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Comparison of Carbon and Nitrogen Storage in Mineral Soils of Graminoid and Shrub Tundra Sites, Western Greenland

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ABSTRACT

Shrub species are expanding across the Arctic in response to climate change and biotic interactions. Changes in belowground carbon (C) and nitrogen (N) storage are of global importance because Arctic soils store approximately half of global soil C. We collected ten (60 cm) soil cores each from graminoid- and shrub-dominated soils in western Greenland and determined soil texture, pH, C and N pools, and C:N ratios by depth for the mineral soil. To investigate the relative chemical stability of soil C between vegetation types, we employed a novel sequential extraction method for measuring organo-mineral C pools of increasing bond-strength. We found that: (i) mineral soil C and N storage was significantly greater under graminoids than shrubs (29.0 ± 1.8 versus 22.5 ± 3.0 kg C m$^{-2}$ and 1.9 ± .12 versus 1.4 ± 1.9 kg N m$^{-2}$); (ii) chemical mechanisms of C storage in the organo-mineral soil fraction did not differ between graminoid and shrub soils; and (iii) weak adsorption to mineral surfaces accounted for 40-60% of C storage in organo-mineral fractions—a pool that is relatively sensitive to environmental disturbance. Differences in these C pools suggest that rates of C accumulation and retention differ by vegetation type, which could have implications for predicting future soil C pool storage.

KEY WORDS: Shrubification, Arctic, Climate Change, Grass, Dwarf Shrub
INTRODUCTION

The Arctic is warming more rapidly than other parts of the world as a result of polar amplification of climate change (Masson-Delmotte et al. 2013). Arctic ecosystems tend to be sensitive to physical disturbance (Reynolds and Tenhunen 1996; Stow et al. 2004), and significant climate-driven changes in the Arctic are expected in plant production and belowground processes (Hill and Henry 2011; Ciais et al. 2013). For example, the expansion and increased growth rate of shrub species across the Arctic has been documented over the last 50 years (Sturm, Racine and Tape 2001; Stow et al. 2004; Tape, Sturm and Racine 2006; Elmendorf et al. 2012; Urban et al. 2014). Woody plant cover is expected to increase by up to 52% by 2050 (Pearson et al. 2013).

Arctic shrub expansion includes increases in the cover, abundance and biomass of woody plant species (Myers-Smith et al. 2011). Deciduous shrub expansion has been clearly linked to temperature and moisture conditions, with shrub expansion being greater on warmer, wetter sites (Elmendorf et al. 2012). Changes in herbivory patterns (Post and Pedersen 2008; Cahoon et al. 2012) and human and natural disturbance to ecosystems influence shrub expansion (Normand et al. 2013; Myers-Smith et al. 2011), as do nutrient availability and soil temperature (Tape et al. 2012). While shrub expansion affects ecosystem processes on local and regional scales, the phenomenon holds global importance due to the critical role of vegetation in carbon (C) uptake and sequestration and the large C stores in high-latitude soils.

Pan-Arctic shifts in vegetation may cause feedbacks to climate (Sturm et al. 2001), but there is much uncertainty as to the magnitude and direction of those feedbacks (Pearson et al. 2013). Whereas some research suggests that attributes of shrubby plant
communities, such as woody, recalcitrant plant litter and increases in aboveground biomass, may increase landscape C storage (Cornelissen, van Bodegom and Aerts 2007), other findings show that increased evapotranspiration and decreased albedo with shrub expansion will amplify regional warming (Chapin et al. 2005; Pearson et al. 2013). This study investigates the effects of shrub expansion on belowground processes, such as soil C and nitrogen (N) cycling.

Arctic soils are of particular importance to global climate because high-latitude soils, including permafrost, contain up to 50% percent of global soil C (Tarnocai et al. 2009; Hugelius et al. 2014). Carbon accumulates in soils over thousands of years as a result of complex interactions between biotic, physical, and chemical mechanisms. In the Arctic, low temperature plays an integral role in preserving soil C by limiting microbial decomposition. Physical and chemical mechanisms of C stabilization such as occlusion in soil aggregates and adsorption to mineral surfaces, stabilize soil C as well (Marschner et al. 2008; Dungait et al. 2012). Soil C is more resistant to microbial degradation when the strength of the organo-mineral association exceeds that of the microbial enzyme active sites (Dungait et al. 2012; Lacroix, Petrenko and Friedland 2016). To this end, it is proposed that C strongly bound to mineral surfaces may not be available for biological degradation under warming scenarios (Davidson and Janssens 2006; Höfle et al. 2013; Tang and Riley 2014). However, we know little about the physical and chemical properties of C stabilization in the active layer of soil (Höfle et al. 2013).

Nitrogen, another critical ecosystem component, may also be affected by shrub expansion. However, limited research has been conducted to understand how mineral soil N pools may change with shifting vegetation. Microbial communities and enzyme
production in Arctic soils are chronically N-limited (Kayoma et al. 2014; Stark, Mannisto and Eskelinen 2014). Arctic shrubs have been shown to increase significantly with N and Phosphorous (P) additions (Shaver et al. 2001), suggesting that shrub species are both N and P limited in ambient conditions. Understanding how N availability may change with shifting vegetation should improve predictions of both shrub expansion and feedbacks to climate change.

This study investigated C and N pools and C accessibility in graminoid-dominated versus shrub-dominated areas in western Greenland. Our study had an explicit focus on deeper, mineral soil because up to 75% of global soil C is stored in subsoil (Jobbágy and Jackson 2000). Furthermore, many previous studies lack measurement of the entire mineral soil profile (Mack et al. 2004). Several recent studies have improved estimates of soil C storage across the Arctic, owing to the measurement and inclusion of permafrost soils in C accounting (Tarnocai et al. 2009; Hugelius et al. 2014; Schuur et al. 2015). To our knowledge, few studies have compared mineral soil C and N pools between graminoid and shrub vegetation types. Johnson et al. (2011) reports higher C pools under graminoid than shrub vegetation for both organic and mineral soil. Furthermore, Bradley-Cook et al. (2016) found that microbial respiration in graminoid mineral soils is more sensitive to increases in temperature than shrub mineral soils, suggesting vulnerability of the graminoid soil C pool to changes in climate. This study contributes an original dataset on mineral soil C and N pools in two dominant Arctic tundra vegetation types and provides baseline data to which future shifts in vegetation and changes in C and N pools can be compared.
The objectives of this study were to: (i) determine whether or not differences in aboveground vegetation and biomass in tundra ecosystems were associated with discernable differences in belowground C and N pools, and (ii) quantify differences in the stabilization of organic compounds by the mineral component of the soil strata under graminoid versus shrub vegetation.

We hypothesized that C and N pools under graminoid vegetation would be higher, given that previous studies have reported higher C pools in soils under graminoid vegetation (Ping et al. 1997; Johnson et al. 2011). Although increases in shrub cover and height can result in greater inputs of litter to above- and belowground C pools (Myers-Smith et al. 2011), this effect may be offset by the insulation effect of winter snow trapping by shrubs. Insulation from snow and warmer soil temperatures have been shown to increase soil C decomposition (Baptist, Yoccoz and Choler 2009; Nowinski et al. 2010). Furthermore, root longevity, which may influence C inputs to soil, is lower in sedges and grasses than in shrubs (<5 years for graminoids versus > 5 years for shrubs; Iversen et al. 2015).

To address our second objective, we employed a novel method of chemically extracting C pools from the organo-mineral fraction of the soil in order to assess the chemical stability of C in graminoid versus shrub soils (Lopez-Sangil and Rovira 2013). The method allowed for the extraction of C from successively more difficult-to-access mineral-bound pools (Gonzalez-Prieto et al. 1989; Lopez-Sangil and Rovira 2013) and offered a unique study of the variation in chemical stabilization of C in Arctic soils. We hypothesized that in shrub-dominated soils, a greater proportion of C would be stored in relatively stable pools, given that lignacious, woody material should persist for longer
periods of time, and, thus, become tightly bound to the mineral soil strata. Lignin is likely to displace other smaller molecules in the electrostatic competition for mineral space (Kleber et al. 2014). In contrast, the relatively labile organic compounds that characterize graminoid plants may be metabolized before being sequestered in more stable organo-mineral fractions.

**MATERIALS AND METHODS**

*Study Areas*

We collected soil cores from two tundra areas near Kangerlussuaq, Greenland in July and August 2011 (Fig. 1). Soils were humus-poor brown gelsols (Jones et al. 2009). The areas were comparable with respect to landscape age, air temperature, soil temperature and soil texture (Table 1a), but they differed in active layer depth and vegetation type and height, a measure linearly related to biomass for dwarf shrubs (Table 1b; Elzein et al. 2011). In both areas, patches of shrubs and graminoid vegetation were evident, and the accumulation of litter types beneath each vegetation type suggested these boundaries persisted for many growing seasons. Sampling took place in the center of vegetation patches in order to avoid dynamic boundaries between the two vegetation types.

We conducted our sampling in two areas that were representative of the general landscape and were affected by the Greenland Ice Sheet (GrIS) to varying degrees (i.e., varied in proximity to the GrIS). The study area closer to the GrIS was hypothesized to be colder and have lower decomposition rates and lower plant productivity. The other study area, while proximate to the terminal edge of Russell Glacier, was farther from the GrIS and, therefore, was hypothesized to experience less climatic influence from the ice
Soil and air temperature data were collected continuously with Thermocron iButtons (Model DS1921G, Embedded Data Systems®) from summer, 2011 to summer, 2012. In each study area, air temperatures were measured at one location, 30 cm aboveground and were shielded from direct sunlight. Soil temperature probes were installed at 5-cm depth at three locations within each vegetation type but not all iButtons were successfully recovered. Temperature data represent 1 to 3 replicates per vegetation type at each study area.

In our study sites, “shrub” areas were dominated by *Betula nana* with interspersed *Salix glauca*. “Graminoid” areas included grasses and sedges and were dominated by *Poa pratensis*. Percent cover of shrub, graminoid, water and fell-field within a 100-m radius of each study site was quantified from a land cover classification map. The land cover map was created in ArcGIS using multi-spectral WorldView2 images (1.34-m resolution). The first study area, referred to as “Low Biomass Area,” had 66% graminoid cover and 29% shrub cover. The second study area, referred to as “High Biomass Area,” had 47% graminoid cover and 49% shrub cover.

**Sample Collection**

We selected each study area for access and for mixed shrub and graminoid vegetation. Within these study areas, we randomly selected five spatially independent plots of each vegetation type for soil sampling. Plots were at least 10 m apart and were on well-drained soils. Soil cores were extracted (described below) from the center of each plot, resulting in 10 soil cores from each study area, or 20 deep soil cores total (10 graminoid and 10 shrub). Vegetation surveys were completed for all vascular plants in a 0.5-m x 0.5-m area in each plot, under which a soil core was collected. Vegetation cover
was assessed visually, with the percent cover of vegetation categories estimated. Biomass was not harvested for the surveys.

The Arctic brown soils were characterized by a relatively thin organic horizon, which ranged between 3 and 10 cm in depth (unpublished data). The data presented here represent the mineral horizons of the soil only, and the measurement of the depth increments began at the organic-mineral interface. The Kangerlussuaq area of Greenland lies close to the boundary between discontinuous and continuous permafrost (Tarnocai et al. 2009). We used a Smart Stick™ to measure the depth of refusal, a proxy for active layer depth, at each of our soil coring locations. Because rocks may intercept the probe, depth of refusal was measured three times at each location of soil core excavation. Mean depth of refusal was 57.6 ± 3.2 cm under shrub and 78.5 ± 3.2 cm under graminoid vegetation. All soil cores, except for one under shrub vegetation, reached the deepest target depth interval (50-60 cm).

Soil cores were extracted using a gas-powered auger (Earthquake™ 9800B) with a diamond tipped, 9.5-cm diameter drill bit and extension tube (Tools Direct™ Premium Red Diamond Drill Bit) as described in Petrenko and Friedland (2014). We carefully removed the organic soil horizon (Oi, and Oe) to the organic-mineral boundary and recorded four measurements of the organic layer depth. Then, we incrementally extracted mineral soil cores from the organic-mineral boundary in the following order: 0-10 cm; 10-20 cm; 20-30 cm; 30-40 cm; 40-50 cm; and 50-60 cm. Cores were extracted from the active soil layer only.
We sieved all soil collected from each depth interval to 12.5 mm following the methods of Huntington et al. (1988). The >12.5-mm fraction was separated into rock and root fractions, weighed in the field (±2.5 g precision), and discarded. Fresh soil weight was used to determine soil moisture. The <12.5-mm fraction was homogenized by thorough stirring in a plastic bin before collecting a weighed subsample for laboratory analyses (Vario, Neurath and Friedland 2014).

**Carbon and Nitrogen Pool Calculations**

Samples were frozen at -18 °C for storage and transport to Dartmouth College. Samples were air-dried upon thawing. Water content of the air-dry samples was determined by oven drying at 105°C for 24 hours then re-weighing. Soils were sieved to 2 mm, and the ≤ 2-mm soil fraction and ≥ 2-mm rock fraction was weighed (Vario, Neurath and Friedland 2014). Total field soil mass from each depth increment was corrected for ≥ 2-mm rock content and soil moisture before calculating bulk density. Bulk density was calculated following the hybrid method of Throop et al. (2012), which uses ≤ 2-mm soil fraction and total core volume to calculate soil mass (g) per unit volume (cm³). Subsamples from each soil sample were ground to fine powder using a ball mill.

To test for inorganic C, 1-g of ground subsample was treated with 3 M hydrochloric acid (HCL), stirred occasionally over one hour, and then reweighed (Loeppert and Suarez 1996). Mass loss was not detected, and the soils were determined to not have quantifiable amounts of inorganic C. As such, only the results of organic C analyses are reported.
Percent C and N were measured on ≤ 2-mm, ground subsamples using a Carlo-Erba elemental analyzer. Mineral soil C pools were calculated according to Huntington et al. (1988). Pools were calculated for each depth increment and then summed for the mineral profile total.

**pH and Texture Analyses**

Air-dried, ≤ 2-mm soil samples were prepared for pH analysis by making a 1:1 mixture with deionized water (DI) according to Thomas (1996). pH was measured with a VWR 8015 electroprobe calibrated with pH 4 and pH 7 buffer solutions. Texture analyses were conducted on the 2-mm soil fraction using the hydrometer method with soil dispersion in sodium-hexametaphosphate (50 g/L) as described by Gee and Bauder (1996). Soils with > 15% organic matter were treated with hydrogen peroxide at a 0.3:1 (m/v) ratio of organic matter to hydrogen peroxide and left to stand for 24 hours before texture analysis. Hydrometer readings were taken at 30 s, 60 s, 1.5 h and 24 h after mixing in columns.

**Sequential Extractions of Carbon Pools**

Sequential chemical extractions were performed on three depth intervals of the mineral soil: 0-20 cm, 20-40 cm, and 40-60 cm. Equivalent weights of ≤ 2-mm soil from two depth layers were bulked in order to test three broader depth intervals. Broader depth intervals were used in this test because of the time intensity of the method and because we did not aim to measure differences in C storage at a high depth resolution. Sequential chemical extractions procedures were adapted from the methods of Lopez-Sangil and Rovira (2013). The method included three parts: 1) shaking and dispersion of soil
samples, 2) isolating the organo-mineral soil fraction, and 3) successive chemical extractions of the organo-mineral soil fraction.

To prepare soil samples for extractions, 20 g subsamples were shaken, sonified, and passed through a 53-µm wet sieve, as described in Lacroix, Petrenko and Friedland (2016). The < 53-µm fraction of the sample was taken as the organo-mineral soil fraction, while the >53-µm was assumed to be particulate organic matter (POM). In this case, the >53-µm fraction was mostly composed of sand with very little visible POM. The < 53-µm soil fraction was flocculated using aluminum potassium sulfate, and the organo-mineral soil fraction was allowed to settle out during a two-day refrigeration (Lacroix, Petrenko and Friedland 2016). The flocculated organo-mineral fraction was transferred to a clean Falcon tube and centrifuged for 15 minutes at 2500 g before performing the sequential chemical extractions.

Sequential extractions were performed in the following order: 0.5 M potassium sulfate (K₂SO₄) to extract organic water-soluble compounds; 0.1 M sodium tetraborate (Na₂B₄O₇) at pH 9.7 to extract C compounds adsorbed to mineral surfaces by weak linkages; 0.1 M sodium pyrophosphate (Na₄P₂O₇) at pH 9.8 to extract C compounds precipitated by cations such as calcium, magnesium, iron (Fe), and aluminum; 0.1 M sodium hydroxide (NaOH) at pH 12 to extract massive soil organic matter bound by stronger mineral linkages; and 0.1 M sodium diethionite (Na₂S₂O₄) at pH 8 with a wash of 0.1 M NaOH to extract organic compounds bound by Fe oxides and hydroxides. After the sequence of extractions, the remaining C in the pellet was assumed to be stable.
For each chemical extraction, 30 mL of the extraction solution was added to the Falcon tube and tubes were shaken by hand to re-suspend the pellet. The tubes were then attached to a table shaker and shaken overnight (approximately 16 hours). Sample tubes were centrifuged for 15 minutes at 2500 g, and the supernatant was collected in a 250-ml bottle. The pellet was extracted with the same solution until the supernatant became significantly clearer or clear. Then the next chemical extraction was performed. After the initial overnight incubation, pellets were re-suspended and shaken for 1 hr before centrifugation and collection of the supernatant (Lopez-Sangil and Rovira 2013). Total extract volume for each chemical ranged between 90-250 ml. Samples were filtered using a vacuum filtration system and Whatman® glass microfiber filters (GF/A) before measuring C content of each sample. Liquid samples were diluted between 1:20 and 1:500 with DI water and analyzed with a Shimadzu TOC-5000A. Several analytical replicates, standards and DI water blanks were analyzed for each day that the machine was in use. In order to accurately compare samples, the mass of C extracted by each chemical was normalized to 10 g dry soil weight for statistical analyses.

Statistical Analyses

After determining by t-tests that there were no significant differences in C and N pools between our two study sites (Fig. A1) and confirming similarities in all tested environmental variables, statistical tests were performed on the dataset as a whole, excluding the effect of site (n=10 for each vegetation type). We made the assumption that replicate soil cores taken within the high and low biomass study areas were independent. This assumption was based on the spatial independence of the patches from which we sampled, as graminoid and shrub patches within each study area were physically
disconnected from each other. Additionally, we sampled over a relatively large area, and in most cases distance between soil cores greatly exceeded the minimum requirement of 10 m. To test the hypotheses that mineral soil C and N are greater under graminoid vegetation, we compared both the total mineral pools to 60 cm depth and those of each individual depth increment. We tested differences in C:N ratios for each depth increment only. Changes in the C:N ratio with depth were assessed using a linear regression.

We compared the physical and chemical properties of soil C between graminoid and shrub soils by calculating both the proportion and the mass of C stored in each C pool targeted by the sequential extraction method. We tested differences between treatments for each chemical pool separately. The C pools are presented as follows: water-soluble, weakly mineral-bound, cation-bound, strongly mineral-bound, iron oxide-bound, and stable.

We used one-sided t-tests, assuming equal variance, to test for differences in C and N pools between vegetation groups. We used two-sided t-tests to test for differences in extraction pool sizes. For datasets that were right skewed, such as masses of C extracted from samples, data were log-transformed to meet normal distribution assumptions of least-squares methods. Significance was determined at $\alpha=0.05$. Analyses were performed with the Plyr package in R (Wickham 2011) and JMP11 software (JMP®, Version 11. SAS Institute Inc.). Figures were drawn in GraphPad Prism® Version 5.0 (GraphPad Software, Inc.).
RESULTS

Soil characteristics

Annual soil temperatures were similar in graminoid and shrub soils at both study areas (Table 1b). Differences in growing season temperature ranged from 0.1-0.3°C. Soil texture was comparable between graminoids and shrubs, with percent clay ranging from 5 to 7% (Table 1b). Soil pH ranged from 5.7 to 6.3 in graminoid- and shrub-dominated soils (Table 1b). Except for the 0-10 depth increment, where soil moisture was statistically significantly higher under graminoids, soil moisture was similar between graminoid and shrub soils at the time of sampling (Fig. A2). Depth of refusal, a proxy for active layer depth, was greater under graminoid vegetation (82 and 75 cm in the low and high biomass areas, respectively) than under shrub vegetation (56 and 59 cm; Table 1b).

Soil carbon and nitrogen

Total C and N pools in the mineral soil to 60 cm were significantly greater under graminoid vegetation than under shrub vegetation (Fig. 2a and b). For C, individual depth increments were not significantly higher under graminoid than shrub vegetation, except for the 50-60-cm increment (p<0.01; Fig. 3a). For N, the 0-10-, 10-20-, and 50-60-cm depth increments were significantly higher under graminoid than shrub vegetation (p<0.05, Fig. 3b).

C:N ratios varied significantly between graminoid and shrub vegetation for the 0-10-, 10-20-, 20-30-, and 30-40-cm depth increments (Fig. 4). The deepest increments that we tested (40-50 and 50-60 cm) showed no difference between graminoid and shrub soils. In graminoid soils, the C:N ratio increased significantly with depth (p=0.001, r-squared=0.90; Fig. 4).
Carbon storage mechanisms

Carbon compounds weakly adsorbed to mineral surfaces accounted for 40-60% of organo-mineral C storage in both graminoid and shrub soils (Fig. 5). The second-largest organo-mineral C pool was SOM more strongly bound to mineral surfaces, accounting for approximately 20-25% of storage. The proportion of C stored in the cation-bound pool was significantly higher in shrub soils than in graminoid soils in the 20-40-cm depth increment (Fig. 5). Aside from this difference, the proportions of C among the targeted organo-mineral pools were similar between graminoid and shrub vegetation in the 0-20-, 20-40-, and 40-60-cm depth increments.

The mass of C stored in the cation-bound pool was significantly higher in shrub soils than in graminoid soils in the 20-40-cm depth increment (Fig. 6). Otherwise, the masses of C stored in different organo-mineral pools were similar between the two vegetation types and among soil depths (Fig. 6).
DISCUSSION

Homogeneity of the Study Areas

Our study sites were chosen based on differences in plant height (a proxy for biomass) across a heterogeneous landscape near the GrIS margin. Plant height has been hypothesized to indirectly affect soil C storage via snow entrapment and subsequent insulation of the soil during the winter season (Sturm et al. 2001; Weintraub and Schimel 2005). However, despite differences in vegetation height between the low and high biomass areas, there were no corresponding differences in soil C and N storage for either the graminoid or shrub soils.

We did not detect differences in air temperature, soil temperature, pH, soil texture or belowground C or N pools between the low and high biomass sites. We expected that differences in vegetation height were correlated with differences in abiotic characteristics, but the environmental variables we measured were remarkably similar between study areas. Both sampling areas were deglaciated approximately 7000 ka (Levy et al. 2012), and landscape age has been shown to have a significant effect on soil characteristics, such as C storage (Bradley-Cook and Virginia 2015). Adiabatic winds from the GrIS, which we did not measure, could be one cause for the observed differences in plant height if the winds increase evapotranspiration in an already arid environment or cause damage to plant tissues (Larcher 2003). One objective of climate-related studies in the Arctic region is not only to determine the direction and magnitude of feedbacks to climate change, but also to assess their generality (Cornelissen, van Bodegom and Aerts 2007). Because our study was confined to one area near the GrIS, we may only extrapolate our findings to other, similar, areas in western Greenland.
Carbon and Nitrogen Pools under Graminoid versus Shrub Vegetation

Our measurements of C pools (22.5 kg m$^{-2}$ under shrubs and 29.0 kg m$^{-2}$ under graminoids) were within the range of values reported in previous studies of tundra soils (Ping et al. 1997; Tarnocai et al. 2009; Johnson et al. 2011). Comparable values from other studies ranged from 22.6 kg m$^{-2}$ (Tarnocai et al. 2009) to 31.4 kg m$^{-2}$ (Ping et al. 1997). The mean difference of 6.5 kg m$^{-2}$ between treatment groups is approximately 4 times the estimated 1.6 kg m$^{-2}$ aboveground C pool in shrub tundra (Wilmking, Harden and Tape 2006). To put this difference into perspective, it is roughly equivalent to 2/3 of the aboveground C pool in a temperate hardwood forest (Fahey et al. 2005). The magnitude of difference between graminoid and shrub soil C pools highlights a critical issue in understanding C feedbacks to climate: mineral soil C pools are much larger than aboveground C pools, and potential C loss from soils with changes in vegetative cover could contribute considerable amounts of C to the atmosphere.

Given our estimate of differences in mineral soil C pools under graminoid versus shrub vegetation, and the assumption that a shift from one vegetation type to another would lead to a new equilibrium in the amounts of soil C and N, it is unlikely that potential increases in aboveground biomass with shrub expansion would offset potential differences in belowground pools. An inherent difference in these mineral soil C pools does not necessarily imply that C should be *lost* from current graminoid soils if/when shrubs encroach in the future, but it suggests rates of C accumulation and retention differ by vegetation type.

We found that N pools were significantly higher under graminoid vegetation, with a mean difference of .5 kg m$^{-2}$. In a long-term N fertilization experiment, meant to
simulate greater nutrient availability in warmer tundra soils, researchers measured a net
loss of 2.0 kg C m\(^{-2}\) over 20 years (Mack et al. 2004). Shrub encroachment onto relatively
N-rich graminoid soils could cause accelerated nutrient cycling and eventual loss of C in
the same way that N fertilization accelerated nutrient cycling in the aforementioned study.
Higher N pools may also increase the likelihood of shrub expansion into graminoid areas,
as shrubs have been shown to expand more rapidly into high-nutrient soil environments,
such as flood plains and stream corridors (Tape et al. 2012). While our study did not
include the specific landscape features that Tape et al. (2012) associated with high
nutrient environments, we were able to confirm that graminoid soils are of greater quality
(lower C:N ratio) and therefore may be susceptible to more rapid shrub encroachment.

Differences in C between vegetation types at individual depth increments were
not significant except for the 50-60-cm increment, whereas N pools were significantly
different in the 0-10-, 10-20-, and 50-60-cm depth increments. In both cases, non-
significant differences in each depth increment summed to significant differences in the
total soil profile. Significantly higher C and N pools in deeper layers of graminoid soils
could be due to buried surface horizons following loess deposits, as described by Ping et
al. (1997), or nutrient leaching to deeper soil layers (Falsone et al. 2012). While we did
not observe buried organic horizons, soil layers from core extractions could not be
reconstructed with confidence. However, we found no evidence of cryoturbation (freshly-
exposed and unsorted soil) at the soil surface.

We found no correlation between soil moisture and C pools in graminoid soils,
suggesting high soil C pools at depth are not due to anaerobic or desiccated conditions.
Soil C pools in graminoid soils were approximately the same in the 0-10-cm and 50-60-
cm depth increments, whereas C pools in shrub soils were higher at the mineral soil surface than at 50-60-cm depth (typically, soil C concentrations decrease with depth (Yoshitake et al. 2011)). This suggests C export to deeper soil under graminoid vegetation, a phenomenon that has been associated with long-term preservation of C in high latitude soils (Falsone et al. 2012). We did measure a positive correlation between soil C pools and soil moisture in shrub soils, but the relationship had a poor fit ($R^2=0.38$) and therefore cannot be reliable in interpreting trends in mineral soil C pools under shrubs. Shrub expansion has been previously shown to be sensitive to soil moisture, however, with more expansion occurring in dryer soils (Tape et al. 2012).

Active layer depth varied between graminoid and shrub areas, which may have influenced C and N storage. The active layer was deeper under graminoid vegetation than under shrub vegetation, but we confirmed that soil moisture and texture were similar between the vegetation types. Winter insulation from snowpack has been shown to increase active layer depth (Nowinski et al. 2010), but this fact contradicts our finding that the active layer is shallower under shrubs, since shrubs typically provide greater winter insulation via snow trapping (Myers-Smith et al. 2011). Our measurement of depth of refusal leaves uncertainties as to the real cause of the shallower soils. The deep soil cores in shrub areas were obstructed by rocks in the 50-60 cm depth range at several locations, and in one location the 50-60-cm depth increment could not be sampled due to rocks. Mean depth of refusal under shrubs was 57.5 cm, which is similar to the depth where rocks were encountered. It is therefore possible that the method for measuring active layer depth was inaccurate in the shallow, rocky soils that we sampled. This logic
does suggest inherent differences in the underlying bedrock conditions in the soils we sampled, though the soil texture did not differ between vegetation types.

C:N ratios were significantly higher in shrub soils than in graminoid soils, and measured values were consistent with other studies in the Arctic (Höfle et al. 2013; Sistla et al. 2013). Higher N availability in graminoid soils could lead to losses in soil C with shrub encroachment, given that nutrient additions to tundra ecosystems has been shown to cause significant C loss (Mack et al. 2004). The C:N ratio increased significantly with depth under graminoid vegetation (Fig. 4), but there was no relationship between C:N ratio and depth under shrub. The difference in C:N ratio patterns with depth may suggest a divergence in nutrient pools between graminoid and shrub soils over time, with shallower soils reflecting the chemistry of the present vegetation.

Our study assumed that vegetation patches had been stable for sufficient time for large differences in C and N content to develop and that our sampling reflected the vegetation class under which soil development had been occurring in the recent past. Two studies of shrub expansion in the Kangerlussuaq area have reported stable shrub cover (Post and Pedersen 2008; Daniels et al. 2011), while one study found shrub encroachment in places subject to human disturbance (Jørgensen, Meilby and Kollman 2013). It is thought that potential shrub expansion in the area has been hindered by caribou and muskox grazing, because in the experimental exclusion of these herbivores, shrub coverage has been shown to increase (Post and Pedersen 2008; Jørgensen, Meilby and Kollman 2013).
Overall, the assumption of prolonged stability in the spatial dimensions of the vegetation patches was supported by our findings, given that current soil properties under the vegetation types were distinctly different from each other and were consistent with expectations of respective vegetation classes. For example, C:N ratios in shrub soils were consistent with published values for C:N ratios in the plant functional types, where grasses typically have lower C:N ratios than woody plants (Hooker et al. 2008). Differences in C and N pools could also have been influenced by soil moisture, since grasses tended to dominate in less well-drained areas in some cases. However, we avoided sampling in visibly wet areas in order to minimize the effect of soil moisture. We found that the 0-10-cm depth increment under graminoid vegetation had statistically significantly higher moisture content than shrub soils, but soil moisture was the same between vegetation groups for all other mineral soil depth increments.

*Physical and Chemical Carbon Storage Mechanisms*

We found that the organo-mineral soil C pool is similarly distributed across chemical fractions in graminoid and shrub soils, which implies that neither graminoid nor shrub soils are inherently more labile in either of the soil types we investigated. The stability of soil C in the organo-mineral fraction appears to be governed by factors other than vegetation type. One pool that was significantly different between graminoid and shrub soils was the cation-bound pool in the 20-40-cm depth increment. This difference may be attributed to higher availability of cations in shrub soils either due to increased rates of weathering in the rooting zone or lower cation uptake by shrubs. Shrubs typically have deeper rooting zones than graminoids (Jackson et al. 1996), which may promote weathering of mineral substrates and increased cation availability.
Weak adsorption by minerals accounted for 40-60% of the C storage in the organo-mineral fraction of the soil across both soil types. Ecosystem disturbances can cause destabilization of C in the weak mineral pool, as soil organic matter is sequestered by relatively weak bonds (Lopez-Sangil and Rovira 2013; Lacroix, Petrenko and Friedland 2016). Although strong mineral bonds are predicted to limit microbial activity (for example, Tang and Riley 2014), our findings suggest that these physical and chemical mechanisms may not slow temperature-dependent decomposition in these soils, especially if the soils are physically disturbed.
CONCLUSION

We found significant differences in mineral soil C and N pools between graminoid and shrub dominated soils, on the order of 6.5 kg C m\(^{-2}\) and .5 kg N kg m\(^{-2}\), respectively. An inherent difference in these mineral soil C pools does not necessarily imply that C should be lost from current graminoid soils if/when shrubs encroach in the future, but it suggests rates of C accumulation and retention differ by vegetation type. Physical and chemical mechanisms of C storage in the organo-mineral fraction of the soil did not differ between graminoid and shrub soils, which suggests that although C and N inputs to belowground pools may change with shifts in vegetation, the chemical accessibility of soil C may remain similar. In the organo-mineral fraction of soil, 40-60% of C was weakly adsorbed to minerals, a pool that is relatively sensitive to environmental (i.e. warming) and physical disturbances. These results have implications for understanding the flux of greenhouse gases from Arctic soils in a changing environment.

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TABLE AND FIGURE CAPTIONS

Figure 1. Map of Low Biomass and High Biomass study areas near the Greenland Ice Sheet. There are shrub and graminoid habitats in each study area. Inset highlights the Kangerlussuaq area of Greenland.

Figure 2. Mineral soil (a) carbon pools and (b) nitrogen pools to a depth of 60 cm in graminoid- and shrub-dominated soils in western Greenland. Error bars represent ± one standard error of the mean.

Figure 3. Mineral soil (a) carbon pools and (b) nitrogen pools in 10-cm depth increments from the surface of the mineral soil to 60-cm depth for graminoid- and shrub-dominated soils in western Greenland. Error bars represent ± one standard error of the mean, and asterisks indicate statistically significant differences.

Figure 4. C:N ratios to 60-cm mineral soil depth under graminoid and shrub vegetation. Trend lines represent linear regressions of C:N ratios with soil depth. Error bars represent ± one standard error of the mean, and asterisks indicate statistically significant differences between vegetation types within the same soil depth.

Figure 5. Proportion of total extractable carbon stored in each of the organo-mineral complex pools. Carbon pools increase in chemical stability from left to right on the x-axis. Error bars represent ± one standard error of the mean, and asterisks indicate statistically significant differences between vegetation types within the same organo-mineral complex pool and soil depth.

Figure 6. Mass of carbon (normalized to 10 g dry weight) stored in organo-mineral complexes of varying accessibility. Carbon pools increase in chemical stability from left
to right on the x-axis. Error bars represent ± one standard error of the mean, and asterisks indicate statistically significant differences.

Table 1. (a) Location and environmental characteristics of Low and High Biomass study areas, and (b) characteristics of graminoid and shrub soils within each study area. Landscape ages are estimates of time since deglaciation based on measurements made at or near our study areas. Yearly temperatures are given for 2011-2012 (summer to summer), and growing season temperatures are given for May-June or May-July, 2012. Data are presented with ± one standard error of the mean.
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Figure 5.
Figure 6.
## TABLES

Table 1.

### (a) Low Biomass Area High Biomass Area

| Coordinates       | 67.149 N 50.113 W | 67.103 N 50.286 W |
|-------------------|-------------------|-------------------|
| Landscape age (ka) | ~7                | 6.9 ± 0.2         |
| Elevation (m)     | 346.6             | 232.5             |
| Air temperature (°C) | -6.0           | -6.8             |
| Growing season air temperature (°C) | 10.6 | 10.7 |

### (b) Low Biomass Area High Biomass Area

| Canopy height (cm) | 9.9 ± 0.8 | 11.2 ± 1.3 | 14.2 ± 1.0 | 20.4 ± 0.5 |
|--------------------|-----------|------------|------------|------------|
| Soil temperature (°C) | -3.3 ± 0.1 | -3.3 ± 0.3 | -2.9 ± 0.2 | -2.9 (n=1) |
| Growing season soil temperature (°C) | 3.5 ± 0.4 | 4.0 ± 0.1 | 3.7 ± 0.5 | 2.9 (n=1) |
| Depth of refusal | 82 ± 4.2 | 56 ± 5.2 | 75 ± 4.7 | 59 ± 4.3 |
| Soil pH | 5.7 ± 0.1 | 6.2 ± 0.2 | 5.8 ± 0.1 | 6.3 ± 0.1 |
| Sand (%) | 58 ± 5 | 51 ± 6 | 40 ± 3 | 45 ± 3 |
| Silt (%) | 36 ± 5 | 43 ± 5 | 52 ± 2 | 48 ± 2 |
| Clay (%) | 5 ± 2 | 6 ± 2 | 8 ± 2 | 7 ± 1 |

Levy et al. (2012)

(a) Location and environmental characteristics of Low and High Biomass study areas, and (b) characteristics of graminoid and shrub soils within each study area. Landscape ages are estimates of time since deglaciation based on measurements made at or near our study areas. Yearly temperatures are given for 2011-2012 (summer to summer), and growing season temperatures are given for May-June or May-July, 2012. Data are presented with ± one standard error of the mean.
Figure A1. Mineral soil pools of (a) carbon and (b) nitrogen for low biomass and high biomass study areas in Western Greenland. Carbon and Nitrogen pools did not differ between study areas for graminoid or shrub soils.
Figure A2. The left panel presents percent moisture (g H$_2$O per g dry soil), and the right panel presents soil bulk density to 60-cm mineral soil depth under graminoid and shrub vegetation. Error bars represent ± one standard error of the mean, and asterisks indicate statistically significant differences between vegetation types within the same soil depth.
Figure A3. Relationship between soil C pool and percent moisture under (A) graminoid and (B) shrub vegetation. Trend line represents linear regressions of C pools with soil moisture.