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Authors: Alexia M. Kelley, and Howard E. Epstein

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Effects of Nitrogen Fertilization on Plant Communities of Nonsorted Circles in Moist Nonacidic Tundra, Northern Alaska

Alexia M. Kelley*† and
Howard E. Epstein*

*Department of Environmental
Sciences, University of Virginia, P.O.
Box 400123, Charlottesville, Virginia
22904-4123, U.S.A.

†Corresponding author:
alexia.kelley@duke.edu

Abstract

Nitrogen availability is considered to be a key limiting factor for plant growth in arctic tundra. Freeze-thaw cycles, which can produce patterned-ground features, may also limit the establishment and growth of arctic plants. In this experiment, we fertilized nonsorted circles, a type of patterned-ground feature, and the surrounding more stable vegetation in moist nonacidic tundra of northern Alaska to determine if nitrogen availability limited plant communities on these disturbance-dominated features. Similar to other studies in moist nonacidic tundra, the fertilized stable vegetation showed an increase in graminoid biomass and a decrease in moss biomass, but no total biomass response. The plant communities on nonsorted circles were less responsive to the addition of nitrogen as compared to the well-vegetated rims. The nonsorted circle vegetation may be limited by additional factors, such as frost heave disturbance, availability of buried seeds, and/or other nutrients. This difference in fertilization response shows that the presence of these features creates spatial heterogeneity in tundra plant community dynamics that should be taken into account when studying tundra responses to environmental change.

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Introduction

Plant growth in arctic tundra is influenced by a variety of environmental factors, such as temperature, growing season length, and light availability (Chapin, 1987), as well as nutrient availability (Chapin et al., 1995; Shaver and Chapin, 1995; Press et al., 1998; Shaver et al., 1998; Shaver and Jonasson, 1999) and physical disturbances (Jonasson and Callaghan, 1992). Nitrogen (N) availability is one of the strongest limiting factors for tundra vegetation (Chapin et al., 1995; Chapin and Shaver, 1996; Shaver and Jonasson, 1999). Microbial decomposition of organic matter by both fungi and bacteria, the primary mechanism that converts N in soil organic matter into forms that are usable by plants (such as NH_4^+ -N, NO_3^- -N, and free amino acids), is limited by the cold climate of these high-latitude regions (Nadelhoffer et al., 1992). The addition of plant-available N in tundra fertilization experiments often results in an overall increase in total biomass (Shaver and Chapin, 1980; Shaver et al., 1986; Chapin et al., 1995) and total cover (Fox, 1992; Robinson et al., 1998; Madan et al., 2007), as well as changes to the structure of the plant community (Henry et al., 1986; Fox, 1992; Press et al., 1998; Robinson et al., 1998; Shaver et al., 2001; Gough and Hobbie, 2003; Madan et al., 2007), as some tundra plant species are better able to compete for N than others (McKane et al., 2002).

The mechanisms by which these plant communities respond to this type of environmental manipulation often depend on the initial amount of vegetative cover. In well-vegetated environments, such as low-Arctic and subarctic tundra, increased nutrient availability causes shifts in the species composition of the plant community through competition (Press et al., 1998). However, in the more sparsely vegetated High Arctic, the plant community shifts through the colonization of bare ground (Wookey et al., 1995; Robinson et al., 1998; Madan et al., 2007). A similar

response was seen in a fertilization experiment in a tundra fellfield community (Fox, 1992).

The presence of small patterned-ground features, such as nonsorted circles (Fig. 1), also impacts plant community dynamics in arctic ecosystems (Jonasson and Sköld, 1983; Cannone et al., 2004; Kade et al., 2005). Nonsorted circles are defined as small circular features (0.5 to 3 m in diameter) that are less vegetated with more exposed bare substrate than the surrounding intercircle tundra, and lack a border of stones (Washburn, 1980; van Everdingen, 2002). Each winter, nonsorted circles undergo a cycle of frost heave as a result of the accumulation of ice lenses in the underlying soils. The amount of frost heave that occurs in nonsorted circles is greater than that in surrounding intercircle tundra (Walker et al., 2004), and the disturbance associated with this frost heave can disrupt the roots of vegetation establishing on these features (Jonasson and Callaghan, 1992). These features play an important role in arctic ecosystems by mixing soils through the process of cryoturbation, which moves carbon-rich organic matter into the permafrost where it is inaccessible to microbial decomposition (Dyke and Zoltai, 1980; Walker et al., 2004; Bockheim, 2007). Across the Arctic, these features can cover over 70% of the ground surface (Walker et al., 2004).

Nonsorted circles, having low vegetative cover (Kelley et al., 2004; Walker et al., 2004), are often thought of as an earlier successional state than the surrounding stable tundra (Haugland and Beatty, 2005). Given favorable climatic conditions, vegetation is eventually able to colonize these features, making them harder to distinguish from the surrounding stable tundra (Chernov and Matveyeva, 1997). However, the exact mechanisms governing this process are not well understood. These features also have a different soil N regime than the surrounding tundra. Specifically, there is less plant-available N [in the forms of NH_4^+ -N, NO_3^- -N, and dissolved organic nitrogen (DON)] in the soils of the

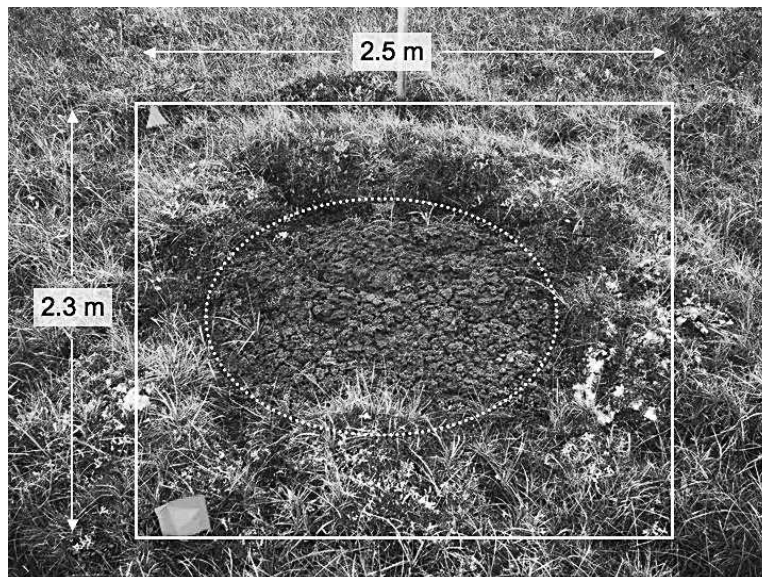


FIGURE 1. Treatment plot containing the nonsorted circle surrounded by more stable, well-vegetated tundra near Franklin Bluffs, Alaska. The white box indicates the border of the plot, in which the fertilization treatment was applied. The dashed white line is the approximate transition between the nonsorted circle and the more stable tundra.

nonsorted circles than the stable tundra (Kaiser et al., 2005; Sorensen et al., 2006; Kelley, 2007). This motivates the question: Are plant communities on nonsorted circles limited solely by the physical disturbance of frost heave, or are they also limited by available N?

In this paper we present the results of a three-year N fertilization experiment on the plant communities of nonsorted circles in northern Alaska. The goal of this study was to determine if N was limiting to plant communities on these frequently disturbed features relative to the more stable tundra that surrounds them. Because of generally low available N on nonsorted circles, we hypothesized that the vegetation on these features is indeed limited by N, but the response of plants to increased N may be reduced relative to the surrounding tundra, due to repeated disturbance associated with annual frost heave.

Methods

SITE DESCRIPTION

This study was conducted in coastal plain tundra of northern Alaska. The study site was located near Franklin Bluffs (69°40'N, 148°43'W) along the Dalton Highway. It is situated in arctic bioclimate Subzone D (Walker, 2000) and is characterized as a moist nonacidic tundra (MNT) (CAVM Team, 2003). The most common type of patterned ground features at this site are partially vegetated nonsorted circles that have some exposed mineral soil. At this particular site, these features cover approximately 25% of the ground surface (Walker et al., 2004). The common species on the nonsorted circles at this site are the forbs *Saxifraga oppositifolia*, *Minuartia arctica*, *Braya bartlettiana*, and *Puccinellia angustata*; the graminoids *Eriophorum angustifolium* ssp. *subarcticum*, *Juncus triglumis*, and *J. biglumis*; the evergreen shrub *Dryas integrifolia*; and the mosses *Bryum wrightii* and *Polyblastia sendneri* (Kade et al., 2005). The remaining 75% of the ground surface is well-vegetated, with the following species: *Dryas integrifolia* (evergreen shrub); the deciduous shrubs *Salix reticulata*, *S. arctica*, and *Arctostaphylos rubra*; the graminoids *Carex bigelowii*, *C. membranacea*, and *Eriophorum angustifolium* ssp. *triste*; the forbs *Papaver macounii*, *Cardamine hyperborea*, *Polygonum viviparum*, *Senecio atropurpureus*, and *Saussurea angustifolia*;

the mosses *Tomentypnum nitens*, *Ditrichum flexicaule*, and *Hypnum bambergeri*; and the lichens *Cetraria islandica*, *Flavoce-traria cucullata*, and *Thammodia subuliformis* (Kade et al., 2005). The Summer Warmth Index (SWI, the sum of monthly temperature averages above 0°C) is 27.0°C mo, average maximum thaw depth is 67 cm, and the soil pH at this site is 7.5 (Walker et al., 2004).

EXPERIMENTAL DESIGN

During the summer of 2003 twenty plots were selected within an area of approximately 1500 m². The plots, which contained an entire nonsorted circle plus the surrounding well-vegetated rim (Fig. 1), ranged in size from 3.1 m² to 10.8 m², depending on the size of the circle. The plots were divided into two halves. One half was used for monitoring plant community dynamics, while the second half was used to monitor nutrient dynamics. The plots were randomly divided into two categories: “control” or “fertilized.” Fertilizer in the form of NH₄NO₃ was added to the fertilized plots every two weeks between mid June and early July (for a total of 3 times) for a total of 10 g N m⁻² y⁻¹ each year between 2004 and 2006. This amount of fertilizer is consistent with that used by several other arctic fertilization studies in northern Alaska (Chapin et al., 1995; Shaver and Chapin, 1995; Shaver et al., 1998, 2001; Gough et al., 2002; Gough and Hobbie, 2003) and was expected to elicit a response in the duration of the study. The distance between the edges of control and fertilized plots ranged from 20 cm to several meters. No leaching of the fertilizer between plots was detected in the nutrient analyses.

NITROGEN AVAILABILITY

N availability was monitored using anion and cation exchange resin probes (PRSTM probes, Western Ag, Saskatoon, Saskatchewan, Canada) during the summer of 2005, the following winter, and the summer of 2006. These probes exchange Na⁺ and HCO₃⁻ with labile nutrients present in the soil solution at rates that are dependent on the initial concentrations within the soil solution and the length of the burial period (Jowkin and Schoenau, 1998). The probes measure the rate at which nutrients are removed from the soil using a mechanism that simulates root

uptake. Four anion and four cation resin probes were placed in the bare/nonsorted circle section of each plot. The probes were left for approximately 8 weeks (14 June to 7 August 2005) during the growing season of 2005, 10 months (7 August 2005 to 1 June 2006) during the winter of 2005–2006, and then 6 weeks (1 June to 15 July 2006) during the growing season of 2006. During the 10-month winter incubation, the soils and probes were frozen for approximately 8 months, during which time little exchange of nutrients was likely to occur. The probes from each plot were grouped together for one sample, extracted in 1 M KCl and analyzed for NH_4^+ -N and NO_3^- -N using a Technicon Autoanalyzer (see Hangs et al., 2004, for more detailed information regarding the chemical analysis). These probes are not used to measure rates of DON availability; however, previous studies at this site indicate that DON pools are approximately twice as large as the total inorganic N pools (Kelley, 2007).

VEGETATIVE COVER

For each plot, the plant community was monitored by measuring percent species cover each year. This was performed during the same week in June each growing season between 2004 and 2006. The first year of data was taken before fertilization had started. To determine percent cover of each species, a 100 point 1×1 m quadrat was placed on each plot. This 1 m^2 area contained part of the nonsorted circle and the surrounding vegetated rim. Each year the point frame was placed in the same location, which was marked with colored pin flags. At each of the 100 points, each species encountered was recorded. If loose litter or standing dead plants were encountered, this was recorded as “litter.” Additionally, if the soil surface was covered in cryptogamic crust or if mineral soil (as opposed to moss or organic soil) was encountered on the surface, this was also recorded. When possible, plants were identified to species, or at least to plant functional type. Data are presented in the following plant functional groups: deciduous shrubs, evergreen shrubs, graminoids, forbs, *Equisetum* spp., mosses, and lichens. Data are also presented for mineral soil, cryptogamic crust, and litter. The percent cover data are presented as change in percent cover between each year of fertilization (2005 and 2006) and the year of pretreatment data (2004). This was done to account for interannual variability in the plant communities that could have been caused by factors such as climate, which are assumed to be equal across all plots.

PHENOLOGY

During the growing season of 2005 it appeared that certain species were responding to the fertilization treatment by flowering earlier or more abundantly in the fertilization plots than in the control plots. As a result, we monitored phenological changes during the growing season of 2006 on both the nonsorted circles and the vegetated rims within each plot to determine if the changes were statistically significant.

The following plant groups or species were monitored from within a week of snowmelt (approximately end of May) to the end of July 2006: *Carex* sp., *Dryas integrifolia*, *Eriophorum vaginatum*, *Salix lanata*, *Salix arctica*, *Saxifraga oppositifolia*, *Silene acaulis*, *Arctostaphylos rubra*, *Tofieldia coccinea*, *Braya bartlettiana*, and *Pedicularis* sp. Between one and three individuals of each species, when present, were flagged on both the circle and vegetated rim of each plot. These plants were monitored every other day for the traits listed in Table 1, which were chosen and modified from those used in the International Tundra Experiment (ITEX)

TABLE 1

Phenology characteristics observed for species in both control and fertilized plots. The numbers are the sample size for each trait.

Species	Phenological traits (n)
<i>Arctostaphylos rubra</i>	First leaf bud burst (10) First open flower (9) First scarleting of leaves (9) Last green leaf turning scarlet (2)
<i>Braya bartlettiana</i>	First greening of leaves (15) First flower stalk (11) First open flower (10) First petal fading (7) Last petal fading (8)
<i>Carex</i> sp.	Emergence of first new leaf (39) First stigmas visible (5) First anthers exposed (4) First yellowing of leaves (16) First seed shed (18)
<i>Dryas integrifolia</i>	First leaf erected (40) Appearance of first color of flower bud (20) First open flower (21) Last petal shed (pulled gently) (20) First twisting of maturing seeds (13) First seed dispersal (pulled gently) (7) First yellowing or browning of leaves (36)
<i>Eriophorum vaginatum</i>	Appearance of first inflorescence bud (14) First open flower (9) First seed shed (9)
<i>Pedicularis</i> sp.	First appearance (3) First flower stalk (4) First flower open (3)
<i>Salix arctica</i>	First leaf bud burst (14) First pollen shed/first stigmas (6) All pollen shed/onset of seed dispersal (4) First yellowing of leaves (2)
<i>Salix lanata</i>	First leaf bud burst (19) First pollen shed/first stigmas (5) All pollen shed/onset of seed dispersal (5) First yellowing of leaves (14)
<i>Saxifraga oppositifolia</i>	First flower open (20) First pollination (3) First capsule open (15)
<i>Silene acaulis</i>	First open flower (4) First open anther (4) First stigma receptive (5) First capsule cracks open (at top) (6)
<i>Tofieldia coccinea</i>	First flower stalk (3) First open flower (3)

(Molau and Edlund, 1996). The date for each characteristic was averaged for each species within a plot.

ABOVEGROUND BIOMASS

In mid July of 2006 aboveground biomass was sampled at each of the 20 plots. Two samples were taken from each plot, one from the nonsorted circle and one from the vegetated rim that surrounds the circle. A 20 cm by 20 cm quadrat was selected to represent the plot vegetation, and an intact sample of aboveground vegetation and soil to a depth of approximately 10 cm was removed from the tundra. Each quadrat was then placed on ice and transported back to the lab, where it was processed within 36 hours of collection. All live vegetation was removed and

TABLE 2

Nitrogen supply rate ($\mu\text{g N cm}^{-2}$ burial period $^{-1}$, mean \pm 1SE) for control and fertilized plots over 3 measurement periods ($n = 60$; summer 2005: 14 June to 7 August; winter 2005: 7 August 2005 to 1 June 2006; and summer 2006: 1 June to 15 July).

Treatment	Summer 2005	Winter 2005	Summer 2006
Control	2.51 \pm 0.40	2.33 \pm 0.78	2.68 \pm 0.44
Fertilized	112.93 \pm 4.68	121.87 \pm 1.81	124.72 \pm 4.33

divided into functional types, which included evergreen shrubs, deciduous shrubs, forbs, graminoids, moss, and lichens. Each of the plant types was divided into the following parts, when applicable: live stem, live foliar, reproductive, and standing dead. Surface litter was also collected. The samples were dried at 50°C to a constant weight, and the final weights were recorded.

The live foliar tissue of the following plant groups was also analyzed for N content: *Dryas integrifolia*, *Salix arctica*, *Arctostaphylos rubra*, *Eriophorum vaginatum*, *Carex* sp., *Saxifraga oppositifolia*, and moss. After the samples had been weighed for aboveground biomass, the plant tissue was ground and then analyzed for N content with a Carlo Erba Instruments NA 2500 elemental analyzer (Milan, Italy) (Hobbie and Gough, 2002).

STATISTICAL ANALYSIS

Statistical analyses were conducted with SAS (version 9.1 for Windows, SAS Institute, Cary, North Carolina, U.S.A.). The biomass data were analyzed with a two-way ANOVA with treatment and cover (i.e. nonsorted circle vs. vegetated rim) as the independent factors. In order to meet the assumption of homogeneity of variance, variables were transformed as necessary. The biomass data for evergreen shrubs, moss, and lichens were log-transformed, while the graminoid biomass data were square root-transformed as this transformation performed slightly better than the log-transformation in terms of adjusting the normality of the data. For these analyses we did not use a Bonferroni adjustment for the multiple tests on the biomass data set, as this is a very conservative approach (Gotelli and Ellison, 2004). However, we do indicate in the table legends which tests would be significant if the adjustment was used. If a significant effect of treatment or a significant interaction was found, orthogonal contrasts were used to compare the control circles to the fertilized circles, and the control rims to the fertilized rims.

TABLE 4

Summary of ANOVA statistics for the change in percent cover data. Significant p -value (<0.05) in bold. Underlined p -values indicate significance at a Bonferroni-adjusted alpha value.

Cover Type	Treatment		Year		Treatment * Year	
	F Value	Pr > F	F Value	Pr > F	F Value	Pr > F
Deciduous Shrub	0.31	0.5822	0.02	0.8859	0.19	0.6676
<i>Equisetum</i> sp.	2.19	0.1560	2.75	0.1147	0.00	1.0000
Evergreen Shrub	4.70	0.0438	9.29	0.0069	3.29	0.0865
Forb	0.75	0.3966	0.42	0.5261	0.58	0.4547
Graminoid	0.60	0.4501	24.22	0.0001	1.41	0.2508
Lichen	7.03	0.0163	1.26	0.2760	2.09	0.1658
Moss	0.01	0.9354	31.73	<.0001	4.49	0.0482
Cryptogamic Crust	1.46	0.2424	13.81	0.0016	0.08	0.7783
Mineral Soil	0.62	0.4418	2.44	0.1357	0.27	0.6090
Litter	0.96	0.3406	134.82	<.0001	1.39	0.2541

TABLE 3

Change in percent cover (mean \pm 1SE) of plant functional types, mineral soil, cryptogamic crust, and litter in control and fertilized treatment plots between 2004–2005 and 2004–2006 ($n = 40$).

Functional Group	2004–2005		2004–2006	
	Control	Fertilized	Control	Fertilized
Deciduous Shrub	-0.5 \pm 0.5	0.0 \pm 0.4	-0.3 \pm 0.7	-0.1 \pm 0.4
<i>Equisetum</i> sp.	0.9 \pm 0.7	0.0 \pm 0.5	0.2 \pm 0.3	-0.7 \pm 0.5
Evergreen Shrub	5.1 \pm 1.6	2.9 \pm 1.8	3.5 \pm 1.7	-3.4 \pm 1.8
Forb	0.4 \pm 1.5	2.4 \pm 0.9	1.6 \pm 1.4	2.3 \pm 1.1
Graminoid	12.7 \pm 2.5	13.1 \pm 3.3	3.1 \pm 3.2	-2.6 \pm 3.1
Lichen	2.1 \pm 1.0	-1.4 \pm 1.1	4.5 \pm 1.6	-1.7 \pm 1.9
Moss	13.9 \pm 3.0	1.1 \pm 0.9	10.2 \pm 2.1	4.4 \pm 1.7
Cryptogamic Crust	2.6 \pm 1.1	8.0 \pm 3.1	13.8 \pm 4.1	17.6 \pm 4.1
Mineral Soil	0.9 \pm 0.8	-1.8 \pm 2.0	-3.1 \pm 2.0	-3.8 \pm 2.9
Litter	0.8 \pm 1.0	0.0 \pm 0.6	25.6 \pm 2.9	30.4 \pm 2.8

The nitrogen content of the foliar tissue and phenology data were analyzed with the same model. Sample size varied for each species, therefore the analyses were adjusted depending on sample size. If samples were present for both cover types and both treatment categories, a two-way ANOVA was used, as described above for the biomass data. If samples for both treatment categories were only present in one cover type, the data were analyzed with a one-way ANOVA. The point frame (species cover) and nutrient availability data were analyzed using a repeated-measures ANOVA comparing fertilization treatment, year/time period and their interaction. As with the biomass data, no adjustment was made to the alpha value used in the cover data.

Results

NITROGEN AVAILABILITY

The fertilized plots had significantly higher N availability than the control plots during all the measurement periods (Table 2; $F = 2236.29$, $p < 0.0001$). There was no significant effect of the sampling period ($F = 2.56$, $p = 0.0921$), nor was the interaction between sampling period and treatment ($F = 2.51$, $p = 0.0959$).

VEGETATIVE COVER

Evergreen shrubs and lichen cover were significantly lower in the fertilized plots (Tables 3 and 4). Cryptogamic crust, evergreen

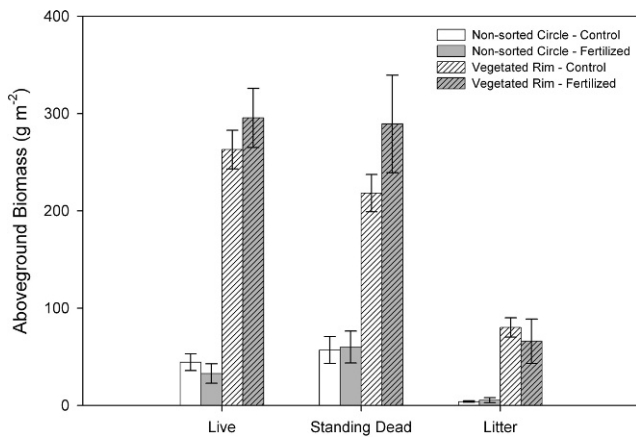


FIGURE 2. Mean aboveground biomass of live, standing dead, and litter in fertilized and control treatment plots on both nonsorted circles and vegetated rims. Bars are means \pm 1SE ($n = 40$). There were no significant differences between treatments within any of the biomass categories.

shrubs, graminoids, litter, and moss varied significantly between the two years. Cryptogamic crust cover increased, while evergreen shrubs and moss decreased. Between the two years the graminoid cover decreased, while there was an increase in the amount of litter. Most of the litter that was found in 2006 was graminoid occurring in the transition between the nonsorted circle and the vegetated rim, and appeared to be the result of vole (*Microtus* sp.) activity (both the presence of burrows and the clipping of vegetation) that was not observed in previous years (personal observation). There was no significant effect of treatment on the presence of vole-related disturbance (A. Kelley, unpublished data). There was a significant effect of the interaction between year and treatment on the change in cover of moss, which was because moss coverage was slightly higher in the control plots than the fertilized plots in 2005, but lower than the fertilized plots in 2006.

PHENOLOGY

Of the traits listed in Table 1, the only species that showed a significant effect of fertilization were *Saxifraga oppositifolia* and *Braya bartlettiana*. There was a significant interaction between the fertilization treatment and cover type on the date of the first *S. oppositifolia* flower opening ($F = 23.58$, $p = 0.0003$), with the flowers on the fertilized vegetated rims opening sooner than the control. However, the opposite effect was seen in the *S. oppositifolia* flowers on the circles with the control flowers opening earlier than the fertilized flowers. The date of the emergence of the flower stalk and the first flower opening of *B. bartlettiana* ($F = 13.5$, $p = 0.0051$, and $F = 9.76$, $p = 0.0142$, respectively) were also significantly influenced by fertilization on the circles (no *B. bartlettiana* individuals were found on the vegetated rims). The emergence of

the *B. bartlettiana* flowering stalk and first open flower occurred earlier in the fertilized plots (data not shown).

ABOVEGROUND BIOMASS

There was no significant effect of the fertilization treatment on aboveground total live biomass, standing dead biomass, or loose litter in either the circles or the vegetated rims (Fig. 2, Table 5). However, there was a significant interaction between the fertilization treatment and cover type on graminoid biomass (Fig. 3, Table 6). The addition of fertilizer significantly increased biomass on the vegetated rims relative to the control vegetated rims, but did not significantly change biomass on the nonsorted circles. Moss was significantly affected by the fertilization treatment, which showed an overall decrease in the moss biomass with the addition of fertilizer.

FOLIAR NITROGEN CONTENT

All the sampled foliar tissue showed greater concentrations of N in the fertilized plots; however statistically, the only significant differences were seen for *Dryas integrifolia* and *Eriophorum vaginatum* from both the nonsorted circles and vegetated rims, and *Carex* spp. on the nonsorted circles only (Table 7).

Discussion

MOIST NONACIDIC TUNDRA

The moist nonacidic tundra at this study site is limited by N, as is indicated by the increase in graminoid biomass (a dominant system component; Table 2) with fertilization. This response is similar to that found by Gough and Hobbie (2003) at a well-vegetated moist nonacidic tundra (MNT) site near Toolik Lake, Alaska, where there was an increase in graminoid and forb biomass, without an overall community response (i.e. no increase in total biomass) with the addition of N fertilizer. The two dominant forms of graminoids (*Eriophorum vaginatum* and *Carex* sp.) in our study showed a significant increase in foliar N concentration with fertilization, indicating that they may be better at competing for N in these systems relative to other species. McKane et al. (2002) showed through a ^{15}N tracer study that tundra plants in moist acidic tundra develop specific soil N niches. For example, *Carex bigelowii* was best adapted to utilizing NO_3^- -N, the least common type of N in acidic arctic systems (Atkin, 1996), as well as in low-arctic nonacidic ecosystems (Hobbie and Gough, 2002; Kelley, 2007). This species may have been able to take advantage of the high amounts of NO_3^- -N added during fertilization. McKane et al. (2002) also found that *Eriophorum vaginatum* was best adapted to naturally available soil N regimes, and therefore would be able to take advantage of the addition of both NH_4^+ -N and NO_3^- -N in our study.

TABLE 5

Summary of ANOVA statistics for the total aboveground biomass data. Significant p -value (<0.05) in bold. Underlined p -values indicate significance at a Bonferroni-adjusted alpha value.

Biomass Categories	Treatment		Cover		Treatment * Cover	
	F-value	Pr > F	F-value	Pr > F	F-value	Pr > F
Live	0.29	0.5906	155.19	<0.0001	1.81	0.2602
Standing Dead	1.65	0.2073	45.94	<0.0001	1.39	0.2456
Loose Litter	2.82	0.1015	44.58	<0.0001	1.32	0.2573

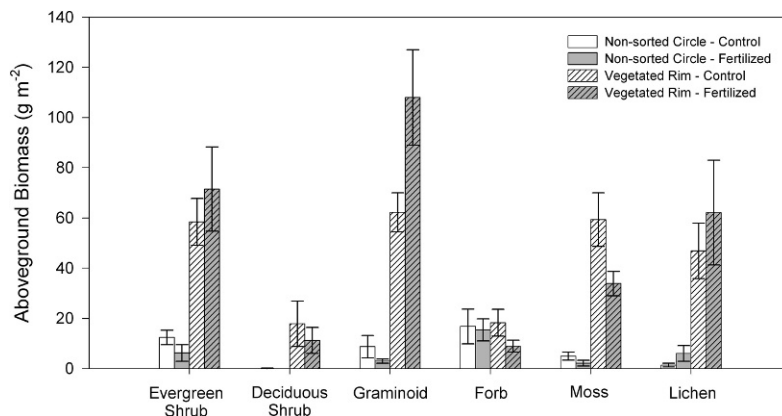


FIGURE 3. Mean live aboveground biomass by functional group in treatment plots on both nonsorted circles and vegetated rims in fertilized and control treatment plots. Bars are means ± 1 SE. Within the graminoids, there was significantly greater biomass in the fertilized vegetated rims than the control rims, but no difference between the control and fertilized nonsorted circles. There was a significant treatment effect on moss biomass, with less biomass in the fertilized plots.

Moss was the only other functional group to show a response to the fertilization and had less biomass in the fertilized plots. This is a common response in fertilization of well-vegetated tundra experiments, and this decrease is attributed to the mosses being shaded out by over-storey vegetation that has increased due to fertilization (Press et al., 1998; Shaver et al., 2001). In tundra ecosystems where the over-storey is not robust enough to shade out the nonvascular species, fertilization experiments often show either no change (Madan et al., 2007) or an increase in total moss cover (Robinson et al., 1998; Gordon et al., 2001). We did not see any increase in moss biomass on the nonsorted circles, which lack an over-storey component to the plant community. This may indicate additional limitations to moss growth. For example, Gordon et al. (2001) found that moss cover increased only with the addition of both N and phosphorus (P) fertilizer, but showed no significant increase with N alone.

Gough and Hobbie (2003) found that the addition of both N and P fertilizer caused the largest community response, although P alone did not show a large response, except for a slight increase in deciduous shrub biomass. This indicated that the addition of P enhanced the response of vegetation to N fertilization, which was especially evident in the large increase in aboveground net primary production of graminoids in their study. Our study found increased concentrations of foliar N, even in species that did not show a significant response to the fertilization in terms of biomass increase (Table 6). If P is an additional limiting factor to the vegetation, the plants may be exhibiting “luxury consumption” (Chapin, 1980; Wookey et al., 1995; Van Wijk et al., 2003) by taking up and storing N until other limiting resources (e.g. P) become more available. Further experimentation is necessary to determine whether P is limiting to the vegetation in this system.

NONSORTED CIRCLES

The response of the vegetation on the nonsorted circles to fertilization was not as pronounced as the vegetated rims. Several functional groups showed weak responses (i.e. no statistical significance) to fertilization, which may be strengthened by increasing the length of the study. Kelley (2007) found greater N concentrations in the organic soils of the stable tundra relative to the mineral soils of the disturbed patterned-ground features at this study site. Net N mineralization also differed between the nonsorted circle soils and the stable tundra soils, with the intercircle tundra exhibiting net immobilization of inorganic nitrogen and the nonsorted circle having positive rates of net N mineralization. This suggests that the intercircle tundra was more limited by N than the nonsorted circles, and may partially explain why the vegetation on the rims showed a greater response than the nonsorted circle vegetation to the fertilization treatment. The increases in foliar N content for plants on nonsorted circles (Table 7) indicate that N availability affects nonsorted circle plant communities, but it is likely that some other mechanism also limits plant biomass on these features relative to the surrounding stable vegetation, such as natural disturbance (e.g. frost heave or needle ice formation) and differences in seed availability.

Frost heave can apply a large amount of stress on the roots of plants that are establishing on the surfaces of nonsorted circles. Jonasson and Callaghan (1992) found that certain types of plants growing on heaving, sorted polygons in subarctic tundra were better able to withstand the amount of force of frost heave because of their root structure, and were often more common on these disturbed surfaces. For example, forbs and graminoids had more fibrous roots that were better at withstanding the force of the soil heaving, unlike the rhizomatous or woody roots of the plants dominant in the stable soils. Additionally, forbs and graminoids

TABLE 6

Summary of ANOVA statistics for the live aboveground biomass data by functional group. Bold type indicates a significant difference between the control and fertilized treatments at an alpha value of 0.05. Underlined *p*-values indicate significance at a Bonferroni-adjusted alpha value.

Functional Group	Treatment		Cover		Treatment * Cover	
	F-value	Pr > F	F-value	Pr > F	F-value	Pr > F
Evergreen Shrub	0.93	0.3402	42.26	<0.0001	3.35	0.0754
Deciduous Shrub	0.43	0.5182	7.73	0.0086	0.40	0.5302
Graminoid	1.49	0.2303	126.96	<0.0001	6.12	0.0182
Forb	1.14	0.2922	0.25	0.6228	0.62	0.4352
Moss	8.11	0.0072	123.09	<0.0001	0.43	0.5154
Lichen	1.17	0.2871	57.10	<0.0001	0.09	0.7615

TABLE 7

Nitrogen concentration of live foliar tissue of vegetation on nonsorted circles and vegetated rims in fertilized and control plots. The numbers following the species indicate the sample size for the nonsorted circles and vegetated rims, respectively. Data are presented as mean with standard error in parentheses. Bold type indicates a significant difference between the control and fertilized treatments within each cover type (nonsorted circle or vegetated rim) at an alpha value of 0.05.

Species (n)	Nonsorted Circles		Vegetated Rim	
	Control	Fertilized	Control	Fertilized
<i>Arctostaphylos rubra</i> (4)	—	—	1.38 (0.20)	2.32 (0.39)
<i>Carex</i> sp. (32)	1.61 (0.17)	2.80 (0.31)	1.68 (0.08)	2.03 (0.11)
<i>Dryas integrifolia</i> (36)	2.09 (0.28)	3.09 (0.38)	1.59 (0.11)	2.58 (0.15)
<i>Eriophorum vaginatum</i> (22)	2.23 (0.07)	4.12 (0.64)	1.83 (0.14)	2.02 (0.18)
Moss (18)	0.87 (0.13)	1.26 (0.18)	0.91 (0.08)	0.93 (0.04)
<i>Salix arctica</i> (1)	—	—	1.57 (1.57)	2.41 (0.45)
<i>Salix reticulata</i> (3)	—	—	1.73 (0.24)	2.01 (2.01)
<i>Saxifraga oppositifolia</i> (6)	1.58 (.42)	2.03 (0.74)	2.38 (2.38)	—

growing on the surfaces of heaving polygons exhibited smaller root diameter and less tensile strength as compared to the individuals growing on stable tundra. At our study site, vertical frost heave measurements for nonsorted circles were approximately 19 cm, while the stable tundra soils exhibited heave of around 2 cm (Walker et al., 2004). On the surfaces of these nonsorted circles, it is common to see individual plants that have been heaved up several centimeters out of the soil (personal observations). The formation of needle ice can uproot certain species (Sigafoos, 1952; Kade and Walker, 2008). Johnson and Neiland (1983) observed that *Carex aquatilis* plants on nonsorted circles had become detached from their rhizomes as a result of needle ice formation.

In a 20-year study of plant succession on nonsorted circles, Johnson and Neiland (1983) did not observe a specific direction of succession (i.e. accumulation of vegetation vs. loss), which was attributed to the high interannual variability of abiotic conditions, such as soil moisture, frost heave, and climate. They concluded that succession of these features was primarily controlled by abiotic factors, and it was rare for “biological forces” to take over. Plant succession on nonsorted circles occurs through two mechanisms: (1) the germination and establishment of seedlings on the bare soils of the features, and (2) the encroachment of vegetation from the surrounding stable tundra (Hopkins and Sigafoos, 1951; Johnson and Neiland, 1983). These mechanisms are the same as those governing predicted response of High Arctic vegetation communities to climate change, and are governed by factors such as increased nutrient availability (Wookey et al., 1995; Robinson et al., 1998; Madan et al., 2007).

We observed that fertilization influenced the flowering phenology of some forb species, which could increase seedling germination in future years. We also observed initial increases in *Braya bartlettiana* seedlings on two of the fertilized nonsorted circles (densities of approximately 3700 seedlings m⁻² as measured in a 10 × 10 cm plot in isolated patches relative to no noticeably dense patches of seedlings in the control plots) in the final year of this study, but a longer study or a greenhouse experiment is needed to determine if this is indeed a result of fertilization. A study of buried seed banks that included the site used in this experiment found that nonsorted circles had a lower density of buried seeds than the stable tundra (Kelley et al., in preparation). Similarly, alpine nonsorted circles had lower buried seed density than the more vegetated surrounding tundra (Sutton et al., 2006). These micro-sites also had increased germination on the nonsorted circles. Although the environmental conditions on nonsorted circles may be conducive to germination, seedling survival was

lower on the nonsorted circles (Sutton et al., 2006), and individuals were smaller in stature (Jonasson and Callaghan, 1992), likely in response to the repeated disturbance associated with frost heave.

Conclusion

Overall, our results showed that nonsorted circle vegetation is not as affected by nitrogen availability as the surrounding vegetated rims, which had increased graminoid biomass and decreased moss biomass in response to N fertilization. This shows that although tundra is generally classified as being N-limited, there are small-scale variations in the controls on arctic plant community dynamics. Possible explanations for these differences in the response of the vegetation to fertilization include differences in frost heave disturbance, available seed, and nutrient availability. These results provide insight into the processes controlling vegetation accumulation on small patterned-ground features, and how heterogeneous tundra may respond to changing environmental conditions, such as increased nutrient availability.

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