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RESEARCH ARTICLE

Plant foliar nutrient response to active layer and water table depth in warming permafrost soils

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Abstract

1. Thawing permafrost in northern latitudes has led to deepening active soil layers and fluctuating water tables. This could increase plant access to permafrost-derived nitrogen (N), phosphorus (P) and other nutrients such as calcium (Ca) and magnesium (Mg), and subsequently increase plant productivity and ecosystem carbon storage and nutrient cycling. We hypothesized that deepening permafrost thaw and water table fluctuations would alter species-specific foliar N:P ratios. Since there is often more P, Ca and Mg available in the deeper mineral soil layers and more N available in the shallow organic layers, we expected that deeply rooted species would decrease foliar N:P ratios due to root proximity to thawing mineral soil, and plants with shallower rooting systems mostly in the organic layer would increase foliar N:P ratios.
2. We assessed foliar and canopy nutrient responses of seven vascular plant species in moist acidic tussock tundra vegetation in the northern foothills of the Alaska Range to variable soil thaw depths and water table levels induced by either a natural thermokarst gradient or a winter warming snow fence experiment.
3. In both the natural thermokarst gradient and the warming experiment, wet or deeply thawed areas generally led to an increase in foliar nutrient concentrations and greater canopy mass and canopy nutrients. For the majority of species, foliar N:P ratios remained proportional or decreased in deciduous species in wet sites, with the exception of one shallowly rooted species that increased foliar N:P ratio in deeply thawed sites. Overall, plant acquisition of P was more related to water table level than to thaw depth, and water table modulated the canopy biomass response of the species at the warming experiment.
4. *Synthesis*. Foliar N:P ratios suggest that plant species in this tussock tundra ecosystem are either remaining or becoming more N-limited as thaw depth deepens and water table level rises, indicating that P is not likely to become the primary limiting nutrient with the progression of permafrost thaw. However, the amount of deeply thawed, wet areas that develop on the landscape as permafrost thaws will be important contributors in the total movement of nutrients above-ground.

KEYWORDS
foliar nutrients, global change ecology, nitrogen, permafrost thaw, phosphorus, thermokarst, warming experiment, water tables

1 | INTRODUCTION

As a consequence of climate change, air temperatures at high latitudes have risen twice as fast as lower latitudes, deepening the seasonally thawed active soil layer that supports plants during the growing season (Grosse et al., 2011; Cohen et al., 2014). In many cases, the newly thawed soil materials have not been active for hundreds to thousands of years and harbour a rich stock of carbon (C), nitrogen (N), phosphorus (P) and other nutrients such as calcium (Ca) and magnesium (Mg; Zimov et al., 2006; Salmon et al., 2018; Strauss et al., 2018). The extent to which plants access and utilize increasingly available soil nutrients can have global consequences for the C cycle. Increased nutrient availability from thawing soils may stimulate plant productivity, offsetting C loss from soil organic matter decomposition (Rustad et al., 2001; Mack et al., 2004; Lavoie et al., 2011; Schuur and Abbott, 2015).

The vast majority of plant species in high-latitude ecosystems are currently limited in growth by the availability of nitrogen, due to low temperatures and correspondingly low N-mineralization by soil biota (Chapin and Shaver, 1986; Hobbie and Gough, 2002). However, some Arctic ecosystems can be both N and P co-limited, especially in organic soils where P inputs from mineral soils are low (Chapin et al., 1991; Shaver et al., 1998; Onipchenko et al., 2012; Ostertag and DiManno, 2016; Hou et al., 2020). Where the permafrost boundary is thawing further into mineral soils, newly thawed soil materials may provide plants with new sources of the rock-weathered minerals P, Ca and Mg (Opfergelt et al., 2018; Mauclet, Hirst, et al., 2021). In addition to exposing novel sources of nutrients from below, warming temperatures may also increase plant nutrient availability by increasing microbial N-mineralization rates in the upper organic soil layer (Rustad et al., 2001; Schimel et al., 2004), and increasing mineral weathering rates on the underlying mineral soils (Weintraub, 2011; Opfergelt et al., 2018).

The geomorphic processes that occur along with permafrost thaw will also affect plant access to new pools of nutrients. Permafrost does not degrade uniformly across the landscape—the melting of ice-rich material within soils leads to heterogeneity in ground subsidence, or thermokarst (Osterkamp and Romanovsky, 1999; Grosse et al., 2016). Thermokarst can lead to the development of collapsed thaw channels or water tracks, which drain surrounding higher areas and create dry areas with shallow thaw depths directly adjacent to deeply thawed areas with high water tables (Schuur et al., 2007; Osterkamp et al., 2009; Belshe et al., 2013; Rodenhizer et al., 2020). Changes in thaw depths and water tables often lead to shifts in plant communities and moss cover, which can indirectly affect plant access to soil nutrients through shading, competition, altered litter regimes or insulating soils with thickening organic layers (Rustad et al., 2001; Osterkamp et al., 2009). More directly, the increased flowing soil water that creates water tracks or saturates soils can alter physical soil properties and provide flushes of nutrients that lead to more rapid nutrient cycling and increased phosphate or nitrogen availability (Chapin et al., 1988; Matthes-Sears et al., 1988; Oberbauer et al., 1989). Recent incubation experiments have demonstrated that thawing permafrost soil in wet, anoxic conditions results in larger micronutrient releases than in drier conditions (Reyes and Lougheed, 2015). However, high soil saturation can also decrease soil oxygen availability and inundate plant roots, which could affect plant access to newly available nutrients at the deepening permafrost soil boundary (Iversen et al., 2015).

The extent to which specific plant species access N, P, Ca and Mg may be dependent on their rooting depths (Wookey et al., 2009; Iversen et al., 2015). Studies in North American and European tundra indicate that deeply rooted forbs and graminoids take up more nutrients at the thaw front, whereas shallowly rooted dwarf shrubs take advantage of nutrients available in shallow soil layers (Oulehle et al., 2016; Zhu et al., 2016; Keuper et al., 2017; Wang et al., 2017; Hewitt et al., 2019). These results suggest that species-specific rooting depths could determine where plants acquire nutrients as permafrost thaws more deeply—but we do not know how increasing thaw depths, fluctuating water tables and rooting depths will interact to affect species-specific plant nutrient response in warming environments, especially with respect to P and other nutrients.

Since high-latitude ecosystems are generally N-limited, many field studies measure changes in foliar or canopy N as a consequence of warming (Hudson et al., 2011; Finger et al., 2016; Salmon et al., 2016; Mörsdorf et al., 2019). However, far fewer warming experiments have focused on accompanying changes in foliar P and other nutrients. Depending on the magnitude of change in N versus P availability that occurs with deepening thaw and fluctuating water tables, and the ability of species to access both nutrients, climate change could effectively move plant communities or specific plant species towards P-limitation or further into N-limitation (Zamin et al., 2014; Beermann et al., 2015; Jiang et al., 2016). Since each plant species has an optimal stoichiometric foliar N:P ratio for plant growth, foliar ratios of N:P can be used as a reliable proxy for N and P access or limitation in ecosystems (Shaver and Chapin, 1995; Koerselman and Meuleman, 1996; Güsewell, 2004; Ostertag and DiManno, 2016). An imbalance in N:P ratio suggests a plant is more easily accessing one element over the other. For example, higher concentrations of N than P will increase the N:P ratio, suggesting either greater access to N or a limited access to P (Koerselman and Meuleman, 1996).

In this study, we assessed the foliar and canopy nutrient concentrations (N, P, Mg, and Ca) of seven vascular plant species of various plant functional types and rooting depths that comprise the majority of biomass at two sites in a moist acidic tussock (MAT) tundra ecosystem in Healy, Alaska, USA. The plant communities at the study sites have been subjected to variable thaw depth and water table level conditions produced by (a) a natural thermokarst gradient and (b) a 10-year winter snow manipulation simulating climate warming (referred to herein as the warming experiment). At both sites, the permafrost boundary is thawing deeper into mineral soils. The concurrent collection of data from these two sites provides a powerful contrast for understanding how plants may respond to changes in soil thaw depth and water table levels under natural disturbance and under a controlled disturbance simulating climate warming.

For the purposes of this paper, we focused on thaw depth and water table levels as driving variables of plant nutrient response. In warming permafrost soils, these two physical processes often co-occur with changes in other abiotic variables that influence biotic processes, such as increased soil temperature and changes in soil moisture. Previous studies at the warming experiment have found that plots with deeper thaw depths (the experimentally warmed plots) also had significantly greater growing season soil temperature and soil moisture (Salmon et al., 2016; Mauritz et al., 2017; Schadel et al., 2018; Taylor et al., 2018). The increased soil moisture was attributed to ground subsidence within the warmed plots, which brought the water table closer to the surface (Schadel et al., 2018; Rodenhizer et al., 2020). Average annual soil temperature in the top 40 cm of the warmed, deeply thawed plots was raised overall by 0.85–1.00°C, although only soils below 20 cm displayed significantly warmer temperatures year-round (Salmon et al., 2016; Mauritz et al., 2017). Significant biological responses also occur in warmed plots, including increased ecosystem respiration, gross primary productivity and N availability (Salmon et al., 2016; Mauritz et al., 2017). With these relationships in mind, we decided to use water table and thaw depth as hypothesized drivers of plant nutrient response.

Since changes in plant nutrient status can be detected above-ground on the foliar level or at the canopy level, we used species-specific foliar nutrient concentrations of N, P, Ca and Mg in conjunction with leaf morphology and canopy mass measurements to assess plant nutrient responses to thaw depth and water table level. In addition, we measured species-specific δ^{15}N content to infer potential changes in N sources (Högberg, 1997; Hobbie et al., 2005; Craine et al., 2009). We hypothesized that plants with known deeper rooting systems would respond to increasing thaw depth with a larger foliar increase in the rock-weathered nutrients P, Mg and Ca compared to N due to plant proximity to mineral soil. In contrast, plants with known shallower rooting systems mostly in the organic layer would respond to thaw depth with a larger foliar increase in N compared to weathering-derived nutrients. We speculated that the influence of water table level would also play a role in plant nutrient acquisition by either restricting plant rooting ability or increasing the flow of nutrients to plant roots due to altered soil properties, and that there may be an interaction between thaw depth and water table level on the nutrient responses of species.

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted at two field sites that lie 1.3 km apart in MAT tundra within the Eight Mile Lake watershed (63°52′59″N, 149°13′32″W), in the northern foothills of the Alaska Range. The first site is a natural thermokarst gradient where three blocks were established in 2003 which differ in age and extent of thaw (Schuur et al., 2007; Vogel et al., 2009). The second site is the Carbon in Permafrost Experimental Heating Research site (CiPEHR), an experimental warming manipulation established in 2008 (Natali et al., 2011). Field permits for these sites are covered by Alaska State Forestry permit LAS24220. These sites (described in detail below) have been well studied and monitored continuously since 2004 (the thermokarst gradient) and 2008 (the warming experiment) for soil temperature, permafrost thaw depth, water table level, CO_2 fluxes, species-specific rooting depths and other vegetation characteristics (Vogel et al., 2009; Lee et al., 2010; Hicks Pries et al., 2013; Hewitt et al., 2019).

The thermokarst gradient site is a natural thermokarst formation that stretches gently downslope (4%) northeast towards Eight Mile Lake for 2–3 km (Vogel et al., 2009). Three blocks, categorized as minimal, moderate and extensive thaw were located on the landscape perpendicular to slope to maximize variation in thaw depth and water table levels (Vogel et al., 2009). The block categories refer to the age and extent of thermokarst features that cover the landscape. The minimal thaw block has the least evidence of thermokarst formation and appears continuous with the unthawed landscape surrounding the sites. The extensively thawed block contains the most thermokarst terrain and microtopography, and thus a larger variation in snow depths that accumulate in thermokarst depressions (Schuur et al., 2007; Vogel et al., 2009). Based on aerial imagery analysis, the extensive thaw block is believed to have begun thawing in the 1950s in response to climate warming (Osterkamp and Romanovsky, 1999; Schuur et al., 2007). Permafrost monitoring in a borehole established in 1985 suggests that the moderate thaw block began thawing in the mid-1980s (Osterkamp and Romanovsky, 1999). Each thaw block contains six plots, approximately 1.5 × 3 m, which contains a permanent non-destructive subplot (70 × 70 cm) where gas flux, biomass and other metrics are measured periodically. We collected data from all six plots at the three thaw blocks ($N = 18$).

The warming experiment consists of a split-block design with six replicate snow fences (1.5 m tall × 8 m long) that trap thick blankets of snow on the leeward side of the fence during the winter (Natali et al., 2011). This manipulation warms the soil on the leeward side of the fence by an average of 2–3°C above the control in the winter and leads to significantly deeper maximum thaw depths in winter soil warming plots compared to ambient plots (in 2017, 37 cm or 1.6 times deeper; Natali et al., 2014; Mauritz et al., 2017). The snow drifts are shovelled off the lee side of the fence prior to snowmelt the first week of April, and ensure that water inputs (in the form of remaining snow depth) and timing of snowmelt are similar across

TABLE 1 Study species and their respective plant functional types, mycorrhizal status, rooting depth categories and max rooting depths in undisturbed tundra near the study site. Rooting depth categories are based on literature values, while max rooting depths were developed in undisturbed tundra proximal to the thermokarst thaw gradient at eight mile Lake (Hewitt et al., 2019)

Species	Plant functional type	Mycorrhizal status	Rooting depth category	Max rooting depth (cm, mean ± *SE*) in undisturbed tundra near study site
Carex bigelowii	Sedge	Non-mycorrhizal	Deep	67 ± 12
Eriophorum vaginatum	Sedge	Non-mycorrhizal	Moderate-Shallow	35 ± 5
Rubus chamaemorus	Forb	Non-mycorrhizal	Deep	67 ± 19
Betula nana	Deciduous Shrub	Ectomycorrhizal	Moderate-Shallow	31 ± 7
Vaccinium uliginosum	Deciduous Shrub	Ericoid	Shallow-Moderate	42 ± 12
Vaccinium vitis-idaea	Evergreen Shrub	Ericoid	Shallow	36 ± 7
Rhododendron tomentosum	Evergreen Shrub	Ericoid	Shallow-Moderate	41 ± 8

control and winter warming plots (Natali et al., 2011). Each snow fence has two winter soil warming plots on the leeward side of the fence, and two control plots on the windward side. Each plot is approximately 1.5 × 1.5 m and contains a permanent non-destructive subplot (60 × 60 cm) where gas flux, biomass and other metrics are measured yearly. For this experiment, we collected data from all four plots at each of the six snow fences ($N = 24$).

From 1977 to 2015, mean annual temperature at the study area was 0.94 ± 0.25°C, and mean annual growing season temperature was 11.91 ± 0.22°C (Mauritz et al., 2017). Average annual precipitation is 378 mm (Natali et al., 2011). Both sites are underlain by continuous permafrost that has a surface temperature of approximately −0.8°C (Osterkamp and Romanovsky, 1999). Soils are characterized by a layer of organic soil (35–55 cm thick) above cryoturbated mineral soils composed of glacial till and loess (Osterkamp et al., 2009; Vogel et al., 2009). Maximum seasonal thaw depths in 2017 in areas of undisturbed tundra at the site ranged from 48 to 81 cm deep (Bonanza Creek LTER data archive).

The vascular vegetation at the thermokarst gradient and the warming experiment is dominated by *Eriophorum vaginatum* (a non-mycorrhizal tussock forming sedge) and *Vaccinium uliginosum* (an ericoid mycorrhizal deciduous shrub), as well as *Rhododendron tomentosum* (an ericoid mycorrhizal evergreen shrub), *Rubus chamaemorus* (a non-mycorrhizal forb), *Vaccinium vitis-idaea* (an ericoid mycorrhizal evergreen shrub), *Carex bigelowii* (a non-mycorrhizal sedge) and *Betula nana* (an ectomycorrhizal deciduous shrub), with considerably smaller amounts of *Empetrum nigrum*, *Andromeda polifolia* and *Oxycoccus microcarpus*. Non-vascular species are primarily feather-moss, particularly *Hylocomium splendens* and *Pleurozium schreberi*, and also *Sphagnum* and *Dicranum* spp. (Schuur et al., 2007).

2.2 | Field methods

We collected soil thaw depth measurements at each plot by inserting a metal probe until it hits permafrost. At the thermokarst gradient, thaw depth was measured at the full plot-level only during maximum thaw depth near the end of August/early September 2017. At the warming experiment, thaw depth was measured weekly at the plot level during the growing season of 2017. Thaw depth at each plot was an average of three measurements surrounding the subplot. In all, 18 wells were installed inside the plots at the thermokarst gradient in May 2017, and four water table measurements were made at those wells during the summer of 2017. At the warming experiment, water table levels were measured three times weekly during the summer months of 2017 at three wells per snow fence side (water table levels taken regularly since 2013). Wells were installed approximately 0.6 m to 1 m below-ground. Although plot-level water table levels were not available in the warming experiment plots, we assigned each plot to the closest well, within 1.5 m of each plot (see Mauritz et al., 2017).

At peak foliar biomass (15–19 July 2017), we collected fully expanded, current year leaves (including petioles) of the seven dominant vascular species (Table 1) at 18 thermokarst gradient plots and 24 warming experiment plots, resulting in a total of 294 foliar samples. Leaves were collected and combined from multiple individuals within the plot for each species (depending on number of individuals within a plot) to account for intraspecies variability. All species were present in every plot, with the exception of two plots where *V. vitis-idaea* and *B. nana* were not present, respectively. We measured vascular plant biomass in the non-destructive subplot in mid-July and early August 2017 using a point-intercept method. At the thermokarst gradient, a 70 × 70 cm aluminium frame with a 64-intersection grid of fishing line (8 cm spacing) was suspended above the subplot within the collection plots. At the warming experiment, a 60 × 60 cm aluminium frame with a 49-intersection grid of fishing line (7 cm spacing) was used to measure biomass within the 60 × 60 cm non-destructive subplot. A pin was dropped vertically at each intersection and the number of points of contact with vegetation was recorded by species. Biomass (g/m^2) was calculated from our point-framing data via species-specific allometric equations developed from previous destructive biomass harvests at the thermokarst gradient site in 2004 and 2012 and verified at the warming experiment (Schuur et al., 2007; Salmon et al., 2016). The foliar portion of biomass was calculated by multiplying total biomass of each species by a species-specific constant developed from the biomass harvest in 2004 (Schuur et al., 2007). Because we sampled biomass within the non-destructive subplot but collected foliage for foliar nutrients within the larger treated plot, some low-presence species that were not detected in our biomass subplot were found in the larger treated plot. These low-presence species were given an allometric biomass value that corresponded to 0.5% of the point-frame, or less than one point of contact.

2.3 | Laboratory methods

Because changes in leaf area can affect foliar nutrient concentrations, we measured specific leaf area (SLA, cm^2/g leaf) by scanning a subset of leaves from each plot at 600 dpi with a flatbed scanner within 12 hr of field collection. Subsets were then oven-dried and weighed to the nearest milligram. We used ImageJ software program (Rasband, W.S., ImageJ 1.52a, U.S. National Institutes of Health) to measure the leaf area of each scan that we used in combination with the dry leaf weights to calculate SLA for each subset. To analyse foliar nutrients, foliar samples were dried at 60°C within 24 hr of collection and hand-chopped in the lab. Leaves were analysed for %N and $\delta^{15}N$ using a Costech elemental analyser attached to a Thermo Fisher Scientific Delta V Advantage continuous flow isotope ratio mass spectrometer (Thermo Fisher Scientific Inc.). To measure foliar P, Ca and Mg, subsamples of foliar tissue (0.2 g) were ashed at 500°C in a muffle furnace and fully digested with 1 ml of 6 N HCl. Foliar Ca and Mg were measured only on samples from the thermokarst gradient. Digests were run for %P using the ascorbate colorimetric method (modified from Murphy J, Riley JP 1962 Anal Chim Acta 27:31) on a microplate reader (PowerWave XS Microplate Reader, Bio-Tek Instruments Inc.) and for %Ca and %Mg using flame atomic absorption spectroscopy (Perkin-Elmer AAnalyst 100, Perkin-Elmer Corporation).

2.4 | Data analysis

All data analyses were completed using R statistical software version 3.4.2 (R Core Team, 2017). Leaf-level nutrient concentrations were calculated on both a mass and leaf area basis for each species. Percent foliar nutrients were converted to foliar nutrient mass (mg/g leaf) and then divided by SLA to get mg/cm^2 leaf. Foliar nutrients calculated on a leaf area basis were either not significantly correlated to thaw or water table depth or did not change the interpretation of results. Canopy nutrient mass in g/m^2 was calculated for each species by multiplying canopy mass (g/m^2) by foliar nutrient mass (mg/g). Total canopy nutrients for each plot were determined by summing the canopy nutrient masses of the seven sampled species. If foliar nutrient values for one or more species were missing from the dataset (where too much sample was lost during the grinding process to run nutrient analyses), those plots were eliminated from the total canopy nutrient analyses so underestimated sums would not affect analyses.

We fit linear mixed-effects models using the R package NLME (Pinheiro et al., 2018) to assess the effects of thaw depth, water table level, and their interaction on species and site-specific foliar and canopy response variables. At the thermokarst gradient, thaw depth and water table did not vary between blocks due to spatial heterogeneity (Appendix Table S1), so random effects of block were included to account for spatial non-independence and other factors related to age and extent of thaw. At the warming experiment, thaw depth and water table were different between treatments (Appendix Table S2) and random effects of fence nested within block were used. Thaw depth, water table level and their interactions were initially included as fixed effects in the models, as well as their polynomial terms if an observed bivariate response suggested that a quadratic relationship existed and there was an ecological basis for believing the relationship may not be linear. Water table level and thaw depth were standardized by subtracting the mean and dividing by the standard deviation. We did not detect multicollinearity between thaw depth and water table at either site based on variance inflation factors ($VIF < 3$; Zuur et al., 2009) and Pearson's product moment correlation analysis ($correlation < 0.7$). We used September 2017 thaw depths and water table levels from each site as they correlated with July thaw depths and water tables and also with long-term thaw depths and water tables (Appendix Tables S1–S2). Model selection between additive models, multiplicative models and models with polynomials was completed using Akaike Information Criteria (AIC; Zuur et al., 2009). Model assumptions of normality, constant variance and independence of residuals were examined, and transformation was unnecessary with the exception of the canopy biomass estimates for *C. bigelowii*, which were square root transformed prior to modelling.

Among the 18 thermokarst gradient plots, a single plot directly in the middle of a thaw channel at the extensive thaw block had an influential and statistically significant leverage on model estimates [based on Cook's distance 4/*n* (Cook, 1975)], indicating that plants in the plot were responding differently than plants in the other 17 plots. This plot had a September 2017 thaw depth of 111 cm, about 1.3 times deeper than the next deepest thaw depth at the thermokarst gradient, 83 cm. It also had an extremely high *V. uliginosum* canopy biomass of 232 g/m^2 (2.4 times higher than the next highest *V. uliginosum* canopy biomass of 97 g/m^2), consistent with *V. uliginosum* measurements in that plot from prior years. Deep thaw in a thaw channel may have different thermal dynamic mechanisms than those in more upland locations, or we could be seeing a trajectory where we see one response during thaw of shallow soil layers, and a different relationship as thaw continues past a certain depth. With only one sample plot in a thaw channel, we did not feel we had adequate sampling to answer that question across the thermokarst gradient site as a whole. We chose to eliminate the plot from our analyses but note it in our discussion of results, as it brings up interesting questions for the future.

3 | RESULTS

Eriophorum vaginatum and *V. uliginosum* comprised the majority of the canopy biomass at the thermokarst gradient (*E. vaginatum*:

75 ± 12 g/m^2, and *V. uliginosum*: 50 ± 5 g/m^2). At the warming experiment, canopy biomass of *E. vaginatum* was much higher (179 ± 21 g/m^2), with *V. uliginosum* being the next most dominant species (50 ± 4 g/m^2). Across both sites, foliar N:P ratios of all species ranged from 7 to 19 with the majority of foliar N:P ratios falling below 14, within the range of literature values for likely N limitation (Koerselman and Meuleman, 1996). The foliar N:P ratio values of two species, *C. bigelowii* and *V. uliginosum*, partially overlapped the range potentially corresponding to N and P co-limitation ($14 < x < 16$; Koerselman and Meuleman, 1996). Surprisingly, we only found one interaction between thaw depth and water table level: the canopy nutrient response of *C. bigelowii* depended on the interaction of both variables (Table 2, Canopy variables). Thus, all other selected models and results presented do not have an interaction term (Appendices S3 and S4).

3.1 | Responses to deepening thaw depths

With deepening thaw, we expected species with shallow rooting depths to show positive responses in terms of foliar or canopy N, and deeply rooting species to show positive responses in terms of foliar or canopy P, Ca and Mg as more mineral soil volume thawed. At both the natural thermokarst gradient and the warming experiment, foliar and canopy nutrient responses to deep thaw were generally positive, although they were also site, species and nutrient specific (Table 2). Thaw depths across the thermokarst gradient ranged from 55 to 83 cm, but no significant differences in thaw depth existed between areas of minimal, moderate and extensive thaw due to high spatial heterogeneity ($F_{2,14} = 0.079$, $p = 0.47$). Thaw depths across the warming experiment ranged from 60 to 110 cm and were significantly deeper in the soil warming plots than in control plots by 32 cm ($F_{1,22} = 88.87$, $p < 0.001$).

Any significant foliar nutrient responses to deepening thaw more often resulted in increases in foliar nutrients, although they were also site, species and nutrient specific (Figure 1). At the thermokarst gradient, foliar N concentrations did not respond to thaw depth (Table 2). Surprisingly, however, the foliar P and Mg concentrations of *R. chamaemorus*, the most deeply rooted species, significantly decreased as thaw depth deepened (Figure 1e). *Betula nana*, however, a moderately deeply rooting shrub, showed increases in foliar P and Mg with thaw (Figure 1b,e). *Rhododendron tomentosum*, a moderately shallow rooted evergreen shrub, also significantly increased foliar P concentrations with thaw (Figure 1). At the thermokarst gradient site, the SLA of *E. vaginatum* decreased (i.e. its leaves became thicker) with deepening thaw depth (Figure 1f). Overall, foliar N:P stoichiometric ratios across the thermokarst gradient remained relatively constant within species as thaw depth varied. At the warming experiment, however, foliar nutrients were more responsive to changes in thaw depth. As thaw depth deepened, foliar N concentrations

TABLE 2 Summary table depicting the directional responses of species-specific foliar and canopy nutrients to the continuous variables of deepening thaw and rising water table, at the thermokarst gradient (hatched) and the warming experiment (solid). Full linear mixed model (LMM) parameters available in Appendices S3–S4. *Ca and mg analyses were only analysed for plant samples from the thermokarst gradient

Foliar variables

Species	*Foliar N (mg/g)*		*Foliar P (mg/g)*		*Foliar N:P ratio*		*Foliar $\delta^{15}N$*		*SLA (cm^2/g)*		*Foliar Ca* (mg/g)*		*Foliar Mg* (mg/g)*	
	Deepening thaw	*Rising water tables*	*Deepening thaw*	*Rising water tables*	*Deepening thaw*	*Rising water tables*	*Deepening thaw*	*Rising water tables*	*Deepening thaw*	*Rising water tables*	*Deepening thaw*	*Rising water tables*	*Deepening thaw*	*Rising water tables*
C. bigelowii	*n.s.*	*n.s.*	*n.s.*	↑	*n.s.*	↓	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.**	*n.s.**	*n.s.**	*n.s.**
E. vaginatum	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	↓	▨↓	*n.s.*	*n.s.**	*n.s.**	*n.s.**	*n.s.**
R. chamaemorus	*n.s.*	*n.s.*	▨↓	↑	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.**	*n.s.**	▨↓	▨↓
B. nana	*n.s.*	*n.s.*	↑	↑	*n.s.*	↓	*n.s.*	*n.s.*	*n.s.*	▨↑	*n.s.**	*n.s.**	▨↑	*n.s.**
V. uliginosum	*n.s.*	*n.s.*	*n.s.*	↑	*n.s.*	↓	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.**	*n.s.**	*n.s.**	*n.s.**
V. vitis-idaea	↑	*n.s.*	*n.s.*	*n.s.*	↑	*n.s.*	↑	*n.s.*	*n.s.*	*n.s.*	*n.s.**	*n.s.**	*n.s.**	*n.s.**
R. tomentosum	↑	*n.s.*	↑	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.**	*n.s.**	*n.s.**	*n.s.**

Canopy variables

Species	*Canopy mass (g/m^2)*		*Canopy N mass (g/m^2)*		*Canopy P mass (g/m^2)*		*Canopy Ca* mass (g/m^2)*		*Canopy Mg* mass (g/m^2)*	
	Deepening thaw	*Rising water tables*	*Deepening thaw*	*Rising water tables*	*Deepening thaw*	*Rising water tables*	*Deepening thaw*	*Rising water tables*	*Deepening thaw*	*Rising water tables*
C. bigelowii	*interaction*		*interaction*		*interaction*		*n.s.**	*n.s.**	*n.s.**	*n.s.**
E. vaginatum	*n.s.*	⌒	*n.s.*	⌒	*n.s.*	⌒	*n.s.**	*n.s.**	*n.s.**	*n.s.**
R. chamaemorus	*n.s.*	⌒	*n.s.*	⌒	*n.s.*	⌒	*n.s.**	*n.s.**	*n.s.**	*n.s.**
B. nana	*n.s.*	▨↑	*n.s.*	▨↑	*n.s.*	*n.s.*	*n.s.**	▨↑	*n.s.**	▨↑
V. uliginosum	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.**	*n.s.**	*n.s.**	*n.s.**
V. vitis-idaea	*n.s.*	*n.s.*	*n.s.*	*n.s.*	▨↓	*n.s.*	*n.s.**	*n.s.**	▨↓	*n.s.**
R. tomentosum	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.**	*n.s.**	*n.s.**	*n.s.**
Total canopy	↑	⌒	↑	⌒	*n.s.*	⌒	*n.s.**	*n.s.**	*n.s.**	*n.s.**

▨↑ ▨↓ Thermokarst gradient: increasing or decreasing

↑ ⌒ ↓ Warming experiment: increasing, nonlinear, or decreasing

n.s. Not significant

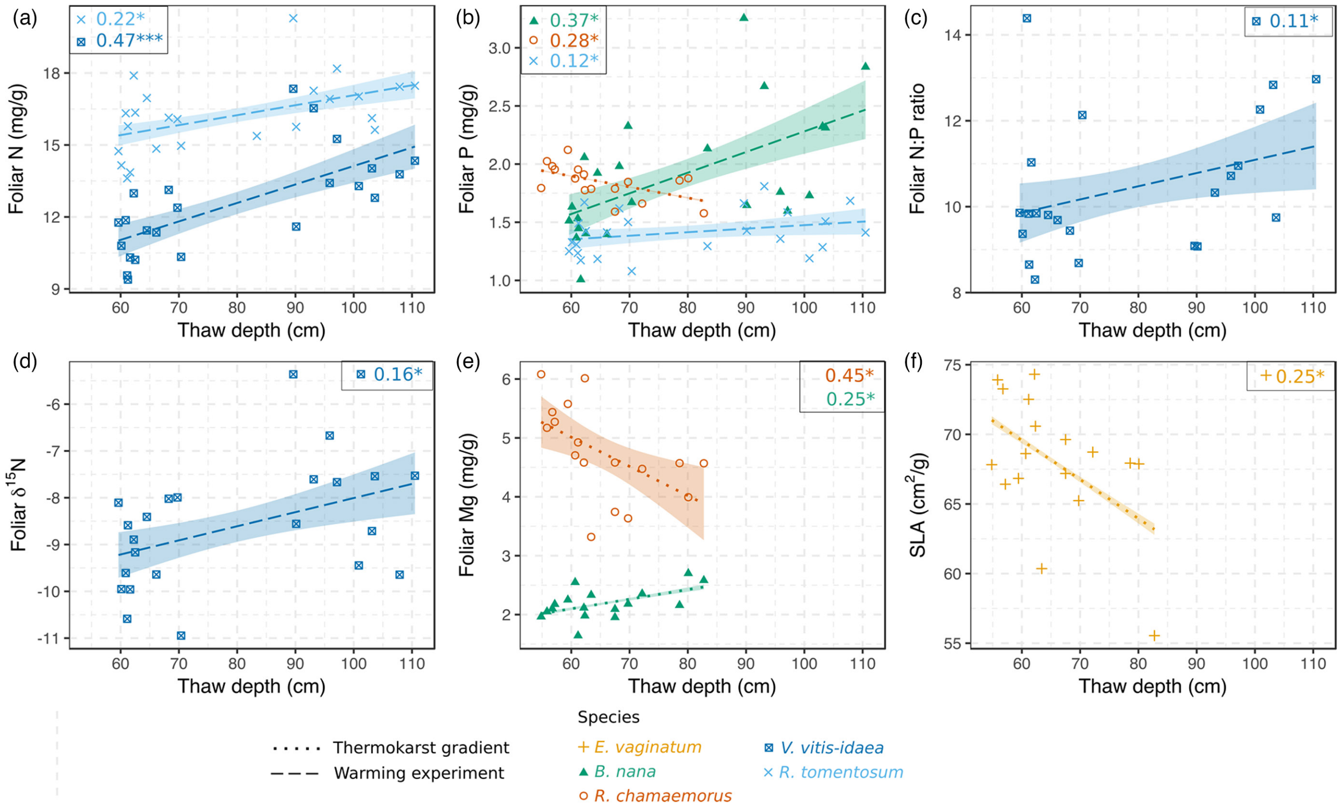

FIGURE 1 Foliar responses to thaw depth at the warming experiment ($n = 24$) and the thermokarst gradient ($n = 17$). Points represent observed values and regression lines are LMM estimates ± standard error (*SE*); full model parameters available in Appendices S3 and S4. Marginal r^2 of each LMM is presented in each panel, representing the proportion of variance explained by the fixed factors. Significance for each relationship is denoted in the corners of each panel: $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$

increased in the shallow and moderately shallow rooted species *V. vitis-idaea* and *R. tomentosum* (Figure 1a). This increase in foliar N led to an increase in the foliar N:P ratio of *V. vitis-idaea*, although these foliar N:P values for *V. vitis-idaea* still remained within the bounds of N limitation (<14) based on literature values (Figure 1c). *Vaccinium vitis-idaea* also became significantly enriched in ^{15}N with deepening thaw depth, showing additional sensitivity to changing edaphic factors (Figure 1d).

We did not observe as many species-specific canopy biomass and nutrient responses to deepening thaw as we had anticipated (Table 2; Figure 2). However, the responses we did observe were consistent with our hypotheses. Surprisingly, at the thermokarst gradient, total canopy biomass (the total combined canopy biomass of all study species in each plot) ranged between 133 and 280 g/m^2 with no apparent relationship to thaw depth. At the warming experiment, however, total canopy biomass significantly increased as thaw depth deepened, as did total canopy N (Figure 2a,b). Interestingly, across both sites thaw depth had no main effect on the canopy biomass of any particular species, although *V. vitis-idaea*, the most shallowly rooted evergreen shrub, displayed a canopy level decrease in P and Mg with deepening thaw depth at the thermokarst gradient (Figure 2c,d). The canopy biomass of *C. bigelowii*, a deeply rooted deciduous sedge, increased with deepening thaw, but only in the presence of a shallow water table (Figure 3a–c).

3.2 | Responses to water table levels

In both the thermokarst gradient and warming experiment, wet areas generally led to positive foliar nutrient responses and/or higher amounts of canopy mass and canopy nutrients, with site- and species-specific responses (Table 2). We expected to see water table levels amplifying or dampening the effects of deepening thaw, but instead water table levels affected foliar and canopy nutrient concentrations more than thaw depth (Table 2). Foliar nutrients were also more responsive at the warming experiment to changes in water table levels than at the thermokarst gradient. This may be due to the fact that water table levels at the thermokarst gradient were not significantly different in areas of minimal, moderate and extensive thaw ($F_{2,14} = 3.14$, $p = 0.07$), and ranged from 0 to 20 cm below-ground, whereas water table levels at the warming experiment ranged from −8 to 36 cm across the whole experiment (negative water tables indicating inundation and standing water) and were shallower in the soil warming plots by 13 cm ($F_{1,22} = 12.94$, $p = 0.002$).

At the thermokarst gradient, water table level had no effect on the nutrient concentrations of most species, with the exception of the forb *R. chamaemorus*, which increased foliar Mg concentrations in wet sites (Figure 4e). Again, foliar N:P stoichiometric ratios across the thermokarst gradient remained relatively constant within species as water table levels varied. In terms of leaf morphology, the

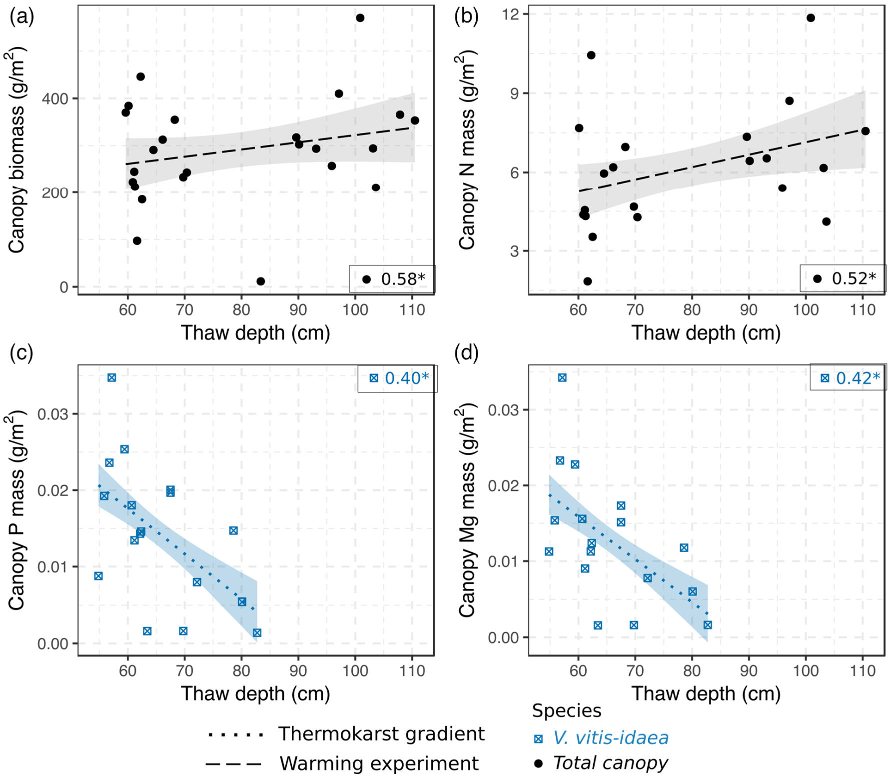

FIGURE 2 Canopy responses to thaw depth at the warming experiment ($n = 24$) and the thermokarst gradient ($n = 17$). Points represent observed values and regression lines are LMM estimates ± *SE*; full model parameters available in Appendices S3 and S4. Marginal r^2 of each LMM is presented in each panel, representing the proportion of variance explained by the fixed factors. Significance for each relationship is denoted in the corners of each panel: $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$

SLA of *B. nana* at the thermokarst gradient increased (leaves became thinner) with rising water tables (Figure 4d). In areas of shallow water table levels at the warming experiment, four deciduous species across functional types (*C. bigelowii*, *V. uliginosum*, *B. nana* and *R. chamaemorus*) displayed increased P concentration (Figure 4a). This increase in foliar P led to a decrease in the foliar N:P ratios of *C. bigelowii*, *B. nana* and *V. uliginosum* in areas of shallow water table, with model estimates decreasing from around 16 between 9 and 14, further towards N-limitation (Figure 4b). *Eriophorum vaginatum*, the dominant evergreen sedge, also became significantly depleted in ^{15}N with rising water table level at the warming experiment, indicating sensitivity to changes in soil environment (Figure 4c).

Rising water tables led to higher amounts of canopy mass or canopy nutrients in some cases (Figure 5), although responses were site and species specific and often nonlinearly related to water table levels (Table 2, Figure 5). At the thermokarst gradient, water table level had no effect on the total biomass of vegetation within plots (Table 2). *Betula nana*, a deciduous shrub, was the only species at the thermokarst gradient whose canopy biomass responded to variation in thaw or water table depth, increasing as water table became shallower (Figure 5a). At the warming experiment, canopy biomass was modulated by water table levels—the canopy biomass of two species responded nonlinearly to shifting water table levels (Figure 5a). Total canopy biomass, total canopy N and total canopy P peaked at water table levels of around 10 cm below-ground, declining in areas of both shallow and deep water table levels (Figure 5a). Canopy biomass for *E. vaginatum* fit a quadratic curve where the highest canopy biomass occurred at intermediate water table levels around 10 cm (Figure 5a). The canopy biomass of *R. chamaemorus*, a forb, was best fit by a cubic curve, in which the canopy biomass peaked around 0–5 cm water table level and then declined and stabilized at deeper water table levels (Figure 5a). In general, changes in the amount of species-specific canopy nutrients largely mirrored the responses of canopy biomass (Figure 5b–e).

4 | DISCUSSION

Our study quantifies changes in species' foliar nutrients in relation to continuous shifts in thaw depth and water table levels, two major physical factors that alter plant environment in thermokarst. While thaw depth is known to be a driver of increased nutrient availability to plants, our study emphasizes that in thawing environments fluctuating water table levels may play a larger role than thaw depth in determining species-specific plant nutrient access and movement of nutrients above-ground in vegetation. Our results indicate that individual species in this tundra system exhibit unique nutrient responses to the variations in thaw and water table level that occur with permafrost thaw and thermokarst development, likely attributable to both rooting depths and increasing nutrient availability in wet areas.

4.1 | Warming increases plant nutrient access

The increases in total canopy biomass and total canopy N observed at the warming experiment as thaw depth increased are consistent with the findings of previous studies at this site which show

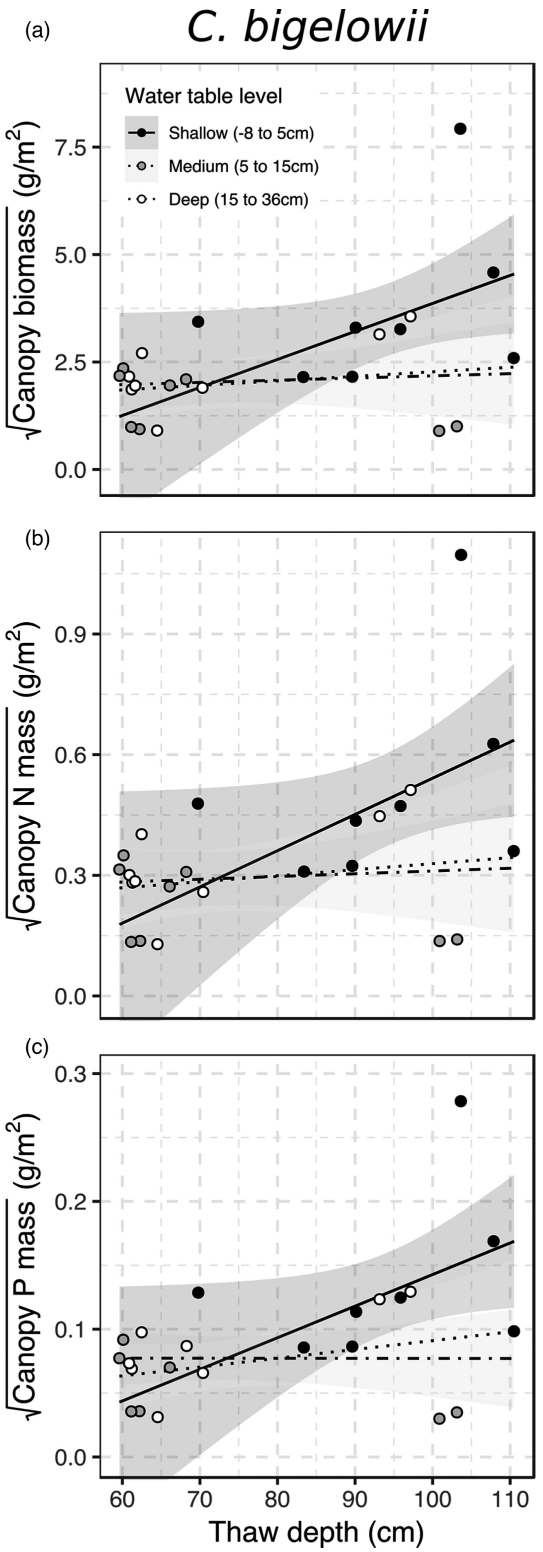

FIGURE 3 At the warming experiment, the canopy biomass and nutrient content of *C. bigelowii* increased with deepening thaw, but only in the presence of a shallow water table (n = 24). *Carex bigelowii* canopy was square root transformed. Regression lines are LMM estimates ± *SE*; full model parameters available in Appendices S3 and S4

increases in total plant growth with continued warming (Natali et al., 2012; Salmon et al., 2016). At the thermokarst gradient, we found no change in total canopy biomass or total canopy nutrients as thaw and water table level varied despite previous studies observing increased biomass at the moderate and extensively thawed blocks (Schuur et al., 2007). These previous studies, however, had a larger spatial and numeric sample size and may have captured a greater amount of the topographic heterogeneity at the moderate and extensively thawed blocks, whereas our sampling did not succeed in capturing the deeply thawed microsites within the thaw channels.

Our observations indicate that particular vascular plant species at the site are overall accessing more nutrients with increasing thaw depths. The decrease in SLA (thicker leaves) for *E. vaginatum* as thaw depth increased at the thermokarst gradient corresponds to prior studies which show declines in the SLA of *E. vaginatum* in response to increased available N and P (under anaerobic conditions, in one case), attributed to increased allocation to nutrient storage or below-ground root mass (Gebauer et al., 1995; Heskel et al., 2012). *Betula nana* is known to be geographically expanding in response to climate change and increasing the amount of woody biomass in Arctic ecosystems (Martin et al., 2017). Any significant responses of N, P, Ca and Mg concentrations in *B. nana* (foliar and/or canopy), while not consistent between sites, were always positive in response to either deeper thaw depths or higher water tables (Table 2). This adds further support to the body of evidence that indicates it is likely to be a crucial player in overall vegetation response to warming climates at high latitudes.

4.2 | Water table levels have a large effect on plant nutrient responses

Wet areas had a positive effect on the nutrient responses (especially of P) and/or biomass of the deciduous study species in particular. Deciduous species (which trade longer nutrient retention times and efficient nutrient resorption for the ability to use nutrients to grow more quickly), may benefit from wet, nutrient-rich areas where nutrients are less limiting. Foliar nutrient concentrations and soil phosphate availability are known to increase in wet tundra due to more rapid nutrient cycling and changes in physical soil properties (Chapin and Shaver, 1981; Matthes-Sears et al., 1988; Oberbauer et al., 1989; Semenchuk et al., 2015). Increased N availability from mass flow of water and nutrients can also stimulate enzymatic phosphatase activity in the soils (Giesler et al., 2012). The observed increases in foliar P in *V. uliginosum*, *C. bigelowii*, *B. nana* and *R. chamaemorus* (and a corresponding decrease in foliar N:P ratio in all but *R. chamaemorus*) in response to wetter conditions may be related to these species' deciduous status and ability to quickly take advantage of higher nutrient availability in wet environments. Deciduous species may be especially important in moving nutrients above-ground in wet areas. Plants at the thermokarst gradient did not show increases in foliar P in plots with shallow water table levels, although there were only two plots at the thermokarst gradient with water tables shallower than 5 cm below-ground.

The increase in canopy biomass (and canopy N, Ca and Mg) that we found in *B. nana* as water tables became shallower corresponds to prior studies which have shown that shrub expansion often occurs in

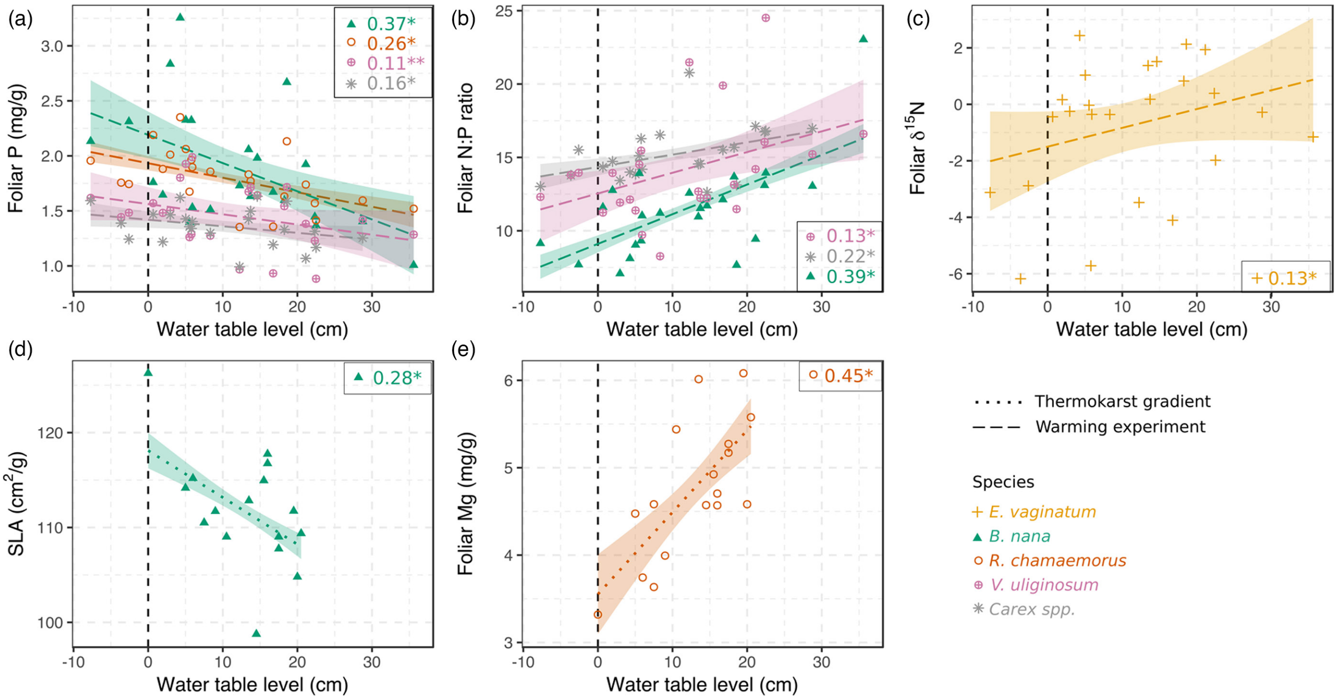

FIGURE 4 Foliar responses to water table levels at the warming experiment ($n = 24$) and the thermokarst gradient ($n = 17$). Points to the left of the vertical dotted line represent plots where the vegetation was submerged. Points represent observed values and regression lines are LMM estimates ± *SE*; full model parameters available in Appendices S3 and S4. Marginal r^2 of each LMM is presented in each panel, representing the proportion of variance explained by the fixed factors. Significance for each relationship is denoted in the corners of each panel: $p < 0.05$*, $p < 0.01$**, $p < 0.001$***

moist and warm habitat such as riverine environments, possibly due to increased nutrient availability (Elmendorf et al., 2012). Associated foliar concentrations of Ca and Mg may correspondingly increase as transpiration increases (Chapin et al., 1975). Under fertilizer additions, *B. nana* leaves have shown increased SLA, which allowed *B. nana* to allocate more resources to woody biomass production (Shaver et al., 2001; Iturrate-Garcia et al., 2020). The increase in SLA (i.e. thinner leaves) that we found in *B. nana* with rising water tables at the thermokarst gradient may be reflective of an increase in nutrient availability. *Rubus chamaemorus* has also been found to be highly responsive to fertilizer additions at both the soil surface and at depth (Keuper et al., 2017). The canopy biomass, canopy N and P, and foliar P concentrations of *R. chamaemorus* were maximized at shallow water table levels at the warming experiment, which suggests that *R. chamaemorus* may also be responding to high nutrient availability in these wet areas.

4.3 | Canopy biomass responds nonlinearly to water table levels

The nonlinear response of total canopy biomass, canopy N and canopy P to water table is consistent with other data from the warming experiment. Total canopy biomass at the warming experiment was driven by the strong quadratic response of *E. vaginatum* canopy mass to water table levels. Other studies at the warming experiment have also found total biomass to be driven almost wholly by changes in the biomass of *E. vaginatum* (Natali et al., 2012; Salmon et al., 2016). We observed biomass of *E. vaginatum* peaking at water tables of about 10 cm below-ground, and the lowest *E. vaginatum* biomass in submerged plots and very dry plots where the water table is deep. Yearly point-framing data at the warming experiment also show browning and decline in *E. vaginatum* in both subsided submerged plots and dry plots (Schuur, unpubl. data). This is likely due to root inundation in submerged plots and decreasing root access to water in dry plots. Nonlinear responses of CO_2 flux, ecosystem respiration and gross primary productivity have also been observed at the warming experiment in response to thaw depth, with water table depth and biomass as significant predictors in the relationship (Mauritz et al., 2017).

Studies at the warming experiment indicate *E. vaginatum* as the primary responding species in terms of biomass in warmed sites with a shallow (but not submerged) water table (Natali et al., 2012; Salmon et al., 2016). This may be partly due to the advantage of its aerenchymous roots in water tracks with enhanced productivity and nutrient cycling (Iversen et al., 2015). The increased canopy biomass (and canopy N and P) of *C. bigelowii* in areas of deep thaw *only* in the presence of a shallow water table also suggests that its aerenchymous rooting traits may give it a competitive ability to reach deep nutrients in deeply thawed, highly saturated environments (Iversen et al., 2015). At the warming experiment, *E. vaginatum* became depleted in ^{15}N as water table level decreased, a pattern also seen in

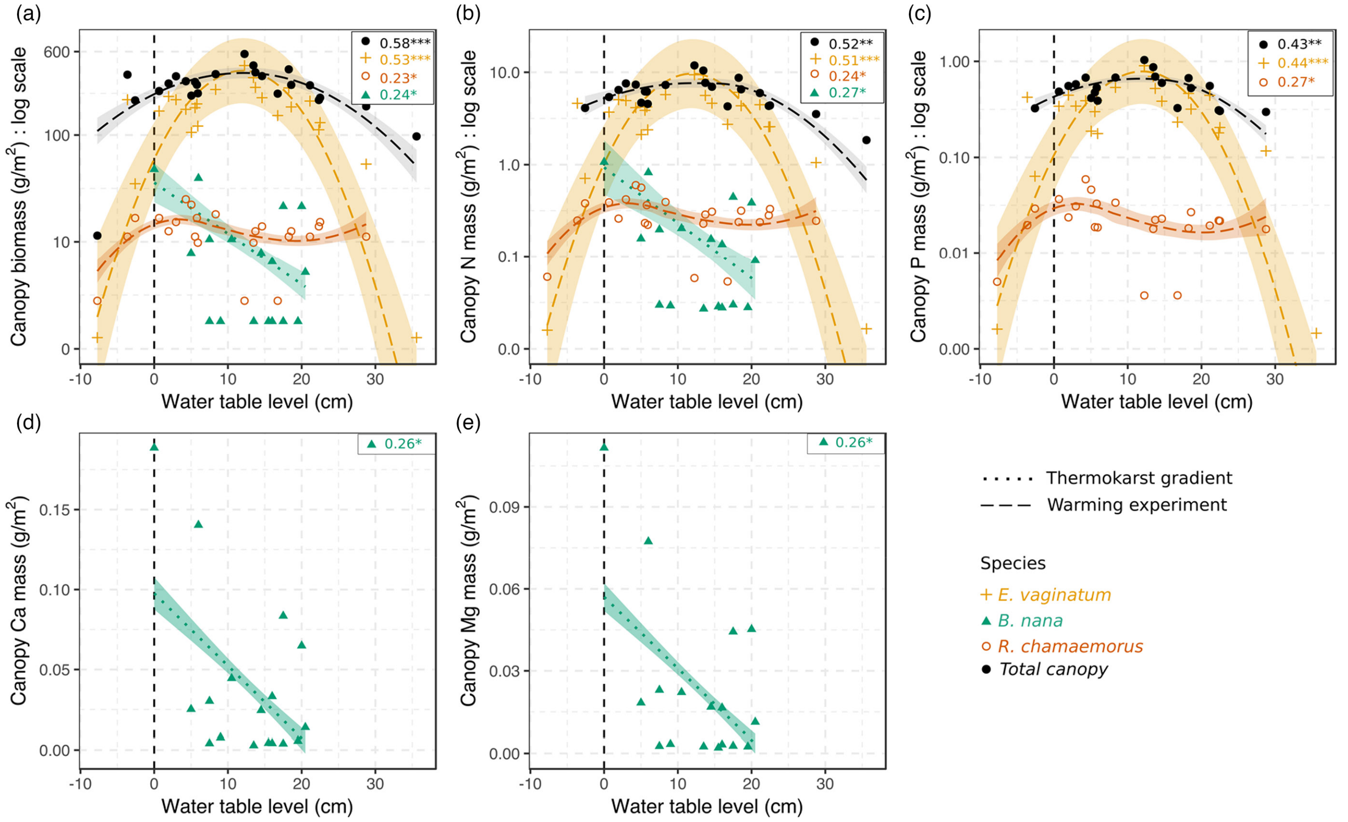

FIGURE 5 Canopy responses to water table level at the warming experiment ($n = 24$) and the thermokarst gradient ($n = 17$). The y-axes in panels a–c were log base 10 transformed for display purposes. Points represent observed values and regression lines are LMM estimates ± *SE*; full model parameters available in Appendices S3 and S4. Marginal r^2 of each LMM is presented in each panel, representing the proportion of variance explained by the fixed factors. Significance for each relationship is denoted in the corners of each panel: $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$

long-term trends at the warming experiment (Salmon et al., 2016; Schuur, unpubl. data). This trend was attributed to altered N cycling and a reliance on an isotopically lighter N source, potentially dissolved organic N, and suggests that fluctuating water tables are altering nutrient pools for *E. vaginatum*.

In addition to nutrients and water, studies have shown that Arctic plants can be limited by shading, biotic competition and other means of interspecies partitioning of resources (Chapin and Shaver, 1985). The differing nonlinear responses of plant species' canopy biomass to water table level at the warming experiment suggest that factors related to plant competition may have affected canopy biomass composition and above-ground nutrient mass. The canopy biomass of *R. chamaemorus*, a low-lying, deep-rooted forb, was low in submerged plots and increased at very shallow water tables, likely due to a balance between increased nutrient availability and decreased oxygen to roots. However, canopy biomass of *R. chamaemorus* was minimized at water tables around 10–20 cm, potentially attributable to shading and competition by the increased canopy biomass of taller graminoids and shrubs. Its biomass increased at deeper water table levels when the canopy biomass of taller shrubs and graminoids dropped off, which could be related to its extremely deep rooting depth and ability to compete for water in drier conditions.

4.4 | Rooting depths and access to nitrogen versus phosphorus

Although species-specific discrepancies in foliar N versus P concentrations were less pronounced than we had hypothesized, certain species-specific responses suggest that rooting depth may still be important in determining which species access nutrients with deeper thaw, especially in terms of N. The increase in foliar N and the foliar N:P ratio in *V. vitis-idaea* with increased thaw depth at the warming experiment, and the canopy-level decreases in P and Mg with increasing thaw depth at the thermokarst gradient, support the hypothesis that shallowly rooted species may be more readily able to access newly available N from shallow mineralization than newly available rock-weathered nutrients at depth. A previous study at the warming experiment by Salmon et al. (2016) found a coordinated increase in surface soil (10 cm depth) inorganic N availability and total foliar N pools over a period of 5 years in the deeply thawed, wet plots. If trends have remained the same, this suggests that *V. vitis-idaea* could be taking advantage of newly available inorganic N in these plots, and the ^{15}N enrichment of *V. vitis-idaea* as thaw depth increased could be due to a decreased reliance on ericoid mycorrhizal symbionts as mineralized N becomes more readily available at shallow depths (Iversen et al., 2015). The increase in foliar N and P in *R. tomentosum* with increases in thaw depth at the warming experiment partially matched our expectation that as a moderate to shallowly rooted species its foliar N concentrations would increase, but also suggests that it may have a greater capacity than *V. vitis-idaea* to access P, perhaps due to increased root growth in warming soils. The growth strategies differ between *R. tomentosum* and *V. vitis-idaea*, and therefore they tend to react differently to environmental conditions, perhaps because *R. tomentosum* is taller and has higher leaf production (Rohrs-Richey & Mulder, 2018). The decreases in foliar P and Mg in *R. chamaemorus* were unexpected as it is the most deeply rooted species (Hewitt et al., 2019). However, it is possible that non-limiting elements within the foliar ratio become diluted as the plant takes up macronutrients for growth (Chapin et al., 1975), or that P is being reallocated to areas other than leaves which were not measured in this study, such as reproductive parts and roots. Root access to plant nutrients at depth is likely to be more nuanced than hypothesized. Deeply rooted plants may increase root biomass throughout the soil profile and thus access nutrients at all depths. Roots or mycorrhizae of shallowly rooted plants that extend deeply enough could access rock-weathered nutrients thawing from shallow mineral soil layers over time (Hewitt et al., 2019).

Foliar N:P ratios indicate that in general most species at this site are accessing P proportionally to N, or in greater proportions than N for deciduous species in wet sites. The only exception to this was *V. vitis-idaea*, the most shallowly rooted species, which increased foliar N concentrations in higher proportions than P as thaw depth increased. This suggests that at least in this MAT ecosystem, although N is increasingly available to plants (Salmon et al., 2016), it will continue to be the amount of available N that determines plant growth, even as more P becomes available with thaw and is moved aboveground in vegetation in wet areas. The observed increase in foliar P in deciduous species in wet sites even under N-limitation could be due to luxury consumption of the non-limiting element P over N by Arctic species, which adds little benefit to the plant in terms of growth, but has implications for P cycling (Van Wijk et al., 2003). It is possible that the type of substrate underlying this site—young colluvial mineral soils (Osterkamp et al., 2009)—might allow for more P availability as permafrost thaws than in other areas of the Arctic where permafrost is thawing into organic soils (Nadelhoffer et al., 1992). Quantifying tundra areas where N or P, or both, are controlling plant growth has important implications for quantifying soil carbon storage (Street et al., 2018).

4.5 | A natural thermokarst gradient versus a warming experiment

Plants in the natural thermokarst gradient and the warming experiment did not respond exactly the same. At the warming experiment, all seven species responded to warming-induced thaw depths or water table levels with increased canopy mass or foliar concentrations of at least one nutrient, whereas only four species at the thermokarst gradient displayed detectable changes in foliar nutrients or canopy mass. While the contrast between a natural thermokarst thaw gradient and a warming experiment adjacent on the landscape is a powerful one, it is important to note the differences inherent in each approach that may make comparison difficult.

Although the warming experiment is spread across the tundra in three blocks, it is still a much smaller spatial disturbance than the thermokarst gradient, which is thawing a large swath of tundra at a constant ambient rate and may thus be developing more complex landscape features such as drainage channels that affect water tables and thaw rates within plots. Natural thermokarst is patchy, and it is also possible that our sampling design at the thermokarst gradient missed sampling microsites in thaw channels, which may have proportionally important nutrient impacts on the landscape.

Differences between plant responses at the thermokarst gradient versus the warming experiment could also be due to factors stemming from the ages and rate of thaw in the two environments. Plots in the warming experiment have been subjected to manipulated thaw for less than a decade—essentially an abrupt thaw event driven by winter warming. Plots in the thermokarst gradient have experienced slower and more continuous climate warming throughout the seasons for 30–50 or more years. Ecosystem response to extreme events can be stronger than to gradual environmental change, which could explain the more significant plant responses we observed at the warming experiment. Both *B. nana* and *E. vaginatum* have been primary responders in tundra warming and fertilization experiments, dependent on various timescales or corresponding to differing environmental conditions such as temperature (Wookey et al., 2009; Elmendorf et al., 2012). We found that *E. vaginatum* is responding in terms of biomass at the younger warming experiment and *B. nana* is responding in terms of canopy and nutrient mass to thaw depth and water table level at the older thermokarst gradient. At the thermokarst gradient, graminoid biomass increased after about 20 years of thaw, but after more than 30 years of thaw deciduous shrubs dominated (Schuur et al., 2007). Many studies have shown that graminoids often respond initially to thaw but then are gradually replaced by shrubs (Shaver et al., 2001; Mack et al., 2004; Elmendorf et al., 2012; Sistla et al., 2013). *Betula nana* was found to increase near-surface long-lived fine root biomass in a fertilization experiment (Sullivan et al., 2007), which could partially explain its successful eventual replacement of *E. vaginatum* (which has an annual root system) in long-term Arctic fertilization experiments (Shaver and Chapin, 1995; Shaver et al., 2001). Recent studies have suggested that initial uptake of nutrients by fast-growing graminoids and other deeply rooted forbs may move nutrients above-ground in the form of more quickly decomposing litter, where shrubs may then access it over longer time-scales (Wookey et al., 2009; Hewitt et al., 2019; Mauclet, Agnan, et al., 2021).

5 | CONCLUSIONS

Our results elucidate species-specific plant nutrient responses to two major alterations in physical environment in thermokarst landscapes: increased thaw depths and fluctuating water tables. We show that total canopy mass and total canopy N increased as thaw depth increased, but that total canopy mass and canopy nutrients were also controlled by water table levels which had nonlinear effects on plant community composition and above-ground biomass. Two out of three shallow to moderately rooted species responded positively in terms of foliar or canopy N to increases in thaw depth, and also showed decreases in canopy P and Mg with thaw depth. In contrast, we found no connection between deeply rooting species and foliar or canopy increases in rock-weathered nutrients, and in fact the most deeply rooted species showed decreases in foliar P and Mg with thaw. Deciduous species, however, often responded strongly to shallow water tables with increased nutrient concentrations or canopy biomass. Our species-specific findings give support for the idea that plant rooting traits are likely important determinants in plant nutrient acquisition, especially for N, but that deciduous traits corresponding to nutrient use efficiency also strongly determine which species may ultimately move nutrients above-ground in increasingly high-nutrient environments of deep thaw and shallow water tables. Our findings suggest that, at least in this MAT tundra thermokarst environment, increased plant access to P may be more related to changes in physical soil properties induced by water table levels than to increased volume of thawed mineral material. Foliar N:P ratios suggest that species in this tussock tundra ecosystem are either remaining in or moving 'further' into N-limitation as thaw depth deepens, water table level rises and more P becomes available. This indicates that in this landscape, P is unlikely to become a limiting nutrient under current thaw trajectories. In both the natural thermokarst gradient and the warming experiment, wet and/or deeply thawed areas generally led to an increase in foliar nutrients and/or higher amounts of canopy biomass and canopy nutrients. This suggests that the amount of deeply thawed, wet areas (such as thaw channels) that develop on the landscape as permafrost thaws will be proportionally important contributors in the total movement of nutrients above-ground when viewed as a sum across the landscape (Becker, Davies and Pollard, 2016; Curasi, Loranty and Natali, 2016). These warm, wet areas may serve as conduits to move more nutrients above-ground following increases in plant biomass and foliar nutrient content, of either graminoids or deciduous species on varying timescales. Determining landscape patterns of nutrient availability and movement will be crucial in quantifying the carbon balance of permafrost ecosystems as climate change impacts the globe.

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CONFLICT OF INTEREST

The authors of this paper have no conflicting interests with the content herein or the *Journal of Ecology*.

AUTHORS' CONTRIBUTIONS

B.L.J., E.A.G.S. and M.C.M. conceived the ideas and designed the methodology; B.L.J., M.M., S.N.M. and M.A.T. collected the data; B.L.J., M.M., R.E.H. and X.W. analysed the data; B.L.J. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13864.

DATA AVAILABILITY STATEMENT

Data are archived with the Bonanza Creek LTER, Institute of Arctic Biology, University of Alaska Fairbank: http://www.lter.uaf.edu/data/data-detail/id/704 (Jasinski et al., 2018a), http://www.lter.uaf.edu/data/data-detail/id/705 (Jasnski et al., 2018b) and http://www.lter.uaf.edu/data/data-detail/id/706 (Jasinski et al., 2018c).

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