceae	*Rubus chamaemorus*	Forb	66.67 (18.85)	43.25 (4.40)	0.82 (0.17)	0.78 (0.09)	94.5 (65.4)	100.05 (30.92)
Cyperaceae	*Eriophorum vaginatum*	Sedge	34.8 (5.49)		0.45 (0.08)		32.02 (8.65)	0
Cyperaceae	*Carex bigelowii*	Sedge	67.4 (11.87)	36.75 (7.28)	0.84 (0.11)	0.62 (0.10)	273.7 (143.62)	131.92 (43.42)
Betulaceae	*Betula nana*	Deciduous Shrub	30.50 (6.66)	26.8 (4.53)	0.40 (0.10)	0.47 (0.09)	45.38 (12.08)	290.05 (118.34)
Ericaceae	*Vaccinium uliginosum*	Deciduous Shrub	42.00 (11.61)	30.25 (4.21)	0.55 (0.16)	0.54 (0.09)	62.32 (23.91)	66.51 (36.48)
Ericaceae	*Empetrum nigrum*	Evergreen Shrub	18.00 (13.00)	23 (1.00)	0.19 (0.12)	0.40 (0.01)	3.27 (2.08)	48.19 (44.52)
Ericaceae	*Rhododendron tomentosum*	Evergreen Shrub	41.40 (8.03)	34.8 (5.60)	0.54 (0.11)	0.60 (0.09)	133.56 (27.56)	273.86 (86.96)
Ericaceae	*Vaccinium vitis-idaea*	Evergreen Shrub	35.75 (6.98)	25.8 (5.52)	0.48 (0.09)	0.46 (0.11)	14.80 (6.57)	30.52 (12.51)
Ericaceae	*Ericoid pool*	Evergreen Shrub	43	27.5 (10.50)	0.57	0.50 (0.21)	0.80 (0.80)	10.52 (6.54)
Ericaceae	*Andromeda polifolia*	Evergreen Shrub	50	22	0.67	0.39	33.00 (33.00)	7.76 (7.76)
Asteraceae	*Petasites frigidus*	Forb		17		0.29	0	11.19
Polygonaceae	*Polygonum bistorta*	Forb		51		0.93	0	83.69

The absorptive fraction of below-ground biomass, the fine root biomass (<2 mm), also varied across plant species ($F = 7.87$, $p < 0.01$, Table 2), but not by vegetation community ($F = 0.84$, $p = 0.39$, Table S2b). Fine root biomass of the pervasive deciduous shrub, *B. nana*, was greater than *E. vaginatum* (*t*-ratio = −3.50, $p = 0.04$), *A. polifolia* (*t*-ratio = 4.30, $p < 0.01$), *E. nigrum* (*t*-ratio = 4.00, $p = 0.01$), and the pooled ericoid fraction (*t*-ratio = 4.50, $p < 0.01$). *Rhododendron tomentosum*, a dwarf shrub abundant in both the inter-tussock spaces and in shrub tundra, had greater fine root biomass than *E. vaginatum* (*t*-ratio = −4.69, $p < 0.01$), several ericoid species including *E. nigrum* (*t*-ratio = −5.14, $p = 0.0001$), *A. polifolia* (*t*-ratio = 5.48, $p < 0.01$), *V. vitis-ideae* (*t*-ratio = 3.58, $p = 0.03$), and the unresolved ericoid pool (*t*-ratio = 5.70, $p < 0.01$). *Carex bigelowii*, a sub-dominant graminoid, had greater fine root biomass than *E. nigrum* (*t*-ratio = 4.37, $p < 0.01$), the pooled ericoid fraction (*t*-ratio = 4.92, $p < 0.01$), and *E. vaginatum* (*t*-ratio = −3.92, $p = 0.01$). The "Other" category containing fine roots of unknown identity, *P. frigidus*, and *P. bistorta* was greater than unresolved ericoid biomass (*t*-ratio = −3.45, $p = 0.05$).

3.2 | Rooting depth profiles

3.2.1 | Maximum rooting depth and plasticity with thaw

The rooting distributions in tussock and shrub tundra follow an asymptotic relationship with depth (Figure 1). The profiles indicated that the majority of root biomass occurred within the top 40 cm across vegetation communities. Plant species significantly explained the absolute maximum rooting depth ($F = 2.73$, $p < 0.01$), while vegetation community was not an important explanatory variable ($F = 3.05$, $p = 0.12$, Table S3). The variation on a species level did not yield significantly different contrasts in maximum rooting depth, yet some patterns in maximum rooting depth emerged and were reinforced when assessing maximum rooting depth in relation to thaw depth. Plant species again was important in explaining the ratio of the maximum root to thaw depth ($F = 2.94$, $p = 0.01$), while again vegetation community was not ($F < 0.001$, $p = 0.81$, Table S3). *Rubus chamaemorus* had a deeper maximum root: thaw depth ratio than *B. nana* (*t*-ratio = 3.77, $p = 0.02$) and *V. vitis-ideae* (*t*-ratio = 3.60, $p = 0.04$). The majority of plants had maximum rooting depths at about 50% of the active layer depth. In tussock tundra, the maximum rooting depth of the plant species ranged from 19% to 84%, and in shrub tundra, 29%–93% of the active layer was colonized (Figure 1, Table 2). Few species had roots occurring close to the thaw front (Figure 1). However, *R. chamaemorus* and *C. bigelowii* were both able to forage close to the thaw boundary and reached on average >80% of the way to the permafrost table in the deeply thawed tussock-dominated plots. *Betula nana* had moderate rooting depths of ~30 cm, reaching about half way to the thaw boundary with the permafrost table. Ericoid species had shallow and moderate rooting depths. Of the ericoids, *E. nigrum* had the shallowest roots (~20 cm), while *R. tomentosum* was the most deeply rooted, with roots extending to around 60% of the active layer (34–41 cm

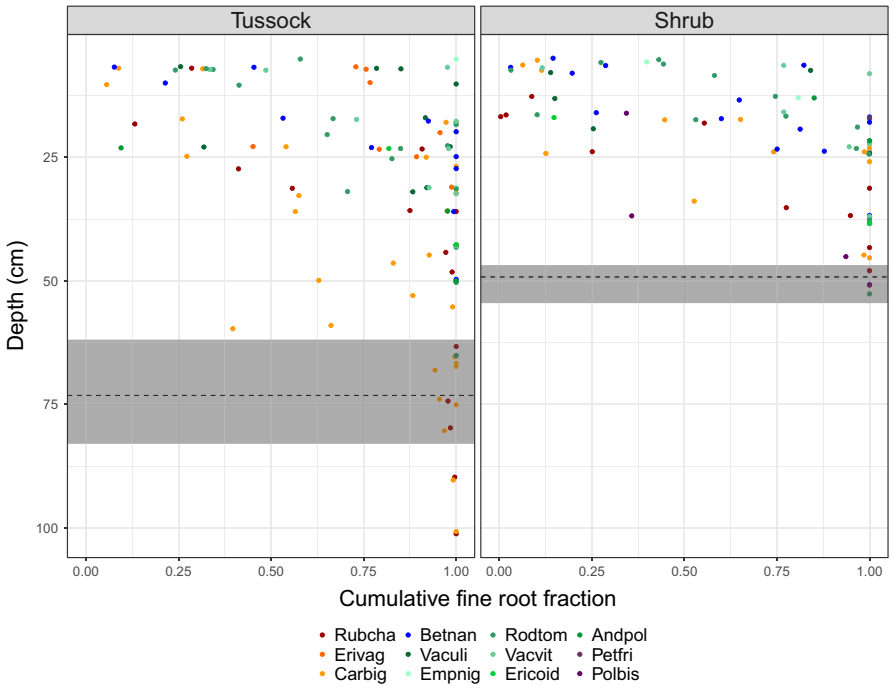

FIGURE 1 Depth profiles of the cumulative dry fine root fraction for plant species in tussock and shrub tundra at Eight Mile Lake. The cumulative fine root fraction was calculated for each species in each plot. Dashed lines represent the average thaw depth of the tussock- or shrub-dominated plots and the shading indicates the range of average thaw depth across both communities. Rubcha = *Rubus chamaemorus*, Erivag = *Eriophorum vaginatum*, Carbig = *Carex bigelowii*, Betnan = *Betula nana*, Vaculi = *Vaccinium uliginosum*, Empnig = *Empetrum nigrum*, Rodtom = *Rhododendron tomentosum*, Vacvit = *V. vitis-idaea*, Ericoid = *ericaceous species pool*, Andpol = *Andromeda polifolia*, Petfri = *Petasites frigidus*, and Polbis = *Polygonum bistorta*. In further analysis *P. frigidus*, *P. bistorta*, and samples with unresolved identities were grouped into an "Other" category [Colour figure can be viewed at wileyonlinelibrary.com]

in shrub and tussock plots). These results show that species vary in their rooting depths and that they respond to variation in thaw depth (i.e., tussock plots are thawed more deeply, but ratios of maximum root to thaw depth do not change).

Both species and the interaction between species and maximum thaw depth were significantly related to maximum rooting depth (thaw $F = 3.58$, $p = 0.09$, species $F = 3.68$, $p < 0.01$, thaw depth × species $F = 2.96$, $p < 0.01$; $R^2_{\text{marginal}} = 0.43$, $R^2_{\text{conditional}} = 0.62$, Figure 2). The maximum rooting depth of both *R. chamaemorus* ($F = 7.85$, $p = 0.04$, $R^2_{\text{marginal}} = 0.56$, $R^2_{\text{conditional}} = 0.95$) and *C. bigelowii* ($F = 44.82$, $p < 0.001$, $R^2_{\text{marginal}} = 0.85$, $R^2_{\text{conditional}} = 0.98$) show a positive response to an increase in thaw depth (Figure 2).

3.2.2 | Traits predictive of rooting depth

Species identity had the greatest explanatory power for maximum rooting depth in relation to thaw depth (Figure S1). The high variable importance score for species was followed by PFT and then mycorrhizal type. Mycorrhizal type had marginal importance. This result was robust whether we grouped mycorrhizal type as NM versus mycorrhizal or broke out the mycorrhizal groups into ERM and ECM. Many species with different mycorrhizal type rooted in a similar zone, ~40%–50% of the active layer depth (Table 2), supporting the random forest findings that species identity is the greatest predictor of maximum rooting depth.

3.3 | Species and traits that provide access to newly thawed permafrost N

3.3.1 | Uptake of deep N tracer 24 hr after isotope addition

There was minimal recovery of tracer in above-ground plant parts (rhizomes excluded, Table 1). Above-ground tracer recovery ranged from 0.01% to 0.32% across plots. Across all species, average tracer recovery was less than 0.03% (Table S4).

The majority of tracer was found in fine roots (3.34% ± 1.41 *SE*) and on average less than 0.07% was recovered in coarse roots and rhizomes. ($F = 20.33$, $p < 0.01$, Bonferroni contrasts $p < 0.01$ for all pairwise comparisons). Within the fine root pool, the percent tracer recovered ranged from 0.02% to 14.04% among plots.

Vegetation community and the interaction between vegetation community and species were important to explaining variation in tracer recovery in fine root biomass (community $F = 25.16$, $p < 0.01$, species × community $F = 3.04$, $p < 0.01$). In the fine root pool, we recovered on average 4.51% ± 2.51 *SE* (range 0.02%–14.04%) of tracer added to tussock tundra and 2.17% ± 1.42 *SE* (range 0.06%–7.58%) of the tracer added to shrub tundra.

The species with the greatest tracer recovered in tussock tundra was *C. bigelowii* and in shrub tundra was *R. chamaemorus*. *Carex bigelowii* in tussock tundra had greater tracer recovery compared to *B.*

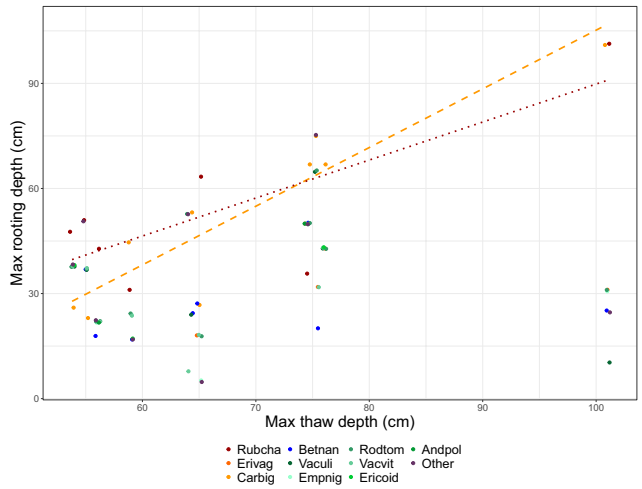

FIGURE 2 Species maximum rooting depth in relation to maximum plot thaw depth. *Rubus chamaemorus* ($R^2_{marginal}$ = 0.56) and *Carex bigelowii* ($R^2_{marginal}$ = 0.85) maximum rooting depths were significantly ($p < 0.05$) related to maximum thaw depth. Dashed line = Carbig, dotted line = Rubcha [Colour figure can be viewed at wileyonlinelibrary.com]

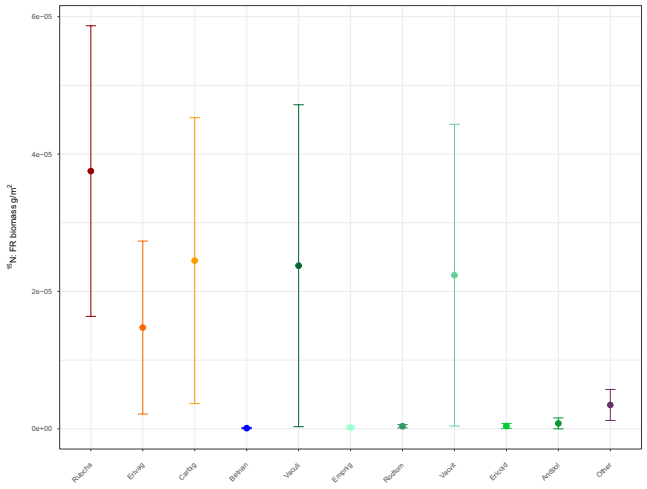

FIGURE 3 Mean proportion of tracer pool (^{15}N g m^2) in relation to dry biomass (g m^2) of fine roots with *SE* [Colour figure can be viewed at wileyonlinelibrary.com]

nana (*z*-ratio = 3.50, p = 0.03), *E. nigrum* (*z*-ratio = 3.64, p = 0.02), *A. polifolia* (*z*-ratio = 3.34, p = 0.05), and the ericoid pool (*z*-ratio = 3.56, p = 0.02) in shrub tundra. *Carex bigelowii* in shrub tundra had greater tracer recovery than *R. chamaemorus* in tussock tundra (*z*-ratio = −3.58, p = 0.02). There were high levels of variability in the percent recovery in root tissue both within and among species. The lowest tracer recovery occurred in evergreen ericoid shrubs (Table S4).

When we assessed the sink strength, defined as the pool of recovered tracer in relation to the biomass of fine roots, of each species across vegetation communities, we found species (Figure 3, F = 2.53, p = 0.02) but not vegetation community (F = 1.95, p = 0.17) was important in explaining this ratio. Strong contrasts in species sink strength emerged. *Rubus chamaemorus* (*z*-ratio = 4.22, $p < 0.01$) and *C. bigelowii* (*z*-ratio = 3.78, $p < 0.01$) had greater sink strength than *B. nana*. *Rubus chamaemorus* also had greater sink strength than *R. tomentosum* (*z*-ratio = 3.48, p = 0.03). Some relatively high biomass species such as *B. nana* and *R. tomentosum* had low tracer to biomass ratios. This is in juxtaposition to relatively moderate biomass species like *C. bigelowii* and *R. chamaemorus* that had large tracer pools in relation to biomass.

3.3.2 | Traits as predictors of N uptake 24 hr after isotope addition

Given the species-level variability in rooting profiles and tracer recovery, we used an exploratory random forest model to assess the importance of plant traits (species, PFT, mycorrhizal type, root: thaw depth ratio, and fine root biomass) in predicting atom percent enrichment of fine root samples. The random forest model indicated that root: thaw depth ratio followed closely by biomass were the only important variables (% MSE root: thaw depth ratio = 0.35, fine root biomass g m^2 = 0.32) in the model explaining atom percent enrichment of fine roots, with all other variables showing predictive power only equal to random permutations.

Furthermore, we tested whether on average, the atom percent enrichment increased with the average root: thaw depth ratio. Analysing the average root: thaw depth ratio allows us to pool species across vegetation communities and consider enrichment levels of species across the rooting profile. We observed that as the average root: thaw depth ratio increased the average atom percent enrichment of fine root material increased (Figure 4, MAD = 0.64, p = 0.04).

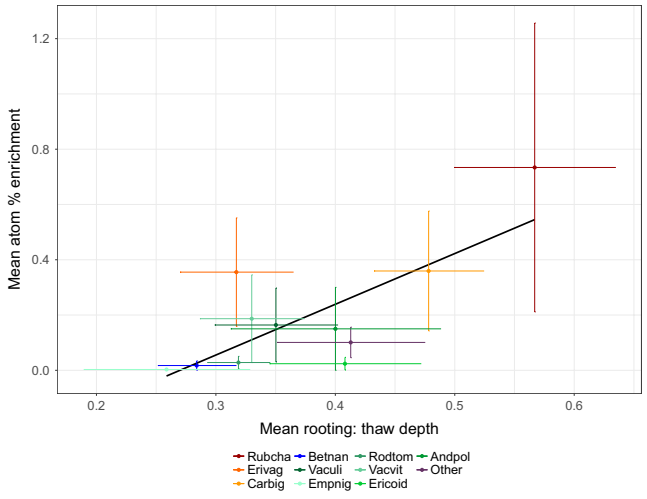

FIGURE 4 Increasing sample depth in relation to thaw depth results in increased fine root atom percent enrichment across all species. Mean for each species with *SE* [Colour figure can be viewed at wileyonlinelibrary.com]

3.3.3 | Foliar atom percent enrichment over the growing season

One of our main goals was to assess which species were able to acquire N late in the growing season, store it over winter and allocate it above-ground during the 2016 growing season. We observed that variation in atom percent enrichment of new leaves over the growing season following isotope addition was affected by time (F = 23.34, p < 0.01), plant species (F = 156.78, p < 0.01), and the interaction between plant species and vegetation community (F = 7.78, p < 0.01). These fixed effects described a high proportion of the variance in foliar atom percent enrichment ($R^2_{marginal}$ = 0.77; $R^2_{conditional}$ = 0.80). *Carex bigelowii* is the first plant to leaf out in early May and it showed foliar enrichment immediately (May 10 0.44% ± 0.15 *SE*). By late May other herbaceous, non-mycorrhizal plant species like the dominant sedge, *E. vaginatum*, and *R. chamaemorus* had higher foliar enrichment than ECM *B. nana* and dwarf ericoid shrubs (Figure 5a–d). Enrichment levels of herbaceous, non-mycorrhizal species (*E. vaginatum*, *C. bigelowii*, *R. chamaemorus*) were consistently higher (Figure 5a,b) than woody dwarf shrubs with ECM and ERM (*B. nana*, *R. tomentosum*, *V. uliginosum*, *V. vitis-idaea* Figure 5c,d) across the growing season in both tussock- and shrub-dominated plots. The enrichment levels of the mycorrhizal dwarf shrubs increased between May and August (Figure 5c,d). However, by August the atom percent enrichment levels of new leaves were still greatest for *C. bigelowii* (3.66% ± 0.94 *SE*), *E. vaginatum* (3.60% ± 0.75 *SE*), and *R. chamaemorus* (3.38% ± 0.79 *SE*, Figure 5a,b), while ECM and ERM evergreen and deciduous shrubs were less enriched (Figure 5c,d).

4 | DISCUSSION

Our tracer study provides insights into how complex plant communities may act as sinks for newly available N as permafrost thaws with warming. We observed immediate uptake of a deep N isotope tracer that simulated the release of newly thawed, permafrost N. Immediate access to deep N was based on fine root depth in relation to the thaw front and biomass more so than species, mycorrhizal type, or PFT. Species with deep, non-mycorrhizal roots were the first to access the tracer and allocate it to new foliar material by the start of the following growing season demonstrating that they stored it over winter. However, woody mycorrhizal species assimilated the tracer into new leaves over the course of the following growing season revealing that a newly thawed permafrost N source has the potential to fertilize graminoid and shrub tundra constituents.

Plant community composition and productivity in tundra ecosystems has been attributed to species-specific nutrient uptake capacity and competitive preference for N form (McKane et al., 2002; Schimel, Kielland, & Chapin, 1996). Yet, others have observed that species-level root traits and physical access influenced by plant–microbe competition (Schimel & Bennett, 2004; Weintraub & Schimel, 2005a; Zhu et al., 2016) regulate the uptake of N. We observed that the most deeply rooted species, with the highest proximity to tracer, were the species with the greatest immediate enrichment levels providing support for the idea that root traits are key to N uptake. Our observations of deeply rooted species late in the growing season are consistent with findings made in the early growing season that report *R. chamaemorus* and *C. bigelowii* follow the progression of the thaw front (Bliss, 1956); however, we did not observe *E. vaginatum* at the thaw front (sensu Bliss, 1956), which could be due to

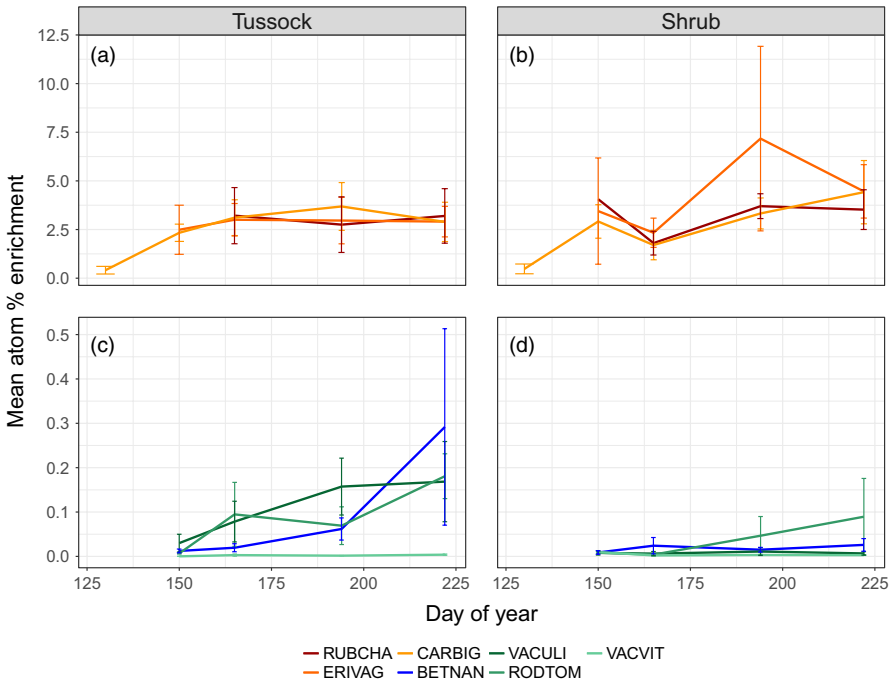

FIGURE 5 Mean atom percent enrichment with *SE* of new leaf tissue for each focal plant over the growing season at EML, Alaska for herbaceous (a, b) and woody (c, d) species in tussock and shrub tundra. Day of year of leaf sampling: 10 May = 130, 30 May = 150, 14 June = 165, 13 July = 194, and 10 August = 222. Note the different scales on the *y*-axis [Colour figure can be viewed at wileyonlinelibrary.com]

our sampling time or a reduced ability to fully document *E. vaginatum* root distributions because we sampled quadrats of tussock tundra composed of tussock and inter-tussock space and *E. vaginatum* roots are concentrated under the tussock crown.

The uptake of nutrients, particularly by herbaceous species, from both shallow and deep soils late in the growing season results in storage of nutrients more so than immediate translocation above-ground (Chapin, Schulze, & Mooney, 1990; Grogan & Jonasson, 2003; Keuper et al., 2017; Larsen, Michelsen, Jonasson, Beier, & Grogan, 2012). The capacity of graminoid and forb species to store and use deep N upon leaf out has been demonstrated in permafrost peatlands with foliar analysis (Keuper et al., 2017). In line with these patterns of late season deep N use, graminoids had the highest ^{15}N tracer concentration in roots in the fall following tracer addition in surficial soils in subarctic heath tundra (Larsen et al., 2012). Variation in assimilation of tracer by species the following growing season may indicate differences in plant phenology and synchrony between above- and below-ground activities.

We observed that the new leaves of mycorrhizal shrubs increased in foliar enrichment over the course of the growing season, which may be explained by two hypotheses: (a) access to tracer at shallower depths increased as roots that initially accessed deep N senesce and decompose resulting in subsequent internal cycling in the soil profile and tracer availability; and/or (b) there was immediate immobilization of the tracer in fungal biomass and eventual transfer to the host plant over longer time periods (Colpaert, Laere, & Assche, 1996; Näsholm et al., 2013). In our current study, we cannot partition the importance of plant mycorrhizal type compared to rooting depth because we observed that plants with similar mycorrhizal habits had similar rooting depths. Instead, we can only speculate that the cold-tolerance of many fungi and root tips (Tibbett & Cairney, 2007) along with the long-distance foraging potential of some ECM taxa poises them to take advantage of newly thawed permafrost resources. The depth distributions, activity, and linkages between deep soil and root-associated mycorrhizal fungi warrant further investigation.

Our current understanding of soil nutrient pools is that they are driven by sink rather than source processes in tundra ecosystems (Weintraub & Schimel, 2005a). Seasonal dynamics of available N pools are closely linked to root growth and below-ground activity. For example, at the onset of peak plant biomass extractable N concentrations decline, likely due to N uptake and microbial immobilization driven by root C inputs (Weintraub & Schimel, 2005b). Later in the fall, high rates of ammonification and N leaching have been observed in lowland tundra (Treat, Wollheim, Verner, & Bowden, 2016). This was attributed to decomposition of soil organic matter in surficial soils not the deeper N-rich transition layer soils coupled with high root mortality and therefore low sink strength. The contrasts between these results and our results in observed sink strength suggest that we need to further study and incorporate late season temporal and vertical N availability in our conceptual model of below-ground N cycling.

The relationships between newly thawed permafrost N uptake, species response to warming, and C allocation patterns informs our understanding of vegetation effects on the permafrost C-climate feedback. Within 5 km of our research site, experimental warming of MAT at the Carbon in Permafrost Experimental Heating Research (CiPEHR) site resulted in increased thaw depth coupled with increased above-ground biomass, net primary productivity (ANPP), and N pools (Natali et al., 2012; Salmon et al., 2016), driven predominantly by changes in the dominant sedge *E. vaginatum*. Furthermore, as foliar N pools increased and foliar ^{15}N signatures shifted, resin-available N in surface soils did not increase suggesting a shift to a deep N source (Natali et al., 2012; Salmon et al., 2016). The results from the CiPEHR warming experiment in relation to our N uptake study demonstrate that deeply rooted, NM graminoids and forbs with low C allocation per unit N have the capacity to use permafrost-derived N immediately, are responsive to warming, and are implicated in the use of newly thawed permafrost N to stimulate ANPP to a magnitude that may offset some C losses from soils as this ecosystem warms.

Furthermore, when we place the experimental results from CiPEHR and our study in the context of the longer term progression of thaw at our research site, we find supporting evidence for permafrost N use by plants that are responding positively to thaw. If we scale our August 2016 atom percent enrichment concentrations by previously acquired foliar biomass estimates of new leaves for three representative species, we can see that the pool of recovered isotope is greater for the ERM and ECM dwarf shrubs than the deeply rooted but low biomass plants like *R. chamaemorus*. New leaves of *R. chamaemorus* in August were on average 3.38% ± 0.79 *SE* enriched, but have low biomass (0.26 g m^2 ± 0.19 *SE* and 1.58% ± 0.43%N); in contrast, the ECM deciduous shrub *B. nana* had lower enrichment (0.14% ± 0.10 *SE*), but greater average new foliar biomass (18.22 g m^2 ± 12.74, 0.69% ± 0.07%N), and the dominant ERM evergreen shrub *R. tomentosum* had similar enrichment to *B. nana* (0.14% ± 0.05 *SE*) and even greater new foliar biomass (23.15 g m^2 ± 6.33 *SE*, 1.30% ± 0.03%N). This scaling of isotope uptake by estimates of new leaf biomass shows 100 μg ^{15}N recovered by *R. chamaemorus*, 200 μg ^{15}N recovered by *B. nana*, and 400 μg ^{15}N recovered by *R. tomentosum*. This highlights that the immediate sink strength of deeply rooted, herbaceous non-mycorrhizal plants might be quite strong, but over longer time frames, regardless of direct or indirect mechanisms, dwarf shrubs show use of substantial amounts of deep N. With the progression of thaw at our site total canopy N has increased along with evergreen and deciduous shrub above-ground biomass, while graminoid biomass decreased (Schuur et al., 2007). This indicates that plant functional types that show a positive response to increased permafrost thaw may be supported by the use of newly thawed permafrost N over longer time-scales.

Uptake of deep permafrost N may contribute to the attenuation of N limitation in MAT and potentially result in increased productivity. Longer term warming and fertilization experiments in MAT result in a compositional shift over decadal time-scales (Mack et al., 2004; Shaver et al., 2001; Sistla et al., 2013; Walker et al., 2006). The same successional trajectory from graminoid to shrub tundra has been observed with increasing permafrost degradation at EML (Schuur et al., 2007). Both directional changes in thaw depth and

improved nutrition in more surficial soils as a consequence of translocated N from newly thawed permafrost may eventually facilitate a transition to more shrub-dominated tundra. At CiPEHR, Natali et al. (2012) observed increased graminoid litter inputs with warming, which decompose quickly (Hobbie, 1996) and would therefore enrich the surface soil with N from newly thawed permafrost. *Betula nana* is a strong competitor for late season ammonium from surficial soils (McKane et al., 2002) and thus is primed to access recycled N transported from depth. If deciduous shrubs like *B. nana* respond to enriched surficial soils or take up N from newly thawed permafrost via mycorrhizal conduits over longer time-scales, we would expect dominance of this shrub to ensue. The long-term potential for increased productivity due to both woody and non-woody plant response to warming at these southerly MAT sites has the potential to affect the balance of C sources from soils with a greater C sink in plant biomass. We suggest there is a strong need for the modelling of regional C balance with a more nuanced treatment of root function and N dynamics.

5 | CONCLUSIONS

Our investigation demonstrates late-season access to a newly thawed permafrost N source is strongly related to below-ground species traits. We observed immediate uptake of tracer by deeply rooted non-mycorrhizal sedges and forbs with low growth potential and therefore modest impacts on the permafrost C-climate feedback. However, over a longer time period higher productivity dwarf shrubs accessed the isotope tracer. Our study shows high potential for newly thawed permafrost N to fertilize both graminoid and shrub tundra communities over longer time periods, which may offset C losses from these ecosystems.

ACKNOWLEDGEMENTS

This project was supported by the National Science Foundation (award number: 1504312). We thank E.A.G. Schuur for facilitating our research at the Eight Mile Lake research site.

AUTHORS' CONTRIBUTIONS

M.C.M. and R.E.H. designed the field experiment; R.E.H. conducted fieldwork, isotope analysis, data analysis, and drafted the manuscript; R.E.H. and H.G. processed field samples; D.L.T. conducted molecular verification of root identities; H.G. corrected root IDs for final analysis. All authors made contributions to manuscript revision and have approved the final version of the manuscript.

DATA ACCESSIBILITY

Data are archived with the Arctic Data Center: https://doi.org/10.18739/A2K06X08R (Hewitt, Taylor, Genet, McGuire, & Mack, 2018).

ORCID

Rebecca E. Hewitt http://orcid.org/0000-0002-6668-8472

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Hewitt RE, Taylor DL, Genet H, McGuire AD, Mack MC. Below-ground plant traits influence tundra plant acquisition of newly thawed permafrost nitrogen. *J Ecol*. 2019;107:950–962. https://doi.org/10.1111/1365-2745.13062