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Effects of increased soil nutrients on seed rain: a role for seed dispersal in the greening of the Arctic?

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Abstract

Warming temperatures in the Arctic are resulting in greater plant growth, particularly deciduous shrubs, in a phenomenon termed the "Greening of the Arctic." Local expansion of deciduous shrubs is most likely resulting from vegetative growth, while the contribution of recruitment from seed is unknown. Here we compare seeds dispersed from plant communities created by experimental nutrient addition for 5 or 22 years with those from a community of sedges, deciduous shrubs, and evergreen shrubs at ambient soil nutrients. Nutrient addition decreased species richness and diversity and shifted the plant community toward dominance by dwarf birch, *Betula nana*, and a forb, *Rubus chamaemorus*. Generally, the composition of the seed rain resembled the adjacent plant community for deciduous shrubs, but not for other growth forms. Total seed abundance and proportion and total abundance of deciduous shrub seeds were greater adjacent to plots fertilized for 22 years. The deciduous shrub seed response was driven by a dramatic increase in seeds dispersed by *Betula,* resulting in lower taxa diversity, but not richness, of seed rain. These results suggest that increased shrub abundance will affect local seed dispersal, providing additional propagules for germination and increasing opportunities for reproduction by seed to be an important factor in the Greening of the Arctic.

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Introduction

Air temperature in the Arctic has been increasing for the past few decades at a faster rate than areas at lower latitudes, and models show that this trend will continue (ACIA, 2004; Pearson et al., 2013; Larsen and Anisimov, 2014). This change in climate has had many effects, including an increase in "greenness" of the tundra (e.g., Raynolds et al., 2006, 2008; Walker et al., 2012), termed the "Greening of the Arctic," attributed primarily to an increase in abundance of deciduous shrubs ("shrubification") over the past 50 years (Tape et al., 2006, 2012; Elmendorf et al., 2012).

This regional increase in shrub density could lead to changes in ecosystem functions, particularly carbon and nitrogen cycling. In winter, shrubs trap more snow, maintaining warmer soil conditions and higher soil nutrient concentrations than under shorter stature vegetation (e.g., Sturm et al., 2005). However, these effects appear to reverse in summer, partly because the shrubs increase shading that keeps the soil cooler (Blok et al., 2009) and deposit more litter, which also insulates the soil (DeMarco et al., 2014). The net results of these and other effects of shrubs on tundra ecosystems are complex and not yet understood (Myers-Smith et al., 2011; Arctic Council, 2013).

Shrub cover appears to be increasing with warming in three ways: open patches surrounded by shrubs are getting filled in via vegetative growth, individual shrubs are getting larger, and new areas are being colonized by seed (Tape et al., 2006; Myers-Smith et al., 2011). The role of seeds in this increase is particularly unclear. Shrubs, and most other arctic plants, propagate primarily by means of asexual, vegetative (clonal) growth (Jonsdottir et al., 1996). Although most tundra plants produce viable seed each year, seedlings are rare, likely because of a combination of low seed production and germination bottlenecks. The few seed addition studies that have been conducted suggest that germination rates would increase if more seeds were dispersed (e.g., Gough, 2006). In fact, field studies have shown that seeds will germinate in the tundra if ground is available and conditions allow (e.g., Moulton and Gough, 2011; Müller et al., 2011). Germination requirements of the shrub species implicated in shrubification have been less studied because they do not occur in the High Arctic where most germination research has been conducted (e.g., Alsos et al., 2013).

Conditions governing sexual reproduction bottlenecks may be changing.Warming may result in individual plants producing more flowers and thus seeds because the period of favorable reproductive conditions is extended (Molau and Larsson, 2000), and plants have more nutrients to allocate to sexual reproduction (Hobbie, 1996). In addition, warmer temperatures may provide more favorable germination conditions (Bell and Bliss, 1980; Douhovnikoff et al., 2010). Disturbances such as herbivores removing or trampling vegetation, thermokarst, or frost heaving are likely required to open up suitable space where seeds may establish (Gartner et al., 1986). For example, seed germination often increases in tundra when vegetation is experimentally removed (e.g., Gough, 2006; Eskelinen, 2010). Seedlings that are rarely seen in the field are often restricted to frost boils, areas of exposed mineral soil resulting from freeze-thaw action (Gartner et al., 1983; Gough, 2006). Because seeds allow plants to move into disturbed areas (Graae et al., 2011), shrubs may be taking advantage of increased disturbance rates in the Arctic that are accompanying global change (ACIA, 2004; Normand et al., 2013). In summary, the relative importance of vegetative growth and seed dispersal as mechanisms for shrub expansion is unclear, though recent evidence suggests that for some deciduous shrubs, recruitment of new individuals from seed may be more common than previously thought (Douhovnikoff et al., 2010).

Our goal in this study was to examine how artificially increasing soil nutrients to favor deciduous shrubs affected the number and species composition of dispersed seeds in moist acidic tussock (MAT) tundra in northern Alaska. When this community is experimentally warmed or fertilized, species richness declines, and the community

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shifts from a mixed community of sedges, deciduous and evergreen shrubs, mosses, and lichens toward dominance by one deciduous shrub, dwarf birch (*Betula nana*, hereafter *Betula*), and one forb (*Rubus chamaemorus*, hereafter *Rubus*) (Hobbie and Chapin, 1998; Shaver et al., 2001; Gough et al., 2012; Sistla et al., 2013). The ramifications of such changes for seed production and dispersal have to our knowledge not been examined for the entire plant community (but see Bret-Harte et al., 2001, for flowering responses to artificial warming and increased nutrients by tundra deciduous shrubs). Thus, our overall goal was to determine if the seed rain mirrors the adjacent plant community under ambient conditions and following fertilization when the community has become shrub dominated. The hypotheses tested were that, relative to ambient nutrients, long-term fertilization would cause (1) the relative proportion of deciduous shrubs in the seed rain to increase and the proportion of evergreen shrubs and graminoids to decrease; (2) a greater total number of seeds to disperse, particularly of *Betula*; (3) taxa richness and diversity of the seed rain to decline; and (4) greater magnitude changes in the seed rain (seed abundance, richness, and diversity) with increased experimental duration. Better understanding how the composition of the seed rain reflects plant community structure is a crucial step in determining how seed availability and dispersal may be contributing to greening in the Arctic.

Methods

STUDY SYSTEM

The experiments used in this study were conducted in MAT as part of the Arctic Long Term Ecological Research (LTER) project at Toolik Lake, Alaska, U.S.A. (68°38′N, 149°34′W) on the North Slope of the Brooks Range. MAT is characterized by moist soil with a mean soil pH in the organic horizon between 3.5 and 4 (Gough et al., 2000). Tussock tundra refers to the presence of small mounds produced by one of the most common plant species, *Eriophorum vaginatum*, or cotton grass, a sedge. Other common vegetation in MAT includes *Sphagnum* mosses, lichens, another sedge *Carex bigelowii*, evergreens: *Vaccinium vitis-idaea* (low bush cranberry) and *Rhododendron palustre* (Labrador tea), deciduous shrubs: *Vaccinium uliginosum* (blueberry) and *Betula*, and forbs such as *Rubus* (cloudberry) and *Polygonum bistorta* (all species hereafter referred to by genus only).

We used two fertilization experiments that are part of the Arctic LTER, established in 1989 and 2006 respectively, for our research. The 1989 MAT site consists of 4 blocks and the 2006 MAT site consists of 3 blocks of 5 × 20 m plots arranged in a single row with 2 m spacing between each. In each of the blocks, one plot was randomly selected to receive 10 g nitrogen (N) $m^{-2}yr^{-1}$ as ammonium nitrate and 5 g phosphorus (P) $m^{-2}yr^{-1}$ as superphosphate in the form of granular fertilizer every June immediately following snowmelt from the initiation of the experiment to the present. Within each block, corresponding unfertilized control plots were left unmanipulated. Data presented here were collected in 2010, thus the 1989 plots had been fertilized once a year for 22 years and the 2006 plots for 5 years.

COMMUNITY COMPOSITION AND INFLORESCENCE PRODUCTION

In late July 2010, aerial cover of the vegetation was assessed in each plot. Eight adjacent 1 m^2 quadrats were used to estimate cover of each vascular plant species, mosses, lichens, and other cover categories, such as leaf litter or frost boil cover, so 8 m^2 was sampled in each plot. Relative abundance was determined by dividing each category by the total cover (also see Gough and Hobbie, 2003).

During the same sampling period, we also quantifed the number of flowers, fruits, and other inflorescence structures in the front 0.2 m^2 area of each quadrat. Because this sampling was only conducted once during the growing season, for the purpose of this study we summed all reproductive structures for each species to generate a total number per species. For example, at the time of sampling, some *Rubus* plants still had flowers while other flowers had matured to fruits. Each flower or fruit was counted as one structure to generate the total number of reproductive structures per plot (hereafter referred to as inflorescences). Only flowers and fruits produced in 2010 were counted; previous year's berries are sometimes still present but were distinguished from new production based on color and shape.

SEED RAIN EXPERIMENT

Methods for quantifying seed rain were adapted from the International Tundra Experiment (ITEX) Manual (Molau, 1996) and Molau and Larsson (2000). Seed rain traps were set out in 2 × 2 m square seed rain plots adjacent to fertilized or unfertilized tundra in late summer 2010 until just after snowmelt in spring 2011. For the 1989 treatment plots, one seed rain plot was established at each long end of the fertilized plots in all four blocks (n = 8) and two control seed rain plots were delineated in an area of unfertilized tundra (n = 2). For the 2006 treatment plots, similarly to the 1989 plots, one seed rain plot was established on each end of the fertilized plots in Blocks 1–3 (n = 6) and four control seed rain plots were establshed (n = 4) in a nearby area of unfertilized tundra. Within each of the square seed rain plots described above, four 0.5 × 0.5 m artificial turf mats were secured to the ground at each of the four corners.

After snowmelt in early June 2011, mats were collected and transported in individual bags to the field laboratory where they were air dried for several days. All contents of each bag were removed, the mats were swept with a paintbrush to remove material followed by visual inspection and removal of vegetation material and seeds with forceps, and all seeds were separated from debris. All seeds were dried at room temperature for a minimum of one week and then transported to the University of Texas–Arlington (UTA).

In the lab at UTA, four different mesh sieves were used (#18, #35, #60, and #170 mesh) to sort the samples. Large litter (such as leaves and sticks) was removed after examining each piece to ensure no seeds were stuck to them. The contents of each sieve level was placed in a separate petri dish and methodically searched under a stereomicroscope. Seeds were counted and identified to species using reference seeds collected in Fall 2010 and online seed databases (USDA, NRCS, 2013). Seeds partially destroyed (apparently from being eaten) and seeds found in mammal feces were not included in the counts. Seeds that could not be identified to species were labeled as "unknown" and grouped by seed morphology.

STATISTICAL ANALYSIS

Relative abundance of the plant community was analyzed by grouping vascular species into growth form and then running a two-way MANOVA with the plant categories included as dependent variables and the two main effects of experiment duration and fertilization treatment. Relative cover was arc sin square root transformed

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prior to analysis. For seed rain, abundance from the four mats in each seed rain plot was summed prior to analysis. The taxa richness of each seed rain plot was calculated as the number of unique vascular plant taxa per plot, and diversity was determined using the Shannon-Weiner Diversity Index. Seed abundance, taxa richness, and taxa diversity were analyzed separately as a two-way ANOVA with experiment duration and fertilization treatment as main effects. Similar analyses were conducted on individual plant growth forms and species as described below. Inflorescence counts were analyzed using a Poisson distribution with a log-link function with duration and fertilization as main effects. All statistical analyses were conducted in SAS Version 9.3 (SAS Institute, Cary, North Carolina).

Results

PLANT COMMUNITY

When all plant cover types were analyzed in a MANOVA, there was a significant interaction between experiment duration and treatment ($F_{6,72} = 52.44$, $P < 0.0001$) resulting from the relatively subtle responses to fertilization after 5 years compared with the dramatic changes after 22 years (Fig. 1). The changes in the older, fertilized plots also helped drive a significant overall treatment effect ($F_{6,72} = 251.42$, $P < 0.0001$) and a significant overall effect of experiment duration ($F_{6,72} = 73.38$, $P < 0.0001$).

Cover of evergreen shrubs, deciduous shrubs, graminoids, and litter also had a significant interaction between experiment duration and treatment (and significant main effects of duration and fertilization, all $P < 0.0001$; Fig. 1) because of the more dramatic responses after 22 years. Deciduous shrubs significantly increased in relative abundance when fertilized, driven primarily by the positive response of *Betula*, particularly after 22 years (Fig. 2). In contrast, evergreen shrubs (including *Rhododendron*) and graminoids (both *Eriophorum* and *Carex*) declined in relative abundance with added nutrients, significantly after 22 years (Fig. 2). Lichens and mosses also significantly declined in relative abundance with fertilization and with the duration of the experiment (Fig. 1).

Similarly, there was a dramatic effect of fertilization on vascular plant species richness and diversity after 22 years that was not evident after 5 years of treatment resulting in a significant interaction and significant main effects (all $P < 0.0001$; Table 1). On average, seven species were lost from plots fertilized for 22 years, with two species, *Betula* and *Rubus*, dominating all plots. This shift was also reflected in a dramatic decline in diversity (Table 1).

The number of inflorescences produced in each treatment mirrored the changes in the plant community for deciduous shrubs in particular (Table 2). This response was driven by the increase in *Betula* catkins in fertilized plots of both experiments, with a more dramatic increase after 22 years (main effect of fertilization: $Z = 35.17$, $P < 0.0001$; Table 2). The number of forb inflorescences also significantly increased with fertilization ($Z = 2.05$, $P = 0.04$). In addition, evergreen inflorescences were lower in both experiments with added nutrients (after 22 years because so few evergreen shrubs remained), while graminoid inflorescences decreased with fertilization only after 22 years (interaction between duration and fertilization: $Z = -5.04$, $P < 0.0001$; main effect of fertilization: $Z = 4.80$, $P < 0.0001$).

SEED RAIN

Seeds from a total of 18 taxa were found in the seed rain mats. These included three separate unknown categories: unknown graminoid, unknown ericaceous, and unknown dicot. The "unknown dicot" category was not included in any of the growth forms discussed below; however, the "unknown graminoid" and "unknown ericaceous" categories were included in graminoid and evergreen shrub categories, respectively. Because of this, our estimates of species richness and diversity may be somewhat conservative.

Similar to plant cover, seed rain composition and seed relative abundance also changed dramatically with longer term fertilization. Total seed abundance and distribution among growth forms were not different in plots fertilized for 5 years in comparison to control plots (Fig. 3, part a). In contrast, more total seeds were collected adjacent to plots fertilized for 22 years compared with controls (main effect of duration was marginally significant $P = 0.08$), primarily because of the greater number (though not significantly so) of deciduous shrub seeds (Fig. 3, part b); unequal sample sizes reduced statistical power for these analyses. *Betula* seeds comprised 99%–100% of the deciduous shrub seeds, paralleling greater abundance of this species in the vegetation after 22 years of fertilization (Fig. 2). Despite dramatic reductions in corresponding cover, the abundance of both graminoid and evergreen shrub seeds were unaffected by the treatments (Fig. 3). The graminoid seeds were almost entirely *Carex*, with just a few *Eriophorum* seeds, somewhat in contrast to the changes in relative abundance of these species in the plant community (Fig. 2). The evergreen shrub seeds from all treatments were dominated by those of *Rhododendron*, a species that decreased in relative abundance in the plant community after 22 years of fertilization (Fig. 2).

Seed rain taxa richness was not significantly affected by fertilization in either experiment, although there was a trend of fewer taxa in the 22 year fertilized plots compared with controls (Table 1). Taxa diversity of the seed rain was also not affected after 5 years of treatment, but appeared to be lower after 22 years, with a marginally significant interaction between duration and treatment ($P = 0.07$, Table 1).

Discussion

GREATER BETULA *ABUNDANCE AND SEED PRODUCTION AFTER 22 YEARS OF FERTILIZATION*

Significant changes occurred in relative abundance of growth forms in the plant community with fertilization, with shifts more dramatic after longer treatment (e.g., Shaver et al., 2001). We did not detect similar compositional changes in the seed rain, except for deciduous shrubs (partially supporting Hypothesis 1). Despite the increase of *Betula* relative abundance after 22 years (3-fold), and the corresponding increase in birch catkin production and seeds dispersed (50-fold and 13-fold, respectively), the total number of seeds of all taxa dispersed from the fertilized plots was greater, but not significantly so, when compared to ambient nutrient plots (Hypothesis 2). No differences in number of seeds overall or for individual growth forms were detected in the seed rain after 5 years despite changes in community relative abundance (particularly an increase in deciduous cover, Fig. 1, part a). After 22 years, evergreen shrub (including *Rhododendron*) and graminoid (mainly *Eriophorum*) cover was substantially lower in the plant community, while relative abundance of *Rubus* was much higher, but these species and growth forms showed no difference in seed quantity in the seed rain among treatments or duration.

Lack of parallel effects in the seed rain with the plant community may be a result of differences in seed dispersal modes between species. For example, *Rubus* berries are most likely bird

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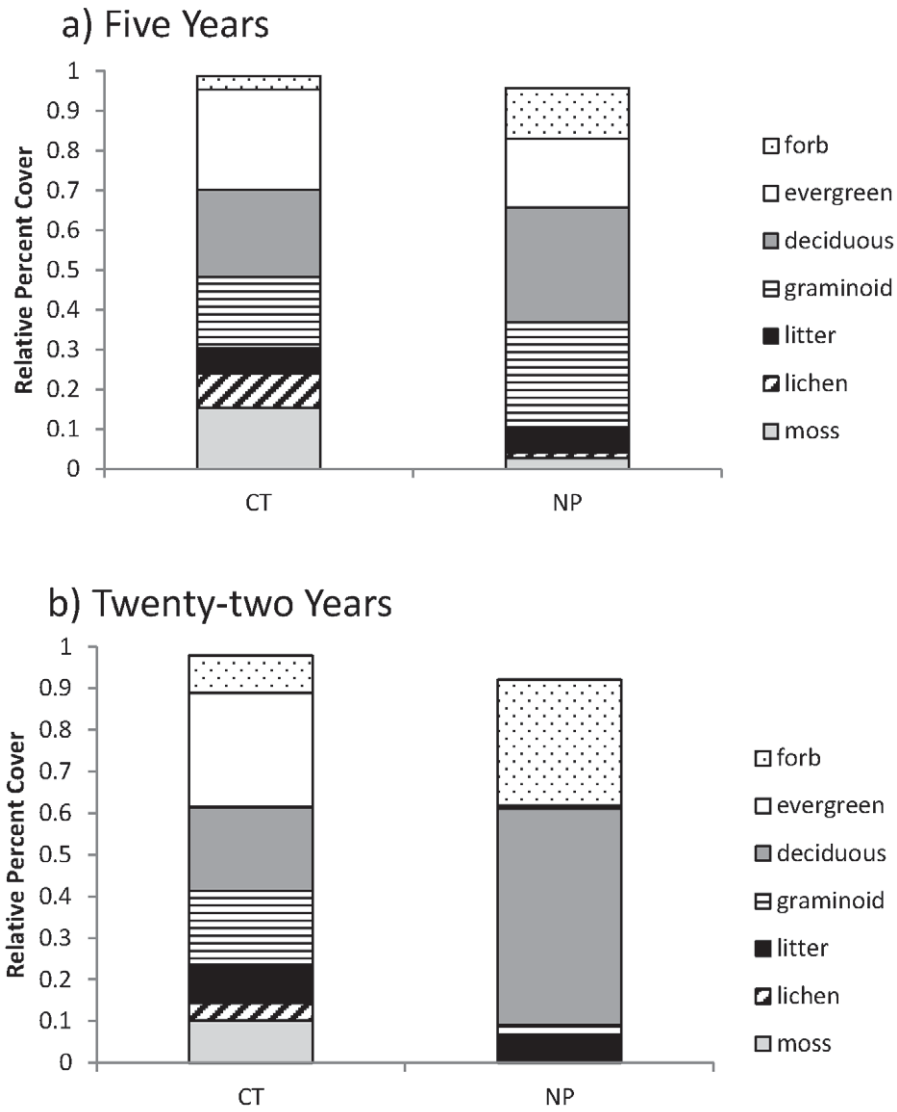


FIGURE 1. Relative abundance of plant growth forms in the plant community measured in moist acidic tundra in 2010 after (a) 5 years and (b) 22 years of treatment. Treatment abbreviations: CT = control, N P= nitrogen plus phosphorus added.

dispersed and thus unlikely to be detected using this seed rain method (Molau and Larsson, 2000). Only three *Rubus* seeds were collected, despite 5–6 berries m^{-2} counted in fertilized plots in both experiments ("Forbs" in Table 2), and these had been completely removed from the berry, broken open and had the center eaten out, rendering them unviable. Wind-dispersed *Rhododendron* seeds are very small and appeared relatively evenly dispersed across the study site, despite this species having less cover in fertilized plots. In contrast, dispersal of *Betula* was highly localized; the control and fertilized seed rain plots were within 50 m of each other, but the large numbers of *Betula* seeds were recorded only adjacent to the fertilized plots, suggesting that the seed rain input from increased abundance of *Betula* will be on a relatively small, local scale.

Taxa richness and diversity of the seed rain changed in parallel to the plant community, partially supporting Hypothesis 3. The magnitude of difference was smaller in seed rain than in plant cover, but taxa diversity was lower in plots fertilized for 22 years when compared with controls. The greater numbers of *Betula* seeds adjacent to the fertilized plots clearly influenced diversity of the seed rain. The slight response in richness was caused by species that were already rare in the seed rain being detected (or not) based on only a few seeds.

Finally, the magnitude of changes in the seed rain, similar to changes in the plant community, was much greater after 22 years than following 5 years of experimental fertilization, as described above, supporting Hypothesis 4. Our study is the first to link an experimental increase in *Betula* abundance directly to increased seed output, suggesting that increases in shrubs occurring vegetatively will likely lead to greater seed production and potentially more opportunities for new individuals to recruit from seed.

POTENTIAL INFLUENCE OF SEED RAIN ON SHRUBIFICATION AND OTHER COMMUNITY RESPONSES TO CLIMATE CHANGE

Despite the fact that most arctic plants primarily reproduce vegetatively, most species also produce viable seeds (Jonsdottir et al., 1996). Seed dispersal has allowed many of these species to repopulate areas following deglaciation and migrate long distances (Alsos et al., 2007). Since disturbance can promote germination, given the dramatic changes in disturbance regimes occurring throughout the Arctic, the ability of plants to disperse

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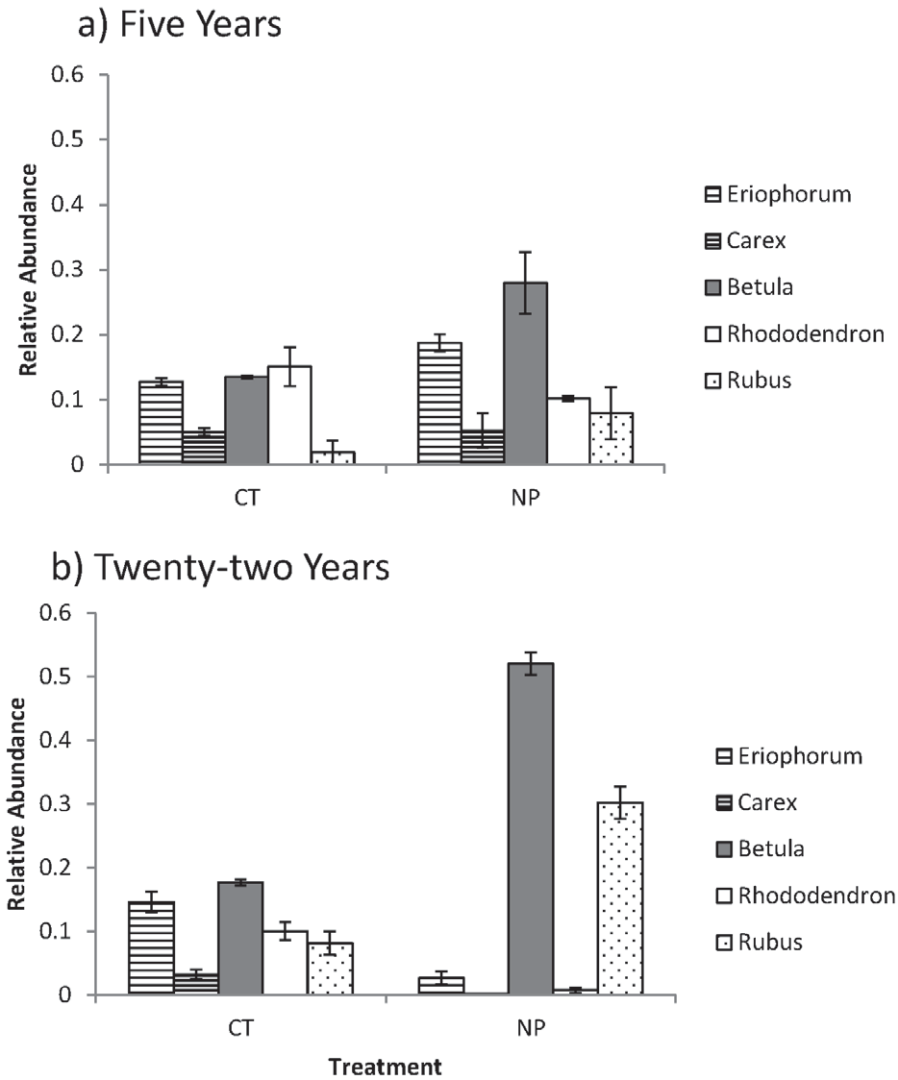


FIGURE 2. Mean relative abundance (±SE) of individual vascular plant species measured in moist acidic tundra in 2010 after (a) 5 and (b) 22 years of treatment. Graminoids: Eriophorum and Carex; deciduous shrub: Betula; evergreen shrub: Rhododendron; forb: Rubus. Treatment abbreviations as in Figure 1.

via seed may again become important to maintaining ecosystem integrity.

The role of seed production, dispersal, and subsequent germination in the process of shrubification and arctic greening is not clear. Repeat aerial photos used to document shrubification often show new individuals establishing adjacent to existing individuals (Tape et al., 2006), which likely is the result of asexual reproduction. *Betula* can "layer" by extending stems horizontally that then become covered with moss, develop roots, and produce a new aboveground individual. This clonal growth response has resulted in the increases in cover documented in long-term warming and fertilization experiments (e.g., Bret-Harte et al., 2001; Sistla et al.,

TABLE 1

Mean species/taxa richness and Shannon-Weiner diversity (H') (/m², ± SE) of the plant community and seed rain sampled in 2010 in moist acidic tundra. Different superscript letters within a row indicate pairwise significant differences among means.

		5 years		22 years	
	Duration Treatment	Control	Fertilized	Control	Fertilized
Plant community	Richness	11 ± 0[a]	10 ± 1[a]	10 ± 1[a]	3 ± 0[b]
	H'	1.57 ± 0.04[c]	1.72 ± 0.09[b]	1.93 ± 0.05[a]	0.74 ± 0.04[d]
Seed rain	Richness	8 ± 1	8 ± 1	10 ± 2	7 ± 1
	H'	1.18 ± 0.03	1.27 ± 0.07	1.35 ± 0.22	0.76 ± 0.17

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TABLE 2

Mean number of inflorescences produced (/m², ± SE) in 2010. Different superscript letters within a row indicate pairwise significant differences among means.

	5 years		22 years	
Duration Growth form/Species	Control	Fertilized	Control	Fertilized
Graminoid	2 ± 2[a]	8 ± 8[b]	10 ± 7[a]	0.2 ± 0.2[b]
Deciduous Shrub	3 ± 3[b]	52 ± 34[a]	2 ± 1[b]	100 ± 42[a]
Betula	1 ± 1[b]	51 ± 32[a]	2 ± 1[b]	100 ± 42[a]
Evergreen Shrub	21 ± 14	8 ± 8	30 ± 12	0
Forb	1 ± 1[b]	6 ± 6[a]	5 ± 2[b]	7 ± 3[a]

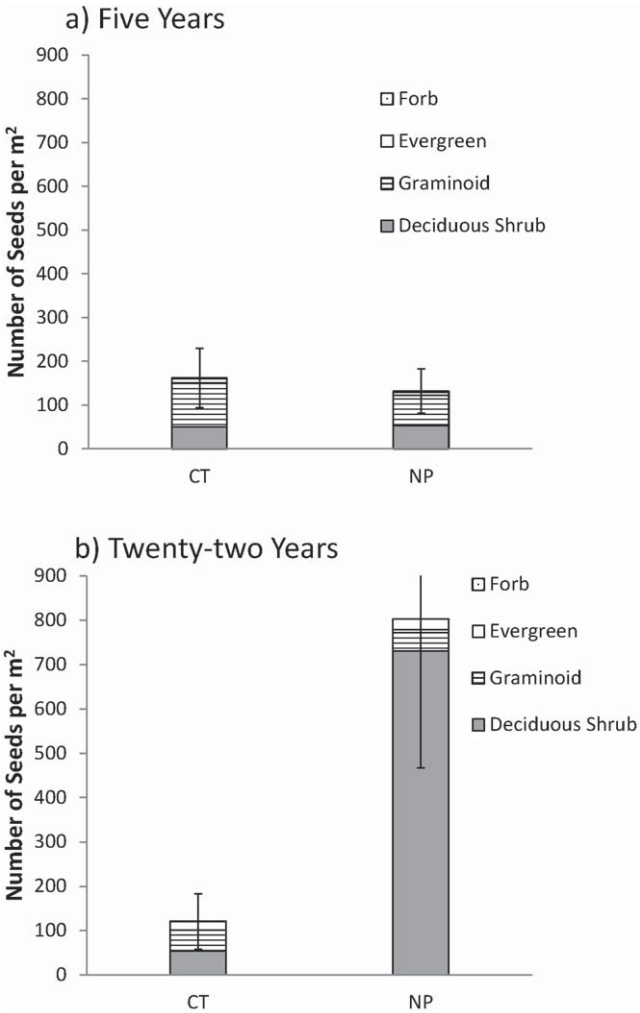


FIGURE 3. Mean relative abundance (±SE) of vascular plant growth forms in seed rain in moist acidic tundra in 2010 after (a) 5 and (b) 22 years of treatment. Treatment abbreviations as in Figure 1.

2013). Although not studied here, presumably increases in seed production also occur as a result of experimental warming, simply because more *Betula* biomass results in more catkins.

Our results suggest that increased *Betula* abundance associated with higher soil nutrient availability results in greater seed dispersal rates. This dramatic response, however, was evident after 22 years but not 5 years, suggesting a threshold for greater seed dispersal had not been met in the shorter-running experiment, despite a substantial increase in number of catkins produced (Table 2). After 8 years of fertilization in the same experiment assessed here at 22 years, *Betula* had more infloresences per ramet and more ramets flowering compared with ambient nutrient plots, suggesting that relative abundance of this species and flowering rate are both greater with increased soil nutrients (Bret-Harte et al., 2001). Greater seed production will lead to more opportunities for successful dispersal and germination, particularly if disturbance accompanies those changes (Gough, 2006).

For recruitment from seed to be an important mechanism for shrub expansion requires not only available seeds but that germination conditions are met. However, predicting how climate warming may affect germination microsite availability is difficult. Studies in tundra have shown that germination is frequently a more limiting factor in plant recruitment than seed dispersal (Cooper et al., 2004; Müller et al., 2011). For example, although *Betula* produces a high proportion of viable seeds (Chester and Shaver, 1982), an appropriate microsite is required for germination to occur (Gartner et al., 1986; Gough, 2006; Moulton and Gough, 2011). Disturbance of the vegetation and moss mat in tundra, such as by freeze-thaw disturbance (Gartner et al., 1983) or animal grubbing, seems to be required for successful seed germination of many species (e.g., Gough, 2006; Milbau et al., 2013). If abiotic stress is alleviated with climate warming and changes in disturbance regime co-occur, recruitment from seed may be promoted as the Arctic continues to warm (Douhovnikoff et al., 2010). However, recent studies suggest that competition may also increase with warming and increased soil nutrient availability, thus potentially restricting germination and subsequent changes in species richness (Eskelinen, 2010; Elmendorf et al., 2012; Olsen and Klanderud, 2014). Lack of understanding of how these factors might counteract each other hampers prediction of rates of woody shrub expansion and treeline throughout the Arctic (Normand et al., 2013).

Determining the net result of the many changes associated with climate warming and shrubification for arctic ecosystems is a current research challenge (Myers-Smith et al., 2011). Our results suggest that when soil nutrient availability increases, as occurs with greater air temperatures (e.g., Rustad et al., 2001), *Betula* cover increases and produces substantially more seeds. If changing disturbance regimes create increases in appropriate microsites for *Betula* seed germination, this species is well equipped to spread into new areas. Concomitant changes in seed production and landscape disturbance frequency could result in an increase in the importance of

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sexual reproduction in the Greening of the Arctic, and in particular, increases in *Betula* during times of warming.

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