

Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra

JENNIE DEMARCO,^{1,†} MICHELLE C. MACK,² M. SYNDONIA BRET-HARTE,³ MARK BURTON,⁴ AND GAUIS R. SHAVER⁵

¹*Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003 USA*

²*Department of Biology, University of Florida, Gainesville, Florida 32611 USA*

³*Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775 USA*

⁴*Nicholas School of the Environment, Duke University, Durham, North Carolina 27708 USA*

⁵*The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA*

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Abstract. Warming Arctic temperatures can drive changes in vegetation structure and function directly by stimulating plant growth or indirectly by stimulating microbial decomposition of organic matter and releasing more nutrients for plant uptake and growth. The arctic biome is currently increasing in deciduous shrub cover and this increase is expected to continue with climate warming. However, little is known how current deciduous shrub communities will respond to future climate induced warming and nutrient increase. We examined the plant and ecosystem response to a long-term (18 years) nutrient addition and warming experiment in an Alaskan arctic tall deciduous shrub tundra ecosystem to understand controls over plant productivity and carbon (C) and nitrogen (N) storage in shrub tundra ecosystems. In addition, we used a meta-analysis approach to compare the treatment effect size for aboveground biomass among seven long-term studies conducted across multiple plant community types within the Arctic. We found that biomass, productivity, and aboveground N pools increased with nutrient additions and warming, while species diversity decreased. Both nutrient additions and warming caused the dominant functional group, deciduous shrubs, to increase biomass and proportional C and N allocation to aboveground stems but decreased allocation to belowground stems. For all response variables except soil C and N pools, effects of nutrients plus warming were largest. Soil C and N pools were highly variable and we could not detect any response to the treatments. The biomass response to warming and fertilization in tall deciduous shrub tundra was greater than moist acidic and moist non-acidic tundra and more similar to the biomass response of wet sedge tundra. Our data suggest that in a warmer and more nutrient-rich Arctic, tall deciduous shrub tundra will have greater total deciduous shrub biomass and a higher proportion of woody tissue that has a longer residence time, with a lower proportion of C and N allocated to belowground stems.

Key words: Arctic; carbon pools; climate change; deciduous shrubs; manipulated warming; meta-analysis; nitrogen pools; nutrient additions; tundra.

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† **E-mail:** jennied@nmsu.edu

INTRODUCTION

Temperatures in the Arctic have increased by 1.5°C over the last century and are expected to

continue to increase at a faster rate than the rest of the globe (Overpeck et al. 1997, Serreze and Francis 2006, Kaufman et al. 2009). Warmer temperatures can stimulate plant productivity

directly in the Arctic by providing a warmer environment for plant growth (Elmendorf et al. 2012a, Sistla et al. 2013) or indirectly by stimulating microbial decomposition of organic matter and releasing more nutrients for plant uptake and growth (Nadelhoffer et al. 1991, Chapin et al. 1995, Michelsen et al. 1996, Schmidt et al. 2002, Aerts et al. 2006, Sistla et al. 2013).

Low and tall deciduous shrub cover is increasing across the Arctic tundra biome (Tape et al. 2006, Forbes et al. 2010, Elmendorf et al. 2012b) and is expected to continue to increase with future warming (Walker et al. 2006, Elmendorf et al. 2012a). The functional traits of low and tall deciduous shrubs may allow them to respond more rapidly to environmental change compared to graminoids, sedges, and evergreen shrubs (Chapin and Shaver 1989, Baddeley et al. 1994, Schmidt et al. 2002, Walker et al. 2006). Previous studies that have directly tested plant community and ecosystem responses to environmental change have been carried out in plant communities dominated by sedges, grasses, creeping and semi-erect deciduous shrubs, or evergreen shrubs. These studies have demonstrated that plant productivity responds strongly to nutrient additions and to a lesser degree to temperature increase (Shaver and Chapin 1980, 1991, Parsons et al. 1994, Boelman et al. 2003, Van Wijk et al. 2003). Nitrogen (N) or N in combination with phosphorus (P) can limit productivity in upland communities such as moist acidic tussock tundra (Shaver and Chapin 1980, Chapin et al. 1995, Shaver et al. 2001), moist non-acidic tussock tundra (Gough and Hobbie 2003), heath tundra (Gough et al. 2002), and dwarf shrub communities (Baddeley et al. 1994, Zamin and Grogan 2012), while wet sedge communities tend to be P-limited (Shaver and Chapin 1995).

Fewer studies have directly tested temperature and nutrient controls over productivity and carbon (C) storage in tall deciduous shrub tundra even though communities dominated by tall shrub tundra make up 26% of the vegetated portion of the circumpolar Arctic (Walker et al. 2005). In addition, woody sites at high latitudes show a stronger sink for C compared to herbaceous sites they are replacing (Cahoon et al. 2012).

There have been no experimental studies reporting the effects of long-term environmental

manipulations on tall deciduous shrub tundra communities. Previous research in other arctic plant communities has shown that the short-term (<5 years) response to environmental manipulations is not always predictive of long-term (>9 years) responses (Chapin et al. 1995, Boelman et al. 2003, Mack et al. 2004). Furthermore, plant communities from different regions within the Arctic do not always respond similarly to the same environmental manipulations (Van Wijk et al. 2003). For example, in a meta-analysis comparing long-term ecosystem level experiments at Toolik Lake, Alaska and at Abisko, northern Sweden, Van Wijk et al. (2003) found that communities from both regions responded to nutrient additions by increasing aboveground plant biomass, particularly the biomass of deciduous shrub and graminoid plants. In Alaska, deciduous shrubs increased from 20% to 60% of the aboveground vascular biomass, replacing most other plant functional groups. In Sweden, by contrast, there was little response from the same species of deciduous shrubs which only increased about 2% from the control aboveground vascular biomass, while graminoids maintained dominance. The lower relative abundance and lesser responsiveness of deciduous shrubs in Sweden may be related to chronically greater herbivory on deciduous shrubs in Sweden. In addition to our limited knowledge of long-term responses to environmental change in tall shrub tundra, we know little about how environmental changes will influence belowground biomass, C and nutrient storage even though the Arctic stores 20–30% of the total amount of terrestrial soil-bound C (McGuire et al. 2009).

Much of what we know about tall deciduous shrub-dominated tundra communities comes from observational studies. These studies show that tall shrub tundra communities are found along gravelly river bars, well-drained floodplains, streams, and in water track areas where the soil temperatures are warmer and nutrient availability is higher (Matthes-Sears et al. 1988). These communities are dominated by deciduous shrubs—willows (*Salix* spp.), birch (*Betula* spp.) or alder (*Alnus* spp.)—and are the most productive of all arctic tundra plant communities (Matthes-Sears et al. 1988, Shaver and Chapin 1991). In addition, 70% of tall deciduous shrub

tundra biomass is produced belowground in stems and roots (Chapin et al. 1980, DeMarco et al. 2011). Shrub tundra soils have larger C and N pools and cycle N in the soil faster than other tundra communities (Weintraub and Schimel 2003, Buckeridge et al. 2010, Chu and Grogan 2010, DeMarco et al. 2011). At the plant level, deciduous shrubs have higher transpiration (Bliss 1960), and higher rates of photosynthesis (Johnson and Tieszen 1976) and nutrient uptake (Kielland 1994) compared to other arctic plant growth forms and respond more quickly to environmental change than evergreen shrubs (Baddeley et al. 1994, Chapin et al. 1995, Bret-Harte et al. 2002).

The objective of our study was to understand controls over plant productivity and C and N stocks in tall deciduous shrub tundra ecosystems in order to predict how these systems will respond to environmental change. In addition, we wanted to understand how the response of tall deciduous shrub tundra compared to the response of other plant communities types within the region that have been subjected to the same treatments. To investigate whether the productivity of this vegetation type is limited by temperature, nutrients, or an interaction between the two we examined the plant and ecosystem response in a long-running (18 years) nutrient addition and warming experiment in Alaskan tall deciduous shrub tundra. We also tested whether these environmental changes altered total ecosystem N and C stocks. To compare the response of tall deciduous shrub tundra to warming and fertilization treatments, we calculated the treatment effect size of the biomass response from seven separate long-term fertilization and warming experiments. We hypothesized that productivity and C and N pools in plant biomass would increase more strongly and consistently with the alleviation of nutrient limitation than they would to a 1–3°C increase in air temperature, within the range of the expected increase in Arctic air temperature by the middle of the 21st century (ACIA 2004). In addition, we predicted that increasing plant productivity in response to nutrients would lead to an increase in C and N pools in soil organic matter due to increased inputs of plant litter. We hypothesized that tall deciduous shrub tundra would respond more to warming and fertilization compared to moist

acidic tundra because deciduous shrubs have higher growth and nutrient uptake rates compared to other plant functional groups.

METHODS

Study site and treatments

This study took place in two large areas of tall deciduous shrub tundra located near Toolik Field Station at the Arctic Long Term Ecological Research (LTER) site (68°38' N, 149°38' W, elevation 760 m) in the northern foothills of the Brooks Range, Alaska, USA. The entire northern foothills region of the Brooks Range is treeless and underlain by continuous permafrost, 250–300 m thick (Osterkamp and Payne 1981). Mean annual air temperature is around –10°C, with average summer temperatures from 7° to 12°C. Mean annual precipitation is 318 mm, with 43% falling as snow in the winter (<http://ecosystems.mbl.edu/ARC>). Average snow depth is 50 cm, although snow distribution can be variable due to redistribution by wind. The snow-free season typically lasts from mid-May to mid-September.

In 1989, two replicate randomized blocks were established in separate patches of tall shrub tundra with each block containing four 5 m × 10 m plots separated by 1-m buffer strips. The two patches were ~1–2 ha in area and were ~400 m apart, both on the east side of Toolik Lake; production, biomass, and C, N, and P budgets of the (unmanipulated) tall shrub tundra at one of these sites (Block 2) were described in detail in Shaver and Chapin (1991). Within each block, plots were randomly assigned to the following treatments: control (C), nutrient addition (NP), elevated temperature (T), and nutrient addition with elevated temperature (NP + T). Nutrients were added annually since 1989 by adding 10 g N/m² of nitrogen (N) as NH₄NO₃ and 5 g P/m² of phosphorus (P) as triple superphosphate [Ca(H₂PO₄)₂ · H₂O] with 45% as P₂O₅ in late May or early June following snow melt. Temperature was manipulated by placing a greenhouse over the shrub tundra during the months of June through August. Greenhouses were built of transparent 0.15-mm (6 mil) plastic stretched over a 2.4 m × 4.9 m (8 feet × 16 feet) wooden frame. To completely enclose the vegetation aboveground, this frame was initially ~1.2 m (4 feet) tall at the edges, sloping to a gabled roof

~1.6 m tall at the center. However, due to the increased growth of the shrubs in the fertilized greenhouses, after ~5 years of treatment it was necessary to increase the height, to 1.8 m (6 feet) at the edges and a total height of ~2.2 m. The greenhouse plastic is removed each autumn prior to snow fall and replaced each spring. The greenhouse plastic is removed during the fall, winter, and spring, allowing snow to drift over the vegetation and establish a temperature regime similar to the control plots (Shaver et al. 2013). Additional details of greenhouse construction and effects on microclimate are provided in Shaver et al. (1998) and Sistla et al. (2013). The sites were initially established and are currently maintained by the Arctic LTER project (<http://dryas.mbl.edu/arc/default.html>). Between the 19th and 27th of July 2007, 18 years after the start of the experiment, we harvested above- and belowground plant material and soils from the treatments within the two blocks to assess changes in biomass, productivity, and C and N stocks with nutrient addition and elevated temperature.

Environment

Two profiles of soil temperature were measured at four soil depths (1–just below bottom of moss layer, 10, 20, 40 cm below the soil surface) within each treatment in Block 2 using copper/constantan thermocouples connected to a data logger (Campbell Scientific CR10, Campbell Scientific, Logan, Utah, USA). Soil temperatures were read every 15 minutes and averaged every three hours. Mean annual soil temperatures, growing season (June–August), and winter season (January–May plus September–December) soil temperatures were calculated using data collected in 2007. Air temperature was not measured the year of this study or any year prior to this study. Air temperatures in greenhouses with the same construction as the ones in our study in moist acidic, moist non-acidic, and wet sedge tundra increased by 5°C relative to the control (Chapin et al. 1995, Shaver et al. 1998, Gough and Hobbie 2003).

Biomass

In mid-July of 2007, we measured aboveground and belowground stem biomass by destructively harvesting all shrubs from three

separate 50 × 50 cm quadrats within each plot for each treatment within each block (total n = 6 quadrats of each treatment), as in Shaver and Chapin (1991) and Bret-Harte et al. (2008). Understory plants and mosses were collected from a 10 × 40 cm area nested within the 50 × 50 cm quadrat. Each quadrat was sorted into species and then into tissue type (e.g., inflorescences, new leaves and stems, old aboveground stems, belowground stems, roots). The separated samples were then dried for a minimum of 48 hours at 60°C and then weighed. Biomass of each species and tissue type, per functional group, and total aboveground biomass were calculated on a per meter squared basis by calculating the mean biomass for either each species and tissue type, each functional group, or total biomass among the three quadrats and then averaging between the two blocks to get a final value for each treatment.

Belowground stems within the organic layer were removed from the same 10 × 40 cm quadrats used to determine aboveground biomass according to methods described in Shaver and Chapin (1991) and Bret-Harte et al. (2008). Belowground stems were separated by species.

Root biomass was sampled from each quadrat within each treatment and block (Mack et al. 2004). Roots in the upper organic soils were removed from 5 × 5 cm slabs of organic soil cut from the side of the quadrat hole down to the mineral soils, and roots in the underlying thawed mineral soils were removed from soil cores taken using a 5-cm diameter corer from the mineral/organic interface to the current bottom of the thaw layer. Two soil cores, adjacent to each other, were removed and combined to provide enough material for processing. Roots were separated by hand from these samples and separated into two size classes; fine (≤2 mm in diameter) and coarse (>2 mm diameter) and were dried at 65°C for a minimum of 48 hours before weighing. Roots and belowground stems from the organic and mineral layer were combined to estimate total belowground root biomass.

Aboveground net primary production

Net primary production (NPP) was calculated for aboveground vascular plants only, after Shaver and Chapin (1991). Aboveground production was separated by parts; new leaves, new

stems, secondary stem growth, and inflorescence/fruit. Leaves included new deciduous and evergreen leaves, all aboveground material for forbs, and the leaf blades and sheaths of the graminoids. Secondary stem growth (annual ring growth) was estimated for woody stems that were produced in previous years, using estimated annual percentage growth rates from Bret-Harte et al. (2002). These rates were 15.8%/year for *Betula nana*, 18.1%/year for all *Salix* species, and 7.9%/year for *Rhododendron tomentosum*. Secondary growth of *Potentilla fruticosa* was assumed to be the average of the secondary growth rates of *Betula nana* and *Salix pulchra*, and came to 16.95%. We assumed negligible secondary growth for *Dryas integrifolia*, *Empetrum nigrum*, *Rubus chamaemorus*, *Vaccinium vitis-idaea* (Shaver and Chapin 1991) and did not include their secondary growth in the ANPP calculation.

Species richness and dominance

Biomass for each species was summed across all replicates within a treatment for construction of rank abundance curves as in Shaver et al. (2001). Species were ranked within each treatment by their biomass, with number one being the most abundant species within that treatment.

Soil properties

Soil properties were determined using a second set of soil slabs for the organic soil and cores for the mineral soil, collected in the same way as the soil samples analyzed for root biomass. Prior to analysis, organic and mineral soils were analyzed separately by first homogenizing each sample by hand and removing the >2 mm diameter fraction (e.g., roots, below-ground stems, coarse woody debris, and rocks). Soil water content was calculated by subtracting the weight of the soil, after being dried at 60°C (organic soils) or 105°C (mineral soils) for 48 h, from the wet weight of the soil and then dividing by the dry weight of the soil. Soil bulk density was determined by dividing the oven dry soil mass by the core volume. Extractable inorganic N pools were determined from these samples (see below).

Carbon and nitrogen pools

Dried plant and organic soil samples were ground to a fine powder in a Wiley-mill with a

#40 mesh screen. Mineral soils were hand ground using a mortar and pestle. Bulk C and N were determined on all plant parts for each species and for both organic and mineral soil layers using an ECS 4010 elemental analyzer (Costech Analytical, Valencia, California, USA).

Pools of dissolved inorganic N (N-NH_4^+ and N-NO_3^-) were measured by extracting 10 g of fresh soil with 50 ml of 0.5 M K_2SO_4 . The soil slurry was agitated on a shaker table for 2 h, allowed to sit overnight in a cooler, and then vacuum filtered through a Whatman GF/A filter. Filtrate was frozen until analyzed colorimetrically, on a segmented flow autoanalyzer (Astoria Analyzer, Astoria-Pacific, Clackamas, Oregon, USA).

Meta-analysis of long-term studies

To compare the treatment responses in our study with responses from other plant community types near Toolik Lake that have been subjected to the same treatments we conducted a meta-analysis comparing the treatment effect size for aboveground biomass between the control and treatments (NP, T, and NP + T) of seven separate long-term experiments. We extracted treatment means, standard errors, and sample size from published papers using the software Data Thief (Tummers 2006) (Appendix: Table A1). Standard deviations were calculated by multiplying the standard error by the square root of the sample size. The extracted means and calculated standard deviations were used to calculate the standardized mean difference for each treatment from each study using an effect size calculator (gemni.gmu.edu) and formula outlined in Hedges (1981) and Lipsey and Wilson (2001). The direction calculation method was used and followed the formula:

$$ES = \frac{\bar{X}_{G1} - \bar{X}_{G2}}{\sqrt{\frac{[S_1^2(n_1-1) + S_2^2(n_2-1)]}{(n_1+n_2-2)}}$$

where \bar{X}_{G1} is the treatment mean, \bar{X}_{G2} the control mean, S_1 the treatment standard deviation, S_2 the control standard deviation, n_1 the treatment sample size, and n_2 the control sample size.

Statistical analysis

For all analyses the three quadrats sampled for each treatment within each block were averaged

Table 1. Mean (\pm SE) soil temperature ($^{\circ}$ C) measured during 2007 across all four treatments. Different letters within the same variable indicate significant differences among treatments.

Layer	C	NP	T	NP + T
Annual				
Moss	-1.33 (0.02)	-2.30 (0.67)	-1.29 (0.18)	-1.45 (0.24)
10 cm	-0.80 ^{ab} (0.10)	-1.63 ^b (0.50)	-0.28 ^a (0.05)	-0.34 ^a (0.03)
20 cm	-0.82 ^{ab} (0.002)	-1.26 ^{ab} (0.27)	-0.11 ^b (0.06)	-0.61 ^a (0.46)
40 cm	-0.86 (0.33)	-0.87 (0.35)	0.04 (0.07)	-0.85 (0.63)
Growing season				
Moss	7.48 ^b (0.29)	7.92 ^b (0.01)	11.87 ^a (2.34)	10.01 ^a (0.13)
10 cm	5.02 (0.16)	5.01 (1.01)	5.78 (0.16)	5.49 (0.30)
20 cm	3.42 (0.07)	3.40 (0.62)	3.86 (0.60)	3.22 (0.50)
40 cm	2.55 (0.28)	3.14 (0.63)	3.10 (0.47)	2.40 (0.60)
Winter				
Moss	-4.29 (0.11)	-5.71 (0.87)	-5.72 (1.01)	-5.72 (1.01)
10 cm	-2.77 ^a (0.19)	-3.88 ^b (0.32)	-2.34 ^a (0.02)	-2.33 ^a (0.14)
20 cm	-2.26 ^{ab} (0.02)	-2.85 ^b (0.15)	-1.47 ^a (0.28)	-1.92 ^{ab} (0.44)
40 cm	-2.02 (0.33)	-2.25 (0.25)	1.03 (0.25)	-1.95 (0.64)

resulting in one value per treatment and block, thus block ($n = 2$) is the statistical replication for this study. Differences among treatments for all variables measured were tested using a three-way analysis of variance (ANOVA) with fertilization (NP) and greenhouse (T) as fixed main effects, block as a random main effect, and fertilization by greenhouse (NP \times T) interaction term. In the initial ANOVAs using a randomized complete block, 2×2 factorial design, block effects were never significant. The analyses were then redone treating blocks as replicates in a 2×2 factorial design. Proportional allocation data were arcsine square root transformed prior to analysis to linearize proportions. ANOVA results were considered significant at a level of $p < 0.10$. We chose this level of significance because of the low level of replication in our experiment; we are constrained here by the initial experiment design. Due to the long-term nature of the experiment and the lack of comparable long-term experimental manipulations in tall shrub tundra communities within the Arctic, we feel even significance at the $p < 0.10$ level can provide important information to make inferences on how these communities will respond to environmental change. All statistical analyses were performed using the software package JMP v. 8.

RESULTS

Environmental data

The greenhouse warming treatment significantly increased mean annual soil temperature by 0.5° and 0.7° C at 10 and 20 cm depths

compared to the unwarmed treatments (10 cm, NP: $F_{1,4} = 3.03$, $p = 0.16$, T: $F_{1,4} = 12.55$, $p = 0.02$, NP \times T: $F_{1,4} = 2.25$, $p = 0.21$; 20 cm, NP: $F_{1,4} = 3.09$, $p = 0.15$, T: $F_{1,4} = 6.43$, $p = 0.06$, NP \times T: $F_{1,4} = 0.01$, $p = 0.93$; Table 1). Warming significantly increased temperatures in the moss layer during the growing season (NP: $F_{1,4} = 0.37$, $p = 0.57$, T: $F_{1,4} = 7.52$, $p = 0.05$, NP \times T: $F_{1,4} = 0.94$, $p = 0.39$) and at the 10 (NP: $F_{1,4} = 7.61$, $p = 0.05$, T: $F_{1,4} = 24.57$, $p = 0.01$, NP \times T: $F_{1,4} = 7.80$, $p = 0.05$) and 20 cm (NP: $F_{1,4} = 3.72$, $p = 0.13$, T: $F_{1,4} = 10.04$, $p = 0.04$, NP \times T: $F_{1,4} = 0.06$, $p = 0.81$) soil depths during the winter (Table 1). In contrast to the warming treatment, the fertilization treatment actually decreased soil temperatures by 1.1° C at the 10-cm depth during the winter. Soil moisture did not significantly differ among treatments (Table 2).

Biomass

Total aboveground biomass increased relative to the control treatment by 98% with nutrient addition alone and 81% with warming alone. There was a significant difference in aboveground biomass with fertilization alone and temperature alone but no significant nutrient by temperature interaction, suggesting that the 326% increase in biomass seen in the nutrient plus warming treatment was an additive effect of warming and increased temperature (Fig. 1). There was no significant difference between blocks in aboveground biomass. Deciduous shrubs made up the greatest biomass compared to biomass from other growth forms for all

Table 2. Mean (\pm SE) soil moisture (g H₂O g soil⁻¹), soil layer depth† (cm), bulk density (g cm⁻³), ammonium (μ g g soil⁻¹), and nitrate (μ g g soil⁻¹) measured across all four treatments. Different letters within the same variable indicate significant differences among treatments.

Soil property	C	NP	T	NP + T
Soil moisture				
Organic	1.68 (0.38)	1.17 (0.08)	0.72 (0.26)	1.47 (0.87)
Mineral	1.12 (0.43)	0.85 (0.26)	0.95 (0.50)	0.76 (0.18)
Soil layer depth				
Organic	15.56 (4.69)	9.17 (2.50)	7.21 (2.54)	11.04 (2.54)
Mineral	13.83 (2.42)	9.23 (2.35)	8.04 (3.13)	10.98 (5.35)
Bulk density				
Organic	0.11 (0.01)	0.10 (0.03)	0.09 (0.03)	0.11 (0.02)
Mineral	0.33 (0.01)	0.46 (0.001)	0.40 (0.04)	0.47 (0.17)
N-NH ₄ ⁺				
Organic	60.04 ^b (3.95)	165.71 ^a (37.02)	65.54 ^b (14.17)	94.24 ^{ab} (17.64)
Mineral	20.06 (2.16)	23.70 (1.51)	18.48 (6.24)	16.86 (5.17)
N-NO ₃				
Organic	1.73 ^b (0.77)	146.48 ^a (80.26)	0.50 ^b (0.01)	6.78 ^b (5.34)
Mineral	2.0 ^{ab} (0.81)	43.77 ^a (35.59)	0.38 ^b (0.19)	2.11 ^{ab} (1.37)

† Soil layer represents soil that was already thawed at the time of sampling.

treatments, while biomass of all other functional groups, except graminoids, declined with the addition of nutrients or warming (Table 3). Total belowground biomass, total belowground stem, and total root biomass did not differ significantly among treatments (Fig. 1).

Aboveground net primary production

Total aboveground vascular net primary production significantly increased in the nutrient treatment but only marginally in the warming treatment; there was no significant nutrient \times warming interaction. Both new leaves and new stems increased in the nutrient addition treatments although this increase was not statistically different from the control. Production of inflorescences/fruit declined with nutrient addition and warming (Fig. 2).

Species richness and dominance

The control site had a total of 21 different vascular plant species (Fig. 3). After 18 years of adding nutrients or increasing temperature, species diversity declined to 12 and 13 species in the nutrient addition and the warming treatments, respectively. The greatest species loss occurred in the NP + T, which had only six vascular species. Deciduous shrubs *Betula nana* and *Salix* spp. were the most abundant species in all four treatments. Warming and added nutrients resulted in a decline in forb, graminoid and evergreen shrub diversity (Fig. 3; Appendix: Table A2).

Soil properties

There was no significant difference in soil layer depth or bulk density among any of the four treatments (Table 2). Soil ammonium concentrations were three times higher in the nutrient treatments compared to the control for organic soils only (NP: $F_{1,4} = 9.51$, $p = 0.04$, T: $F_{1,4} = 2.29$, $p = 0.20$, NP \times T: $F_{1,4} = 3.12$, $p = 0.15$) and did not change with warming at either soil depth. Soil nitrate concentrations were 84 and four times greater in the NP and NP + T treatments for the organic (NP: $F_{1,4} = 22.74$, $p < 0.01$, T: $F_{1,4} = 14.83$, $p = 0.02$, NP \times T: $F_{1,4} = 6.97$, $p = 0.06$) soil and 22 times greater in the mineral soil (NP: $F_{1,4} = 7.01$, $p = 0.06$, T: $F_{1,4} = 8.96$, $p = 0.04$, NP \times T: $F_{1,4} = 0.65$, $p = 0.46$) for the NP treatment only. For both organic and mineral soils, nitrate concentrations significantly decreased in the warming treatment relative to the control (Table 2).

Carbon and nitrogen pools

The total ecosystem C pool did not differ across treatments. However, nutrient addition significantly increased the aboveground C pool, with the nutrient plus temperature treatment having the greatest aboveground C pool (Fig. 4). The belowground C pool was not significantly different across treatments. Total ecosystem N pools were also not significantly different across treatments. There was, however, a significant increase in aboveground N pool with fertilization (Fig. 4). Belowground N pools were not signif-

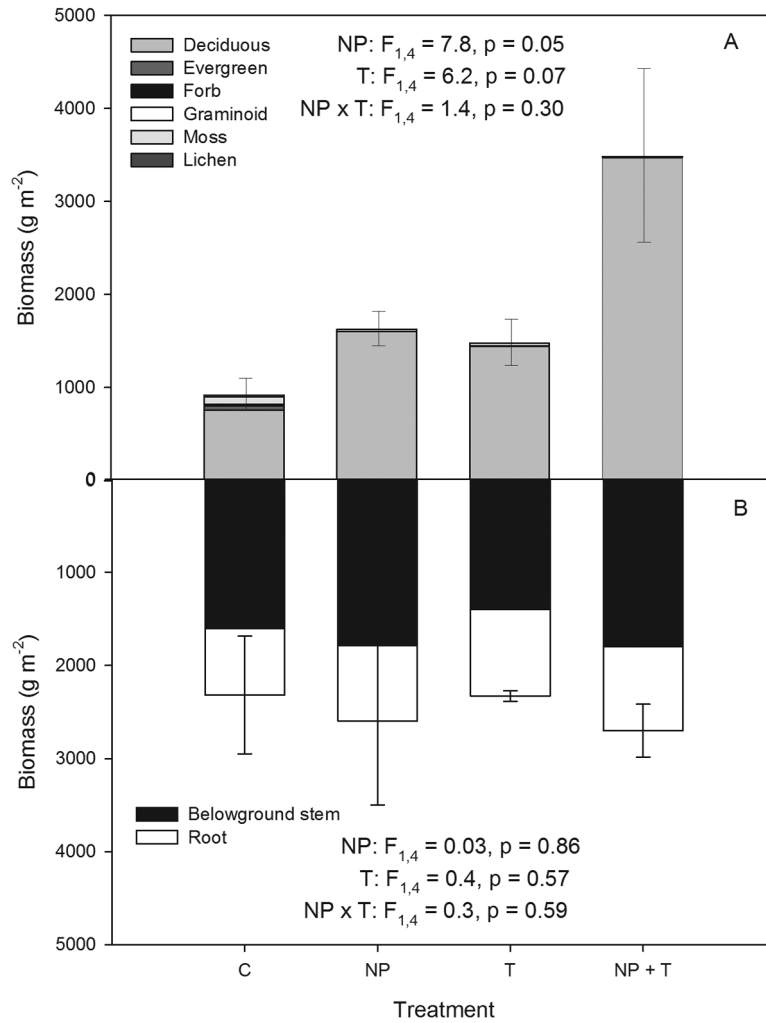


Fig. 1. (A) Mean (\pm SE) aboveground biomass (g m^{-2}) from tall shrub tundra harvested in the eighteenth year of treatment, separated by functional group and (B) mean (\pm SE) belowground biomass (g m^{-2}) separated by roots and belowground stem. Degrees of freedom, F-values, and significance of main effects and interactions in a two-way analysis of variance are also shown for aboveground and belowground biomass separately. Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T).

icantly different across treatments.

Added nutrients plus warming increased C pools in shoots, woody standing dead, and litter by four, four, and eleven times, respectively relative to the control. N pools also increased two-fold in shoots, four times in woody standing dead, 17 times in litter, and one and half times in roots in the added nutrients plus warming treatment, relative to the control. There were no significant differences in C or N pools across treatments for belowground stem, organic soil, or mineral soil (Fig. 4; Appendix: Table A3).

Allocation

The fertilization and warming treatments increased proportional biomass and C and N allocation to aboveground stems, and warming alone decreased proportional allocation of biomass and C and N to belowground stems. For N allocation, the interaction between fertilization and warming was only significant for aboveground stems. Allocation of biomass and C to roots significantly decreased in the fertilization treatment only. There was no effect of warming or nutrient addition on biomass, C, or N

Table 3. Mean ± SE aboveground biomass (g m⁻²) for the most abundant species and functional groups.

Growth form/species	Total biomass			
	C	NP	T	NP + T
Forb				
<i>Artemisia alaskana</i>	0.5 ± 0.4	0	4 ± 4	0
<i>Polemonium acutiflorum</i>	0.7 ± 0.7	0	0	2 ± 2
<i>Polygonum bistorta</i>	2 ± 0.5	0.1 ± 0.1	0.2 ± 0.2	0
<i>Valeriana capitata</i>	1 ± 1	3 ± 2	0.03 ± 0.03	0
Total	6 ± 4	3 ± 2	5 ± 3	1 ± 1
Graminoid				
<i>Arctagrostis latifolia</i>	0	0	0	10 ± 10
<i>Calamagrostis canadensis</i>	3 ± 3	3 ± 0.1	18 ± 18	3 ± 3
<i>Calamagrostis lapponica</i>	0	2 ± 2	2 ± 2	0
<i>Carex bigelowii</i>	2 ± 2	0	0	0
<i>Carex podocarpa</i>	5 ± 5	0	0.2 ± 0.2	0
<i>Poa arctica</i>	2 ± 2	15 ± 15	5 ± 5	0
Total	11 ± 3	20 ± 18	25 ± 15	14 ± 14
Deciduous				
<i>Betula nana</i>	205 ± 41	390 ± 130	573 ± 573	86 ± 86
<i>Potentilla fruticosa</i>	46 ± 46	31 ± 31	0	0
<i>Rubus chamaemorus</i>	0.4 ± 0.4	0	0	0
<i>Salix glauca</i>	338 ± 338	443 ± 133	109 ± 109	2116 ± 2116
<i>Salix pulchra</i>	169 ± 162	736 ± 230	761 ± 414	1268 ± 1255
Total	758 ± 262	1601 ± 201	1443 ± 269	3470 ± 947
Evergreen				
<i>Empetrum nigrum</i>	33 ± 33	0	0	0
<i>Rhododendron tomentosum</i>	1 ± 1	0	0	0
<i>Vaccinium vitis-idaea</i>	10 ± 7	0	1 ± 1	0
Total	43 ± 41	0	1 ± 1	0
Mosses				
<i>Sphagnum</i> spp.	32 ± 32	0	0	0
Non- <i>Sphagnum</i> spp.	47 ± 2	1 ± 1	2 ± 2	0
Total	79 ± 34	1 ± 1	2 ± 2	0
Lichen				
	22 ± 22	0	0	0

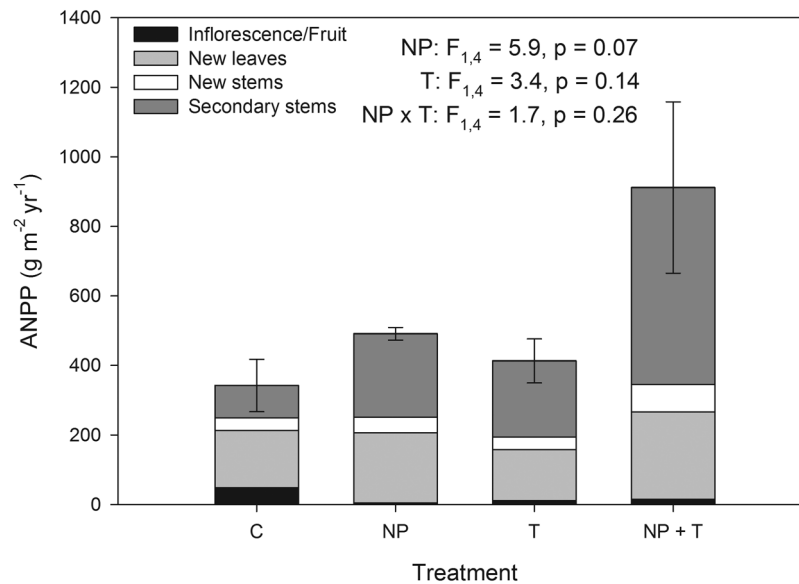


Fig. 2. Aboveground vascular net primary production (ANPP) across treatments and separated by plant parts. Degrees of freedom, F-values, and significance of main effects and interactions in a two-way analysis of variance are also shown. Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T).

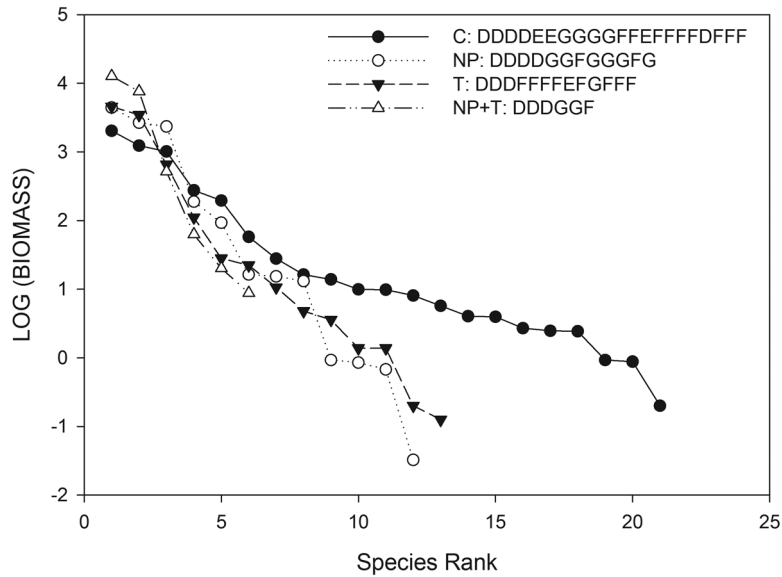


Fig. 3. Vascular plant biomass rank-abundance curves in the 2007 harvest, 18 years after initiation of treatments. The sequence in abundance of growth forms represented by each species in each treatment is also shown, with the relative number of repeated letters indicating abundance: forb (F), graminoid (G), deciduous (D), and evergreen (E).

allocation to leaves (Fig. 5; Appendix: Tables A4 and A5). Nutrient addition resulted in a decrease in C:N ratio in leaves (NP: $F_{1,4} = 13.5$, $p = 0.02$) and roots (NP: $F_{1,4} = 5.8$, $p = 0.07$). In contrast, warming caused an increase in C:N ratio in aboveground stems (T: $F_{1,4} = 10.5$, $p = 0.03$). There was no difference in C:N ratios in belowground stems with warming or nutrient addition (Fig. 6).

DISCUSSION

Controls over biomass and productivity

Overall, our study supported our hypothesis that plant productivity would increase more strongly with the alleviation of nutrient limitation than an increase in air temperature. Aboveground biomass and ANPP increased with nutrient additions and with increased temperature, with the strongest response occurring in the nutrient plus warming treatment. The larger response seen with nutrient additions compared to the warming treatment is not surprising given the annual fertilization addition is about double the nutrient requirement for aboveground production in shrub tundra (Shaver and Chapin 1991) while the warming treatment only in-

creased soil temperatures by 0.5°C , within the range of natural variation in this ecosystem. The increase in deciduous shrub biomass and decrease in graminoids and moss with warming is consistent with recent results from a synthesis of 61 warming experiments across the tundra biome (Elmendorf et al. 2012a). The lack of a positive interaction between nutrient additions and temperature suggests that the response seen was an additive one and that biomass and productivity in tall deciduous shrub tundra is either co-limited by nutrients and temperature, or by the indirect effect of temperature on nutrient availability.

As with other ecosystems in the region, the tall deciduous shrub community responded to the NP treatment by increasing both biomass and ANPP. When compared to moist acidic tundra, moist non acidic tundra, and dry heath tundra studied within the same region, tall shrub tundra response to NP was proportionally much greater (Fig. 7). The NP treatment had a six, two, and eight times larger effect on aboveground biomass in shrub tundra compared to dry heath tundra, moist non-acidic tundra, and moist acidic tundra, respectively. Moist non-acidic tundra and moist acidic tundra actually showed a negative effect of T and NP + T compared to the positive effect seen

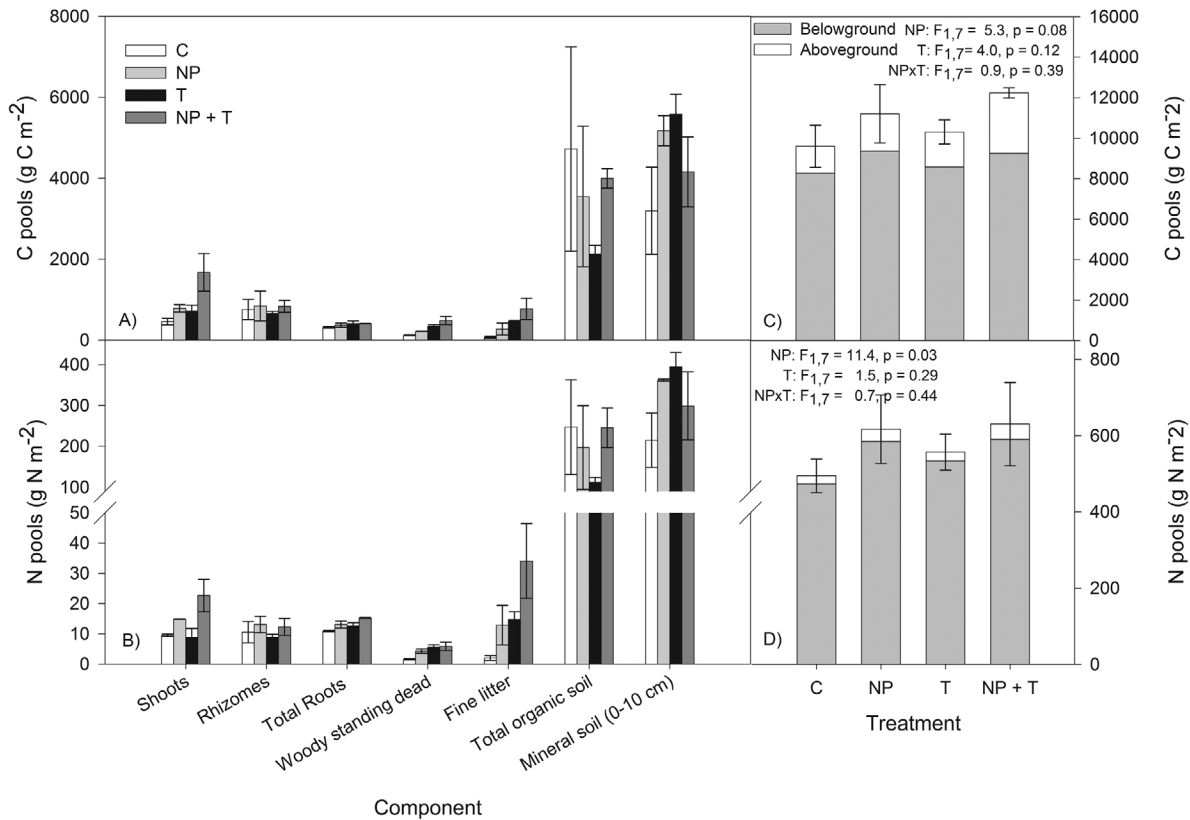


Fig. 4. (A, B) Mean (\pm SE) ecosystem carbon (C) and nitrogen (N) pools in the July 2007 harvest, 18 years after the initiation of treatments. (C, D) Mean (\pm SE) total ecosystem C and N pools separated by above and belowground for each treatment. Degrees of freedom, F-values, and significance of main effects and interactions in a two-way analysis of variance are also shown for the total aboveground pools only. Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T).

in shrub tundra for the same treatments. Treatment responses in shrub tundra were more similar to treatment responses in wet sedge when compared across all vegetation types. The similar response between these two ecosystem types may indicate the importance of both phosphorus and nitrogen availability for biomass and productivity. Productivity in wet sedge plant communities has been shown to be limited by P (Shaver and Chapin 1995) and nutrient additions in tall deciduous shrub communities in Canada suggest potential for productivity to be co-limited by N and P (Zamin and Grogan 2012). The importance of P in arctic tall shrub tundra should be considered in future studies.

The elevated inorganic N concentrations measured in the soil in the nutrient addition treatments suggest that the added nutrients

provided a direct source of plant available nutrients that resulted in an increase in biomass and productivity. In contrast, inorganic N concentrations in the warming treatments soils were either not different from the control or were significantly lower. This lack of change in inorganic N with warming is similar to findings from other long-term warming treatments (Sorenson et al. 2008). The warming only increased annual soil temperatures by 0.5°C which may not be enough to significantly stimulate an increase in net N-mineralization. Studies that show increases in net N-mineralization with manipulated warming report soil temperature increases at 1°C or greater (Schmidt et al. 1999, DeMarco et al. 2011). Studies that have added nutrients at low levels (<10 g N/m²/yr) have not seen an increase in plant growth (e.g., Zamin and Grogan

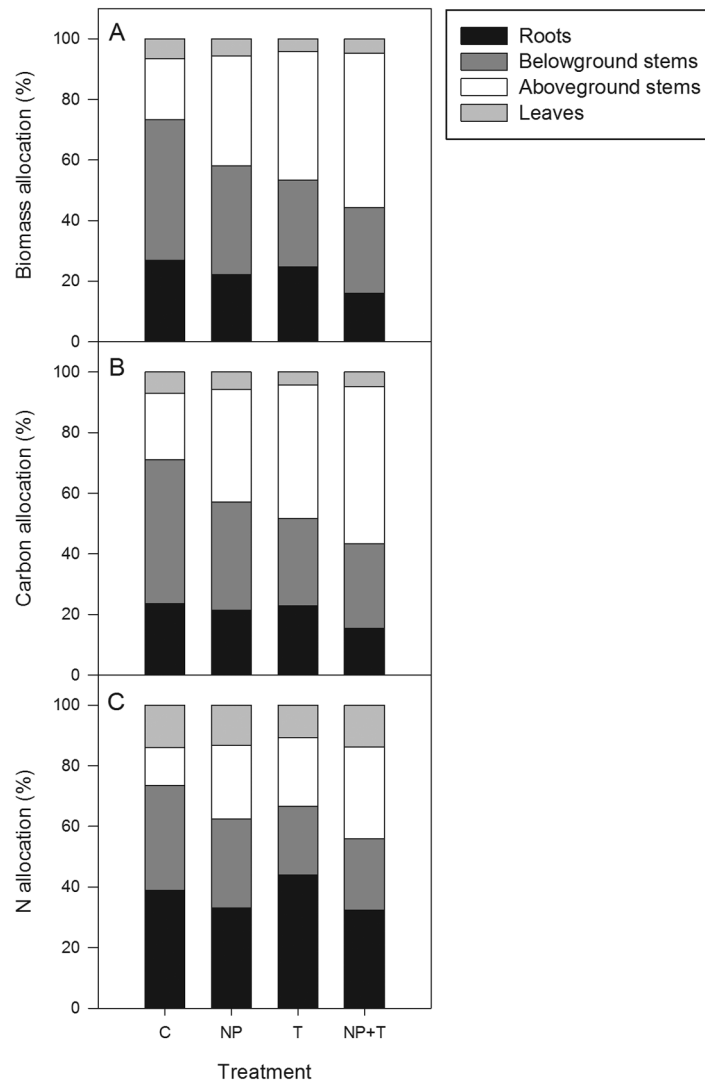


Fig. 5. The proportion of (A) biomass, (B) carbon, and (C) nitrogen allocated to leaves, aboveground stems, belowground stems, and roots within each treatment. Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T).

2012), suggesting that any small stimulation in net N-mineralization due to warming would probably not result in a large increase in plant productivity. In addition growing evidence suggests that soil microbial activity in arctic soils is limited by N (Lavoie et al. 2011), thus any nitrogen released by mineralization may have been immediately immobilized by microbes. The biomass response seen in the warming treatment may have been the result of direct air temperature effects on C assimilation and photosynthesis and not due to an indirect effect of increased

nutrient availability caused by stimulation of soil microbial mineralization. The increased C:N ratio seen in the aboveground stems of the warming treatment suggests that there was a stimulation in productivity with no additional increase in N storage. Although aboveground biomass, ANPP and total C pools increased marginally, there was no change in total N pools. This may have occurred if warming increased the efficiency of C uptake per unit N. Thus, any plant uptake of N that was made available through enhanced mineralization in the warming treatment may

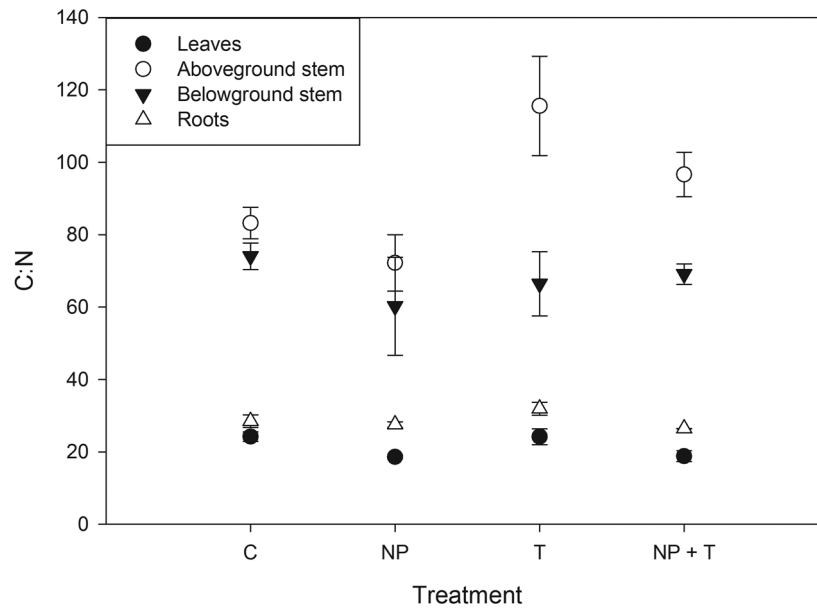


Fig. 6. Mean (\pm SE) carbon to nitrogen ratios of plant tissues across treatments.

not have been detected in the plant N pools.

The large increase in aboveground biomass and ANPP in the NP+T treatment may be explained as an additive effect of the fertilizer on total nutrient uptake plus an effect of the warming on C accumulation rates, especially early and late in the growing season. Total aboveground biomass increased by 98%, 81%, and 326% in the NP, T, and NP + T treatments relative to the control. Warming manipulations can result in early leaf expansion (Chapin and Shaver 1996, Arft et al. 1999). In the NP + T treatment, this increased growth and photosynthetic activity would be supported by a higher soil nutrient availability early in the growing season. The significant increase in ANPP seen in the NP + T treatment suggests that greater growth and C assimilation did occur relative to the other treatments. Results from other tundra manipulation studies have suggested that temperature can constrain early-season growth while nutrients constrained late season growth (Chapin and Shaver 1996). Thus the potential warming response of early leaf out and the measured increase in ANPP in combination with the increased nutrient availability from fertilization may have contributed to the stronger biomass and ANPP response seen in the nutrient plus warming treatment.

Such a large response to nutrients plus warming compared to warming or nutrients alone has not been seen in the studies of other ecosystems within this region that have manipulated both nutrients and temperature together (Chapin et al. 1995, Gough and Hobbie 2003), but it has been seen in sub-arctic systems in Sweden (Jonasson et al. 1999). The ecosystems studied in Alaska vary more in their plant functional type composition than our riparian shrub system or the systems studied in Sweden, which were dominated by evergreen shrubs. Our system was dominated by deciduous shrubs that have been shown to respond positively to short term (<5 years) warming treatments (Dormann and Woodin 2002) and long-term (9 years) fertilization treatments (Chapin et al. 1995, Shaver et al. 2001), therefore it would make sense that we would see a greater ecosystem response when nutrients and warming are manipulated together. Changes in nutrients and temperature had no effect on belowground biomass and this lack of response is similar to the few studies that have also measured belowground biomass with nutrient additions (Mack et al. 2004) or with nutrients and warming (Gough and Hobbie 2003). Our results suggest that both nutrients and temperature are important for driving deciduous shrub growth and that when nutrients and tempera-

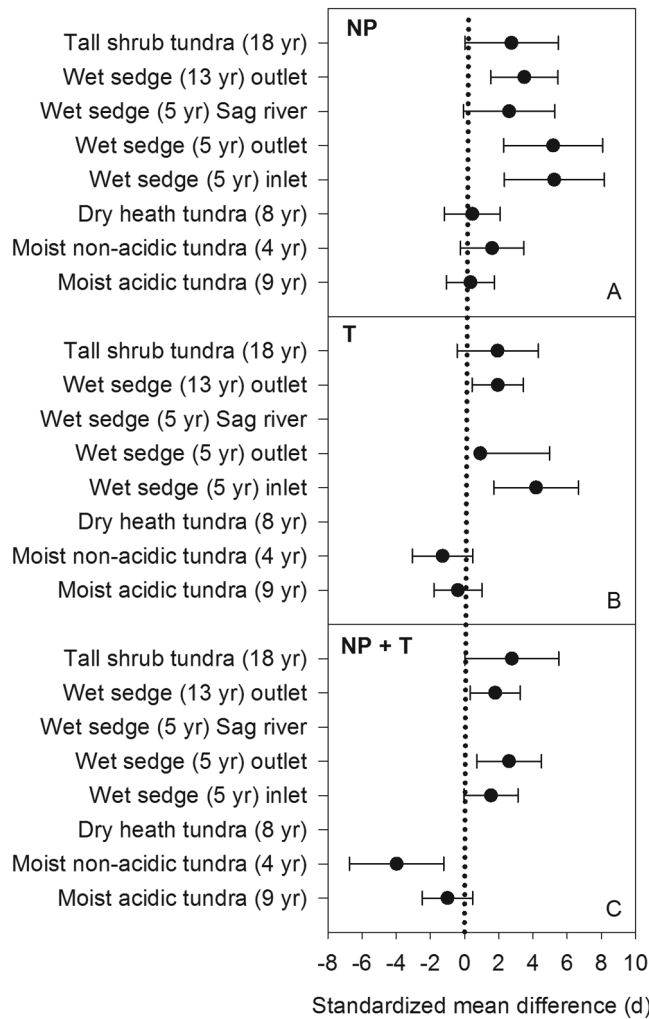


Fig. 7. The effect size of the standardized mean difference of aboveground biomass between control and (A) nutrient additions (NP), (B) temperature (T), (C) nutrient additions plus temperature (NP + T) plots of eight long-term studies (including this study) conducted near Toolik Lake Field Station, AK. Bars represent upper and lower limit 95% confidence intervals. Dates represent length of study in years.

tures are elevated shrub communities are able to respond more strongly than other plant communities within the region.

Changes in C and N pools

Our low sample size and the heterogeneous nature of the soil prevented us from being able to detect any differences in soil C and N pools that may have occurred across our treatments. The increases in C and N stored in shoots, woody standing dead, and litter were not enough to offset total ecosystem C and N pools. Mack et al. (2004) also found that C and N pools in shoots,

standing dead, and litter all increased after 19 years of added nutrients in moist acidic tundra located in the same region. However, in contrast to our study, they were able to detect a decrease in C pools in deeper soil layers that was substantially larger than the increase in aboveground C pools. More data are needed from soils collected in tall deciduous shrub tundra to determine whether a similar pattern occurs in tall deciduous shrub tundra with warming and fertilization. The total amount of N added over the 18 years in the fertilized treatments was 180 g/m². The total N stock in the control was

between 451 and 539 g/m². If the entire N added had stayed within the system the total N stock of the fertilized treatments should be approximately 631–719 g/m², slightly more than the actual measured N stocks of the fertilized plots in 2007, which were between 527 and 740 g/m². This suggests some of the added N or the original N was lost from the system perhaps from leaching, denitrification, or some other mechanism. Losses of added N have been seen in other long-term fertilization experiments (Mack et al. 2004).

Species richness and dominance

We saw a striking decrease in species richness and functional group representation with both fertilization and warming. This loss is not surprising, because this system is dominated by deciduous shrubs that produce a dense canopy, which allows only shade tolerant species to survive below. Loss of species richness with environmental manipulations has been seen in other warming (Chapin et al. 1995, Gough and Hobbie 2003, Hollister et al. 2005) and nutrient addition (Chapin et al. 1995, Gough et al. 2002, Gough and Hobbie 2003) experiments with greatest loss seen in NP + T treatment for at least one other experiment (Chapin et al. 1995, Bret-Harte et al. 2001, Bret-Harte et al. 2008). The complete loss of evergreens with fertilization has also been seen in other nutrient addition studies, mostly in the Alaskan Arctic, and has been attributed to the strong growth and biomass response of deciduous shrubs shading out the understory evergreens (Chapin et al. 1995). In contrast, in sub-arctic Sweden evergreen shrub biomass has been shown to increase with additional nutrients and warming while deciduous shrub biomass decreased (Jonasson et al. 1999). These Swedish ecosystems were initially dominated by evergreen shrubs and had few deciduous shrubs present. In addition, their study was of shorter duration than this study. It is possible that deciduous shrubs at these sites may take longer to become dominant.

Shifts in allocation

Nutrient additions and warming resulted in changing the proportion of aboveground biomass, C, and N invested in long lived woody stems with the greatest increase seen in the nutrient plus warming treatments. This pattern

was driven by changes in biomass allocation within the deciduous shrubs, which increased allocation to aboveground stems. Changes in aboveground allocation were not detected in the other functional groups in this experiment. In contrast, the proportional allocation of biomass, C, and N to belowground stems decreased, primarily in the nutrient plus warming treatment. Again this was driven by changes in allocation within deciduous shrubs although graminoids also decreased allocation to belowground stems with warming and nutrient addition.

An increase in wood production in response to warming and nutrients, as seen in this study, could have important implications for ecosystem C cycling. Woody stems store more C than non-woody plant material and can take longer to decompose compared to other plant parts (Hobbie 1996). If there was no simultaneous decrease in belowground soil C stocks, future warming in conjunction with increased nutrients in the North American Arctic could result in a negative feedback to the atmosphere, where more C is taken up by shrub growth and stored in tissue that has a longer C turnover time, thus decreasing net ecosystem respiration. However, there may be a threshold at which further increases in air temperature could lead to decreased production due to drought stress or increased herbivory and increases in soil C loss via respiration, resulting in a net ecosystem C loss to the atmosphere. Research by Cahoon et al. (2012) suggests that, in arctic and subarctic regions, woody plant communities with soil temperatures less than 10°C are net C sinks while woody plant communities with soil temperatures greater than 10°C are net C sources; consistent with this observation, continuous increases in soil temperature driven by a warmer climate could drive shrub tundra communities into becoming a net C source. More measurements of soil C and N dynamics in warming and nutrient treatments are needed to better understand how the belowground component of the ecosystem will respond and contribute to total ecosystem C and N and feed back to global C cycling.

Our study has provided insight into how tall deciduous shrub ecosystems may respond to environmental change and has demonstrated

that the magnitude of the response to environmental change varies among arctic vegetation types. Models that simulate the response of arctic vegetation to global climate change need to include a full range of vegetation types across regions, with variable magnitude of response to climate change. More long-term data sets that represent more of the dominant vegetation communities within the Arctic are needed to increase our understanding and our ability to predict how the Arctic will respond to environmental change.

Conclusions

Vegetation initially dominated by tall deciduous shrubs in the Alaskan Arctic responded to long-term environmental changes of increased nutrients and warming by increasing biomass and productivity of the dominant functional group, deciduous shrubs, resulting in an increase in C and N stored in aboveground shoots, woody standing dead, and litter. In addition, nutrient addition and warming shifted allocation of biomass, C, and N to aboveground stems and reduced allocation to belowground stems. Species richness declined with these manipulations, while dominance by a small number of deciduous shrub species increased. In all cases, the effects of environmental manipulations were more pronounced in the nutrient plus warming treatments. A future Arctic that is warmer and has more plant-available nutrients has the potential to alter tall deciduous shrub ecosystems by increasing total deciduous shrub biomass and greater allocation to woody tissue that has a longer residence time. These changes should be considered when making predictions about the response of arctic vegetation to future climate change.

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SUPPLEMENTAL MATERIAL

APPENDIX

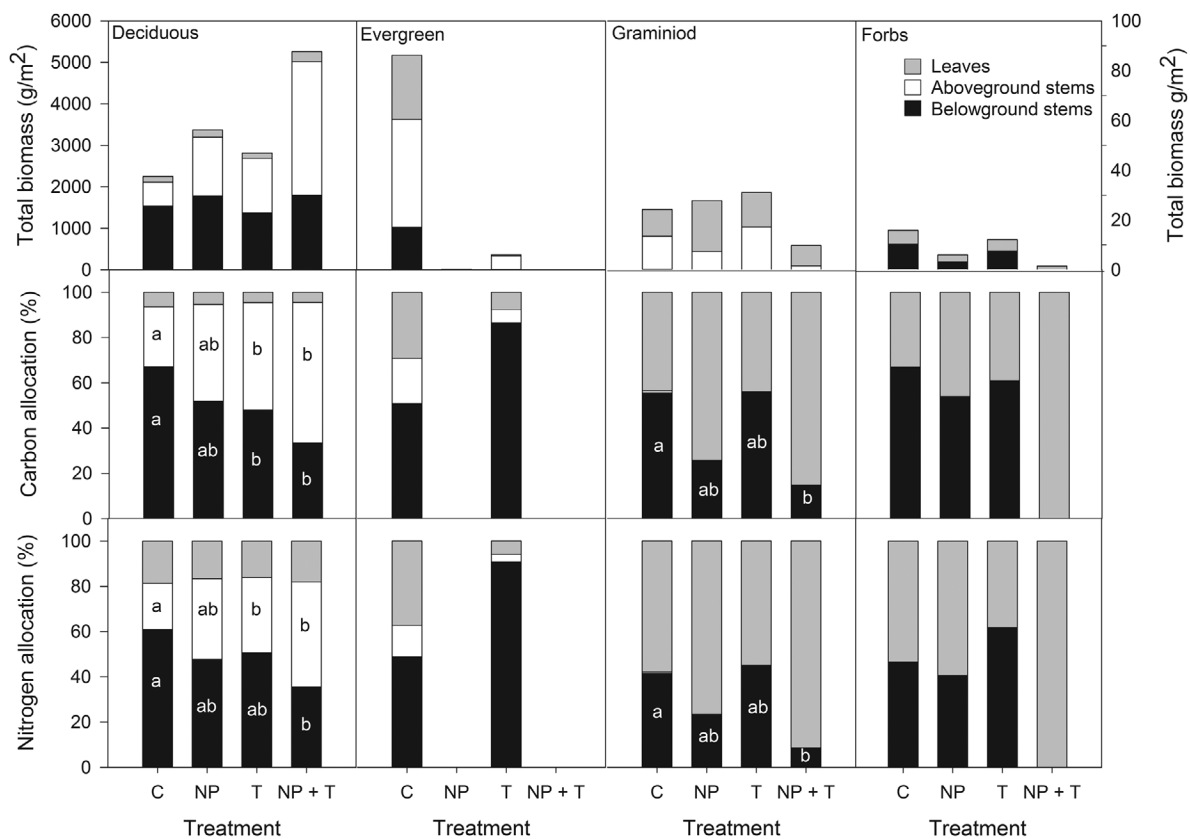


Fig. A1. Total biomass and the percent of C and N allocated among leaves, aboveground stems, and belowground stems within each functional group across treatments. Different letters indicate significantly different groups across treatments within the same plant part. For total biomass, evergreens, graminoids, and forbs are graphed on the same scale.

Table A1. Mean (\pm SD) of aboveground biomass (g m^{-2}) samples at eight separate long-term studies (including this study) conducted near Toolik Lake Field Station, AK. Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T).

Citation	Vegetation type	Length of study (yr)	n	C	NP	T	NP + T
Chapin et al. 1995	Moist acidic tundra	9	4	1019 (164)	1082 (198)	955 (164)	824 (222)
Gough and Hobbie 2003	Moist non-acidic tundra	4	3	409 (54)	476 (23)	339 (55)	215 (43)
Boelmann et al. 2003	Wet sedge-outlet	13	5	95 (18)	215 (45)	132 (20)	153 (42)
Shaver et al. 1998	Wet sedge-inlet	5	4	64 (24)	318 (64)	197 (38)	154 (88)
	Wet sedge-outlet	5	4	68 (16)	310 (64)	174 (48)	229 (86)
	Wet sedge-Sag river	5	2	231 (21)	345 (58)		
Gough et al. 2002	Dry heath tundra	8	3	204 (62)	238 (85)		
This study	Tall shrub tundra	18	2	818 (321)	1624 (262)	1473 (355)	3485 (1322)

Table A2. Vascular plant species rank by treatment based on aboveground biomass with number one being the most abundant species; no number indicates that species was not present in the plot; Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T).

Functional group	Species	C	NP	T	NP + T
Forb	<i>Aconitum delphinifolium</i>	21			
	<i>Anemone richardsonii</i>	14			
	<i>Artemisia alaskana</i>	16		6	
	<i>Petasites frigidus</i>	19			
	<i>Polygonum sp.</i>	15			6
	<i>Polygonum bistorta</i>	11	11	11	
	<i>Pyrola secunda</i>	17			
	<i>Senecio lugens</i>			9	
	<i>Stellaria longipes</i>	20		3	
	<i>Valeriana capitata</i>	12	7	12	
Graminoid	<i>Arctagrostis latifolia</i>				4
	<i>Calamagrostis canadensis</i>	8	6	4	5
	<i>Calamagrostis lap</i>		8	7	
	<i>Carex bigelowii</i>	9	12		
	<i>Carex hypnophyllum</i>		10		
	<i>Carex podocarpa</i>	7		10	
	<i>Carex vaginatum</i>		9		
Deciduous shrub	<i>Poa arctica</i>	10	5	5	
	<i>Betula nana</i>	2	3	2	3
	<i>Potentilla fruticosa</i>	4	4		
	<i>Rubus chamaemorus</i>	18			
Evergreen shrub	<i>Salix glauca</i>	1	2	3	1
	<i>Salix pulchra</i>	3	1	1	2
	<i>Empetrum nigrum</i>	5			
	<i>Rhododendron tomentosum</i>	13			
	<i>Vaccinium vitis-idaea</i>	6		8	

Table A3. Two-way ANOVA results comparing carbon and nitrogen pools across treatments (NP, T, NP + T) within the same component. Asterisks represent the level of significance with *P < 0.1, **P < 0.05, ***P < 0.01, ****P < 0.001. In the initial ANOVAs using a randomized complete block, 2 × 2 factorial design, block effects were never significant. The analyses were then redone treating blocks as replicates in a 2 × 2 factorial design. Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T).

Component	Pool (g/m ²)	NP	T	NP × T
Shoots	Carbon	F _{1,4} = 6.6*	F _{1,4} = 5.3*	F _{1,4} = 1.6
	Nitrogen	F _{1,4} = 9.7**	F _{1,4} = 1.3	F _{1,4} = 1.9
Belowground stems	Carbon	F _{1,4} = 0.3	F _{1,4} = 0.04	F _{1,4} = 0.03
	Nitrogen	F _{1,4} = 1.2	F _{1,4} = 0.2	F _{1,4} = 0.03
Total roots	Carbon	F _{1,4} = 0.4	F _{1,4} = 2.2	F _{1,4} = 0.4
	Nitrogen	F _{1,4} = 9.4*	F _{1,4} = 6.3*	F _{1,4} = 0.1
Woody standing dead	Carbon	F _{1,4} = 5.0*	F _{1,4} = 21.9***	F _{1,4} = 0.2
	Nitrogen	F _{1,4} = 2.8	F _{1,4} = 9.4**	F _{1,4} = 1.7
Fine litter	Carbon	F _{1,4} = 2.8	F _{1,4} = 8.6**	F _{1,4} = 0.1
	Nitrogen	F _{1,4} = 4.5*	F _{1,4} = 5.7*	F _{1,4} = 0.4
Total organic soil	Carbon	F _{1,4} = 0.1	F _{1,4} = 0.9	F _{1,4} = 1.8
	Nitrogen	F _{1,4} = 0.4	F _{1,4} = 0.5	F _{1,4} = 0.2
Mineral soil (0–10 cm)	Carbon	F _{1,4} = 0.3	F _{1,4} = <0.01	F _{1,4} = 0.2
	Nitrogen	F _{1,4} = 0.1	F _{1,4} = 0.02	F _{1,4} = 0.3

Table A4. Two-way ANOVA results comparing biomass, carbon, or nitrogen allocation across treatments (NP, T, NP + T) within the same plant part. Asterisks represent the level of significance with *P < 0.1, **P < 0.05, ***P < 0.01, ****P < 0.001. In the initial ANOVAs using a randomized complete block, 2 × 2 factorial design, block effects were never significant. The analyses were then redone treating blocks as replicates in a 2 × 2 factorial design. Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T)

Plant part	NP	T	NP × T
Biomass allocation			
Leaves	F _{1,4} = 0.005	F _{1,4} = 2.3	F _{1,4} = 0.6
Aboveground stems	F _{1,4} = 26.7***	F _{1,4} = 58.1***	F _{1,4} = 3.6
Belowground stems	F _{1,4} = 2.1	F _{1,4} = 11.5**	F _{1,4} = 1.8
Roots	F _{1,4} = 5.5*	F _{1,4} = 2.2	F _{1,4} = 0.7
Carbon allocation			
Leaves	F _{1,4} = 0.07	F _{1,4} = 2.9	F _{1,4} = 1.0
Aboveground stems	F _{1,4} = 27.0***	F _{1,4} = 65.3***	F _{1,4} = 3.6
Belowground stems	F _{1,4} = 3.5*	F _{1,4} = 15.3**	F _{1,4} = 2.4
Roots	F _{1,4} = 4.3*	F _{1,4} = 2.1	F _{1,4} = 1.5
Nitrogen allocation			
Leaves	F _{1,4} = 0.4	F _{1,4} = 0.5	F _{1,4} = 1.0
Aboveground stems	F _{1,4} = 91.9****	F _{1,4} = 62.5****	F _{1,4} = 6.6*
Belowground stems	F _{1,4} = 0.8	F _{1,4} = 12.6**	F _{1,4} = 1.3
Roots	F _{1,4} = 5.7*	F _{1,4} = 0.3	F _{1,4} = 0.6

Table A5. Two-way ANOVA results comparing carbon and nitrogen allocation across treatments (NP, T, NP + T) within the same plant functional group and plant part. In the initial ANOVAs using a randomized complete block, 2 × 2 factorial design, block effects were never significant. The analyses were then redone treating blocks as replicates in a 2 × 2 factorial design. Asterisks represent the level of significance with *P < 0.1, **P < 0.05, ***P < 0.01, ****P < 0.001. Treatments: control (C), nitrogen and phosphorus fertilization (NP), warming (T), and fertilization plus warming (NP + T)

Plant part	NP	T	NP × T
Deciduous shrubs			
Nitrogen allocation			
Leaves	F _{1,4} = 0.9	F _{1,4} = 0.6	F _{1,4} = 1.8
Aboveground stems	F _{1,4} = 10.8*	F _{1,4} = 26.7***	F _{1,4} = 5.8*
Belowground stems	F _{1,4} = 5.0*	F _{1,4} = 16.5**	F _{1,4} = 1.2
Carbon allocation			
Leaves	F _{1,4} = 0.2	F _{1,4} = 4.2	F _{1,4} = 0.9
Aboveground stems	F _{1,4} = 9.7**	F _{1,4} = 35.5***	F _{1,4} = 4.3
Belowground stems	F _{1,4} = 6.6*	F _{1,4} = 20.9**	F _{1,4} = 2.3
Evergreen shrubs			
Nitrogen allocation			
Leaves	F _{1,4} = 7.7*	F _{1,4} = 0.8	F _{1,4} = 0.8
Aboveground stems	F _{1,4} = 8.5**	F _{1,4} = 0.9	F _{1,4} = 0.9
Belowground stems	F _{1,4} = 1.5	F _{1,4} = 0.2	F _{1,4} = 0.2
Carbon allocation			
Leaves	F _{1,4} = 6.9*	F _{1,4} = 0.5	F _{1,4} = 0.5
Aboveground stems	F _{1,4} = 6.4*	F _{1,4} = 0.3	F _{1,4} = 0.3
Belowground stems	F _{1,4} = 1.6	F _{1,4} = 0.3	F _{1,4} = 0.2
Graminoids			
Nitrogen allocation			
Leaves	F _{1,4} = 0.1	F _{1,4} = 0.6	F _{1,4} = 1.0
Aboveground stems	F _{1,4} = 1.5	F _{1,4} = 0.5	F _{1,4} = 0.5
Belowground stems	F _{1,4} = 15.4**	F _{1,4} = 3.5	F _{1,4} = 0.9
Carbon allocation			
Leaves	F _{1,4} = 0.03	F _{1,4} = 0.3	F _{1,4} = 1.6
Aboveground stems	F _{1,4} = 1.1	F _{1,4} = 0.9	F _{1,4} = 0.9
Belowground stems	F _{1,4} = 8.9**	F _{1,4} = 4.1	F _{1,4} = 0.01
Forbs			
Nitrogen allocation			
Leaves	F _{1,4} = 1.1	F _{1,4} = 0.03	F _{1,4} = 0.2
Belowground stems	F _{1,4} = 1.2	F _{1,4} = 2.1	F _{1,4} = 0.1
Carbon allocation			
Leaves	F _{1,4} = 0.9	F _{1,4} = 0.02	F _{1,4} = 0.4
Belowground stems	F _{1,4} = 1.7	F _{1,4} = 3.8	F _{1,4} = 0.001