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Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low arctic tundra

Tara J. Zamin[1]*, M. Syndonia Bret-Harte[2] and Paul Grogan[1]

[1]*Department of Biology, Queen's University, Kingston, ON, Canada; and* [2]*Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA*

Summary

1. Climate change in arctic tundra is projected to increase soil fertility, which may alter plant community composition and ecosystem processes by shifting niche space to favour particular species' life-history strategies. The rate and magnitude of change in soil fertility may be critical to determining plant community responses, and so effects of slow increases in nutrient availability due to climate warming may differ substantially from those of chronic high-level fertilizer additions.

2. We investigated above- and below-ground plant biomass responses to experimental summer warming and above-ground responses to nutrient additions (low-level N and factorial N and P) in a mesic birch hummock tundra community in the central Canadian Low Arctic after eight years of experimental treatment.

3. Plant community biomass responses to experimental warming were fundamentally different from those of high-level N and/or P additions, mainly due to opposing effects on the evergreen shrubs. Evergreen shrub above-ground biomass increased 66% with greenhouse warming, but decreased on average 70% with high-level N and/or P additions, driven by the strong responses of *Rhododendron subarcticum*. Because of this evergreen response, greenhouse-warming increased total above-ground biomass by 32% and total below-ground biomass by 70%, but did not significantly change the total above-ground/below-ground biomass ratio. However, warming increased the shoot/root ratio of *Betula glandulosa* threefold.

4. Increased soil fertility created interactions between N and P availability, whereby increased P availability led to a substantial increase in inorganic N availability. Meanwhile, the growth of several species that span a range of different functional groups was stimulated by the separate N and P additions. These factorial fertilization results highlight the importance of understanding climate warming impacts on availability of both of these nutrients in order to predict plant community responses.

5. *Synthesis.* Our results strongly suggest that the trajectory of mesic tundra vegetation change with warming depends critically on the rate of increase in soil fertility. The relatively large greenhouse-induced biomass increase in evergreen compared to deciduous shrubs suggests that carbon balance and albedo feedbacks to warming will be restricted in mesic tundra ecosystems, at least in their early responses to climate change.

Key-words: climate change, determinants of plant community diversity and structure, greenhouses, life-history strategy, nitrogen, nutrient addition, phosphorus, shrub growth, soil fertility, tundra vegetation

Introduction

Soil fertility is a fundamental constraint on primary production in arctic tundra (Chapin *et al.* 1995; Bret-Harte *et al.* 2001; Dormann & Woodin 2002; van Wijk *et al.* 2004; Zamin & Grogan 2012) and therefore impacts of climate change on soil nutrient availability will be integral to the region's response to warming, as it relates to carbon balance and albedo (Sturm *et al.* 2005; Weintraub & Schimel 2005; Loranty, Goetz & Beck 2011; Natali *et al.* 2011). Warmer air will raise soil temperatures and is expected to increase soil fertility as a result of enhanced decomposition of organic matter due to faster microbial activity (Nadelhoffer *et al.* 1991; Shaver *et al.* 2006; Brzostek *et al.* 2012) and the extended duration over which temperatures are favourable for microbial activity (Rustad *et al.* 2001). Although direct effects of higher temperatures on shoots may contribute, studies isolating above- and below-ground warming impacts clearly indicate that tundra plant growth responses to warming are driven primarily by temperature-enhanced nutrient availability below ground (Hartley *et al.* 1999).

Plant growth rates and community structure are dramatically altered by the extent to which the below-ground environment changes (Chapin *et al.* 1995; Jonasson *et al.* 1999;

*Correspondence author: E-mail: tjzamin@gmail.com

Shaver & Jonasson 1999; Bret-Harte *et al.* 2008; Campioli, Leblans & Michelsen 2012). Fertilization studies that have greatly increased soil N and P availability report a strong increase in the abundance of deciduous shrubs and a strong decrease in evergreens (Chapin *et al.* 1995; Bret-Harte *et al.* 2008), while those that have increased nutrient availability by relatively small amounts report moderate increases in the abundance of *both* deciduous and evergreen shrubs (Jonasson *et al.* 1999; Campioli, Leblans & Michelsen 2012). Overall, tundra plant growth responses to warming seem to be more in line with the latter fertilization studies, as evidenced from both experimental warming manipulations (Molau & Alatalo 1998; Jonasson *et al.* 1999; Walker *et al.* 2006; Campioli, Leblans & Michelsen 2012; Michelsen, Rinnan & Jonasson 2012; Sistla *et al.* 2013) and a meta-analysis of vegetation change in control plots over the past 30 years (Elmendorf *et al.* 2012b). Since increases in soil fertility with climate warming are expected to be slow relative to those induced by fertilization studies (Hobbie, Nadelhoffer & Hogberg 2002), differing plant community responses to warming and fertilization may reflect changes in critical components of niche space that favour particular plant species' life-history strategies (Grime 1979; McKane *et al.* 2002).

The different life-history strategies of evergreen and deciduous shrubs result in different physiological constraints that may be important drivers of their respective responses to warming. Evergreen shrubs are well adapted to growing in high-stress and low-nutrient environments due to their conservative nutrient use, slow relative growth rates, low specific leaf area and low leaf nitrogen (Chapin 1980; Reich, Walters & Ellsworth 1997). By contrast, deciduous shrubs are best adapted to lower-stress environments where their relatively high root biomass or specific root length (Aerts & Chapin 2000), high specific leaf area and high leaf nitrogen (Chapin 1980; Reich, Walters & Ellsworth 1997) optimize nutrient uptake and photosynthesis. These two functional groups exemplify the fundamental trade-off between rapid acquisition versus conservation of resources (Diaz *et al.* 2004). Thus, if climate warming greatly increases soil nutrient availability in the Arctic, deciduous shrubs are expected to increase in abundance relative to evergreens.

Although deciduous shrubs have increased substantially in certain areas of the Arctic as the climate has warmed over the last 50 years (Tape, Sturm & Racine 2006; Forbes, Fauria & Zetterberg 2009; Blok *et al.* 2011; Ropars & Boudreau 2012; Tremblay, Lévesque & Boudreau 2012; Arctic Council 2013; Jeffries, Overland & Perovich 2013), these patterns are based on changes in the percentage cover or inferred photosynthetic activity (i.e. NDVI). It has recently become clear that such measures do not necessarily imply an increase in total biomass, because many species alter their shoot morphology in response to warming (Campioli, Leblans & Michelsen 2012; Campioli *et al.* 2013) or alter below-ground biomass (Sistla *et al.* 2013). Changes in allocation then need to be taken into account in analysing plant responses to climate warming, as they may affect ecosystem response independent of changes in inferred biomass.

As above- and below-ground resource constraints change with warming, tundra plants may shift allocation from root to shoot growth or from photosynthetic to woody tissue in order to maintain optimal foraging (Gleeson & Tilman 1992). Some arctic plant species have high developmental plasticity that enables them to change biomass allocation in response to changing resource conditions (Bret-Harte *et al.* 2001; Hudson, Henry & Cornwell 2011; Campioli, Leblans & Michelsen 2012; Heskel *et al.* 2012), but the extent of plasticity has not been evaluated for all species within the community. In addition to allocation shifts within species, changes in the relative abundances of species with different life-history strategies and plant traits may have ecosystem-wide impacts, including feedbacks to soil nutrient availability via litter quality and quantity (Cornwell *et al.* 2008). Thus, changes in plant allocation and species' relative abundance induced by warming may interact with changes in soil fertility, to either accelerate or decelerate further change in the plant community.

The extent to which warming will increase arctic soil fertility remains largely unknown (Hobbie, Nadelhoffer & Hogberg 2002; Giesler *et al.* 2012). Most warming studies have reported only modest changes in either inorganic N or P availability, but not in both (Chapin *et al.* 1995; Robinson *et al.* 1995; Jonasson *et al.* 1999; Biasi *et al.* 2008; Sorensen, Michelsen & Jonasson 2008; Lamb *et al.* 2011). Medium-term factorial nutrient addition studies have pointed to *independent co-limitation* of tundra plant growth by N and P (Zamin & Grogan 2012), such that growth increases with the addition of each nutrient alone, but increases more so (either additive, sub- or super-additive) with the addition of both nutrients (Harpole *et al.* 2011). Understanding the relative impacts of increases in soil N and P availability on tundra plant growth will improve our ability to predict plant community outcomes and changes in carbon stocks with warming.

Here, we investigate changes in plant biomass and allocation after eight years of experimental summer warming and nutrient additions (low-level N and factorial N and P) in mesic birch hummock tundra to enable improved projections of the mechanisms through which tundra plant communities may change in a warmer Arctic. We test the following hypotheses:

1 Experimental summer warming increases the above- and below-ground biomass of the most abundant deciduous and evergreen shrub species, *Betula glandulosa* and *Rhododendron subarcticum*, with strongest increases in leaf biomass and a net increase in above-ground/below-ground biomass ratios.

2 Experimental summer warming and high-level nutrient addition manipulations favour different plant life-history strategies and therefore result in fundamentally different changes in mesic tundra plant community structure.

3 The magnitude and rate of change in soil fertility affect plant species' growth responses differently, with high-level increases in N availability stimulating deciduous shrubs and restricting evergreen shrubs relative to that of low-level increases in N availability.

4 Above-ground growth of all vegetative tissues of the principal mesic tundra plant species is *independently co-limited* by the availability of soil N and P.

Materials and methods

SITE AND TREATMENTS

This study was conducted in the central Canadian Low Arctic near the Tundra Ecosystem Research Station at Daring Lake, Northwest Territories (64º 52′ N, 111º 33′ W). Average annual air temperature is −8 ± 0.5 °C (Bob Reid, Aboriginal Affairs and Northern Development Canada, *unpublished data 1997–1999 and 2009–2011 continuous record*), ranging from an annual minimum of −38 ± 0.7 °C in January to a maximum of 20 ± 0.4 °C in July (Bob Reid, Aboriginal Affairs and Northern Development Canada, *unpublished data 1996–2011 discontinuous record*). Annual precipitation typically ranges from 200 to 300 mm (Lafleur & Humpheys 2008), with 138 ± 13 mm as rain falling primarily in June–September (Bob Reid, Aboriginal Affairs and Northern Development Canada, *unpublished data 1996–2011*). The region is underlain by continuous permafrost (>160 m depth), with an active layer that varies by vegetation type from 0.3 to 1.2 m depth at maximum (Dredge, Kerr & Wolfe 1999; Lafleur & Humpheys 2008). In the birch hummock vegetation type, the organic soil layer depth typically ranges from 6 to 11 cm (Buckeridge *et al.* 2010), with a pH 4.3 ± 0.3 and C concentration of 46.5 ± 1.7 (Chu & Grogan 2010).

This research was conducted in mesic birch hummock tundra, part of the erect dwarf shrub tundra category of arctic vegetation types (CAVM 2003), where the maximum shrub height is 30 cm, and the vegetation is dominated by evergreen shrubs (*Rhododendron subarcticum* Harmaja [formerly *Ledum decumbens* (Aiton) Lodd. ex Steud.], *Vaccinium vitis-idaea* L., and *Andromeda polifolia* L.), which constitute ~48% of the above-ground vegetation biomass (data this study), and lichens (predominantly *Cetraria spp.* and *Cladina spp.*), which constitute ~25% of the above-ground vegetation biomass (data this study; see Nobrega & Grogan 2008 for more information). *Betula glandulosa* Michx. is the most abundant deciduous shrub, constituting ~7% of the above-ground vascular plant biomass (data this study).

Nutrient addition and summer warming manipulations were established in early July 2004 on flat patches of similar birch hummock tundra vegetation within a 200 × 300 m area of a gently sloping valley. The nutrient addition plots (5 × 7 m) included the following randomly located treatments: low N (1 g N m^{-2} yr^{-1}; n = 5), high N (10 g N m^{-2} yr^{-1}; n = 5), high P (5 g P m^{-2} yr^{-1}; n = 5) and high N+P (10 g N m^{-2} yr^{-1} and 5 g P m^{-2} yr^{-1}; n = 5), with the high N and P application levels chosen to match those of acidic tussock tundra manipulations near Toolik Lake, Alaska (Chapin *et al.* 1995), and heath manipulations at Abisko, Sweden (Jonasson *et al.* 1999). Granular ammonium nitrate (NH_4NO_3) and triple superphosphate (45% P_2O_5; both agricultural grade) were applied once yearly, generally in late summer. The warming treatment (n = 5) included A-frame greenhouses (1.8 m × 4.7 m) covered with heavy polyethylene film (150 micron) that reduced mean daytime photosynthetically active radiation by 32% (Farnsworth 2007). The film was put up in early-mid June and taken down in late August–early September each year from 2004 onwards. Small vent holes (20 cm tall) in the apex of each end of the greenhouses allowed for air flow that prevented extreme temperatures and relative humidity levels. Control plots (n = 5) were located among the treatment plots in the same stretch of valley. Initial vegetation assessments with the point-intercept method indicated that community structure (i.e. abundances of each growth form: deciduous shrubs, evergreen shrubs, graminoids, forbs, mosses and lichens) and overall vascular plant abundance (i.e. total hits per plot) were similar among all plots prior to the start of the experimental manipulations (G.H.R. Henry and P. Grogan, unpubl. data).

ENVIRONMENTAL MEASUREMENTS

To assess the environmental effects of the greenhouse warming treatment, soil temperatures at 2, 5 and 10 cm were measured using hand-held digital soil thermometers (Kliva Ltd., Riga, Latvia) at 6 tussock and 6 inter-tussock locations within each greenhouse and control plot (in randomized treatment order) through the day on 5 dates over the 2006 growing season. Data were pooled across microsites (e.g. tussocks and inter-tussocks) to generate plot means for statistical analyses. Soil moisture was measured simultaneously with a hand-held 12-cm-long dielectric permittivity probe (Hydrosense, Campbell Scientific, Logan, Utah) using an identical sampling approach. In addition to the manually collected data, multiyear temperatures in the air and soil (at 2, 5, and 10 cm depth) in replicate pairs of greenhouse and control plots (n = 2 probes per plot per depth for two replicate plots of each treatment) were measured each hour and recorded as an average every 4 h from 2008 onwards using thermocouple probes connected to CR10X dataloggers (Campbell Scientific, Logan, Utah).

To determine treatment effects on soil organic and inorganic nutrient availability, soil samples were collected on 12–13 July 2011. For each sampling, one organic soil core (rectangular: 5 × 5 cm to 10 cm depth) was taken from each plot, in a place with even microtopography or on the side of a tussock (i.e. not on the top of a tussock or in an inter-tussock). If the organic layer was shallower than 10 cm, underlying mineral soil was discarded. Soils were processed at the field laboratory within several hours of collection. All above-ground plant material and lichens were cut off, the soil core was weighed for bulk density determination, and then all roots >2 mm in diameter were removed. The soil was then homogenized by hand and subsampled to determine soil moisture and nutrient pools (5 subsamples of 10 g fresh weight each).

For soil nutrient determinations, the five soil subsamples of 10 g fresh weight were treated as follows. Three subsamples were extracted in either 0.5 M K_2SO_4 (for ammonium-N, total dissolved C, and total dissolved N determination), 0.5 M $NaHCO_3$ (for phosphate-P analysis; pH 8.5) or Type I purity H_2O (for nitrate-N analysis; NCCLS Type I resistivity: 10–18 MΩ-cm). In each case, 50 mL of the corresponding solution was added to the soil sample, and the sample was shaken manually 3 times over the next hour, allowed to sit for 30 min, and then filtered through glass fibre filters (Fisher G4; 1.2 μm pore space) using a vacuum. The remaining two subsamples from each core were chloroform-fumigated for 24 h in a darkened vacuum dessicator jar (Brookes *et al.* 1985) and then extracted in either 0.5 M K_2SO_4 (for microbial biomass C and N) or 0.5 M $NaHCO_3$ (for microbial biomass P) using the same shaking and filtering procedures listed above. All extracts were frozen at −20 °C until analysis.

Concentrations of NH_4^+-N, NO_3^--N and PO_4^{3-}-P in the extracts were determined colorimetrically using automated flow analysis (Bran-Leubbe Autoanalyser III, Norderstadt, Germany) and the indophenol, sulphanilamide (Mulvaney 1996) and molybdate–ascorbic acid methods (Kuo 1996), respectively. Total dissolved nitrogen (TDN) in the extracts was determined by chemiluminescence analysis (TOC-TN autoanalyzer, Shimadzu, Kyoto, Japan), and dissolved organic nitrogen (DON) was calculated as the difference between

TDN and the inorganic N pools (NH_4^+-N and NO_3^--N). The final C and N concentrations in the extracts were corrected for the dilution associated with initial soil moisture in each individual sample, and areal pool sizes (g m^{-2}) were calculated using the sample's bulk density and organic layer depth. Microbial biomass C, N and P was calculated as the difference between the fumigated and non-fumigated extractable C, N and P samples, without using a correction factor to adjust for the low extractability of cell wall components (Jonasson *et al.* 1996).

VEGETATION ANALYSIS

Vegetation composition was assessed using the point-intercept method (Jonasson 1988; Bean & Henry 2003) on a randomly selected 1.0 m^2 subplot within each plot between 31 July and 12 August 2011. Although growth was probably minimal over this period since phenological peak biomass at this site is around 1 August, plots were nonetheless measured in a random order across treatments. One hundred intercepts were measured per subplot using a small pin (diameter <1 mm), with all above-ground hits recorded. One 40 × 40 cm area within each point-framed 1.0 m^2 subplot was harvested on 13 or 14 August 2011 and used to calibrate the point framing hits data. In the greenhouse and control plots, this harvest included the underlying organic soil layer (to a maximum sampling depth of 10 cm measured from the green-brown transition in the moss layer), which contains over 85% of the root biomass (Churchland *et al.* 2010). In the four fertilized treatments, only above-ground tissue was harvested by cutting horizontally just below the green–brown moss transition in order to include all litter and lichens. Thus, the transition point used to distinguish above-ground from below-ground stem tissue was the same in all plots across the study. Additionally, the number of inflorescences and fruits of each species was counted in a 1.0 m^2 quadrat in each plot, starting on 26 June 2011.

Residual surface litter mass, constituting past years' senesced leaves and small twigs on the ground surface, was also collected. For all plots, the harvested quadrats (40 cm × 40 cm by 10 cm deep for the greenhouses and controls; and 1–2 cm deep for the fertilized plots) were turned upside down in the laboratory and fingers loosely worked in between the plant shoots to remove the surface litter. For several of the fertilized plots where there was insufficient live biomass to hold the harvested quadrat together, the litter was collected in the field and included all loose unattached dead leaves and stems atop the soil or moss surface in the 40 × 40 cm sampling area.

In sorting the greenhouse and control harvests, great care was taken to keep shoots and roots attached so that the latter could be identified to species level. We worked our fingers carefully and methodically around the soil from the bottom of the core upwards, releasing soil and untangling coarse roots and larger fine roots. In all plots, harvested vascular plants were sorted to the species level and then differentiated into above- (all treatments) and below-ground tissues (greenhouse and controls only). 'Above-ground' biomass for vascular shoots was delineated by the transition of green to brown in the moss layer, by structural changes in the shoot, or by the absence of fine roots. Above-ground biomass was sorted to age- and tissue-specific pools using the bud scars on the stems to differentiate current year's (termed 'new') growth from all previous years' live growth (termed 'old'). For the five shrub species this included new leaves (termed 'leaves' for deciduous species), old leaves (evergreens only), new stem and old stem. For the only graminoid (*Eriophorum vaginatum*), above-ground biomass was sorted into leaf sheaths, leaf blades and live inflorescence shoots, the latter of which were rare and therefore not included in this analysis. In *Rubus chamaemorus*, the only forb, all above-ground biomass was classified as 'shoot'. Mosses were sorted into *Sphagnum spp*. and non-*Sphagnum* mosses (vast majority acrocarpous; pers. obs.), and lichens were sorted to the species level. Below-ground biomass in the greenhouse and control harvests were sorted to the following size classes: below-ground stem ≥ 5 mm diameter (*B. glandulosa* and *R. subarcticum* only); coarse roots and stems <5 mm and >2 mm diameter (*B. glandulosa*, *R. subarcticum*, and *V. uliginosum* only); and fine roots and rhizomes ≤2 mm diameter (all vascular species, termed 'rhizomes' in *Rubus*).

The bulk soil from each 40 × 40 × 10 cm harvest was collected and weighed for bulk density determination, then subsampled for soil moisture determination. Any remaining coarse roots were collected and termed 'unidentified coarse roots'. 'Unidentified fine roots' were determined by taking a small subsample of soil (~20 g fresh weight) of known mass and carefully picking out all fine roots. The ratio of fine roots to subsampled soil, corrected for moisture content in both cases, was then used to calculate the total unidentified fine root biomass in the whole harvest. Only living roots, based on tissue turgor and colour, were included in the unidentified coarse and fine root biomass.

In order to calibrate the point framing hits data to above-ground biomass, we used a power model as it yielded higher explained variance than a linear model (Jonasson 1988; see Table S1 in Supporting Information for equations and linear regression parameters). Separate calibrations were determined for leaves and stems in the shrub species. All other species, including each lichen species had one calibration equation for all above-ground biomass. In the case of shrub species, once we had extrapolated the total leaf and total stem biomass for a given species to the 1.0 m^2 scale, we used the ratio of its new leaves/old leaves and new stem/old stem in the 0.16 m^2 harvest to calculate the amount of new leaves, old leaves (evergreens only), new stem and old stem at the 1.0 m^2 scale. The same procedure was used to calculate the relative biomass of leaf blades and sheaths in *Eriophorum vaginatum*, and the biomass of *Sphagnum* and non-*Sphagnum* mosses. For the litter, we scaled the mass from the 40 × 40 cm harvest directly up to 1.0 m^2.

STATISTICAL ANALYSES

We used a combination of Student's *t*-tests and analyses of variance (ANOVAS) to analyse for treatment effects. Effects of warming on soil temperatures collected at 5 dates throughout the 2006 growing season were analysed with a repeated measures ANOVA. The impacts of warming or low N addition on soil nutrient pools were each tested with *t*-tests, while the impacts of high-level N and P additions on soil nutrient pools were investigated with a two-way ANOVA (general linear model (GLM) with N addition and P addition as main effects, and a N by P interaction). For the vegetation analyses, each tissue type within a species was analysed separately (e.g. 4 separate analyses for new leaves, new stem, old leaves and old stem for *R. subarcticum*). The impact of warming on a given species' tissue type was tested with a *t*-test, the effect of magnitude of N addition tested with a one-way ANOVA, and the effects of factorial high N and P addition were investigated with a two-way ANOVA. *Post hoc* Tukey tests were run to explore any significant effects in the ANOVAS. For species in which there were multiple tissue types analysed (e.g. all shrubs and *E. vaginatum* above-ground tissues), Bonferroni corrections were applied at the species levels (see Table S2 for Bonferroni thresholds). All test statistic information is included in Tables 2–5. All means are reported in Table S3 for soil and S4 for plant data.

Table 1. Differences between greenhouse and control summer air and soil temperatures

	Diel mean (SE)*	12–4 pm mean (SE)*	12–4 pm max*	Daytime mean increase†
Temperature				
Air	2.2 (0.16) °C	5.9 (0.38) °C	13.8 °C	
Soil – 2 cm depth	2.4 (0.08) °C	4.6 (0.27) °C	9.4 °C	3.6 °C
Soil – 5 cm depth (sr)	2.1 (0.05) °C	2.8 (0.15) °C	5.3 °C	3.3 °C
Soil – 10 cm depth	2.4 (0.04) °C	2.4 (0.11) °C	4.5 °C	2.2 °C

Symbols in parentheses following variable name indicate the data transformations used to achieve homogeneity of variances for the statistical tests on this data: no symbol, not transformed; sr, square-root-transformed. See Figs S1 and S2 for effects of greenhouses on air and soil temperatures throughout the growing season.

*Multiyear 4-hourly datalogger records between 15 June and 25 August in 2008, 2009 and 2011 (n = 2 probes per plot per depth for two replicate plots of each treatment).

†Multimicrosite (e.g. tussock and intertussock) hand-held soil probe data from 5 dates throughout the 2006 growing season (n = 12 measurements per plot for all five replicate plots of each treatment).

All data were transformed if necessary to achieve normality and homoscedasticity. When these assumptions could not be met, the data were converted to ranks using fractional ranking, prior to analysis by ANOVA (Akritas 1990). Since an ANOVA on rank data cannot test for interactions (Quinn & Keough 2002), the N × P interaction effect was not analysed in these analyses. Similarly, when the rank data did not satisfy the assumptions of normality and homoscedasticity, a non-parametric Wilcoxon rank-sum test was run on the warming, N or P addition analyses (e.g. 2 treatments; N × P interaction term not analysed) and a Kruskal–Wallis rank-sum test was run for the magnitude of N addition analysis (e.g. 3 treatments). All data transformations and cases where Wilcoxon or Kruskal–Wallis tests were used are indicated next to the test statistic in Tables 1, 2, 5, S6, and S7.

We used a redundancy analysis (RDA) to investigate impacts of the warming and fertilizer treatments on overall plant community structure. As the underlying environmental gradient was less than 2.5 standard deviation units, a linear ordination method was appropriate (Legendre & Birks 2012). The ordination was conducted on the total above-ground biomass for each vascular plant species and total functional group biomass for lichens and mosses in each plot, and soils data from the treatment plots were used as environmental constraints. In the ordination diagram, each plot point is derived from a combination of the responses of the individual species (displayed in blue), and the relative locations of the points are a function of their similarity to each other. Differences in community composition as measured by the redundancy analysis were tested using a one-way ANOVA on the axis 1 site (i.e. plot) scores (n = 5 per treatment), followed by a *post hoc* Tukey test. All statistical analyses were performed with JMP 9 (SAS Institute Inc 2010) and R (R Core Team 2012), and the ordination was performed in R 2.15.0.

Results

ENVIRONMENTAL VARIABLES

Multiyear datalogger records indicated that the greenhouses increased summer mean diel air and soil temperatures by 2.1–2.4 °C (Table 1 and Fig. S1). Throughout the growing season, warming of both air and soil temperatures tended to be greatest in mid-late July (Fig. S1), and afternoon temperature anomalies in the air and close to the soil surface were approximately twice those of the diel mean anomalies (Table 1 and Fig. S2). The greenhouse-induced increase in daytime soil temperatures measured in different microsites was similar in magnitude to that seen in the multiyear datalogger records and was statistically significant at all sampled depths (2 cm depth: $F_{9,40}$=40.8, $P < 0.01$; 5 cm depth: $F_{9,40}$=79.8, $P < 0.01$; 10 cm depth: $F_{9,40}$=83.6, $P < 0.01$; Fig. S1). Lastly, the greenhouses did not alter soil moisture at 0–8 cm depth or 0–4 cm depth (Table S5), presumably because of subsurface lateral water flow from around the greenhouse edges.

Soil solutions NH_4-N, NO_3-N, DON or PO_4-P pools in mid-July were not significantly affected by greenhouse warming (Fig. 1), but were consistently enhanced by the nutrient treatments. Low-level N addition significantly increased NH_4-N and DON pools fivefold and twofold above control levels ($T = -2.7$, $P = 0.03$; and $T = -3.0$, $P = 0.02$, respectively; Fig. 1a,c), but did not significantly alter NO_3-N (Fig. 1b). High-level N additions increased DON and NO_3-N pools 15-fold and 3000-fold ($W = 81$, $P = 0.02$ and $F_{1,19}$=69.2, $P < 0.01$, respectively). There was a significant interaction between N and P additions on NH_4-N pools ($F_{1,19}$=15.2, $P < 0.01$), because the positive effects of N addition were lessened by the addition of P, such that soil NH_4-N was increased 300-fold and 100-fold in the high N and high N+P plots, respectively. Lastly, high-level P additions increased PO_4-P pools 42-fold ($F_{1,19}$=240.8, $P < 0.01$; Fig. 1d) and tended to increase NH_4-N and NO_3-N pools, although these latter effects were not significant (see Tables S6 and S7 in Supporting Information for all soil pool statistics).

WARMING EFFECTS ON VEGETATION BIOMASS

Across all vascular plants, *Rhododendron subarcticum* responded the most strongly and consistently to warming, with all seven tissue types increasing in biomass 1.5–4.0 times, and reproductive effort (i.e. number of inflorescences) increasing 0.7-fold (Table 2, Table S8 and Fig. 2). The greatest increase was in the old leaves and below-ground stems, which increased 3.1- and 4.0-fold, respectively, above control levels. By contrast, responses of the other abundant evergreen (*Vaccinium vitis-idaea*) to warming were generally negligible, except for a 3.8-fold increase in reproductive effort (Table 2,

Table 2. Statistical results for the analyses of greenhouse warming impacts on above- and below-ground tissues of the major vascular plant species in birch hummock tundra. 'New' is current year's growth. 'Old' is all past years' live growth. 'Inflor', inflorescences. Bold values indicate tests that are significant following Bonferroni correction (degrees of freedom = 8); see details on Bonferroni correction thresholds per tissue type in Table S2

	New leaves *T* (P)	Old leaves *T* (P)	New stem *T* (P)	Old stem *T* (P)	# Inflor. *T* (P)	Fine roots *T* (P)	Coarse roots *T* (P)	Below-ground stem *T* (P)	Above-ground total *T* (P)	Below-ground total *T* (P)	Total (above + below) *T* (P)	Leaf: fine roots *T* (P)	Shoot: root *T* (P)
Betula glandulosa	**3.02 (0.017)**	NA	2.27 (0.053)^{cr}	2.15 (0.064)^{rc}	***W* = 25 (0.007)**	2.73 (0.026)†	0.02 (0.980)	−1.30 (0.231)	**2.63 (0.030)**†	−0.37 (0.721)^{sr}	0.57 (0.687)†	*W* = 14 (0.841)	***W* = 0 (0.011)**
Vaccinium uliginosum	0.43 (0.676)	NA	0.80 (0.448)	*W* = 10 (0.691)	*W* = 7 (0.280)	0.54 (0.603)†	−0.25 (0.806)†	NA	0.79 (0.452)†	0.46 (0.658)	0.67 (0.525)	*W* = 14 (0.841)	1.35 (0.213)
Rhododendron subarcticum	**4.81 (0.001)**	**4.44 (0.002)**†	**7.94 (<0.001)**	3.07 (0.015)	−1.87 (0.098)	**4.61 (0.002)**	**4.36 (0.002)**	**8.30 (<0.001)**^{sr}	**4.07 (0.004)**	**5.14 (<0.001)**	**5.14 (<0.001)**	*W* = 16 (0.548)	*W* = 16 (0.548)
Vaccinium vitis-idaea	0.76 (0.470)†	2.61 (0.031)	0.96 (0.364)	2.24 (0.056)^{sr}	**−2.56 (0.034)**†	−1.47 (0.180)	NA	NA	1.64 (0.140)	1.47 (0.180)	−0.46 (0.659)	***W* = 2 (0.032)**	**2.73 (0.026)**
Andromeda polifolia	−0.02 (0.988)	1.42 (0.193)	0.47 (0.652)	0.58 (0.587)	0.04 (0.969)†	0.22 (0.834)	NA	NA	0.44 (0.670)	0.22 (0.834)	0.31 (0.762)	*W* = 9 (0.530)	0.71 (0.497)
Eriophorum vaginatum	blades: 2.55 (0.034)	sheaths: 2.02 (0.078)^{sr}			0 (1.0)	**2.55 (0.034)**			2.27 (0.053)^{sr}	**2.55 (0.034)**	**2.45 (0.040)**	*W* = 16 (0.548)	0.53 (0.609)
Rubus chamaemorus	shoot: *W* = 13 (1.0)				*W* = 6.5 (0.192)	Rhizome: *W* = 14 (0.833)			*W* = 13 (1.0)	*W* = 14 (0.833)	*W* = 13 (1.0)	*W* = 15 (0.656)	*W* = 15 (0.656)

Symbols following *P* values indicate the data transformations used to achieve homogeneity of variances: no symbol, not transformed; †log-transformed; sr, square-root-transformed; cr, cube-root-transformed; rc, reciprocal transform; *W*, Wilcoxon rank-sum test on raw data; NA, part does not exist for this species.

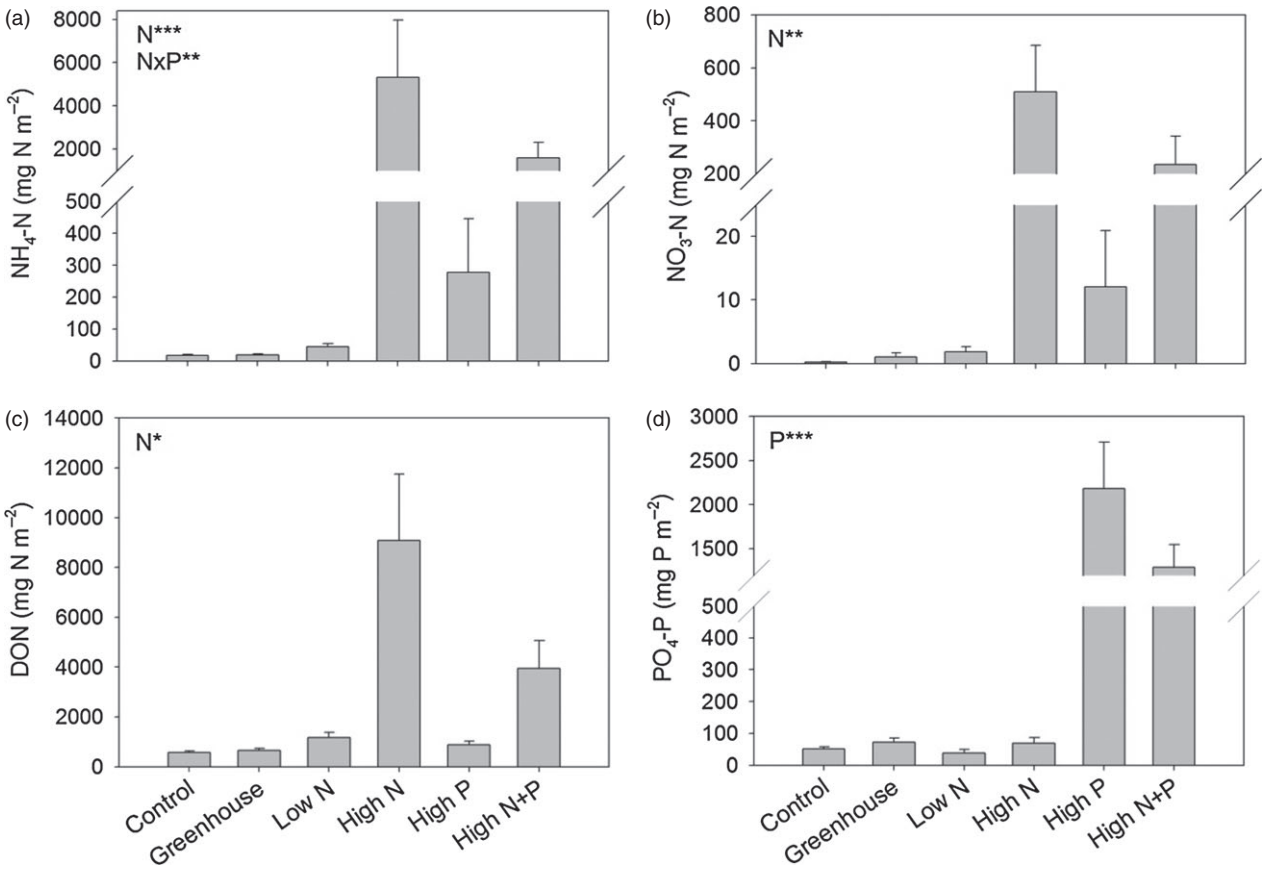


Fig. 1. Experimental summer warming and nutrient addition treatment effects on mid-July ammonium (a), nitrate (b), dissolved organic N (c) and phosphate (d) pools in the soil organic layer of mesic birch hummock tundra. Error bars are standard errors (n = 5). Statistically significant effects from the factorial high-level N and P addition analyses are indicated by $P < 0.0001$***; $P < 0.001$**, $P < 0.01$*, $P < 0.10$‡, with all statistical information provided in Tables S6 and S7. There were no statistically significant greenhouse effects.

Table S8 and Fig. 2). However, the proportion of *V. vitis-idaea* inflorescences that set fruit (16 ± 5%) was unaffected by warming (Table S8). *Betula glandulosa* responded to warming with 2.4-fold increases in leaf biomass (Table 2 and Fig. 2). Since warming enhanced *B. glandulosa* above-ground biomass, but not total below-ground biomass, its overall shoot/root ratio increased markedly, from 1:3 to nearly 1:1 (Table 2). *B. glandulosa's* reproductive effort declined with warming from 9 ± 4 inflorescences per square metre to 0 in all greenhouse replicate plots (Table 2). *Eriophorum vaginatum* blades and fine roots increased about twofold with warming, though this change was only marginally significant (Table 2 and Fig. 2). Lastly, lichen species' responses to warming varied from strongly negative to no impact (Table 3 and Fig. 3). Warming halved the biomass of the two most abundant lichen species (*Cetraria cucullata* and *Cladina rangiferina*) and negatively affected the other relatively abundant species, such as *Bryocaulon divergens*, *Cetraria nivalis* and *Cladina mitis,* with marginally significant decreases of 37–67%.

Across the whole community, summer greenhouse warming for 8 years increased total above-ground biomass by 124 g m^{-2} (32%) and total below-ground biomass by 276 g m^{-2} (70%) (Table 4 and Fig. 4a,b), although there was no statistically significant change in overall shoot/root ratio. These increases were dominated by the strong responses of evergreen shrubs, which increased 122 g m^{-2} (66%) above-ground (with a 200% increase in apical productivity) and 195 g m^{-2} (82%) below-ground (Table 4 and Fig. 4a,b,c). Deciduous shrub above-ground biomass increased 28 g m^{-2} (145%) with warming (with a 100% increase in apical productivity) but with no change below-ground (Table 4 and Fig. 4a,b,c). Graminoid above- and below-ground biomasses were increased by 85% and 96%, respectively, with warming. In contrast, lichen biomass decreased 49 g m^{-2} (50%) with warming. Residual litter mass was unaffected (Fig. 4d).

EFFECT OF LEVEL OF N ADDITION ON PLANT BIOMASS

The magnitude of N addition affected total community above-ground biomass, with the low-level N addition having no impact but the high-level N addition significantly decreasing biomass (Table 4 and Fig. 4a). This latter effect was driven primarily by the responses of evergreen shrubs (Fig. 4a), whose shoot biomass was reduced by 79% in high N addition plots. By contrast, deciduous shrub total above-ground biomass was unaffected by either low or high N addition (Table 4 and Fig. 4a).

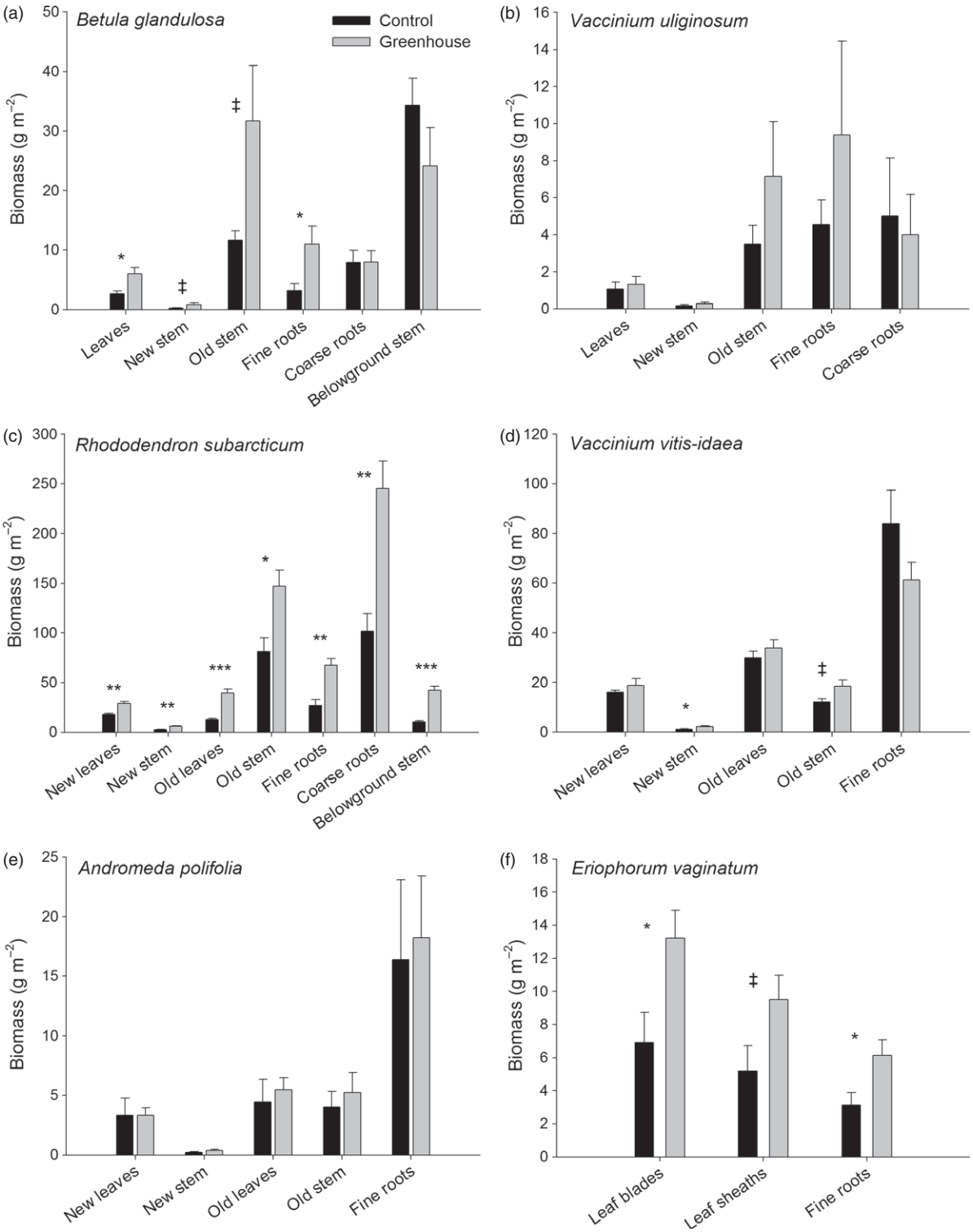


Fig. 2. Vascular plant species above- and below-ground biomass responses to warming in mesic birch hummock tundra for the deciduous shrubs (a, b), evergreen shrubs (c, d, e) and graminoid (f) growth forms. Error bars are standard errors (n = 5). Statistically significant effects are noted using the nomenclature of Fig. 1, with further details provided in Table 2. Responses of *Rubus chamaemorus* are not shown, as they are represented by the forb group in Fig. 4.

EFFECTS OF FACTORIAL HIGH N AND P ADDITIONS ON PLANT GROWTH

Betula glandulosa, *E. vaginatum* and *R. chamaemorus* above-ground growth was stimulated by high-level N and P additions (Table 5 and Fig. 5), although the relative importance of each nutrient varied among species and plant tissue type (Table 5). In *B. glandulosa*, leaf growth was most significantly increased by P, whereas new stem growth was

Table 3. Statistical results for the warming, magnitude of N addition, and factorial N and P additions analyses on biomasses of mosses and lichens. Bold values indicate tests that are significant following Bonferroni correction [degrees of freedom = 8 (warming *t*-test); 2, 12 (N-level ANOVA); and 1, 19 (factorial N and P ANOVA)]. NA, interaction not available due to rank data or Wilcoxon tests; see nomenclature in Table 2 caption

	Warming *T* (P)	N level *F* (P)	High N effect *F* (P)	High P effect *F* (P)	High N × P interaction *F* (P)
Mosses					
Sphagnum spp.	1.31 (0.228)†	χ^2 = 6.31 (0.043)	**7.02 (0.018)^{rsq}**	0.12 (0.737)^{rsq}	0.37 (0.552)^{rsq}
Non-*Sphagnum spp.*	−1.39 (0.201)	2.16 (0.158)	0.22 (0.648)	2.10 (0.167)	1.67 (0.215)
Total moss	0.37 (0.719)^{sr}	**9.24 (0.004)**	1.43 (0.249)	3.37 (0.085)	1.18 (0.293)
Lichens					
Alectoris ochroleuca	−2.20 (0.059)	3.34 (0.070)	**6.22 (0.024)**	2.27 (0.152)	1.12 (0.292)
Bryocaulon divergens	**−7.73 (<0.001)^{sq}**	0.96 (0.411)	1.76 (0.203)	**5.69 (0.030)**	0.29 (0.596)
Cetraria cucullata	**−6.97 (0.001)**	**4.36 (0.038)**	**20.10 (<0.001)**	**6.40 (0.022)**	0.30 (0.592)
Cetraria islandica	−0.77 (0.466)	0.78 (0.479)‡	2.05 (0.172)	1.07 (0.315)	0.32 (0.580)
Cetraria laevigata	−1.40 (0.198)	χ^2 = 4.40 (0.111)	**6.27 (0.024)**	0.12 (0.892)	0.55 (0.468)
Cetraria nivalis	**−7.51 (<0.001)^{sq}**	1.27 (0.315)	3.10 (0.098)‡	**8.08 (0.012)‡**	NA
Cladina mitis	**−7.28 (<0.001)**	**5.30 (0.022)**	**4.50 (0.050)**	**8.63 (0.001)**	2.39 (0.141)
Cladina rangiferina	**−3.88 (0.005)†**	3.11 (0.082)	2.87 (0.110)	**8.62 (0.001)**	0.16 (0.692)
Cladonia gracilis	−2.26 (0.054)	0.53 (0.601)	3.02 (0.102)	**5.73 (0.030)**	0.19 (0.665)
Masonhalea richardsonni	−1.75 (0.118)	χ^2 = 3.50 (0.174)	3.74 (0.071)†	0.54 (0.472)†	0.31 (0.588)†
Total lichen	**−9.37 (<0.001)**	**6.77 (0.011)**	**18.59 (<0.001)**	**13.98 (0.002)**	0.02 (0.890)

Symbols following the *P* value indicate the data transformations to achieve homogeneity of variances: no symbol, not transformed; †log-transformed; ‡rank-transformed; sr, square-root-transformed; cr, cube-root transformed; rc, reciprocal transform; sq, square-transformed; rrt, reciprocal square-root-transformed; rsq, reciprocal square-transformed; *W*, Wilcoxon rank-sum test on raw data; NA, interaction not available due to rank data or Wilcoxon tests.

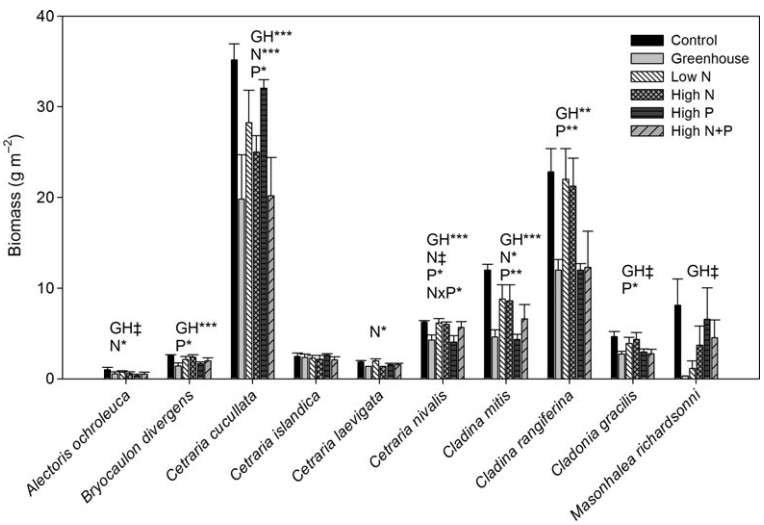


Fig. 3. Lichen species responses to the summer warming and fertilization treatments. Statistically significant effects from the greenhouse (GH) warming analyses and factorial high-level N and P addition analyses are indicated using the nomenclature of Fig. 1. Our analysis of varying levels of N addition indicated no significant effects of the low N treatment. Only the 10 most abundant lichen species are shown. Error bars are standard error (n = 5).

significantly enhanced by both nutrients, but especially by N (Table 5 and Fig. 5). In *E. vaginatum,* leaf blade growth increased with both N and P additions, while for sheath growth there was a significant interaction between N and P addition, because growth only increased with the addition of both nutrients (Table 5 and Fig. 5). Lastly, *R. chamaemorus* shoot growth was strictly P-limited (Table 5 and Fig. 5). In contrast to the above three species, most above-ground tissues of the four ericaceous dwarf shrubs (both deciduous and evergreen) were negatively affected by high N and P additions (Table 5 and Fig. 5). In particular, the biomass of *R. subarcticum* and *V. vitis-idaea* declined substantially in the high N + P plots, primarily as a result of elevated N effects (Table 5 and Fig. 5).

Compared to the controls, total above-ground biomass in the high N plots and high N+P plots was reduced by 182 g m^{-2} (47%) and 93 g m^{-2} (24%), respectively (Table 4 and Fig. 4a), in association with a significant interaction whereby the negative effects of N addition were lessened by the presence of P. These community-level effects were driven largely by the responses of evergreens, in which biomass in the high N, high P and high N+P plots was only 21%, 49% and 18% of control levels, respectively (Table 4 and Fig. 4a). Lastly, there was a significant interaction between N and P addition for residual surface litter mass, in which a tendency for elevated litter mass in the high N plots was eliminated by the addition of P (Fig. 4d). The die-off of evergreens in the high N plots resulted in very high litter

Table 4. Statistical results for the warming, magnitude of N addition, and factorial N and P additions analyses on functional group biomass and productivity. Bold values indicate tests that are significant following Bonferroni correction; see nomenclature in Table 3 caption

	Warming *T* (P)	N addition level *F* (P)	High N effect *F* (P)	High P effect *F* (P)	High N × P interaction *F* (P)
Above-ground biomass					
Deciduous shrubs	**2.42 (0.042)**[†]	1.93 (0.188)	1.84 (0.194)[rrt]	4.15 (0.059)[rrt]	3.39 (0.084)[rrt]
Evergreen shrubs	**4.52 (0.002)**	**16.04 (<0.001)**	**42.57 (<0.001)**	**9.99 (0.006)**	**8.3 (0.011)**
Graminoids	2.27 (0.053)[sr]	0.62 (0.552)	**9.97 (0.006)**	**13.13 (0.002)**	**5.82 (0.028)**
Forbs	*W* = 13 (1.0)	0.53 (0.601)	0 (1.0)[‡]	**6.0 3 (0.026)**[‡]	NA
Moss	0.37 (0.719)[sr]	**9.24 (0.004)**	1.43 (0.249)	3.37 (0.085)	1.18 (0.293)
Lichen	**−9.37 (<0.001)**	**6.77 (0.011)**	**18.59 (<0.001)**	**13.98 (0.002)**	0.02 (0.890)
Total	**2.95 (0.019)**	**16.79 (<0.001)**[sr]	**15.03 (<0.001)**	0.15 (0.708)	**8.7 (0.009)**
Total litter	−1.29 (0.233)	2.33 (0.140)	2.57 (0.128)	0.15 (0.708)	**9.61 (0.007)**
Apical above-ground growth					
Deciduous shrubs	2.31 (0.050)	1.92 (0.190)	4.04 (0.062)[†]	**8.53 (0.010)**[†]	1.09 (0.311)[†]
Evergreen shrubs	***W* = 0 (0.008)**	**19.22 (<0.001)**	**36.67 (<0.001)**	1.32 (0.267)	2.67 (0.122)
Graminoids	2.27 (0.053)[sr]	0.62 (0.552)	**9.97 (0.006)**	**13.13 (0.002)**	5.82 (0.028)
Forbs	*W* = 13 (1.0)	0.53 (0.601)	0 (1.0)[‡]	**6.0 3 (0.026)**[‡]	NA
Total	**−5.62 (<0.001)**	**6.55 (0.012)**	*W* = 48 (0.912)	***W* = 94 (<0.001)**	NA
Below-ground biomass					
Deciduous shrubs	0.08 (0.939)				
Evergreen shrubs	**3.71 (0.006)**				
Graminoids	**2.55 (0.034)**				
Forbs	*W* = 14 (0.833)				
Total	***W* = 3.9 (0.047)**				
Above-ground + below-ground biomass					
Deciduous shrubs	0.95 (0.369)				
Evergreen shrubs	**4.63 (0.002)**				
Graminoids	**2.45 (0.040)**				
Forbs	*W* = 13 (1.0)				
Total	**3.40 (0.009)**				

mass and very low remaining live biomass and apical production (Fig. 4a,c,d).

EFFECTS OF WARMING AND NUTRIENT ADDITION TREATMENTS ON VEGETATION COMMUNITY STRUCTURE

Plant community above-ground growth responses to experimental warming and to high-level fertilization had fundamentally different trajectories after eight years of the treatments, as revealed by the redundancy analysis (Fig. 6). The greenhouse and high-level N+P addition plots clustered at opposing ends of the first axis ($F_{5,24}$=24.1, $P < 0.01$), diverging from the control plots in differing directions. The first RDA component explained 80.0% of the variance and correlated with increasing soil organic and inorganic N and P availability. The second RDA component explained an additional 11.8% of the variance and was strongly associated with increasing soil moisture and decreasing bulk density. *B. glandulosa* and *E. vaginatum* were positively associated with the high levels of soil N and P availability, whereas *R. subarcticum* was strongly negatively associated with these variables. *Post hoc* Tukey tests on the RDA axis 1 scores revealed that the high N and high N+P were similar to each other but significantly different from the control, while the greenhouse treatment was also different from the control and dissimilar from any other treatment.

Discussion

CONTRASTING EVERGREEN GROWTH RESPONSES TO EXPERIMENTAL WARMING AND HIGH-LEVEL NUTRIENT ADDITIONS

Evergreen shrub biomass increased under experimental summer warming but decreased under high-level N and/or P additions. The decreased nutrient stress associated with high-level fertilization was detrimental to *R. subarcticum* and beneficial to *B. glandulosa* as expected based on life-history strategies (Grime 1979; Chapin 1980), but this dynamic was not matched in the experimental warming plots where both species increased in abundance. Because evergreens were the dominant functional type, their contrasting responses drove the ecosystem trajectories to these treatments in opposing directions, with important implications for nutrient cycling and carbon storage. Enhanced production of recalcitrant evergreen litter may act as a negative feedback that would slow warming-induced increases in soil fertility (Hobbie 1992) and consequently restrict overall plant community biomass responses.

Warming did not alter total above-ground/below-ground biomass allocation across the entire vegetation community, but considerably increased it in *B. glandulosa*. The overall lack of response is likely because the ecosystem response is dominated by evergreens, and their allocation did not change

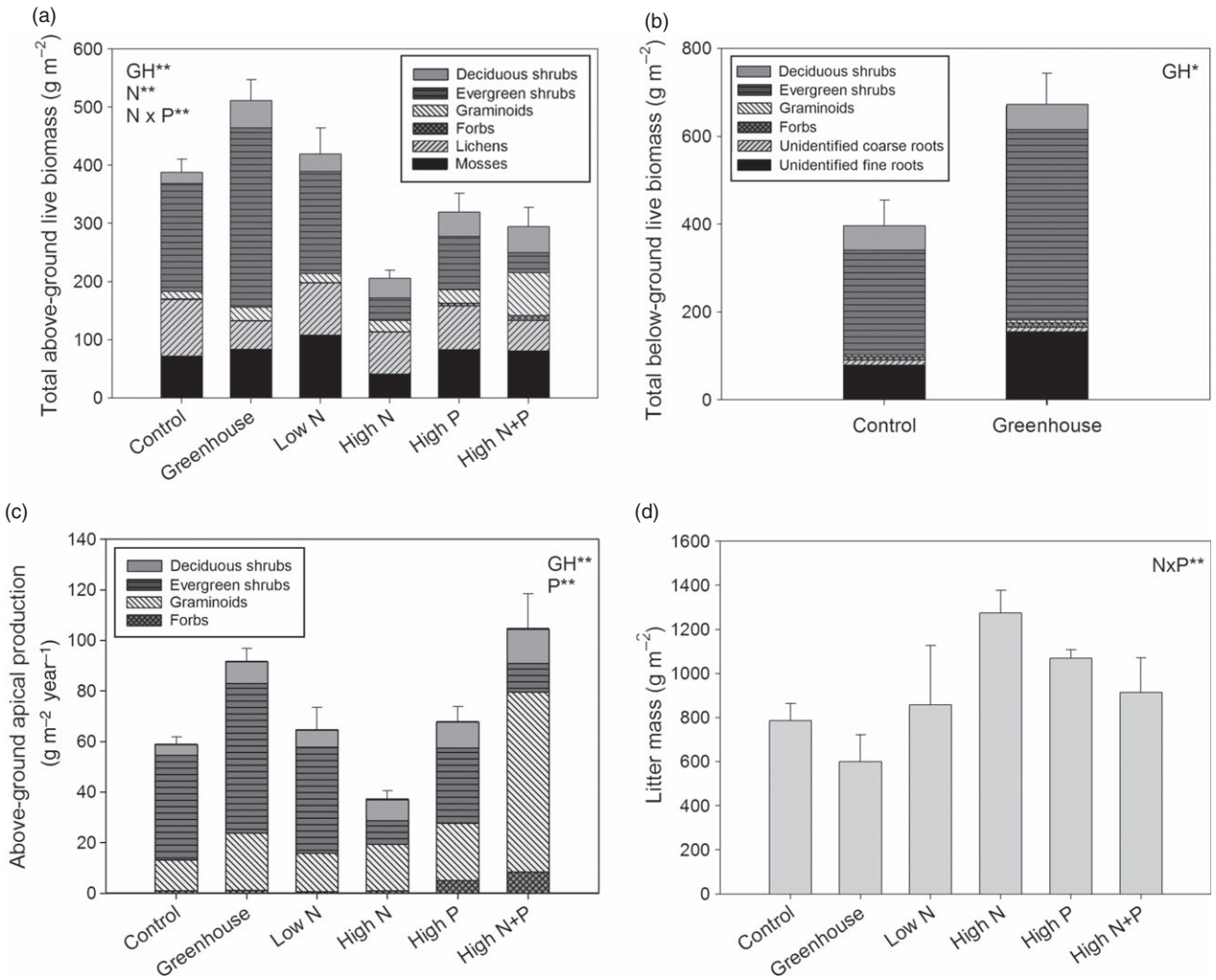


Fig. 4. Experimental summer warming and fertilization effects on above-ground plant biomass (a), below-ground plant biomass (summer warming only) (b), above-ground apical production (c) and residual (late summer) surface litter (d). Statistically significant effects are indicated using the nomenclature of Fig. 1. Error bars represent standard errors (n = 5).

significantly. The lack of change in above-/below-ground allocation indicates that below-ground biomass will continue to be an important C sink in early responses of mesic tundra to warming. However, an increase in the relative abundance of *Betula* over the longer term could change this situation. The threefold increase in shoot/root ratio of *B. glandulosa* with warming indicates that the growth response in this species is directed more towards enhancing its ability to capture C than to taking up nutrients (Chapin 1980; Garnier 1991). This pattern suggests that further increases in nutrient availability may promote above-ground community dominance by *Betula* if this species preferentially acquires those nutrients.

The extent of increase in soil fertility altered the relative success of *B. glandulosa* and *R. subarcticum*. Strong positive growth responses of evergreen shrubs have been documented after 14 years of long-term experimental warming (Sistla *et al.* 2013). However, the responses of older tissues in *R. subarcticum* that we document here indicates that this species must have been positively responsive within a few years of the start of our experiment, which is surprising given its relatively conservative nutrient use strategy and slow growth rate compared to deciduous species (Chapin, Johnson & McKendrick 1980; Chapin & Shaver 1996). Nonetheless, evergreens can take up nutrients earlier in the growing season than deciduous shrubs (Welker *et al.* 1995; McKane *et al.* 2002; Larsen *et al.* 2012), enabling them to take advantage of nutrient pulses in the soil solution that occur around snowmelt (Buckeridge & Grogan 2010). Furthermore, ericoid mycorrhizas produce proteases (Read 1991), which may increase access to newly mobilized dissolved organic N from proteins in soil. In summary, the evergreens may have had an advantage at acquiring nutrients in the warmed soils where fertility is still relatively low, due to their biomass dominance (Churchland *et al.* 2010; Vankoughnett 2010) and nutrient acquisition strategies (Chapin 1980; Read 1991; McKane *et al.* 2002; Larsen *et al.* 2012).

Evergreens are particularly sensitive to high levels of inorganic nutrients (Chapin *et al.* 1995), even though over half of evergreen N uptake is from inorganic forms (McKane *et al.* 2002). This sensitivity is in part determined by the form in which the nutrients are added and the site characteristics. High-level N and P addition led to increases in evergreen

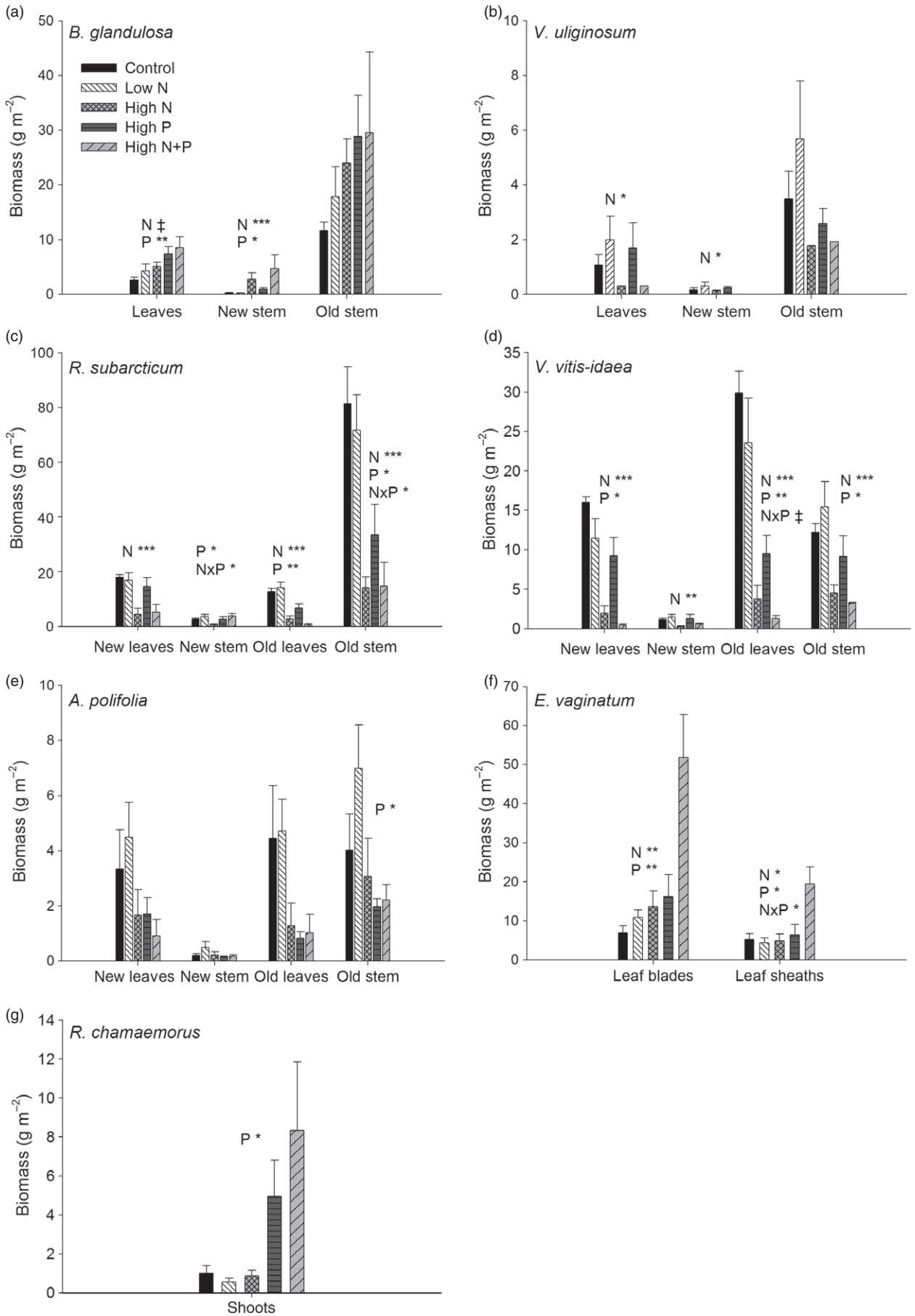
Table 5. Statistical results for the magnitude of N addition analysis and factorial N and P additions analysis on tissues of the major species in birch hummock tundra. Bold values indicate tests that are significant following Bonferroni correction. For details on nomenclature, see Table 3

	N level *F* (P)	High N effect *F* (P)	High P effect *F* (P)	High N × P interaction *F* (P)
Betula glandulosa				
Leaves	1.87 (0.196)	3.14 (0.095)^{sr}	**13.51 (0.002)^{sr}**	0.85 (0.371)^{sr}
New stem	**15.36 (<0.001)†**	**22.34 (<0.001)†**	5.03 (0.040)†	1.21 (0.288)†
Old stem	1.95 (0.184)‡	2.91 (0.107)^{rsq}	4.98 (0.040)^{rsq}	**10.45 (0.005)^{rsq}**
Above-ground biomass	**4.20 (0.041)‡**	**5.61 (0.031)^{rc}**	**8.33 (0.011)^{rc}**	**8.14 (0.012)^{rc}**
Vaccinium uliginosum				
Leaves	χ^2 = 4.45 (0.108)	***W* = 25 (0.015)**	*W* = 48 (0.882)	NA
New stem	χ^2 = 0.79 (0.675)	***W* = 10 (0.003)**	*W* = 42 (0.567)	NA
Old stem	**6.24 (0.014)‡**	*W* = 50 (1.0)	*W* = 56 (0.675)	NA
Above-ground biomass	χ^2 = 3.33 (0.189)	***W* = 25 (0.015)**	*W* = 46 (0.728)	NA
Rhododendron subarcticum				
New leaves	**12.80 (0.001)**	**21.26 (<0.001)**	0.29 (0.599)	0.73 (0.406)
New stem	**7.74 (0.007)**	0.47 (0.502)	6.39 (0.022)	5.37 (0.034)
Old leaves	**16.81 (<0.001)**	**52.96 (<0.001)**	**13.40 (0.002)**	2.90 (0.108)
Old stem	**10.21 (0.003)‡**	**18.56 (<0.001)**	5.61 (0.031)	5.88 (0.028)
Above-ground biomass	**10.21 (0.003)‡**	**26.33 (<0.001)**	**4.96 (0.041)**	**5.90 (0.027)**
Vaccinium vitis-idaea				
New leaves	**18.0 (<0.001)‡**	**55.16 (<0.001)†**	5.94 (0.027)†	0.09 (0.774)†
New stem	**9.81 (0.003)^{sr}**	**12.93 (0.002)^{cr}**	1.28 (0.274)^{cr}	1.69 (0.213)^{cr}
Old leaves	**17.29 (<0.001)^{sr}**	**46.08 (<0.001)^{cr}**	**11.83 (0.003)^{cr}**	3.55 (0.078)^{cr}
Old stem	χ^2 = 7.02 (0.030)	**39.62 (<0.001)^{rc}**	5.78 (0.029)^{rc}	0.00 (0.974)^{rc}
Above-ground biomass	**19.01 (<0.001)^{sr}**	**78.29 (<0.001)**	**18.43 (<0.001)**	**9.37 (0.008)**
Andromeda polifolia				
New leaves	1.60^{sr} (0.242)	1.95 (0.181)†	0.67 (0.425)†	0.22 (0.648)†
New stem	0.93 (0.422)^{rc}	0.40 (0.536)^{rc}	0.01 (0.940)^{rc}	0.40 (0.535)^{rc}
Old leaves	2.67 (0.110)^{cr}	1.30 (0.272)^{rc}	0.64 (0.434)^{rc}	0.18 (0.673)^{rc}
Old stem	4.63 (0.032)‡	*W* = 29 (0.119)	*W* = 19 (0.020)	NA
Above-ground biomass	2.28 (0.145)‡	1.37 (0.259)†	1.39 (0.256)†	0.27 (0.612)†
Eriophorum vaginatum				
Blades	1.56 (0.250)	**9.51 (0.007)^{cr}**	**11.61 (0.004)^{cr}**	2.25 (0.153)^{cr}
Sheaths	0.07 (0.932)	5.20 (0.037)	**8.80 (0.012)**	5.65 (0.030)

shrub biomass at Abisko or other Scandinavian sites (Parsons *et al.* 1994; Press *et al.* 1998; Jonasson *et al.* 1999; Grellmann 2002; van Wijk *et al.* 2004), while it substantially decreased evergreen biomass at Toolik Lake, Alaska (Chapin & Shaver 1996; Gough, Wookey & Shaver 2002; Bret-Harte *et al.* 2008; Gough *et al.* 2008, 2012), and in this study. Across all of these studies, the same level of N and P additions increased soil NH_4-N and PO_4-P pools 0- and twofold at Abisko, Sweden, respectively (Jonasson *et al.* 1999), but 30-fold and 300-fold at Toolik Lake, Alaska (Chapin *et al.* 1995). This suggests that evergreens are more sensitive to dried fertilizer applied in pellet form than to liquid fertilizer (Chapin *et al.* 1995; Jonasson *et al.* 1999) and are more sensitive in poorly drained sites than in better drained sites (Chapin *et al.* 1995; Jonasson *et al.* 1999).

Mechanisms that could explain this sensitivity to substantial increases in soil inorganic nutrient availability include detrimental changes in phenology or physiology (Callaghan *et al.* 2004; Martin *et al.* 2010; Rixen *et al.* 2012) and negative competitive interactions (Chapin *et al.* 1995; Gough, Wookey & Shaver 2002). Increased plant nutrient concentrations may have restricted or delayed winter hardening, resulting in reduced shoot tolerance to freezing and higher mortality in spring or autumn (Robinson *et al.* 1998; Martin *et al.* 2010; Rixen *et al.* 2012), although these responses may be species specific (Taulavuori *et al.* 2001; Callaghan *et al.* 2004). Alternatively, the substantial increases in leaf nutrient concentrations that result from high-level fertilization (Shaver & Chapin 1980; Chapin *et al.* 1995) may have interfered with normal physiological functioning for some ericaceous species (Bubier *et al.* 2011). Negative competitive interactions are probably not the explanation at our Daring Lake site since high-level fertilization caused distinct patches of dead evergreens far away from deciduous shrubs (pers. obs.). Altogether this indicates that when predicting the plant functional types that may be most successful in a warmer world, it is important not only to consider the eventual ecological niche, but also the changes that lead to it.

Fig. 5. Vascular plant species above-ground biomass responses to nutrient addition treatments for the deciduous shrubs (a, b), evergreen shrubs (c, d, e), graminoid (f) and forb (g) growth forms. Statistically significant effects from the two-way ANOVA of high-level N and P additions are indicated using the nomenclature of Fig. 1. Our analysis of varying levels of N addition indicated no significant effects of the low N treatment. Error bars are standard errors (n = 5).



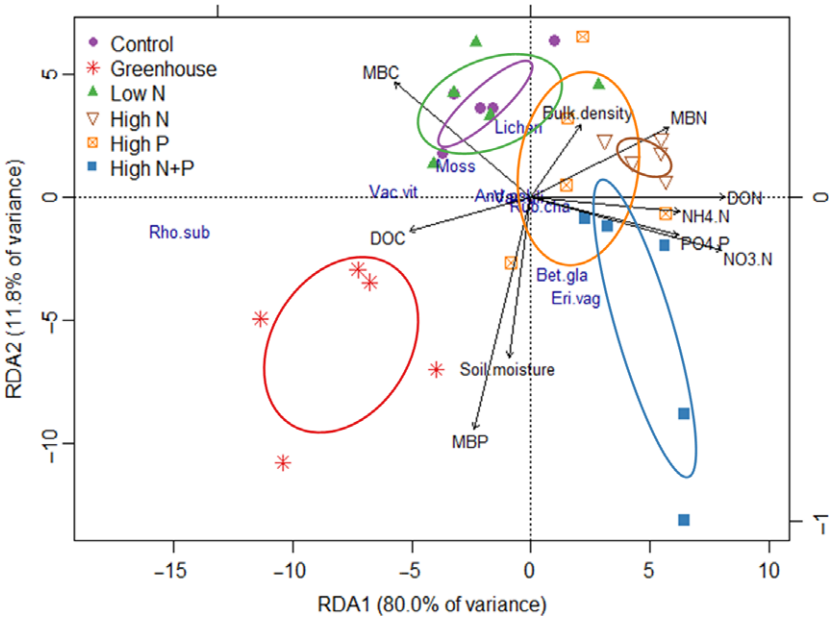


Fig. 6. Redundancy analysis of vascular plant species total above-ground biomass responses to the experimental warming and fertilization treatments. Species abbreviations: Bet.gla, *Betula glandulosa*; Vac.uli, *Vaccinium uliginosum*; Vac.vit, *Vaccinium vitis-idaea*; Rho.sub, *Rhododendron subarcticum*; And.pol, *Andromeda polifolia*; Eri.vag, *Eriophorum vaginatum*; Rub.cha, *Rubus chamaemorus*. Soil pools abbreviations: DOC, dissolved organic C; DON, dissolved organic N; MBC, microbial biomass C; MBN, microbial biomass N; MBP, microbial biomass P. All soil pools are in g m^{-2} to the sampling depth. The bottom and left axes correspond to the variable loadings, and the top and right axes correspond to the site (plot) axis scores.

LONGER-TERM WARMING IMPACTS AND PLANT COMMUNITY RESPONSES

It is unclear whether the responses we observed here are likely to be consistent over time. At Toolik Lake, evergreen responses increased after 14 years of warming (Sistla *et al.* 2013), but in some other sites vegetation responses seem to be consistent (Michelsen, Rinnan & Jonasson 2012), with only the magnitude increasing over time (Campioli, Leblans & Michelsen 2012; Elmendorf *et al.* 2012a; Campioli *et al.* 2013). Shrubs and graminoid responses to warming have varied as a function of time and temperature and/or moisture (Elmendorf *et al.* 2012a). Overall, evergreen shrubs have shown much larger variation in responses after 10 years of warming and a trend for more negative long-term responses in drier sites (Elmendorf *et al.* 2012a). In addition to direct effects of warming, hydrological changes due to permafrost degradation are likely to result in drier soils in many arctic sites, which could be negative for evergreens (Elmendorf *et al.* 2012a), though short-term drying in mesic sites may be transiently favourable for some evergreens, such as *V. vitis-idaea* (Molau 2010).

The mesic conditions at Daring Lake may have contributed to a stronger warming impact on total vegetation biomass than has been seen in studies of equal or longer duration in other low arctic tundra sites (Chapin *et al.* 1995; Wahren, Walker & Bret-Harte 2005; Elmendorf *et al.* 2012a), with the exception of the 14-year harvests of a greenhouse warming treatment reported by Sistla *et al.* (2013). We conclude that the combination of a moderate greenhouse air temperature increase and intermediate soil moisture levels at our site resulted in relatively strong greenhouse effects on soil temperatures compared to most other warming studies in permafrost-dominated ecosystems (Wookey *et al.* 1993; Hobbie & Chapin 1998; Robinson *et al.* 1998; Jonasson *et al.* 1999; Sorensen, Michelsen & Jonasson 2008). Furthermore, this combination of enhanced soil temperature at intermediate soil moisture created the optimal conditions for enhanced microbial decomposition of organic matter (Nadelhoffer *et al.* 1991; Rustad *et al.* 2001; Brzostek *et al.* 2012), with the available nutrients acquired by plants before our mid-July sampling.

Although evergreens dominated community responses after eight years, the strong response of *Betula glandulosa* may allow it to gain a competitive advantage and dominate in the longer term, by shading out the rest of the community. Ongoing climate warming has been correlated with increases in deciduous shrub cover (Goetz *et al.* 2005; Tape, Sturm & Racine 2006; Forbes, Fauria & Zetterberg 2009; Jia, Epstein & Walker 2009; Elmendorf *et al.* 2012b; Epstein *et al.* 2012), yet experimental studies indicate that increases in *B. glandulosa* are primarily due to growth increases in existing rather than newly initiated ramets (Zamin & Grogan 2012). Therefore, *Betula* dominance may be restricted by this growth pattern and by landscape heterogeneity that will provide refuges for evergreen shrubs, herbaceous plants and lichens.

Lichens are an important C stock in many tundra ecosystems and have been observed to decline with mid- to long-term experimental warming (Chapin *et al.* 1995; Press *et al.* 1998; Gough & Hobbie 2003; Hollister, Webber & Tweedie 2005; Walker *et al.* 2006; Hudson & Henry 2010; Elmendorf *et al.* 2012a; Lang *et al.* 2012). While these lichen declines in experimental warming treatments are often in correlation with the expanding vascular plant canopy (Press *et al.* 1998; Cornelissen *et al.* 2001; van Wijk *et al.* 2004; Walker *et al.* 2006; Lang *et al.* 2012), this inverse relationship is not supported by long-term monitoring that shows increases in vascular plant abundance without declines in lichens (Hudson & Henry 2009; Elmendorf *et al.* 2012b). An important experimental artefact, unique to greenhouse warming studies and not to open-topped chamber studies, is that the former exclude precipitation, which may disproportionately affect non-vascular species that derive their water and nutrients primarily through rainfall or dew

(Brodo, Sharnoff & Sharnoff 2001). This means that long-term declines in lichens and their associated carbon storage may not be as dramatic as predicted by warming experiments.

Other potential confounding effects known to be associated with the greenhouse treatments are unlikely to substantially affect plant responses to warming, because these effects are small and often work in opposing directions. We saw no effects of greenhouses on soil moisture. Greenhouses modestly decrease PAR (Chapin *et al.* 1995), which may reduce growth and alter competitive interactions. However, photosynthetic rates of tundra plants can be higher inside greenhouses (Bret-Harte *et al.* 2001), when factors such as increased temperature and moisture availability can more than counterbalance any negative effects of modest decreases in light intensity. Concurrently, greenhouses may enhance growth by reducing growing season herbivory and/or pollination; however, neither of these changes are likely to have been large in our greenhouses. Hare browsing on *Betula* shoots was observed between September–May (pers. obs.), and caribou are generally present in September and October, when the greenhouse plastic was removed. Furthermore, warming did not change the rate of fruit set in *V. vitis-idaea,* suggesting that pollination was adequate. Altogether, the strong greenhouse impacts on biomass are most likely due to genuine effects of temperature.

INTERACTIONS BETWEEN SOIL N AND P AVAILABILITY

In our study, increased soil fertility unexpectedly created interactions between soil N and P availability. High levels of P addition increased NH_4-N and NO_3-N availability 15-fold in our plots, although this increase was not statistically significant due to high variation. We do not believe that increased N availability in the high P plots was due to contamination via leaching from nearby plots fertilized with high levels of N, as this would have affected all of the fertilized plots equally, and we did not see this effect in nearby plots treated with low levels of N (Fig. 1). Two possible biological explanations are P-stimulated increases in biotic N fixation and/or protease production by either plant roots or microbes. Increased P availability has been shown to increase rates of N fixation and/or abundance of N-fixing organisms (Smith 1992; Crews 1993; Weiss, Hobbie & Gettel 2005; Benner & Vitousek 2007; Benner *et al.* 2007; Stewart, Coxson & Siciliano 2011b). N fixation in birch hummock vegetation at this site has been estimated at 0.137 g m^{-2} $year^{-1}$ (1.37 kg ha^{-2} $year^{-1}$) mostly from cyanobacterial moss associations (Stewart, Coxson & Grogan 2011a), and we did see slightly increased moss biomass with P addition. Increased P availability may also increase root exudation of proteases, either by increasing root biomass (Jonasson *et al.* 1999; van Wijk *et al.* 2003) or by increasing ATP and plant energy status. In addition, microbial protease exudation may increase with added P, because soil microbial biomass N/P ratios are highly constrained around 6.9 on average (Cleveland & Liptzin 2007), so an increase in P availability may increase microbial N requirement. Overall, this suggests that increased soil N and P availability alters biological processing of these important nutrients.

Our results clearly indicate that the extent to which tundra vegetation biomass and carbon stocks change with warming will be affected by the relative increases in soil N and P availability. The N-P factorial additions indicated consistent independent co-limitation of N and P on the growth of most above-ground tissues for *B. glandulosa* and *E. vaginatum*. While the growth of *R. chamaemorus* shoots was strictly P-limited and the growth of *B. glandulosa* leaves was more strongly enhanced by P addition, this was in the context of subtle increases in N availability in the P-alone plots. Altogether, these results demonstrate a need for increasing our understanding of P versus N limitation in arctic tundra, including the mechanisms through which P limits tundra plant growth and the impact of climate change on soil P availability and N/P stoichiometry. As controls on soil N availability are primarily biotic and controls on P availability are part biotic and part geochemical (Schlesinger 1997), warming impacts on each elemental cycle may differ substantially, with consequent impacts on the stoichiometry of soil soluble nutrient pools and plant biomass responses.

In conclusion, evergreen shrubs are likely to dominate early responses to warming in mesic shrub tundra, contrary to the predictions from high-level fertilization studies that greatly enhanced soil nutrient pools. Since evergreen shrubs tend to have relatively slow growth rates, low stature and produce recalcitrant litter, their increased growth may act as a negative feedback to slow down the increase in soil fertility with warming. However, as *B. glandulosa* and other relatively fast-growing species respond to warming-enhanced soil fertility and increase their stature and canopy cover, a threshold may be crossed over which evergreens become shaded out above ground and out-competed for the enhanced nutrient supply below-ground. The rate and magnitude of change in soil fertility with warming and interactions between N and P availability may dictate the plant species' life-history strategies that will be most successful in this changing climate and consequently the future carbon balance and albedo of mesic tundra systems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Effect of greenhouse on mean diel air and soil temperatures measured using dataloggers through three growing seasons (a), and on daytime soil temperatures measured manually in one summer (b).

Figure S2. Greenhouse treatment increase in mean diel temperature (a) and 4 pm temperatures through the growing season (b).

Table S1. Linear regression parameters used for the hits: biomass calibration.

Table S2. Bonferroni correction thresholds for the species-level analyses.

Table S3. Dissolved organic, inorganic, and microbial soil C, N and P pools in the warming and fertilization treatments.

Table S4. Plant part- and age-differentiated biomass for all species and functional groups in the warming and fertilization treatments.

Table S5. Effect of greenhouses on soil moisture.

Table S6. Effects of greenhouse warming and low-level N additions on dissolved organic and inorganic C, N, and P pools.

Table S7. Effects of factorial N and P additions on dissolved organic and inorganic C, N, and P pools.

Table S8. Number of inflorescences and fruits for vascular plant species in the greenhouse warming and control plots.

