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Enhanced plant leaf P and unchanged soil P stocks after a quarter century of warming in the arctic tundra

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Abstract. Phosphorus (P) limits or co-limits plant and microbial life in multiple ecosystems, including the arctic tundra. Although current global carbon (C) models focus on the coupling between soil nitrogen (N) and C, ecosystem P response to climate warming may also influence the global C cycle. Permafrost soils may see enhanced or reduced P availability under climate warming through multiple mechanisms including changing litter inputs through plant community change, changing plant–microbial dynamics, altered rates of mineralization of soil organic P through increased microbial activity, and newly exposed mineral-bound P via deeper thaw. We investigated the effect of long-term warming on plant leaf, multiple soil and microbial C, N, and P pools, and microbial extracellular enzyme activities, in Alaskan tundra plots underlain by permafrost. Here, we show that 25 yr of experimental summer warming increases community-level plant leaf P through changing community composition to favour relatively P-rich plant species. However, despite associated increases in P-rich litter inputs, we found only a few responses in the belowground pools of P available for plant and microbial uptake, including a weak positive response for citric acid–extractable PO_4 in the surface soil, a decrease in microbial biomass P, and no change in soil P (or C or N) stocks. This weak, neutral, or negative belowground P response to warming despite enhanced litter P inputs is consistent with a growing number of studies in the arctic tundra that find no long-term response of soil C and N stocks to warming.

Key words: climate change; experimental warming; extracellular enzyme activity; long-term; phosphorus; toolik LTER; tundra.

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INTRODUCTION

Phosphorus (P) is an important component of living organisms, and there is growing evidence that it is limiting or co-limiting to plant or microbial life in many terrestrial biomes, including the Arctic (Shaver and Chapin 1995, Zamin and Grogan 2012, McLaren and Buckeridge 2019, Hou et al. 2020). Tundra responses to warming have focused experimentally on the response of soil nitrogen (N) because of historic evidence that arctic ecosystems are primarily N-limited (Shaver and Chapin 1980, 1995). The underlying paradigm is that N-mineralization rates will increase with warming soils (Rustad et al. 2001, Salazar et al. 2020), and that resulting increases in plant growth and decreases in soil C stocks (Mack et al. 2004) could contribute to potential catastrophic losses of C from arctic ecosystems with implications at the global scale (McGuire et al. 2018). In arctic permafrost systems, P is cycled within the active layer and organic soils, and access to mineral stores of P is reduced or non-existent (Chapin et al. 1978, Giblin et al. 1991, Jonasson et al. 1999).

Therefore, C-P cycles may also be tightly coupled like C-N cycles in arctic tundra (Sundqvist et al. 2014). Further, ecosystem responses to warming-induced increases in N availability may depend on the P-status of the ecosystem; while enhanced N can result in decreases in soil C stocks in arctic tundra (Mack et al. 2004), enhanced N and P together may result in a gain in soil C stocks (Street et al. 2018). Thus, arctic P cycling deserves attention in a global warming context.

Despite receiving less attention than soil C and N response to warming, there is evidence that warming may impact multiple aspects of P cycling, including soil available P and the release of P by microbes, although there are fewer reported studies of P stocks in plants and soil. A recent meta-analysis on the effects of warming on soil available N in cold biomes found no effects on inorganic N pools, despite increases in N mineralization rates with warming (Salazar et al. 2020). Similarly, reported warming-driven increases in P pools and stocks in arctic ecosystems are conflicting; we have summarized these studies in Fig. 1a and in Appendix S1: Table S1. Generally, warming appears to increase or have no effect on soil extractable P, rates of P mineralization, or soil P stocks, although microbial biomass P, microbial P acquisition, and plant P are more variable (Fig. 1a, Appendix S1: Table S1). The internally cycled P pools available to plants and microbes are composed of multiple forms of P and their availability is controlled by different mechanisms (Herndon et al. 2019), each of which may respond independently to warming. To understand the response of P access and availability to warming, and potential coupling with C, will require further investigation with a broader range of P-extraction methods, and simultaneous investigation in soil, microbes, and plants.

There are several direct and indirect ways that biologically available tundra P may be affected by climate warming. Specifically, we suggest four critical and direct responses to temperature that may be important drivers of enhanced or reduced P cycling (Fig. 1b): (1) *Increased microbial activity* may change the release of phosphate from soil organic matter, dissolved organic phosphorus (DOP), or mineral apatite in the upper mineral soil when accessible, positively, through short-term temperature stimulation of enzyme activity (Keiser et al. 2019), or negatively, through long-term loss of soil organic matter. (2) *Altered plant–microbial dynamics*, as a result of changes in plant or microbial community structure and competition, may change the availability of P in tundra soil in unpredictable directions (McLaren and Buckeridge 2019). For example, increases in deciduous shrubs reported with warming in tundra soils should increase the biomass of ectomycorrhizal fungi, known scavengers for soil P (Read and Perez-Moreno 2003). (3) Altered (positive or negative) *vegetation P uptake and litter recycling* (DOP availability) may occur via temperature-related plant community shifts, growth dilution, or biomass changes (Chapin et al. 1995, Jonasson et al. 1999, Schmidt et al. 2002, Jónsdóttir et al. 2006, Kaarlejärvi et al. 2012). The balance between changed litter inputs vs. changed root nutrient exchange may lead to differences in P availability with warming at the soil surface vs. at depth. (4) Enhanced access to mineral P, via *increased thaw depth* (Frey et al. 2007), reported in response to warming in tundra soils (Sistla et al. 2013), may result in higher accessible mineral P stocks and higher potential P availability at the bottom of the active layer.

To explore these proposed mechanisms, we investigated plant community structure, plant litter, soil and microbial P pools, and microbial enzyme activity in long-term warming manipulation (greenhouse) plots in the Alaskan tundra. We included a biologically based soil extraction protocol (DeLuca et al. 2015) to deepen our understanding of the multiple P pools available to plants and soil microorganisms. We have previously seen this ecosystem respond to warming with changes to the vegetation community (Chapin et al. 1995, Sistla et al. 2013), soil N and P mineralization (Nadelhoffer et al. 1991, Schmidt et al. 2002), soil enzyme activity (Sistla and Schimel 2013), microbial community shifts (Deslippe et al. 2011), and food-web rearrangement (Sistla et al. 2013), leading us to favour the following hypotheses:

1. Summer warming (greenhouse manipulation) increases plant litter, soil, and microbial P.
2. The warming effect is stronger at the surface, because plant litter feedbacks dominate P-cycling controls. Alternatively, P availability

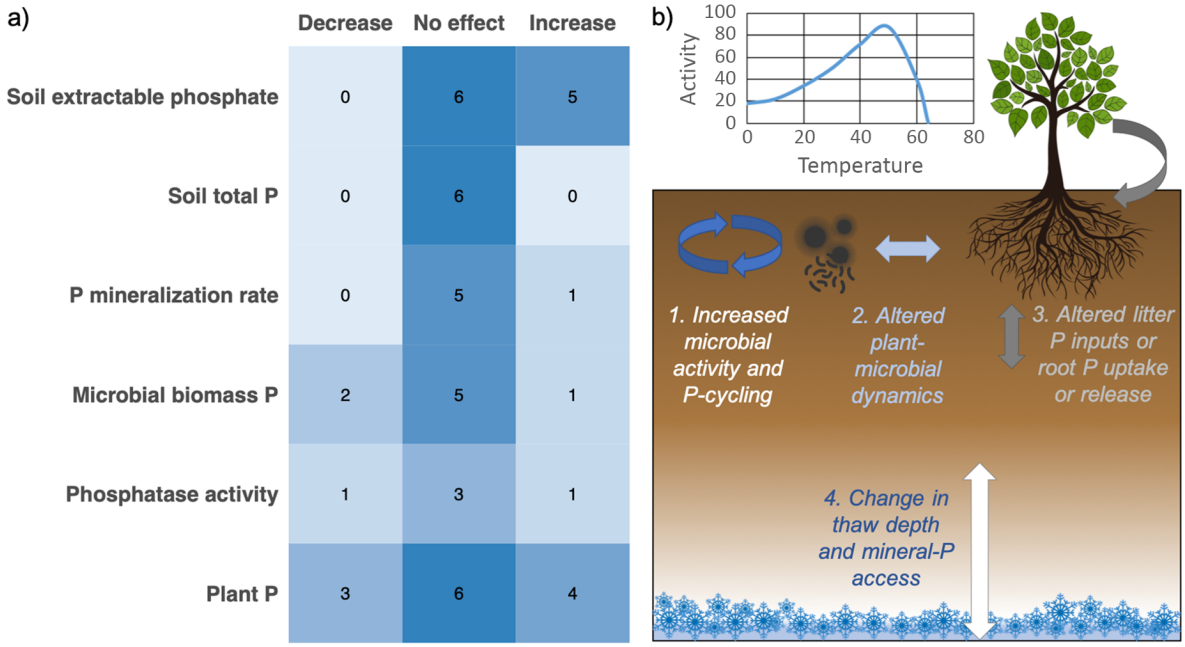

Fig. 1. (a) State of the knowledge for tundra P response to warming. Summary of our literature review on how tundra and cold peat P pools and functions respond to experimental warming manipulations. The numbers and corresponding colour saturation in each tile represent supporting studies (or different supporting plant species within studies) and details of the studies are available as Appendix S1: Table S1. The results from this study are included in the tally. (b) Four proposed mechanisms for how summer warming may increase P availability to tundra plants and soil microbes. Warming may (1) increase microbial enzyme activity, releasing more P from organic and mineral complexes; (2) alter plant-microbial dynamics by changing the community or activity of either group, and their competition for P; (3) increase or decrease the amount and/or P content of plant litter or root exudates through changes to the plant community composition or biomass; and (4) increase microbial and plant root accessibility to mineral P, as the active layer depth increases.

may be higher in the (active) mineral soils, due to documented changes in thaw depth with warming (Sistla et al. 2013).

Materials and Methods

Site description

The study was conducted at Toolik LTER in the foothills of the Brooks Range, Alaska (68°38′N and 149°43′W, elevation 760 m). Annual average temperature is −7°C, and temperatures are typically above freezing between June and August, with an average temperature of 10°C in July. The area is underlain by continuous permafrost ca. 200 m thick, so there is no deep drainage of soil water and little or no connection with groundwater, with the depth of the active layer ca. 30–50 cm, typically including the organic horizon (ca. 10–15 cm depth) and the upper mineral layer. We conducted this study in the moist acidic tundra ecosystem. The moist acidic tundra is tussock tundra, the most widespread vegetation type in Alaskan upland tundra, with an average organic soil pH of 3–4. Maximum thaw occurs in late August to early September. Soils are Gelisols (formed over permafrost), with high organic content.

Experimental design

Warming treatments are maintained by the Toolik Long-Term Ecological Research (LTER) project. These are spatially paired control (10 × 5 m) and greenhouse (2.5 × 4 m) plots replicated in four blocks separated by at least 10 m, established in 1989. Passive summer

warming is created using wooden "A" frame greenhouses (GH) covered with clear polyethylene sheets annually in late May or early June when the ground is snow free and uncovered at the end of August. The GH reduces photosynthetically active radiation and direct precipitation inputs, but does not negatively influence plant growth (Deslippe et al. 2011) nor affect soil moisture (Deslippe et al. 2011, Sistla et al. 2013) because of lateral water flow into the plots and uneven microtopography allows air circulation beneath the greenhouse bases (Clemmensen et al. 2006). Air temperature in the GH is elevated 2.1°C on average during the summer, organic soil temperature elevated 1.3°C (Deslippe et al. 2011), and the influence on soil temperature extends into the mineral horizon (Deslippe et al. 2011, Sistla et al. 2013). As the plant community changed in composition, the warming treatment effects on soil temperature shifted from being strongest in the summer early in the experiment (1996) to stronger in the winter in later years (2000 and 2008) (Sistla et al. 2013). The most recently reported (August 2014) data collections (Shaver and Rastetter 2019) suggest that thaw is deeper in the greenhouse plots (55 ± 0.71 cm) than the control plots (47 ± 1.70 cm) (Student's *t*-test, $t = 4.5$, $P = 0.01$).

Plant species cover and nutrient content

In July 2015, we quantified the percent cover of vascular and non-vascular plants, bare ground, and plant litter (separated into naturally senesced litter and litter which had been processed by tundra voles ["vole litter"]) in eight contiguous 1 × 1 m replicate quadrats in each plot. Vascular plants were identified to species while mosses and lichens were grouped across species. Proportional cover was calculated by summing the percent cover of all plants and then calculating the relative abundance of each species to standardize across plots. Plant species were grouped into functional groups (graminoids, evergreen shrubs, deciduous shrubs, forbs, lichens, and mosses) for analyses.

We collected leaf material from the dominant species from four functional groups, which collectively comprised ca. 50% of the proportional ground cover: *Eriophorum vaginatum* (graminoids), *Rhododendron palustre* (evergreen shrubs), *Betula nana* (deciduous shrubs), and *Rubus chamaemorus* (forbs). For each replicate plot, fully expanded leaves were collected from a minimum of three individuals of each species and combined to make a single sample. Although we collected green leaf material, only a portion of leaf P (ca. 20–60% depending on species) is retranslocated from leaves in the fall, and leaves with higher P content result in litter with higher P content for multiple tundra species (Berendse and Jonasson 1992). Leaves were dried at 70°C for 72 h and then ground before nutrient analysis (see section 'Soil and plant total carbon, nitrogen, and phosphorus', below).

Soil sampling and preparation

Organic and mineral soil horizons were sampled August 2–3, 2015. Tussocks of *E. vaginatum* were avoided, and sampling occurred in the dominant intertussock areas. A single 10 × 10 cm column of soil was collected using a serrated knife from each plot to the top 5 cm of the mineral layer. All organic horizons were separated into the upper organic (0–5 cm depth) and lower organic (5 cm – mineral layer) soils.

Soils were separated into three layers (upper organic, lower organic, and mineral soils) in the field, bulk density subsamples were collected from the centre of each layer using a sharp knife, dimensions were measured, and then all samples were returned to the field lab. Bulk density samples were weighed, then oven dried for 48 h at 60°C to calculate gravimetric water content and for total CN analysis. The remainder of each core were homogenized by hand and all large roots (>1 mm diameter) and rocks (>2 mm diameter) removed before further processing. The homogenized soil was frozen at −20°C and shipped to University of Texas at El Paso for further analysis.

Soil and microbial extraction and analyses

Soil samples (5 g fresh mass) were thawed and extracted with 25 mL of 0.5 mol/L K_2SO_4 by shaking for 2 h and then filtered through glass filter paper. Duplicate samples for estimates of microbial biomass flush were quantified using a modification of the fumigation-extraction technique (Brookes et al. 1985). Five grams of soil were combined with 2 mL of ethanol-free chloroform and incubated at room temperature for 24 h in a stoppered 250 mL Erlenmeyer flask. Following incubation, flasks were vented and

extracted as above. Both fumigated and non-fumigated extracts were analysed for extractable organic carbon (EOC) and extractable total nitrogen (ETN) on a Shimadzu analyser (TOC-VCPN; Shimadzu Scientific Instruments, Columbia, Maryland, USA). Ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (PO_4) in non-fumigated extracts and PO_4 in fumigated extracts were analysed using colorimetric microplate assays (BioTEK Synergy HT microplate reader; BioTek Instruments, Winooski, Vermont, USA). The protocol for NH_4^+ followed the Berthelot reaction (Rhine et al. 1998), NO_3^- analysis used a modified Griess reaction (Doane and Horwáth 2003), and phosphate was analysed with a malachite green assay (D'Angelo et al. 2001). Microbial biomass C, N, and P flushes were calculated as the difference between EOC, ETN, or PO_4-P in fumigated and non-fumigated extracts, with no correction factor applied.

Biologically based phosphorus (BBP) extractions

We used the biologically based phosphorus (BBP) extraction protocol (DeLuca et al. 2015) which uses four extractants to mimic strategies used by plants or microbes to access P: calcium chloride ($CaCl_2$; dilute salt to simulate P available in soil pore water), citric acid ($C_6H_8O_7$; P sorbed to clay or weakly bound to the soil matrix made accessible through organic acids released by plant roots and microbes), hydrochloric acid (HCl; P strongly bound to mineral surfaces which may be less accessible to plants and microbes), and phosphatase (labile organic P available through enzyme hydrolysis) (DeLuca et al. 2015, Crain et al. 2018). Extractions were conducted in parallel by shaking 0.5 g of each sample with 10 mL of each of the four extractants – 0.01 mol/L $CaCl_2$, 0.01 mol/L $C_6H_8O_7$, 0.02 EU/mL phosphatase solution in a 50 mmol/L sodium acetate buffer and 1 mol/L HCl, followed by centrifugation for 30 min at 3020 rev/min. PO_4 was then determined on the supernatant from each extraction colorimetrically, as above.

Soil microbial extracellular enzyme analysis

We examined the activity of seven hydrolytic enzymes that are involved in the microbial acquisition of C, N, and P: C-acquiring enzymes (β-glucosidase, cellobiohydrolase, β-xylosidase, α-glucosidase), N- and C-acquiring enzymes (N-acetylglucosaminidase [NAG]), and P-acquiring enzymes (phosphatase and phosphodiesterase). Extracellular enzyme methodology was modified from Saiya-Cork et al. (2002) and McLaren et al. (2017, 2018). Frozen samples were thawed immediately prior to exoenzyme assays. One gram of soil was blended with buffer (sodium acetate buffer, pH = 4.5). Aliquots of slurries were pipetted onto 96-well plates, with eight replicates per soil. Fluorescing, 4-methylumbelliferone (MUB)–tagged substrate was added to each assay. Assays were incubated at 20°C for 3.5 h with half-hourly measurements ensuring activity was measured in the linear range of the reaction. Sample fluorescence (i.e., cleaved substrate) was read with a BioTek Synergy HT microplate reader at 360 nm excitation, 460 nm emission. For each substrate, we measured the background fluorescence of soils and substrate and the quenching of MUB by soils and used standard curves of MUB to calculate the rate of substrate hydrolysed.

Soil and plant total carbon, nitrogen, and phosphorus

Subsamples of plant leaves and soil were dried, ground, and processed for total C, N, and P content. Total C and N content was determined using a dry combustion C and N analyser (Elementar PyroCube). Total P content in organic soils and plants was determined on samples after ashing at 500°C and then digested using 6 mol/L HCl, and the total P was determined as the phosphate in the digest using the malachite green assay (D'Angelo et al. 2001). Total P content in mineral soils was measured following lithium metaborate fusion at 950°C, and resultant solutions were analysed by inductively coupled plasma emission spectrometer (ICP-AES) (Feldman 1983).

Statistical methods

Statistical analyses were performed in R v3.6.3 (R Core Team 2020) using the base package (linear models). To assess the effect of warming on the plant community, we used a two-way ANOVA, followed by pairwise contrasts of functional group percent cover between treatment and control. To investigate warming effects on plant CNP content and C:N:P ratios, we used linear models with functional group and treatment

(greenhouse or control) and their interaction as fixed factors. Soil and microbial CNP pools and microbial activity were assessed with a linear model that included treatment (greenhouse or control), soil depth, and their interaction as fixed factors. All variables were assessed for normality and heteroscedasticity and, with the exception of the nutrient ratios, were log-transformed to meet model assumptions. Statistics were conducted with a significance cut-off of alpha = 0.1 to maintain a standard of reporting from these plots (e.g. Sistla et al. 2013). Significant results are reported in the main text, and all variable means (g/g and g/m^2) and their significant statistics are reported in the appendix (Appendix S1: Table S2).

Results

Plant community and CNP responses to warming

The plant functional group cover changed in response to warming, as increased litter ($P = 0.004$), deciduous shrubs ($P = 0.050$) and forbs ($P = 0.059$), and decreased graminoids ($P = 0.033$) and lichen ($P = 0.008$) (Fig. 2a). Relative abundance of evergreen shrubs, moss, vole litter, and bare ground did not change in response to warming (Fig 2a.)

Species-specific plant C, N, P or C:N:P ratios did not change in response to warming, although they did differ between the four functional group–dominant species assessed ($P < 0.0001$ for C, N, and P and Fig. 2b–d). *R. palustre* (evergreen shrub) had a higher C content than all species, *B. nana* (deciduous shrub) had higher C than *E. vaginatum* (graminoids) and *R. chamaemorus* (forbs), and *E. vaginatum* had higher C than *R. chamaemorus*. In contrast, *B. nana* had a higher N and P content than all other species, and *E. vaginatum* and *R. chamaemorus* had similar N and P contents and higher N than *R. palustre*. Differences between species in their C, N, and P contents resulted in differences in species-specific C:N:P ratios (Appendix S1: Fig. S1). *R. palustre* had a higher C:N ratio than all other species ($P < 0.0001$), and *B. nana* had a lower C:N ratio than *E. vaginatum* ($P = 0.0001$) and *R. chamaemorus* ($P = 0.031$). *B. nana* also had a lower C:P ratio than *E. vaginatum* (trend, $P = 0.078$) and *R. chamaemorus* ($P = 0.001$), whereas *R. palustre* had a higher C:P than *B. nana* ($P = 0.0005$). *R. chamaemorus* had a higher N:P ratio than *B. nana* ($P = 0.004$), *E. vaginatum* ($P = 0.023$), and *R. palustre* ($P = 0.009$).

Warming and interactions with soil depth

Summer warming interacted with soil depth for microbial biomass CNP pools (MBC $P = 0.045$; MBN $P = 0.025$, MBP $P = 0.006$; Fig. 3a–c). MBC was higher in the lower organic soil, but only in the control plots ($P = 0.047$). MBN was higher in the upper organic warmed soils ($P = 0.062$), whereas MBP was lower in the warmed soils ($P = 0.006$), specifically in the lower organic ($P = 0.02$) and mineral ($P = 0.05$) soils. Summer warming interacted with soil depth for BBP-citric acid-extractable PO_4 ($P = 0.084$), in that it was enhanced only in the warmed surface organic soil ($P = 0.037$; Appendix S1: Fig. S3b). Summer warming reduced phosphodiesterase ("PhosD") potential activity, independent of depth ($P = 0.069$; Appendix S1: Fig. S2d). None of the other soil or microbial variables, including total C, N, and P (Fig. 2d–f), showed a warming response or an interaction with warming and depth (Appendix S1: Fig S2–S5). There were several significant microbial, enzymatic, and CNP pool differences between soil depths, independent of warming (Appendix S1: Table S2).

Discussion

Aboveground effects

We found that twenty-six years of summer warming did not change either the leaf P or N content for any species, which does not support our first hypothesis that summer warming would increase plant P, at least at the individual species level. This lack of response reflects similar results of shorter-term warming studies conducted at this site where no effect of warming was detected on plant nutrients (Chapin et al. 1995, Shaver and Jonasson 1999) and at other tundra sites (Hudson et al. 2011, Zamin et al. 2017). Further, a meta-analysis of tundra field experiments reports no effect of warming treatments on leaf chemistry (Dormann and Woodin 2002). The few reports of decreased N and P content in the tissue of warmed plants (Jonasson et al. 1999, Jónsdóttir et al. 2006, Kaarlejärvi et al. 2012) are primarily attributed to dilution of nutrients within plants as they increase in size with warming.

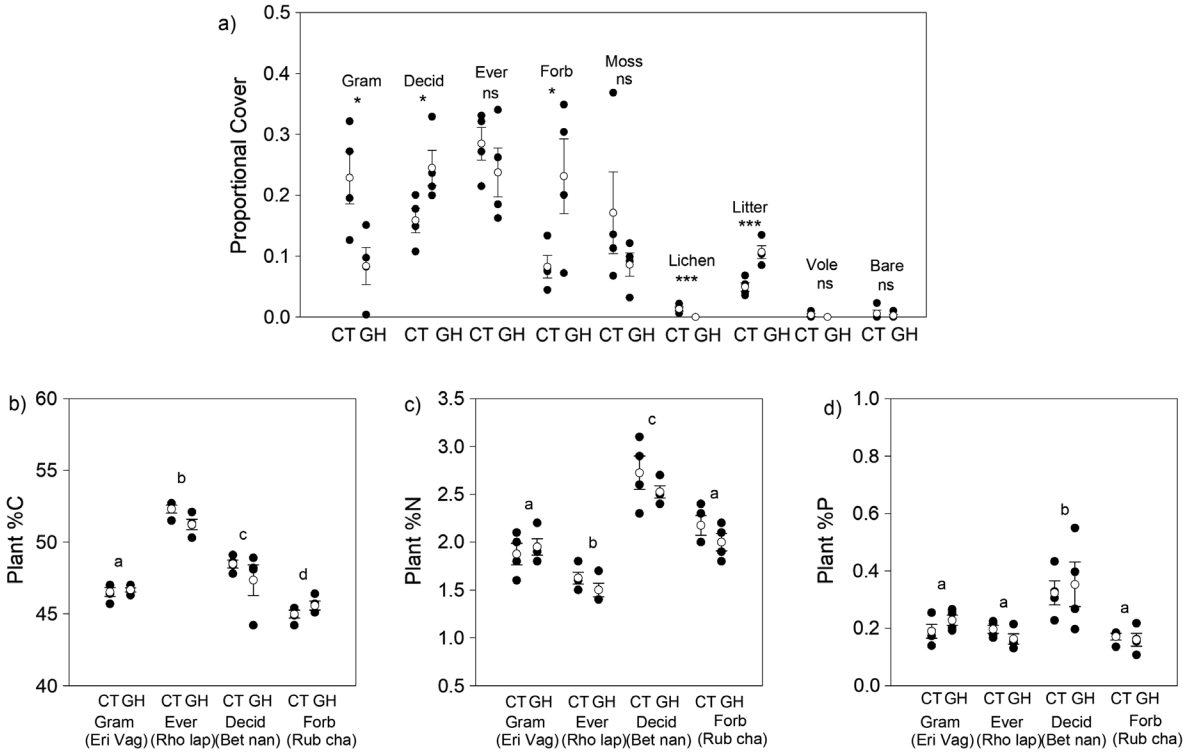

Fig. 2. The effects of long-term summer warming on plant community cover and nutrient concentrations. The proportional cover of vegetation functional groups (a) and % C (b), %N (c), and %P (d) in leaves of dominant species from all vascular plant functional groups is presented from warmed and control plots in moist acidic tundra. The treatment "CT" has received no warming treatment and "GH" has been enclosed in a poly-ethylene greenhouse during growing seasons since 1989. Refer to text for further experimental details. Open circles and error bars are means (n = 4) ± 1 SE and solid circles are individual data points. Functional groups in (a–d) are graminoid (Gram), deciduous shrubs (Decid), evergreen shrubs (Ever), herbaceous forbs (Forb), moss, lichen, litter, litter processed by small mammals (Vole) and bare ground (Bare). The species in b–d are "Eri vag" = *Eriophorum vaginatum*; "Rho pal" = *Rhododendron palustre*; "Bet nan" = *Betula nana*; "Rub cha" = *Rubus chamaemorus*. Significant effects of warming on functional group cover (a) are marked with asterisks above the paired CT and GH data points. *P < 0.1, **P < 0.01, ***P < 0.001. Significant effects of species identity (b–d) are indicated with letters above the means.

Although individual plant species did not shift in their P content with warming as we hypothesized, we did find shifts in the composition of the plant community with warming, with decreases in the cover of graminoids and lichens but increases in deciduous shrubs, forbs, and plant litter. Similar results have been reported from this and other warming experiments in moist acidic tundra at Toolik Lake after shorter periods of warming, with increases in shrubs reported after 9 yr (Chapin et al. 1995), forbs after 15 yr (Sistla et al. 2013), and increases in litter but decreases in graminoid cover after 20 yr of warming (Sistla et al. 2013). This reported increase in shrub abundance with warming is also the most consistently reported effect on tundra plant communities, as described in multiple meta-analyses (Dormann and Woodin 2002, Elmendorf et al. 2012).

While changes in leaf chemistry within species may be absent or minor, with the combination of shifts in plant community composition (Fig. 2a) and differing leaf nutrient concentrations between species (Fig. 2b–d), warming may drive changes in community-level litter inputs of P and N. Simultaneous examination of changes in plant

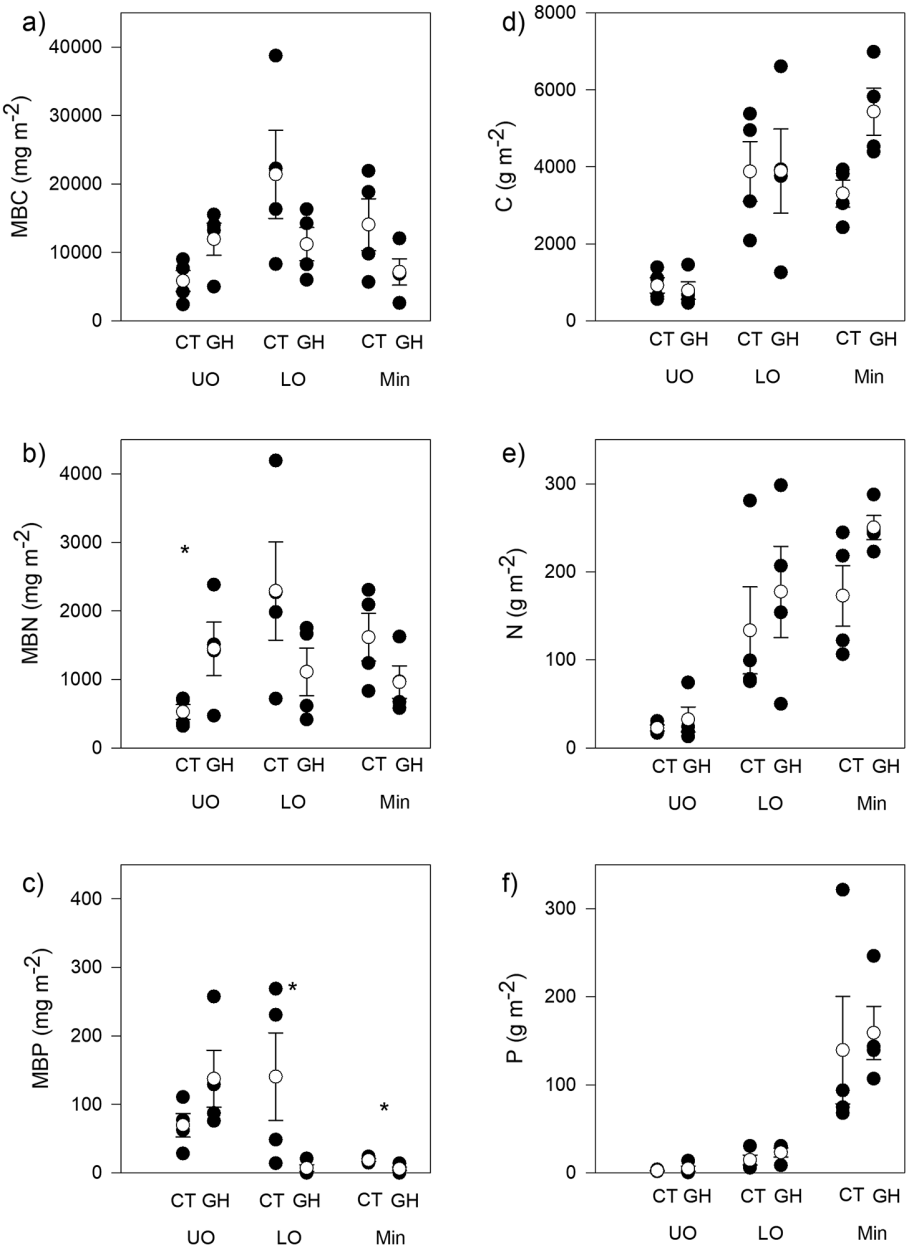

Fig. 3. The effects of long-term summer warming on soil microbial and total C, N, and P. Microbial biomass carbon (MBC; a), nitrogen (MBN; b) and phosphate (MBP; c), and total soil carbon (C; d), nitrogen (N; e) and phosphorus (P; f) are presented in warmed (GH) and control (CT) plots in the moist acidic tundra (a–c) each in the upper (0–5 cm) and lower organic (>5 cm) and mineral (min) soil. The treatment "Control" has received no warming treatment and "GH" has been enclosed in a poly-ethylene greenhouse during growing seasons since 1989. Refer to text for further experimental details. Open circles and error bars are means (n = 4) ± 1 SE and solid circles are individual data points. Effects of warming, $^*P < 0.1$.

community composition and plant chemistry, and thus evaluation of N and P plant stocks, in response to warming, is rare. In the studies conducted at Toolik Lake, AK, after 14 or 15 yr of warming there was no change in either N or P stocks contained in plant biomass (Shaver and Jonasson 1999, Sistla et al. 2013). In a recent study at the Scandinavian forest–tundra ecotones

which combined measures of plant community composition and leaf nutrient concentrations of the dominant shrubs, the effects of warming on the weighted average community-level leaf N was either negative or neutral, while warming decreased community level leaf P because of minor shifts in plant chemistry but increases in the abundance of deciduous shrubs (Kaarlejärvi et al. 2012). In this study, increased cover of the deciduous shrub *B. nana*, with a higher leaf N and P than the dominant species which it replaces (*E. vaginatum* and *R. palustre*), resulted in increased community-level leaf N and P with warming, providing support for our first hypothesis, *at the community level*. Further, communities with higher cover of deciduous shrubs have higher annual litterfall in comparison to communities with higher cover of evergreen shrubs or graminoids, which retain their litter for multiple years. In a nearby fertilization experiment, fertilization increased the cover of shrubs from 20% to 52% and resulted in greater than six times the annual litter fall (McLaren, *unpublished data*). The combination of higher leaf litter inputs (Fig. 2a), a higher cover of deciduous shrubs (Fig. 2a), and the higher N and P content of these leaves (Fig. 2c–d) should also result in significantly higher inputs of N and P into warmed soils, which, in our second hypothesis, we predict may lead to larger warming effects in upper soils. While we only considered leaf, and not whole plant N and P stocks, shrubs retain woody tissue over multiple years and the majority of aboveground litter inputs are leaf tissue. In shrub-dominated plots in this ecosystem, less than 10% of total litter input by mass was composed of woody tissue (McLaren, *unpublished data*). Further, evergreen shrubs likely do not store P in their stems, while deciduous shrubs translocate P from stems into leaves in the spring (Chapin et al. 1980) and changes in woody litter inputs from increases in deciduous shrub cover would also be likely to increase, rather than decrease, P litter inputs into the soil.

Belowground effects

We show an effect of warming on plant community composition and implicit support for mechanisms that would enhance P availability in warmed soils from our own and previously collected data, including increased litter P (this study), warmer surface soils (Shaver and Jonasson 1999, Deslippe et al. 2011, Sistla et al. 2013), and deeper thaw depth (Shaver and Rastetter 2019). Despite this and our in-depth sampling of P pools, we found little support for the belowground component of our first hypothesis, that warming will increase soil and microbial P, or our second hypothesis, that warming effects on P would be higher at the surface from increased litter P inputs. Despite measuring multiple belowground P pools (Appendix S1), only citric acid–extractable PO_4 was higher in the warmed surface soils, representing the P that is weakly bound and accessible after plant organic acid release. Otherwise, we found few of the predicted positive effects of long-term warming on microbial function or nutrient availability in our study soils, and instead report a decrease in MBP. MBN was enhanced in the upper warmed soils in this study, consistent with a recent meta-analyses of warming effects on N that found no cold biome-wide effect on mineral N (NH_4, NO_3), but enhanced MBN and root N (Salazar et al. 2020). This weakly supports our second hypothesis with regards to N and places our system in line with the global average N response to warming but does not resolve our weak P response.

Previous evidence of belowground P response to warming has been mixed, so our weak P response to warming for microbial processes is consistent with some previous studies and not with others. Specifically, our lower microbial biomass P (MBP) in the warmed soils was consistent with the same response to 19 yr of warming in Finnish heath (Stark et al. 2018). However, it is inconsistent with a lack of warming effect on MBP after 10 yr of warming in Alaskan wet sedge and tussock tundra (Schmidt et al. 2002) or after 2 and 10 yr of warming in Tibetan alpine meadow (Wang et al. 2014). It is also inconsistent with increased MBP after 6 months of warming in Swedish heath tundra (Jonasson et al. 2004). We also saw no effect of warming on phosphatase activity and a decrease in phosphodiesterase activity (phosphatases mineralize P from inositol phosphates, and orthophosphate monoesters, such as sugar phosphates, whereas phosphodiesterases mineralize P from monoester and diester phosphates, including nucleic acids and phospholipids). We are not aware of previous attempts to quantify phosphodiesterase activity

in tundra organic soils in response to warming, although both enzyme classes are important for meeting microbial P requirements. The lack of phosphatase response we found is consistent with previous studies at this site after 19 yr of warming (Sistla et al. 2013) and in a Tibetan alpine meadow (Wang et al. 2014), but inconsistent with increased activity in incubated northern US boreal peatland soils (Keiser et al. 2019) or decreased activity after 19 yr of warming in Finnish heath (Stark et al. 2018). Our decreased phosphate acquisition activity aligns with our lower MBP and does not support our hypothesis – or the broader paradigm – that warming will increase microbial activity.

As with the microbial response to warming, the response of soil P availability to warming is inconsistent across studies. No response to warming on belowground PO_4 pools, consistent with many of our belowground P pools, is supported at a nearby wet sedge site after 6 yr of warming (Shaver et al. 1998), after 5 yr in a subarctic fellfield (Jonasson et al. 1999), 12 yr in a Swedish heath (Jonasson et al. 2006) and after 2 and 10 yr in a Tibetan alpine meadow (Wang et al. 2014). In contrast, enhanced PO_4 pools with warming, such as the citric acid–extractable PO_4 in this study, have been reported after 1 yr in a boreal peatland (Munir et al. 2017), after 5 yr in Swedish heath tundra (Jonasson et al. 1999) and after 12 yr in Canadian arctic birch hummock tundra (Gu and Grogan 2020). Microbial activity and PO_4 pools may vary across a season (McLaren et al. 2018), and the single sampling date in some of the above studies, including in this study, may contribute to inconsistencies across study sites. In contrast, soil P stocks summarize the net effect of plant inputs and microbial activity. Our lack of response with P stocks is consistent with no response after 2 and 10 yr of warming in alpine meadow or 5 yr in Swedish heath tundra (Jonasson et al. 1999, Wang et al. 2014) and indicate that warming has no long-term net effect on belowground P. This is consistent with growing global evidence that long-term warming does not alter C stocks in ways that are predicted from short-term warming manipulations (van Gestel et al. 2018, Bouskill et al. 2020, Jian et al. 2020). Therefore, we suggest that inconsistencies between tundra systems in response to warming encompass both seasonal variation, ecosystem specificity, and differences in duration of warming. Our supporting literature has compared different tundra or peatland ecosystems and warming durations, because there were inadequate investigations of P responses to warming to avoid this comparison. We emphasize here, the value of establishing more combined short- and long-term ecosystem climate manipulations in multiple tundra ecosystem types with further attention to P.

Why do plant and litter changes not result in warming effects belowground?

Increases in litter quality and quantity have been shown to increase tundra soil C and N pools (Aguirre et al. 2021) and logically should also increase P pools. Here, we show that plant communities changed in composition, and consequently their inputs of P-rich litter increased, in response to warming. How is it possible to have no increase in stocks with increased inputs? Logically, outputs must also increase to balance inputs, and, although enhanced microbial turnover of plant litter may contribute to increased soil losses, we did not detect enhanced microbial enzymatic P acquisition or soil solution P, indicating this probably was not an important mechanism. It is possible that we are not detecting these soil solution losses by measuring at the wrong time of year. For instance, elevated soil PO_4 has been detected in this site in spring (McLaren et al. 2018), and enhanced winter P leachate losses have been shown to occur at thaw after winter warming (Buckeridge and Grogan 2010), consistent with warmer winter soil temperature in these plots in association with enhanced shrub growth and deeper snow (Sistla et al. 2013). Nonetheless, we did see implied evidence of increased plant P uptake through community shifts towards plants with higher P content in their leaves, suggesting efficient plant P cycling in warmed soils is an important mechanism.

The transfer from litter to plant-available nutrients requires microbial activity, so why did we detect no increase in microbial activity and soil available P pools with warmer soils and higher substrate inputs? In defence of our methods, soil P enzyme activity consistently increases with temperature according to kinetic theory (Shaw and Cleveland 2020), although meta-analyses indicate this increase is minor for hydrolytic

enzymes in systems like ours with low warming magnitude and low mean annual temperatures (Xiao et al. 2018). Soil microorganisms in our system did not respond to warming with increased P-acquisition (i.e. phosphatase or phosphodiesterase activity), possibly because warming may have restricted enzyme production through enhanced N or P limitation (Schimel and Weintraub 2003), which is consistent with our decline in MBP. Alternatively, at the time of our measurements (mid-summer in the latter years of the experiment by which point plant communities had changed substantially), the soil temperatures were likely not different between the treatments, and soil properties are likely dominated by plant presence, rather than warming treatments directly, at the peak of the growing season. Alternatively, the lack of warming response in microbial activity may be a result of soil microbial acclimation, because the 25-yr warmed microbes could have changed their resource demand or resource use efficiency after prolonged exposure to warmer conditions (Billings and Ballantyne 2013). This last reason is supported by multiple studies that find the temperature sensitivity of soil activity declines with time, summarized in a recent meta-analysis that shows microbial respiration in warmed plots does not differ from controls after 10 yr of warming (Romero-Olivares et al. 2017).

Conclusions

We provide theoretical evidence for four potential mechanisms for warming to enhance or alter tundra soil P, including changes to plant P inputs, soil microbial activity, and soil thaw depth. We emphasize three main conclusions with regards to the ecosystem P response to 25 yr of warming in the arctic tundra. First, we found community level increases in plant leaf P and increases in plant litter mass, presumably resulting in increased plant leaf litter P inputs to soil. Second, we measured multiple belowground pools and found only a weak positive response of citric acid–extractable PO_4, a decline in MBP, and a decline in potential phosphodiesterase activity. Overall, the warming response of belowground P pools and microbial activity was less than we hypothesized. However, our belowground results fit within the broad scope of tundra warming responses, and this reported variability is likely because of differences across studies in the ecosystem type, manipulation duration, and seasonality of sampling. That said, there are few studies that measure warming responses to above and belowground P stocks, so we encourage researchers who regularly measure tundra C and N stocks in response to global change to also include P analyses. Finally, we suggest that the lack of long-term belowground effect of warming on P stocks that we report here (similar to the C and N stocks response in this and other studies) may be due to microbial acclimation to warming. Therefore, the surface soil and microbial resilience to warming displayed at this and other sites implies that the persistent paradigm linking warming to C loss through enhanced nutrient availability may be overemphasized as a positive feedback to climate warming.

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Data Availability

Data (McLaren 2021*a*, 2021*b*) are available from the Environmental Data Initiative Data Portal: https://doi.org/10.6073/pasta/1c57b6613111c9d05c0225de12fd1098, https://doi.org/10.6073/pasta/d4f567844673857239eec0cb61c6f543

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3838/full