

Soil Nitrogen Transformations Associated with Small Patterned-Ground Features along a North American Arctic Transect

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ABSTRACT

Small patterned-ground features (PGFs) in the Arctic have unique soil properties that vary with latitude and may greatly affect tundra biogeochemistry. Because nitrogen availability can strongly limit arctic vegetation growth, we examined how soil nitrogen transformations differ between PGFs and the surrounding inter-PGF tundra along an arctic latitudinal gradient. We collected soils at eight sites from the Alaskan Low Arctic to the Canadian High Arctic. The soils were incubated for 21 days at 9 °C and 15 °C and analysed for changes in total inorganic nitrogen, nitrate and extractable organic nitrogen (EON). We found greater nitrogen immobilisation in the surrounding inter-PGF soils than in the PGF soils. Along the latitudinal gradient, differences in net nitrogen mineralisation and EON cycling between PGF and inter-PGF soils were strongly influenced by the presence of a pH boundary within the Low Arctic and the transition between the High and Low Arctic, with greater immobilisation in the nonacidic and Low Arctic sites, respectively. Incubation temperature affected EON flux but did not affect net nitrogen mineralisation or nitrification. These results show that spatial heterogeneity at several scales can influence soil nitrogen dynamics, and is therefore an important influence on arctic ecosystem function. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS: Alaska; Canada; latitudinal gradient; micro-site; nitrogen cycling; tundra

INTRODUCTION

The Arctic contains a great variety of terrestrial ecosystem types as a result of variable environmental conditions such as climate, parent material and soil properties (Walker *et al.*, 1998; Przybylak, 2000; CAVM Team, 2003; Hamilton, 2003; Epstein *et al.*, 2004; Berner *et al.*, 2005). The interactions of climate and soils in the Arctic often cause differential frost heave, which can result in the occurrence of patterned-ground features (PGFs) in arctic tundra soils. PGFs comprise up to 74 per cent of the ground surface area at the local scale (Raynolds *et al.*, 2008) (Table 1), and typically have little to no vegetation on the surface relative to the surrounding inter-PGF tundra (Washburn, 1980).

The characteristics of PGFs change with latitude and climate. In northern polar deserts, PGFs are usually identified as small polygons ~20 to 40 cm in diameter and are typically barren (Figure 1a). The cracks that border these

features are relatively protected from wind, allowing for the growth of some vegetation (Svoboda and Henry, 1987). Further south in the High Arctic, the predominant PGF form is the non-sorted circle ~0.5 to 3 m in diameter (Figure 1b). In the High Arctic, these features are still relatively barren compared to the surrounding tundra. Non-sorted circles are also present in the Low Arctic, where they become more vegetated (Figure 1c) with decreasing latitude. In the most southern parts of the Low Arctic, the PGFs are hard to distinguish from the inter-PGF tundra (Walker *et al.*, 2004). The greatest contrasts between the vegetation cover of the PGF and the inter-PGF tundra occur in the mid-latitude regions of this arctic transect.

Although many studies have described these small PGFs and their formative processes (Washburn, 1980; Daanen *et al.*, 2008; Kessler and Werner, 2003; Peterson and Krantz, 2008), the important role that they play in controlling ecosystem properties has only recently been recognised. Most of these studies have described patterned-ground plant communities and soils (Zoltai and Tarnocai, 1981; Bockheim *et al.*, 1998; Haugland and Beatty, 2005; Kade *et al.*, 2005; Boike *et al.*, 2007; Michaelson *et al.*, 2008;

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Table 1 Description of study sites along the National American Arctic transect.

Site (Subzone)	Latitude Longitude	Dominant PGF form	Per cent PGF coverage ¹	Dominant plant community ¹		Soils ²	Depth of organic horizon (cm) ³		SWI (°C) ³	pH ⁴		Frost heave (cm) ^{3,5}
				PGF	Tundra		PGF	Tundra		PGF	Tundra	
Isachsen (A)	N 78° 47' W 103° 35'	Unvegetated, small non-sorted polygons	60	<i>Puccinellia angustata-Papaver radicatatum</i> community	<i>Saxifraga-Parmelia omphalodes</i> ssp. <i>glacialis</i> community	Fine, mixed, active, hypergelic Glacic Aquiturbel	0	9.3	5.7	6.5	6.4	9.5
Mould Bay (B)	N 76° 13' W 119° 17'	Unvegetated, small non-sorted polygons	64	<i>Hypogymnia subobscura-Lecanora epibryon</i> community	<i>Orthotrichum speciosum-Salix arctica</i> community	Coarse-silty, mixed, superactive, hypergelic Typic and Mollic Aquiturbel	0	3.0	7.7	7.5	7.1	4
Green Cabin (C)	N 73° 13' W 119° 33'	Unvegetated non-sorted circles	37	<i>Puccinellia angustata-Potentilla vahliana</i> community	<i>Dryas integrifolia-Carex rupestris</i> community, <i>Dryas integrifolia</i> variant	Sandy, mixed, active, hypergelic Typic Molliturbel	0	1.6	16	8.4	7.9	4.7
Howe Island (C)	N 70° 18' W 147° 59'	Unvegetated non-sorted circles	59	<i>Mycobolimbia lobulata-Polyblastia sendmeri</i> community	<i>Dryas integrifolia-Salix ovalifolia</i> community	Coarse-loamy, mixed, superactive, pergelic Aquic Molliturbel	0	0.4	14.8	8.6	7.9	4
Franklin Bluffs(D)	N 69° 40' W 148° 41'	Partially vegetated non-sorted circles	28	<i>Junco biglumis-Dryadetum integrifoliae</i> typicum	<i>Dryado integrifoliae-Caricetum bigelowii</i>	Silty, mixed, superactive, pergelic Ruptic-Histic Aquiturbel	0.1	16.8	24.2	8.1	8	19
Sagwon MNT (D)	N 69° 26' W 148° 40'	Partially vegetated non-sorted circles	72	<i>Junco biglumis-Dryadetum integrifoliae pedicularetosum</i>	<i>Dryado integrifoliae-Caricetum bigelowii</i>	Coarse-silty, mixed, superactive, pergelic Aquic Ochreturbel	0.6	11.4	26.5	7.9	7.6	15
Sagwon MAT (E)	N 69° 25' W 148° 41'	Well-vegetated non-sorted circles	6	<i>Anthelia juratzkana-Juncus biglumis</i> community	<i>Sphagno-Eriophoretum vaginait</i>	Coarse-silty, mixed, superactive, pergelic Ruptic-Histic Aquiturbel	1.7	9.2	26.5	5.1	5.3	9
Happy Valley (D)	N 69° 08' W 148° 50'	Well-vegetated non-sorted circles	14	<i>Cladino-Vaccinietum vitis-idaea Racomitrium lanuginosum</i> var.	<i>Sphagno-Eriophoretum vaginait</i>	Coarse-silty, mixed, superactive, pergelic Ruptic-Histic Aquiturbel	11.4	11.0	29.5	4.8	5.3	9.5

¹Raynolds *et al.* (2008) for an additional description of the plant communities, see Kade *et al.* (2005) and Vonlanthen *et al.* (2008). ²Ping *et al.* (2008) and Raynolds *et al.* (2008). ³SWI data from V. Romanovsky. ⁴Walker *et al.* (2008). ⁵Methods for frost heave measurements are described in Romanovsky *et al.* (2008). PGF = Patterned-growth feature; SWI = Summer Warmth Index (°C); MNT = moist nonacidic tundra; MAT = moist acidic tundra.

Ping *et al.*, 2008; Vonlanthen *et al.*, 2008; Walker *et al.*, 2008). Much less attention has been given to ecosystem processes, and studies of nutrient cycling in these features have historically focused on a single site (Jonasson, 1986; Biasi *et al.*, 2005a; Kaiser *et al.*, 2005; Sorensen *et al.*, 2006). In this study, we compare nitrogen (N) cycling in soils from PGFs at multiple sites along a full latitudinal gradient in the North American Arctic. To our knowledge, this is the first such study.

N is one of the most limiting nutrients for plant growth, especially in arctic tundra, where cold temperatures limit the microbial processes of decomposition and N mineralisation (Shaver and Chapin, 1980, 1995; Nadelhoffer *et al.*, 1992). Hence, plant productivity in arctic tundra is often more limited by the availability of N than the direct limitations of temperature on plant growth (Chapin *et al.*, 1995). Understanding the controls on N cycling provides insight into important ecosystem functions such as net primary productivity. Much of our knowledge about arctic N cycling has come from studies that have been focused in specific geographic areas, such as subarctic Sweden (Jonasson *et al.*, 1993; Schmidt *et al.*, 2002), the Low Arctic in northern Alaska (Chapin *et al.*, 1980; Hobbie and Gough, 2002) and the High Arctic in Svalbard (Solheim *et al.*, 1996; Robinson *et al.*, 1998). Some studies have compared nutrient cycling among different tundra sites (Giblin *et al.*, 1991; Nadelhoffer *et al.*, 1991; Schmidt *et al.*, 2002) and between a single site in the High Arctic and a single site in the sub-Arctic (Robinson *et al.*, 1995). However, no study has made a comprehensive comparison across the high-latitude tundra subzones *sensu* the CAVM Team (2003).

The goals of this study were to determine how potential soil N cycling differs in PGFs compared to that in inter-PGF tundra soils and how these patterns vary in soils collected along a latitudinal gradient in the Arctic. Given high quantities of relatively undecomposed dead organic matter (OM) with high carbon to N (C:N) ratios throughout much of the arctic tundra, net N immobilisation by microorganisms is commonly observed (Hobbie *et al.*, 2002). We hypothesise that (1) there will be greater rates of net N immobilisation (i.e. more negative net N mineralisation) in inter-PGF tundra soils relative to the PGF soils because the greater vegetation biomass in the inter-PGF tundra will result in higher inputs of organic material available for microbial decomposition. As OM content decreases with increasing latitude, we also hypothesise that (2) net N immobilisation will decrease with increasing latitude, especially within the inter-PGF tundra soils. Along the latitudinal transect, we expect that (3) the greatest differences in N cycling between PGF and inter-PGF tundra will occur at the mid-latitudinal sites, where there is the greatest contrast in vegetation coverage and therefore OM accumulation. Finally, we expect that (4) the soils incubated at higher temperatures will exhibit greater net rates of N immobilisation as microbial activity is stimulated.

METHODS

Study Sites

The eight study sites are located along a North American Arctic transect (NAAT) (Raynolds *et al.*, 2008; Walker *et al.*, 2008), which spans the complete arctic temperature gradient, from the Low Arctic in northern Alaska through the High Arctic and polar desert in the Canadian Arctic Archipelago (Walker, 2000; CAVM Team, 2003). The sites are, from south to north, Happy Valley, Sagwon moist acidic tundra (MAT), Sagwon moist nonacidic tundra (MNT), Franklin Bluffs, Howe Island, Green Cabin, Mould Bay and Isachsen (Table 1). The climate of these sites becomes colder to the north, with the Summer Warmth Index (i.e. the sum of mean monthly temperatures $> 0^{\circ}\text{C}$) declining from 29.5°C at Happy Valley to 5.7°C at Isachsen. As a result, there is a shift in the types of vegetation (Kade *et al.*, 2005; Vonlanthen *et al.*, 2008) (Table 1), and a decrease in the amount of above-ground biomass (Epstein *et al.*, 2008; Walker *et al.*, 2008). We refer to Howe Island, Green Cabin, Mould Bay and Isachsen as High Arctic sites, and the remaining four as Low Arctic sites. The latter are further divided into Low Arctic acidic sites (Happy Valley and Sagwon MAT) and Low Arctic nonacidic sites (Sagwon MNT and Happy Valley). Because of the logistical constraints associated with working at several sites along an 1800-km long gradient we conducted a controlled laboratory incubation study to impose similar conditions on the soil samples. Maps and detailed descriptions of the study sites along the NAAT are given by Raynolds *et al.* (2008) and Walker *et al.* (2008).

Soil Collection and Preparation

At each site, large samples of soils (between 2 and 5 kg of wet soil) were collected from three PGFs and three surrounding inter-PGF tundra areas (within 10 to 30 cm of the PGF) to a depth of 10 cm. This depth was chosen to sample the most biologically 'active' layer of the soil, while remaining consistent across all the sampling sites, despite differences in organic horizon depth (Table 1). All soils were collected during a 3-week period between the end of July (Canadian sites) and the beginning of August 2005 (Alaskan sites). The soils were shipped back to the University of Virginia and frozen for 6 months at -20°C . The soils from the individual PGFs were not pooled in order to determine intra-site variability. After 6 months, each set of soils was temporarily thawed at 4°C to remove large roots and rocks ($> 2\text{ mm}$) and homogenised by hand. The soils were then refrozen within 12 h until the incubation. Although repeated cycles of freezing and thawing have been shown to affect N cycling in arctic soils (Schimel and Clein, 1996), arctic tundra soils often undergo repeated freeze-thaw cycles during the spring as the active layer begins to thaw (Nobrega and Grogan, 2008).

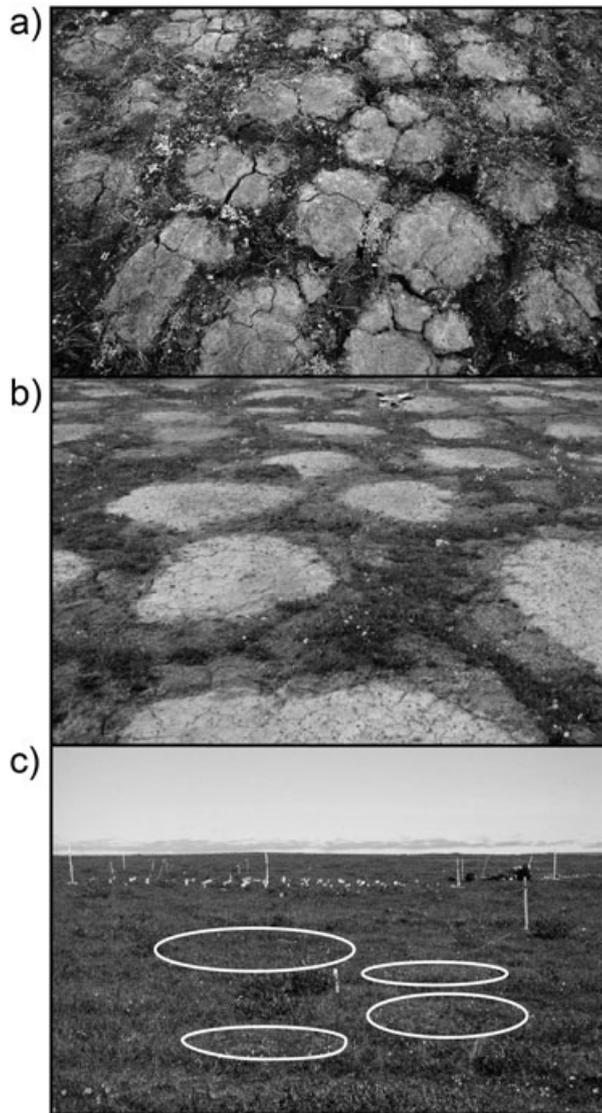


Figure 1 Photographs of dominant patterned-ground features along the latitudinal gradient: (a) barren non-sorted polygons in polar desert; (b) barren non-sorted circles in the High Arctic; and (c) vegetated circles (as indicated by white circles) in the Low Arctic.

Total Soil Carbon and Nitrogen

A sub-sample of each soil was weighed and then dried at 50 °C to constant dry weight in order to determine its gravimetric water content. The dried sample was ground, fumigated with concentrated HCl to remove carbonates (Harris *et al.*, 2001), and analysed for total organic carbon (OC) and total N with an NA 2500 elemental analyser (CE Instruments, Milan, Italy).

Incubation and Nutrient Analysis

In this study, we examine the potential rates of change of N fluxes by way of laboratory incubation. Although this

technique does not give *in-situ* rate measurements, it does have some important advantages, such as allowing us to make comparisons along the transect while using similar environmental conditions. Additionally, by focusing on potential rates of N flux we look at the capability of the soils to produce various N products based on the quality and quantity of the soil OM.

Soils were thawed at ~4 °C for ~12 h, and three sub-samples of each soil (5 g for predominately organic-rich soils and 10 g of predominately mineral soils) were extracted in 50 mL of 0.5 M K₂SO₄ for initial values of inorganic and extractable organic N (EON). The samples were then shaken for 2 h and filtered. Three additional sub-samples, at field moisture conditions, were placed into polyethylene vials and covered with gas-permeable plastic wrap to avoid water loss. No additional water was added to the soils over the course of the incubation. The soils were incubated at either 9 °C or 15 °C for 21 days. The lower temperature (9 °C) is within the range of those found during the summer months at our field sites. The purpose of the 6 °C difference between the two incubations was to determine if increasing temperature affected fluxes of N. At the end of the incubation, the soils were extracted in 50 ml of 0.5 M K₂SO₄, as described above. The filtered extracts were analysed for NH₄⁺-N and NO₃⁻-N with a QuickChem 8500 Series Flow Injection Analyzer (Lachat Instruments, Loveland, CO). The filtered extracts were also analysed for EON via persulfate digestion (Cabrera and Beare, 1993; Doyle *et al.*, 2004), which converts all N into NO₃⁻-N. The amount of EON was calculated by subtracting the extractable inorganic N (the sum of NH₄⁺-N and NO₃⁻-N) from the total N value obtained from the digested sample.

Calculation of Pools and Rates and Data Analysis

Because of the method used to obtain the soil samples we were unable to calculate bulk density of the soils. We therefore present the data in terms of grams of soil dry weight. The flux rates were calculated as the difference between the final and initial concentrations of the pool divided by the dry weight of the soil sample and the length of incubation. Net N mineralisation was defined as the difference in total inorganic N (NH₄⁺-N and NO₃⁻-N), and net nitrification as the difference in NO₃⁻-N concentrations. Net N transformation rates in arctic soils are often negative, indicating a high microbial demand for N, because the microbial community is severely limited by N availability (Mack *et al.*, 2004; Schimel and Bennett, 2004).

Fluxes of the sub-samples for each soil were averaged prior to statistical analysis. Statistical analyses were conducted with SAS (version 9.1 for Windows, SAS Institute, Cary, NC). The data were analysed with a multi-factorial ANOVA. For gravimetric soil moisture, total OC, total N, C:N ratios and pools of extractable N, a two-way ANOVA was conducted, with site and cover type (i.e. PGF or inter-PGF tundra) as the independent variables. For the incubation data, the independent variables were site, cover type and temperature (of the incubation), resulting in a three-

way ANOVA. When necessary, variables were transformed to meet the assumption of homogeneity of variance. Bonferroni-adjusted comparisons were made between cover types within each site using Tukey tests. When the effect of incubation temperature was significant, Bonferroni-adjusted comparisons were made between cover types within each temperature treatment, and between temperature treatments within each cover type.

RESULTS

Soil Characteristics

OC (%C) and total N (%N) were greater in the vegetated inter-PGF tundra soils relative to the PGF soils in the Low Arctic sites (Franklin Bluffs, Sagwon MNT, Sagwon MAT and Happy Valley), which have more organic-rich soils (Figure 2), but not significantly different in the High Arctic sites (Isachsen, Mould Bay, Green Cabin and Howe Island). Differences in %C were significant for site, cover type and their interaction ($F_{7,32} = 50.8$, $p < 0.0001$; $F_{1,32} = 269.4$, $p < 0.0001$; $F_{7,32} = 32.4$, $p < 0.0001$, respectively), as were differences in total N ($F_{7,32} = 63.4$, $p < 0.0001$; $F_{1,32} = 353.9$, $p < 0.0001$; $F_{7,32} = 35.7$, $p < 0.0001$, respectively). C:N ratios did not differ significantly among PGF soils across sites (Figure 2). The three most southern sites (Happy Valley, Sagwon MAT and Sagwon MNT) were the only sites to show significant differences in C:N ratios between the PGF and tundra soils (site: $F_{7,32} = 17.1$, $p < 0.0001$; cover: $F_{1,32} = 39.0$, $p < 0.0001$; interaction: $F_{7,32} = 4.8$, $p = 0.0010$). Similar to %C and %N, soil moisture was greater in the inter-PGF tundra soils relative to the PGF soils for the four most southern sites in the Low Arctic (Figure 2; site: $F_{7,32} = 97.2$, $p < 0.0001$; cover: $F_{1,32} = 342.4$, $p < 0.0001$; interaction: $F_{7,32} = 11.0$, $p < 0.0001$).

Rates of Potential Nitrogen Fluxes

Rates of net N mineralisation were negative in almost all the soil samples, indicating net immobilisation of inorganic N in these soils (Figure 3; Table 2). Rates of net N immobilisation in the inter-PGF tundra were significantly greater than in the PGF soils at both Franklin Bluffs and Sagwon MNT. Additionally, incubation temperature had no significant effect on the flux of inorganic N in these soils.

Net nitrification rates varied across the sites, with no apparent pattern along the latitudinal gradient (Figure 3; Table 2). Howe Island and Franklin Bluffs were the only sites that had a significant difference between the PGF and inter-PGF tundra soils. Net nitrification at Howe Island was significantly greater in the inter-PGF soils, while at Franklin Bluffs net nitrification was greater in the PGF soils. As with net N mineralisation, incubation temperature had no significant effect on these fluxes.

Similar to net N mineralisation, we found an overall net decrease in EON concentrations (i.e. net consumption of EON) in the incubated soil samples (Figure 3; Table 2). The overall rate of EON change in the PGF soils was similar across all the sites. However, at the four southern sites of the Low Arctic, we found greater rates of net EON immobilisation in the vegetated inter-PGF tundra soils than in the PGF soils. Contrary to net N mineralisation, there was a significant effect of incubation temperature on the net change in EON concentrations, particularly in the vegetated inter-PGF tundra soils at Low Arctic sites. The nonacidic sites (Franklin Bluffs and Sagwon MNT) displayed greater net immobilisation of EON in the 9 °C incubation, whereas the acidic sites (Happy Valley and Sagwon MAT) displayed greater EON immobilisation in the 15 °C incubation.

DISCUSSION

In arctic tundra, the influence of PGFs can be seen on landscape surfaces in differences in plant communities, soil structure and permafrost dynamics. These characteristics interact to cause heterogeneity of ecosystem processes such as soil N cycling at local scales, as observed in this study. As expected, potential rates of net inorganic N immobilisation were greater in the inter-PGF tundra soils compared to the PGF soils (Figure 3), supporting our first hypothesis. However, these relative differences in N cycling between PGF and inter-PGF soils varied among the sites along the latitudinal gradient, supporting our third hypothesis. Understanding why these differences occur at both the local and regional scale requires investigations into the controls on N cycling, such as OM quantity and quality, microbial communities and soil environmental conditions.

PGFs undergo cyclical disturbance (in the form of enhanced frost heave) that slows rates of vegetation colonisation and corresponding OM accumulation on the PGF surfaces relative to the surrounding tundra (Haugland and Beatty, 2005). This reduced OM layer and associated low soil N concentrations may impede plant growth on these features (Kelley and Epstein, 2009), further perpetuating the slow rates of OM accumulation on the PGFs (as indicated by low %C and %N in the PGF soils in Figure 2).

Frost-heave disturbance also influences the type of vegetation growing on PGF surfaces. For example, the plant community on PGFs is dominated by forbs, graminoids and non-vascular plants that are more resistant to physical disturbance (Jonasson and Callaghan, 1992). The PGF plant communities at our study sites have higher proportions of forb and lichen biomass and lower proportions of shrubs and mosses that contain more recalcitrant material than the inter-PGF tundra (Walker *et al.*, 2008). The varying community composition between the PGF and the inter-PGF tundra vegetation can influence rates of decomposition and nutrient cycling through the quality of litter produced (Hobbie, 1992, 1996).

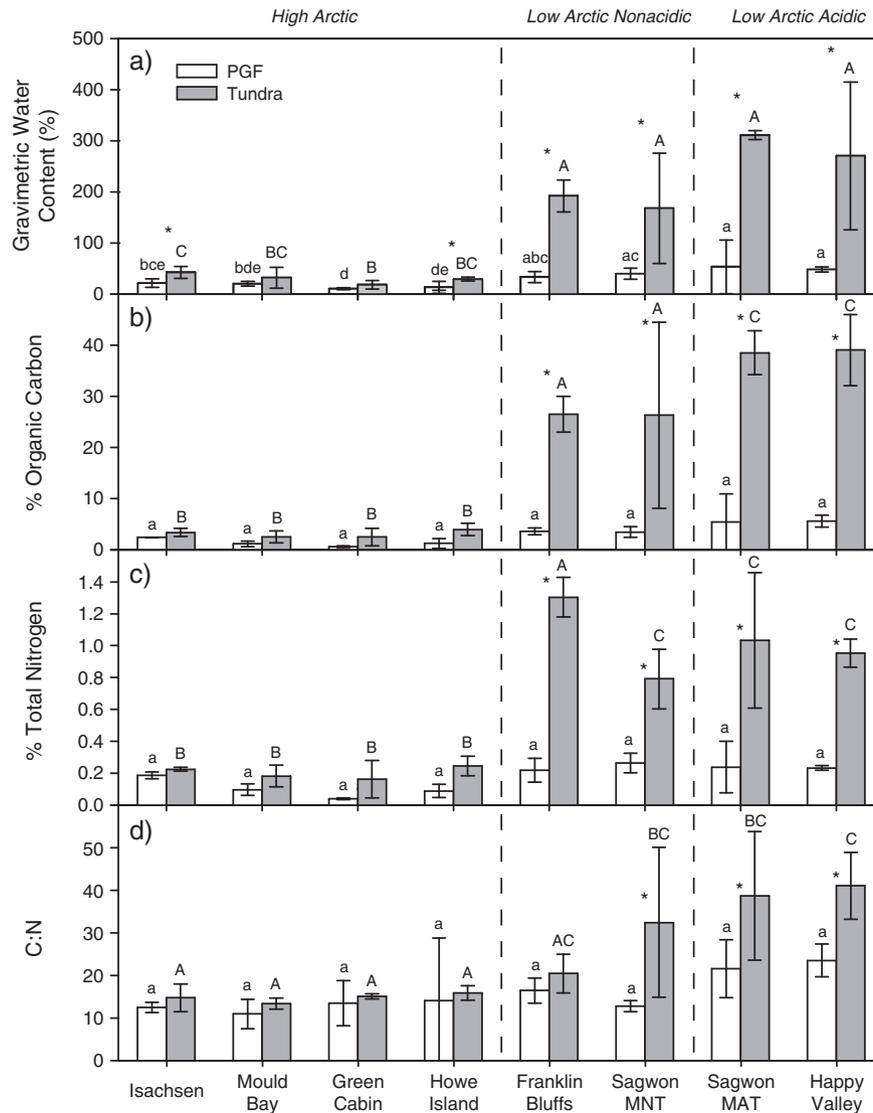


Figure 2 (a) Gravimetric water content; (b) % organic carbon; (c) % total nitrogen; and (d) C:N ratios of patterned-ground features (PGF) and tundra soils in eight sites along a North American arctic transect (mean \pm 95% confidence intervals, $n=3$). The lowercase letters above each bar indicate significant differences in PGF soils among the sites, while the uppercase letters indicate significant differences in tundra soils among the sites. * This symbol indicates a significant difference between the PGF and tundra soils within a site. Dashed lines indicate, from left to right, the border between the High Arctic and the Low Arctic, and Low Arctic nonacidic tundra and Low Arctic acidic tundra.

As hypothesised, the differences in N cycling between the PGF and inter-PGF soil varied among the study sites, and may be driven by differences in the quality and quantity of OM that vary along the latitudinal gradient. The lack of statistical difference in net N mineralisation, nitrification or EON change in the PGF soils among any of the sites corresponds with the amount of OM in these same samples. Because there is little to no OM accumulation on the surfaces of PGFs, there is little substrate for decomposition. However, the inter-PGF soils have distinct OM layers that vary in quality and quantity (Figure 2), and this becomes evident in the N-cycling patterns. For example, the largest difference in net N mineralisation between PGF and inter-

PGF soils occurred at Franklin Bluffs and Sagwon MNT (Figure 3). Contrary to our second hypothesis, net N mineralisation patterns did not follow the expected latitudinal trend, indicating that some other control was influencing these patterns. For example, these two sites were located in moist nonacidic tundra (MNT) of the Low Arctic, differentiating them from sites in the moist acidic Low Arctic or the High Arctic. The transitions between these regions have been identified as important within the Arctic, occurring over smaller geographic distances relative to the size of the entire region (Epstein *et al.*, 2004).

Our data show the influence of a distinct pH boundary on fluxes of inorganic N (Figure 3a and b), similar to several

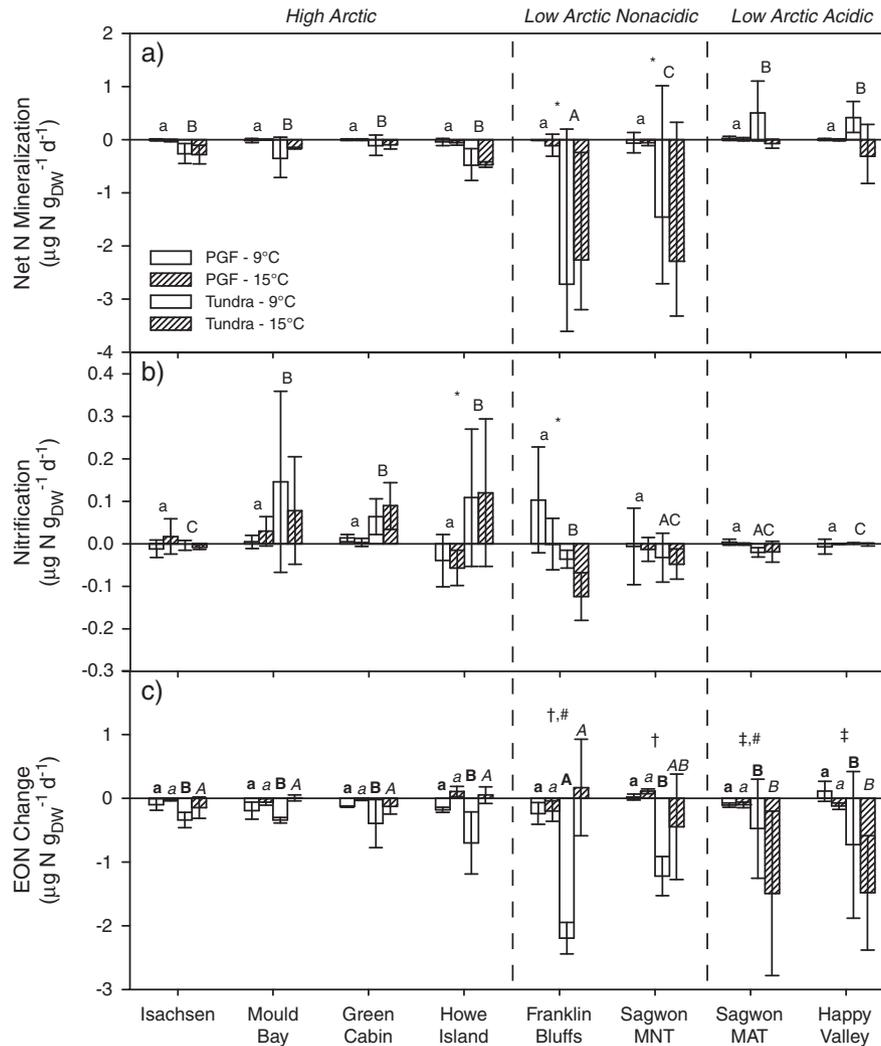


Figure 3 Rates of (a) net nitrogen mineralisation; (b) net nitrification; and (c) net change in extractable organic nitrogen (EON) in patterned-ground features (PGF) and tundra soils in eight sites along a North American arctic transect for 9°C and 15°C incubations (mean ± 95% confidence intervals, n=3). For net N mineralisation and net nitrification, the lowercase letters above each bar indicate significant differences in PGF soils among the sites, while the uppercase letters indicate significant differences in tundra soils among the sites. * This symbol indicates a significant difference between the PGF and tundra soils within a site. For net change in EON, the lowercase letters above each bar indicate significant differences in PGF soils among the sites, while the uppercase letters indicate significant differences in tundra soils among the sites with bold letters referring to the 9°C incubation and italic letters referring to the 15°C incubation. † This symbol indicates a significant difference between the PGF and tundra soils at 9°C; ‡ This symbol indicates a significant difference between the PGF and tundra soils at 15°C. # This symbol indicates a significant difference in the tundra soils between the two incubations. Dashed lines indicate, from left to right, the border between the High Arctic and the Low Arctic, and Low Arctic nonacidic tundra and Low Arctic acidic tundra.

Table 2 ANOVA summary for net nitrogen mineralisation, net nitrification and net change in extractable organic nitrogen.

Factor	Net N mineralisation		Net nitrification		Net change in EON	
	F-value	p > F	F-value	p > F	F-value	p > F
Site	7.6	< 0.0001	4.2	0.0007	5.2	0.0001
Cover	21.7	< 0.0001	2.5	0.1189	73.6	< 0.0001
Temperature	0.3	0.6218	1.6	0.2052	11.4	0.0013
Site x Cover	7.1	< 0.0001	8.5	< 0.0001	5.3	< 0.0001
Site x Temperature	0.5	0.8267	1.3	0.2785	9.2	< 0.0001
Cover x Temperature	0.2	0.6824	0.1	0.7462	5.6	0.0209
Site x Cover x Temperature	0.6	0.7761	0.5	0.8688	7.1	< 0.0001

Note: Values in bold indicate significant factors. EON = Extractable organic nitrogen.

other studies (Hobbie and Gough, 2002; Hobbie *et al.*, 2002; Nordin *et al.*, 2004). This transition from moist acidic to MNT corresponds with a shift in parent material that affects soil pH, and therefore also influences the type and amount of vegetation present. In our Low Arctic acidic tundra sites, the total biomass in the inter-PGF tundra was 3–24 per cent greater than on the PGFs, while in the Low Arctic nonacidic sites, it was 34–51 per cent greater (Walker *et al.*, 2008). Additionally, there is a large difference in the plant community structure and species present (Hobbie and Gough, 2002; Hobbie *et al.*, 2005; Kade *et al.*, 2005; Walker *et al.*, 2008). Eskelinen *et al.* (2009) found that variation in the plant community correlated significantly with soil OM quality when comparing nonacidic and acidic tundra in northern Finland. The litter of plant species present in nonacidic and acidic tundra decomposes at different rates (Hobbie and Gough, 2004), indicating that the source of soil OM in these differing habitats could strongly affect the processes controlling nutrient availability. The differing vegetation community and soil OM quality in nonacidic tundra relative to acidic tundra can also be associated with different microbial communities, which can, in turn, affect rates of N cycling (Eskelinen *et al.*, 2009).

The transition from the Low Arctic to the High Arctic is strongly influenced by climate, resulting in a landscape that changes from virtually completely vegetated – with dwarf-erect shrubs, non-tussock graminoids and mosses – to barren or semi-barren, vegetated primarily by prostrate shrubs and forbs (Polunin, 1951; Yurtsev, 1994; Walker, 2000; Epstein *et al.*, 2004). As biomass decreases with latitude, the thickness of the organic layer also decreases (Table 1). While the thickness of the organic horizon is generally much smaller in the High Arctic than in the Low Arctic, the difference in the organic horizon between PGF and inter-PGF is not nearly as distinct in the High Arctic sites compared to that in the Low Arctic sites. As a result, we observed much more similar C:N ratios between the PGF and inter-PGF in the High Arctic (Figure 2d), as well as smaller differences in net N mineralisation and EON change (Figure 3). In the High Arctic, PGFs are essentially barren (except for lichen crusts) with little OM being added to the soil, which may explain why the N flux rates in these soils were so small. Although there is more OM in the inter-PGF soils at these sites, flux rates also remained very low (Figure 3), possibly due to the colder temperatures of the High Arctic (Table 1) that may limit the activity of microbial communities.

In addition to OM quality and quantity, other site factors such as microbial community and temperature can also influence soil N flux. Microbes are responsible for the conversion of N-containing OM into forms that are usable by plants (NH_4^+ -N, NO_3^- -N and some amino acids). Other studies have shown greater microbial biomass in inter-PGF tundra soils than in PGF soils (Kaiser *et al.*, 2005; Kelley, 2007), which indicates that less microbial activity may be, in part, driving the differences in net N fluxes between the PGF and inter-PGF tundra soils. Additionally, differences in the composition

of the microbial community may also affect these responses (Biasi *et al.*, 2005b; Eskelinen *et al.*, 2009). Further studies characterising the soil microbial community and function are needed to determine what role the composition of these communities has in nutrient-cycling differences between these cover types.

Contrary to our fourth hypothesis, not all N cycling was increased at the higher incubation temperature. In fact, the influence of incubation temperature on N flux depended on the type of N examined. Net immobilisation of inorganic N did not increase with higher incubation temperature (Figure 3). Increased ambient temperature can speed up biochemical reactions, but the fact that we saw no effect of incubation temperature on net N immobilisation indicates that there is some other factor that is more limiting net N immobilisation than the ambient temperature. However, we did see a significant effect of temperature on EON flux. The presence of carbon in EON compounds may make its flux more sensitive to temperature as microbes can use these compounds as a carbon source. In this study, the influence of incubation temperature appeared to be mediated by the substrate pH. EON change was significantly different in the PGF relative to the inter-PGF during the 9 °C incubation at Franklin Bluffs and Sagwon MNT (Low Arctic nonacidic sites), while in the acidic tundra sites significant differences between the PGF and inter-PGF occurred during the 15 °C incubation. This difference in response associated with substrate pH could be caused by microbial community differences (Haynes, 1986), as well as differences in the carbon quality of the EON. The depolymerisation of soil organic N is thought to be the rate-limiting step in overall N cycling, and is the precursor to N mineralisation (Schimel and Bennett, 2004). The observed difference in temperature sensitivity of EON change compared to net N mineralisation may be occurring at the depolymerisation step; therefore, net N mineralisation may be more limited by the availability of N-containing monomers than by temperature.

Because of the method used to sample the soils for this study we were unable to calculate bulk density and, as a result, rates of potential N flux on an aerial basis. Given the large differences in OC content in the soils (Figure 2), it is likely that the bulk densities of the PGF soils are much higher than the inter-PGF soils, which would shift the magnitude of the differences between the PGF and inter-PGF soils. However, in a separate study focusing on the same sites in northern Alaska (Happy Valley, Sagwon MAT, Sagwon MNT and Franklin Bluffs), Kelley *et al.* (2007) found that field measurements of net N mineralisation rates and net nitrification rates calculated on an aerial basis were still significantly different between PGF and inter-PGF soils. Similarly, bulk density across the sites is likely to vary based on differences in soil texture (Walker *et al.*, 2011). Although the lack of bulk density data prevents us from extrapolating data to the ecosystem level, our results still show marked differences in N cycling associated with PGFs, as well as distinct latitudinal trends.

CONCLUSIONS

Although ecosystem processes such as nutrient cycling and net primary productivity are strongly determined by macroclimatic factors in the Arctic, regional and local-scale properties also have a strong influence. In this study, we determined that spatial heterogeneity associated with PGFs in arctic tundra ecosystems can cause large differences in N dynamics, which may explain the strong variation in other ecosystem properties such as net primary productivity, OM accumulation and plant community composition. The degree of difference in N cycling between the PGF and inter-PGF tundra varied along the latitudinal gradient, with the largest differences occurring in the mid-latitudinal regions. The differences in N cycling observed between PGF and inter-PGF soils along the latitudinal gradient are

likely influenced by vegetation controls on soil OM, microbial community composition and environmental differences such as soil moisture. Differences in N cycling, in turn, may influence the amount and type of vegetation present at all of these sites. However, further work on ecosystem properties such as gross N flux measurements and microbial community composition and function is needed to understand the precise mechanisms driving these trends.

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REFERENCES

- Berner J, Callaghan TV, Fox S, Furgal C, Hoel AH, Huntington H, Instanes A, Juday GP, Källén E, Kattsov VM, Klein DR, Loeng H, Martello ML, McBean G, McCarthy JJ, Nuttall M, Prowse TD, Reist JD, Steverson A, Tanskanen A, Usher MB, Vilhjálmsson H, Walsh JE, Weatherhead B, Weller G, Wrona FJ. 2005. *Arctic Climate Impact Assessment*. Cambridge University Press: New York.
- Biasi C, Wanek W, Rusalimova O, Kaiser C, Meyer H, Barsukov P, Richter A. 2005a. Microtopography and plant-cover controls on nitrogen dynamics in hummock tundra ecosystems in Siberia. *Arctic, Antarctic, and Alpine Research* **37**: 435–443.
- Biasi C, Rusalimova O, Meyer H, Kaiser C, Wanek W, Barsukov P, Junger H, Richter A. 2005b. Temperature-dependent shift from labile to recalcitrant carbon sources of arctic heterotrophs. *Rapid Communications in Mass Spectrometry* **19**: 1401–1408.
- Bockheim JG, Walker DA, Everett LR, Nelson FE, Shiklomanov NI. 1998. Soils and Cryoturbation in Moist Nonacidic and Acidic Tundra in the Kuparuk River Basin, Arctic Alaska, USA. *Arctic and Alpine Research* **30**: 166–174.
- Boike J, Ippisch O, Overduin PP, Hagedorn B, Roth K. 2007. Water, heat and solute dynamics of a mud boil, Spitsbergen. *Geomorphology* **95**: 61–73. DOI: 10.1016/j.geomorph.2006.07.033
- Cabrera ML, Beare MH. 1993. Alkaline Persulfate Oxidation for Determining Total Nitrogen in Microbial Biomass Extracts. *Soil Society of America Journal* **57**: 1007–1012.
- CAVM Team. 2003. *Circumpolar Arctic Vegetation Map*, scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. US Fish and Wildlife Service: Anchorage, Alaska.
- Chapin FS, Miller PC, Billings WD, Coyne PI. 1980. Carbon and nutrient budgets and their control in coastal tundra. In *An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska*, Brown J, Miller PC, Tieszen LL, Bunnell FL (eds). Dowden, Hutchinson and Ross: Stroudsburg, Pennsylvania; 458–486.
- Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA. 1995. Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology* **76**: 694–711.
- Daanen RP, Misra D, Epstein H, Walker D, Romanovsky V. 2008. Simulating non-sorted circle development in arctic tundra ecosystems. *Journal of Geophysical Research-Biogeosciences* **113**: G03S06.
- Doyle A, Weintraub MN, Schimel JP. 2004. Persulfate Digestion and Simultaneous Colorimetric Analysis of Carbon and Nitrogen in Soil Extracts. *Soil Science Society of America Journal* **68**: 669–676.
- Epstein HE, Beringer J, Gould WA, Lloyd AH, Thompson CD, Chapin III FS, Michaelson GJ, Ping CL, Rupp TS, Walker DA. 2004. The nature of spatial transitions in the Arctic. *Journal of Biogeography* **31**: 1917–1933.
- Epstein HE, Walker DA, Reynolds MK, Jia GJ, Kelley AM. 2008. Phytomass patterns across a temperature gradient of the North American arctic tundra. *Journal of Geophysical Research-Biogeosciences* **113**: G03S02. DOI: 10.1029/2007jg000555lissn 0148–0227
- Eskelinen A, Stark S, Mannisto M. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. *Oecologia* **16**: 113–123.
- Giblin AE, Nadelhoffer KJ, Shaver GR, Laundre JA, McKerron AJ. 1991. Biogeochemical Diversity Along a Riverside Toposequence in Arctic Alaska. *Ecological Monographs* **61**: 415–435.
- Hamilton TD. 2003. Glacial Geology of the Toolik Lake and Upper Kuparuk River Regions. University of Alaska Fairbanks, Institute of Arctic Biology, Fairbanks, AK.
- Harris D, Horwath WR, van Kessel C. 2001. Acid Fumigation of Soils to Remove Carbonates Prior to Total Carbon or Carbon-13 Isotopic Analysis. *Soil Science Society of America Journal* **65**: 1853–1856.
- Haugland JE, Beatty SW. 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography* **32**: 145–153.
- Haynes RJ. 1986. The Decomposition Process: Mineralization, Immobilization, Humus Formation, and Degradation. In *Mineral Nitrogen in the Plant-Soil System*, Haynes RJ (ed). Academic Press, Inc.: London; 52–126.
- Hobbie SE. 1992. Effects of Plant-Species on Nutrient Cycling. *Trends in Ecology & Evolution* **7**: 336–339.
- Hobbie SE. 1996. Temperature and Plant Species Control Over Litter Decomposition in Alaskan Tundra. *Ecological Monographs* **66**: 503–522.
- Hobbie SE, Gough L. 2002. Foliar and Soil Nutrients in Tundra on Glacial Landscapes of Contrasting Ages in Northern Alaska. *Oecologia* **131**: 453–462.
- Hobbie SE, Gough L. 2004. Litter Decomposition in Moist Acidic and Non-Acidic Tundra With Different Glacial Histories. *Oecologia* **140**: 113–124.
- Hobbie SE, Miley TA, Weiss MS. 2002. Carbon and nitrogen cycling in acidic and nonacidic tundra with different glacial histories in northern Alaska. *Ecosystems* **5**: 761–774.
- Hobbie SE, Gough L, Shaver GR. 2005. Species Compositional Differences on Different-Aged Glacial Landscapes Drive Contrasting Responses of Tundra to Nutrient Addition. *Journal of Ecology* **93**: 770–782.

- Jonasson S. 1986. Influence of frost heaving on soil chemistry and on the distribution of plant growth forms. *Geografiska Annaler* **68 A**: 185–195.
- Jonasson S, Callaghan TV. 1992. Root Mechanical-Properties Related to Disturbed and Stressed Habitats in the Arctic. *New Phytologist* **122**: 179–186.
- Jonasson S, Havström M, Jensen J, Callaghan TV. 1993. In situ mineralization of nitrogen and phosphorus of arctic soils after perturbations simulating climate change. *Oecologia* **95**: 179–186.
- Kade A, Walker DA, Reynolds MK. 2005. Plant communities and soils in cryoturbated tundra along a bioclimate gradient in the Low Arctic, Alaska. *Phytocoenologia* **35**: 761–820.
- Kaiser C, Meyer H, Biasi C, Rusalimova O, Barsukov P, Richter A. 2005. Storage and mineralization of carbon and nitrogen in soils of a frost-boil tundra ecosystem in Siberia. *Applied Soil Ecology* **29**: 173–183.
- Kelly AM. 2007. Soil Nitrogen Cycling and Vegetation Dynamics Associated with Arctic Patterned-Ground Features, Department of Environmental Sciences: University of Virginia, Charlottesville; 169.
- Kelley AM, Epstein HE. 2009. Effects of Nitrogen Fertilization on Plant Communities of Nonsorted Circles in Moist Nonacidic Tundra, Northern Alaska. *Arctic, Antarctic, and Alpine Research* **41**: 119–127.
- Kessler MA, Werner BT. 2003. Self-Organization of Sorted Patterned Ground. *Science* **299**: 380–383.
- Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin III FS. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431**: 440–443.
- Michaelson GJ, Ping CL, Epstein H, Kimble JM, Walker DA. 2008. Soils and frost boil ecosystems across the North American Arctic Transect. *Journal of Geophysical Research-Biogeosciences* **113**: G03S11.
- Nadelhoffer KJ, Giblin AE, Shaver GR, Laundre JA. 1991. Effects of Temperature and Substrate Quality on Element Mineralization in 6 Arctic Soils. *Ecology* **72**: 242–253.
- Nadelhoffer KJ, Giblin AE, Shaver GR, Linkins AE, Chapin III FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J. 1992. Microbial processes and plant nutrient availability in arctic soils. In *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*, Chapin FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds). Academic Press, Inc.: San Diego, California; 281–300.
- Nobrega S, Grogan P. 2008. Landscape and Ecosystem-Level Controls on Net Carbon Dioxide Exchange along a Natural Moisture Gradient in Canadian Low Arctic Tundra. *Ecosystems* **11**: 377–396.
- Nordin A, Schmidt IK, Shaver GR. 2004. Nitrogen Uptake by Arctic Soil Microbes and Plant in Relation to Soil Nitrogen Supply. *Ecology* **85**: 955–962.
- Peterson RA, Krantz WB. 2008. Differential frost heave model for patterned ground formation: Corroboration with observations along a North American arctic transect. *Journal of Geophysical Research-Biogeosciences* **113**: G03S04.
- Ping CL, Michaelson GJ, Kimble JM, Romanovsky VE, Shur YL, Swanson DK, Walker DA. 2008. Cryogenesis and soil formation along a bioclimate gradient in Arctic North America. *Journal of Geophysical Research-Biogeosciences* **113**: G03S12.
- Polunin N. 1951. The real Arctic: Suggestions for its delimitation, subdivision and characterization. *Journal of Ecology* **39**: 308–315.
- Przybylak R. 2000. Temporal and Spatial Variation of Surface Air Temperature over the Period of Instrumental Observations in the Arctic. *International Journal of Climatology* **20**: 587–614.
- Reynolds MK, Walker DA, Munger CA, Vonlanthen CM, Kade AN. 2008. A map analysis of patterned-ground along a North American Arctic Transect. *Journal of Geophysical Research-Biogeosciences* **113**: G03S03.
- Robinson CH, Wookey PA, Parsons AN, Potter JA, Callaghan TV, Lee JA, Press MC, Welker JM. 1995. Responses of Plant Litter Decomposition and Nitrogen Mineralisation to Simulated Environmental Change in a High Arctic Polar Semi-Desert and a Subarctic Dwarf Shrub Heath. *Oikos* **74**: 503–512.
- Robinson CH, Fisher PJ, Sutton BC. 1998. Fungal Biodiversity in Dead Leaves of Fertilized Plants of *Dryas Octopetala* From a High Arctic Site. *Mycological Research* **102**: 573–576.
- Romanovsky VE, Marchenko, SS, Daanen R, Sergeev DO, Walker DA. 2008. Soil climate and frost heave along the Permafrost/ Ecological North American Arctic Transect. In *Proceedings of the Ninth International Conference on Permafrost*. Kane DL, Hinkel KM (eds). Institute of Northern Engineering: Fairbanks, AK; **2**: 1519–1524.
- Schimel JP, Bennett J. 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* **85**: 591–602.
- Schimel JP, Clein JS. 1996. Microbial Response to Freeze-Thaw Cycles in Tundra and Taiga Soils. *Soil Biology and Biochemistry* **28**: 1061–1066.
- Schmidt IK, Jonasson S, Shaver GR, Michelsen A, Nordin A. 2002. Mineralization and Distribution of Nutrients in Plants and Microbes in Four Arctic Ecosystems: Responses to Warming. *Plant and Soil* **242**: 93–106.
- Shaver GR, Chapin FS. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. *Ecology* **61**: 662–675.
- Shaver GR, Chapin FS. 1995. Long-Term Responses to Factorial, NPK Fertilizer Treatment by Alaskan Wet and Moist Tundra Sedge Species. *Ecography* **18**: 259–275.
- Solheim B, Endal A, Vigstad H. 1996. Nitrogen Fixation in Arctic Vegetation and Soils From Svalbard, Norway. *Polar Biology* **16**: 35–40.
- Sorensen PL, Jonasson S, Michelsen A. 2006. Nitrogen fixation, Denitrification, and Ecosystem Nitrogen Pools in Relation to Vegetation Development in the Subarctic. *Arctic, Antarctic, and Alpine Research* **38**: 263–272.
- Svoboda J, Henry GHR. 1987. Succession in marginal arctic environments. *Arctic and Alpine Research* **19**: 373–384.
- Vonlanthen C, Walker DA, Reynolds MK, Kade A, Kuss P, Daniels FJA, Matveyeva NV. 2008. Patterned-ground plant communities along a bioclimate gradient in the High Arctic, Canada. *Phytocoenologia* **38**: 23–63.
- Walker DA, Auerbach NA, Bockheim JG, Chapin FS, Eugster W, King JY, McFadden JP, Michaelson GJ, Nelson FE, Oechel WC, Ping CL, Reeburg WS, Regli S, Shiklomanov NI, Vourlitis GL. 1998. Energy and trace-gas fluxes across a Soil pH boundary in the Arctic. *Nature* **394**: 469–472.
- Walker DA. 2000. Hierarchical Subdivision of Arctic Tundra Based on Vegetation Response to Climate, Parent Material and Topography. *Global Change Biology* **6**: 19–34.
- Walker DA, Epstein HE, Gould WA, Kade AN, Kelley AM, Knudson JA, Krantz WB, Michaelson G, Peterson RA, Ping CL, Reynolds MK, Romanovsky VE, Shur Y. 2004. Frost-Boil Ecosystems: Complex Interactions Between Landforms, Soils, Vegetation and Climate. *Permafrost and Periglacial Processes* **15**: 171–188. DOI: 10.1002/ppp.487
- Walker DA, Epstein HE, Romanovsky VE, Ping CL, Michaelson GJ, Daanen RP, Shur Y, Peterson RA, Krantz WB, Reynolds MK, Gould WA, Gonzalez G, Nickolsky DJ, Vonlanthen CM, Kade AN, Kuss P, Kelley AM, Munger CA, Tarnocai CT, Matveyeva NV, Daniels FJA. 2008. Arctic

- patterned-ground ecosystems: A synthesis of field studies and models along a North American Arctic Transect. *Journal of Geophysical Research-Biogeosciences* **113**: G03S01. DOI: 10.1029/2007JG000504
- Walker DA, Kuss P, Epstein HE, Kade AN, Vonlanthen CM, Reynolds MK, Daniels FJA. 2011. Vegetation of zonal patterned-ground ecosystems along the North America Arctic bioclimate gradient. *Applied Vegetation Science* **14**: 440–463. DOI: 10.1111/j.1654-109X.2011.01149.x
- Washburn AL. 1980. *Geocryology*. Wiley: New York.
- Yurtsev BA. 1994. Floristic division of the Arctic. *Journal of Vegetation Science* **5**: 765–776.
- Zoltai SC, Tarnocai C. 1981. Some non-sorted patterned ground types in northern Canada. *Arctic and Alpine Research* **13**: 139–151.