

Biogenic silica accumulation varies across tussock tundra plant functional type

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Abstract

1. Silica (SiO_2) accumulation by terrestrial vegetation is an important component of the biological silica cycle because it improves overall plant fitness and influences export rates of silica from terrestrial to marine systems. However, most research on silica in plants has focused on agricultural and forested ecosystems, and knowledge of terrestrial silica cycling in the Arctic, as well as the potential impacts of climate change on the silica cycle is severely lacking.
2. We quantified biogenic silica (BSi) accumulation in above and below-ground portions of three moist acidic tundra (MAT) sites spanning a 300 km latitudinal gradient in central and northern Alaska, USA. We also examined plant silica accumulation across three main tundra types found in the Arctic (MAT, moist non-acidic tundra and wet sedge tundra (WST)).
3. Biogenic silica concentrations in live *Eriophorum vaginatum*, a tussock-forming sedge that is the foundation species of tussock tundra, were not significantly ($p < .05$) different across the three main sites. Concentrations of BSi in live above-ground tissue were highest in the graminoid species ($0.55 \pm 0.07\%$ BSi in sedges from WST, and $0.27 \pm 0.01\%$ in *E. vaginatum* across the three MAT sites). Both inter-tussock tundra species and shrubs contained substantially lower BSi concentrations than *E. vaginatum*.
4. Our results have implications for how shifts in vegetation cover associated with climatic warming may alter silica storage in tussock tundra vegetation. Our calculations suggest that shrub expansion via warming will increase BSi storage in Arctic land plants due to the higher biomass associated with shrub tundra, whereas conversion of tussock tundra to WST via permafrost thaw would produce the opposite effect in the terrestrial plant BSi pool. Such changes in the size of the terrestrial vegetation silica reservoir could have direct consequences for the rates and timing of silica delivery to receiving waters in the Arctic.

KEYWORDS

Arctic, biogenic silica, shrub expansion, tundra, tussock, wetland

1 | INTRODUCTION

Research on the biologically controlled component of the global silica (SiO_2) cycle has mostly focused on aquatic ecosystems, namely the

uptake and remineralisation of silica by freshwater and marine diatom species (Litchman, Klausmeier, & Yoshiyama, 2009; Martin-Jezequel, Hildebrand, & Brzezinski, 2000). Unlike most other silica accumulating species on Earth, diatoms have an obligate relationship with silicon (Si),

requiring the element in the same molar proportions as nitrogen (N) (Redfield, Ketchum, & Richards, 1963). As a consequence, the amount of silica reaching coastal receiving waters has direct implications for global carbon cycling, as roughly a quarter of global net primary production is directly attributed to marine diatoms (Tréguer & De La Rocha, 2013).

Similar to diatoms in aquatic systems, land plants also incorporate large quantities of silica within their tissue (Cooke & Leishman, 2011; Raven, 2003). In fact, silica is found in every species of plant ever examined, and is unique in never being toxic to plants even in extremely high concentrations (Epstein, 1994). Silica also exhibits extreme concentration ranges in plants, from <0.1 to >10% by dry weight (Epstein, 1994). While silica in plants is not a required nutrient *per se*, its presence in plant tissue has a well-documented ability to improve overall plant fitness, increasing the ability of plants to withstand numerous types of biotic and abiotic stressors (Raven, 2003). Terrestrial plants take up dissolved silica (DSi) from surrounding soil solution via their roots, transport it in solution via the xylem, and deposit it as biogenic silica (BSi), an amorphous form of silica, most commonly in roots and transpiration termini (e.g. leaves) (Epstein, 1994; Frew, Allsopp, Gherlenda, & Johnson, 2016; Raven, 2003). Silica uptake by land plants, known as the terrestrial silica pump, represents a major component of the global silica cycle, equal to roughly one-third that of diatoms in the ocean (Carey & Fulweiler, 2012a).

The ultimate source of silica for biological uptake is weathering of the lithosphere, as silica is the most abundant molecule found in the Earth's crust. While geochemical factors undoubtedly play a large role in regulating rates of export to coastal systems (West, Galy, & Bickle, 2005), the uptake of silica by land plants serves to retain silica on the terrestrial landscape before it is exported to downstream receiving waters (Struyf & Conley, 2012). The degree to which this "silica filter" (Struyf & Conley, 2012) influences export rates from terrestrial to aquatic systems varies enormously, with 20%–80% of DSi found in soil solution having passed through terrestrial vegetation (Clymans et al., 2016). In turn, shifts in vegetation land cover can alter the quantity of silica stored on land and change the rates of silica export to the coastal oceans (Carey & Fulweiler, 2012b; Clymans, Struyf, Govers, Vandevenne, & Conley, 2011; Cornelis & Delvaux, 2016; Struyf & Conley, 2012).

Sedges and grasses are particularly well-known terrestrial accumulators of silica (Epstein, 1994; Raven, 2003), which means that biomes dominated by these plant types, namely agricultural, wetland, grassland, and Arctic biomes, are considered to have especially important effects on the global budget of silica (Carey & Fulweiler, 2012a). Nevertheless, compared to other regions on Earth, knowledge of silica in Arctic land plants is severely lacking.

Arctic landscapes are a mosaic of different vegetation types at multiple scales (Walker et al., 2005). At large scales Arctic tundra can be divided into broad climatic zones, with decreasing amounts of taller vegetation as latitude increases (Walker et al., 2005). At smaller scales, distribution of vegetation is dictated by sharp gradients in topography and bedrock (Giblin, Nadelhoffer, Shaver, Laundre, & McKerrow, 1991; Walker, 2000). Unlike our understanding of how much carbon is stored in above-ground tundra biomass (Epstein et al., 2012), there is

little knowledge of how much BSi is stored in tundra ecosystems, not to mention how such storage varies across the heterogeneous Arctic landscape.

Arctic landscapes are experiencing the effects of climate change to a much larger degree than lower latitude regions (Serreze & Barry, 2011). In response to warming, Arctic land cover is changing rapidly, with increases in primary productivity and shrub cover at the landscape and plot scales (Elmendorf et al., 2012; Goetz, Bunn, Fiske, & Houghton, 2005; Pearson et al., 2013; Sturm, Racine, & Tape, 2001). Warming experiments conducted across the Arctic suggest that dominance of the tundra plant communities will shift from more conservative growth forms, such as mosses and sedges, to faster growing deciduous shrubs (Walker et al., 2006).

Tussock tundra covers approximately 11% of the non-glaciated Arctic (Walker et al., 2005) and is especially dominant on the north slope of Alaska, where it eventually gives way to wet sedge tundra (WST) as one moves northward on the coastal plain (Walker et al., 2016). Tussock tundra is made up of a combination of plant functional types, with the dominant sedge *Eriophorum vaginatum* providing the typical tussock topography characteristic of these landscapes, while shrubs and mosses grow in the inter-tussock spaces (Chapin & Shaver, 1985; Chapin, van Cleve, & Chapin, 1979). To date, no study has quantified BSi accumulation in tussock tundra vegetation, one of the most common types of vegetation cover in the Arctic.

The objective of this study was to quantify BSi storage in above and below-ground portions of tundra vegetation and determine how this changes across plant functional types. To do this, we quantified BSi accumulation in dominant plant species across three tundra types (moist acidic tundra (MAT), moist non-acidic tundra (MNT), and WST). Further, because of the large spatial coverage of the MAT on the North Slope of Alaska (USA), we also quantified BSi concentrations at three MAT sites situated along a 300 km north–south gradient, which allowed us to determine how BSi accumulation changes over large spatial scales. In addition to providing baseline information on silica availability in Arctic plants, our results shed light on how shifting Arctic vegetation cover will alter the amount of silica stored in the global terrestrial vegetation reservoir.

2 | MATERIALS AND METHODS

2.1 | Site description

We conducted this study on three established research sites (Coldfoot, Toolik Lake, and Sagwon) located along a 300 km north–south gradient in Alaska (USA) (Souther, Fetcher, Fowler, Shaver, & McGraw, 2014) (Figure 1, Table 1). Toolik Lake and Sagwon are dominated by classic MAT. Coldfoot is located south of the tree line and although not technically tundra, it has extremely similar vegetation, except for a recent (last 30 years) encroachment of black spruce trees (*Picea mariana*) near the site. All three sites have tussock-forming *E. vaginatum*, along with the sedge *Carex bigelowii*, deciduous shrubs (*Betula nana*, *Salix* spp., *Vaccinium uliginosum*), evergreen shrubs (*Vaccinium vitis-idaea*, *Cassiope tetragona*) and feather and *Sphagnum* moss species

growing between tussocks (herein referred to as “inter-tussock” vegetation). Because of the similarity in vegetative composition of these sites, and for the comparison between sites, we refer to all three sites as MAT, even though we acknowledge that Coldfoot is somewhat dissimilar to the two more northern sites. We also sampled two other common tundra types at Toolik Field Station (in addition to the MAT)—MNT and WST, which is comprised on a mix of wetland *Carex* and *Eriophorum* species, particularly *C. rotundata*.

2.2 | Plant harvest

Plant samples were harvested in late June 2015, which was the period of peak biomass according to phenology data (days 180–200) in 2015 (Parker et al., in revision). At each site, above-ground harvests were conducted at three haphazardly chosen 0.25 m² plots (except Coldfoot, where five plots were established). Plots were located at least 5 m apart from one another. At each plot, replicate samples (at least 3 g) of all species present in both the tussock and inter-tussock portions of tundra within the plots were collected. Above-ground portions of bryophytes and graminoids were cut roughly 1 cm above the litter layer. We collected entire branches of shrubs, but only non-woody portions were analysed for BSi, as these are the portions of the plants where majority of BSi is deposited (Clymans et al., 2016; Cornelis, Ranger, Iserentant, & Delvaux, 2010; Epstein, 1994; Raven, 2003). Sample sizes for species growing in the inter-tussock region were lower than for tussock-forming species (*E. vaginatum*), as *E. vaginatum* was present in all tussock plots, whereas inter-tussock plots

contained a larger variety of species, but not all species were found in each plot at each site. At Coldfoot, the most southern site, we also sampled tree needles from five randomly chosen *P. mariana* trees, as this species has encroached noticeably over the last ~30 years.

Below-ground vegetation was collected with soil cores (3.5 cm diameter) down to the depth of permafrost thaw (7 to >30 cm depth). Two replicate cores were taken within the same 0.25 m² plot used for above-ground sampling. Cores were frozen immediately upon collection and sub-divided into five sub-sections based on depth (0–2 cm, 2–5 cm, 5–10 cm, 10–15 cm, 15–20 cm), although in some instances permafrost prevented cores from being collected at 20 cm depth. After sub-sectioning, cores were thawed and sieved (0.5 mm mesh) to separate below-ground vegetation from soil. Due to the challenge of separating below-ground material after freezing and drying, below-ground vegetation was not separated for live versus dead material, nor for roots versus rhizomes. However, above-ground vegetation samples were separated for live and dead material. Both above- and below-ground vegetation was thoroughly washed with deionised water, dried at 70°C for 48 hr, and then ground using a Wiley mill.

2.3 | Chemical analysis

Plant samples were analysed for BSi content using the wet alkaline chemical extraction in 1% Na₂CO₃ solution, which quantifies total Si content in the plants (Conley & Schelske, 2002). Thirty (±1) mg of material was digested in flat-bottom polyethylene bottles and placed in a hot water shaking bath (85°C at 100 rpm for 4 hr). During every digestion an internal laboratory BSi standard was included for quality control (always within 6% precision). Aliquots of DSI from the BSi extractions were analysed on a Lachat flow analyser using the molybdenum blue colorimetric method, with sodium hexafluorosilicate (Na₂SiF₆) used as the silicate standard. External DSI standards (Hach) were used to ensure accuracy and were always within 5% of the expected value. Above-ground samples were also analysed for carbon (C) and nitrogen (N) content. To do this, roughly 5 mg of dried ground sample was weighed into tin capsules and subsequently analysed using a Thermo Scientific Flash 2,000 NC elemental analyser.

All samples were processed at the Marine Biological Laboratory (USA). We used a nonparametric Kruskal–Wallis one-way ANOVA to determine if significant differences in BSi concentrations existed between field sites and between plant functional types (three or more groups of data), with post-hoc analysis completed via a Dunn test (Zar, 2010). When evaluating differences between two groups of data, we

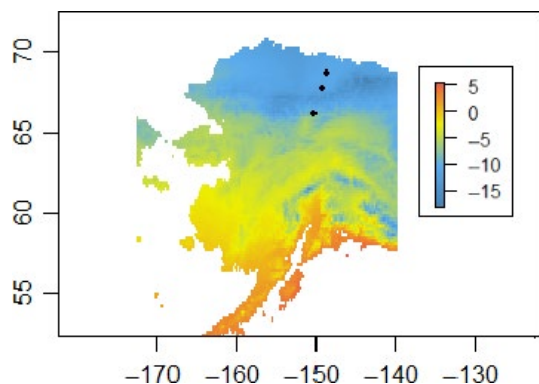


FIGURE 1 Map of field sites (solid circles). Colour refers to mean annual temperature (°C) in the state of Alaska (USA). Map created using “MAPS,” “MAPDATA,” and “RASTER” packages in R

TABLE 1 Site description and characteristics for three tundra sites

Site name	Latitude	Longitude	Elevation (m)	Annual precipitation (mm)	Thawing degree days ^a
Coldfoot	67.250	−150.183	320	414	1,615
Toolik lake ^b	68.617	−149.300	930	275	1,227
Sagwon	69.425	−148.696	305	204	912

^a2001–2011.

^bArctic Long Term Ecological Research (LTER) station. Location of MNT and Wet Sedge study site. Data from Souther et al. (2014).

used a Mann–Whitney–Wilcoxon test (e.g. for dead vs. live plants). All analysis and statistics were done in R (version 3.3.2) (R Core Team, 2015). Reported values represent mean $\pm$ SE. BSi concentrations represent percent SiO₂ by dry weight, with the exception of elemental ratios where the molecular weight of Si was used.

2.4 | Mass of BSi in above-ground tissue

We scaled the BSi concentration data to mass of BSi per unit area in the live above-ground tissue of wet sedge and tussock tundra types using biomass estimates from Shaver and Chapin (1991). For shrub (deciduous and evergreen) BSi estimates, we partitioned total shrub biomass into woody and non-woody tissue by assuming that 20% of total biomass represents leaf tissue (Johnson & Tieszen, 1976). In addition to using our measurements of BSi in shrub leaves, we estimated BSi in non-leaf above-ground tissue based on literature values of bark and woody debris observed in six temperate tree species ($0.02 \pm 0.004\%$ BSi) (Clymans et al., 2016; Cornelis, Ranger, et al., 2010).

3 | RESULTS

3.1 | Concentrations of BSi in above-ground tissue

Concentrations of BSi showed large variation across species and plant functional types. Across the three MAT sites, BSi concentrations in plant functional types ranged from $0.14 \pm 0.003\%$ in lichens to $0.31 \pm 0.02\%$ BSi in graminoid species (*C. bigelowii* and *E. vaginatum*). Across the three MAT sites, *C. bigelowii* exhibited consistently higher BSi concentrations compared to all other species ($0.45 \pm 0.04\%$), with *E. vaginatum* having the second-highest amount of BSi ($0.27 \pm 0.01\%$). The wetland sedges (dominated by *C. rotundata*) harvested from the WST contained the highest BSi concentrations within our study, with $0.55 \pm 0.07\%$ BSi observed in live above-ground tissue, while $1.44 \pm 0.15\%$ BSi and $1.43 \pm 0.71\%$ BSi were observed in dead above-ground and below-ground biomass respectively (Table 2).

BSi concentrations in live *E. vaginatum* were not significantly different across the three MAT sites. We observed no trends in above-ground BSi content that correlated with latitude (Table 2), as the mid-latitude site (Toolik) had the highest BSi concentrations in live *E. vaginatum* ($0.31 \pm 0.02\%$). Concentrations in dead *E. vaginatum* at the three MAT sites ($0.38 \pm 0.02\%$ BSi) were significantly ($p < .01$) higher than in the live tissue ($0.27 \pm 0.01\%$ BSi), but no significant variation in dead material was observed between sites. In the MNT site, BSi concentrations in the live *E. vaginatum* fell within the range observed for MAT ($0.28 \pm 0.02\%$ BSi), although concentrations in the dead MNT *E. vaginatum* were significantly ($p < .02$) higher than what was observed in MAT ($0.52 \pm 0.05\%$ BSi) (Table 2).

Species growing in inter-tussock tundra generally had lower BSi concentrations than *E. vaginatum*. This was true in all instances, except for *C. bigelowii* found in the inter-tussock at Sagwon ($0.41 \pm 0.07\%$ BSi, $n = 2$), and *C. tetragona* (1.38% BSi by wt., $n = 1$) observed at the MNT site (Table 2). The rush *Equisetum*, which was present in the two

inter-tussock MNT plots, did not have greater BSi concentrations than the other species ($0.18 \pm 0.03\%$ BSi, $n = 2$).

Evergreen and deciduous shrubs contained lower BSi concentrations than graminoid and bryophyte species (Figure 2). For example, average BSi concentrations of *Betula nana* and *Salix* spp. were 0.15 ± 0.02 ($n = 6$) and 0.18 ± 0.004 ($n = 3$) % BSi respectively, compared to concentrations of 0.45 ± 0.05 and 0.27 ± 0.02 observed in *C. bigelowii* ($n = 5$) and *E. vaginatum* ($n = 9$) respectively. Similarly, *P. mariana* sampled at Coldfoot also contained relatively low concentrations of BSi within their needles (0.13 ± 0.01 , $n = 5$). On the other hand, bryophytes (mosses) contained relatively high concentrations with an average of $0.26 \pm 0.02\%$ BSi ($n = 9$) observed across MAT sites.

3.2 | Above-ground elemental ratios

Across all species C content of leaves ranged from 38.0% to 55.0% with a mean of $44 \pm 0.27\%$, whereas N content ranged from 0.39% to 3.53% ($1.56 \pm 0.08\%$) and C:N ratios ranged from 11 to 115 (39 ± 1.95). C:N ratios in the MAT live *E. vaginatum* tussock plots ranged from 16.3 (Toolik) to 25.0 (Sagwon). Si:N ratios ranged from 0.045 at Sagwon to 0.073 at Toolik, and Si:C ratios ranged from 0.0023 at Sagwon to 0.0037 at Toolik. No significant differences in any of the nutrient ratios were observed between the three MAT sites. Average C concentrations were higher in *E. vaginatum* from the MNT site ($45.2 \pm 0.9\%$) compared to the MAT sites ($44.1 \pm 0.2\%$), but elemental ratios of C:N, Si:C and Si:N for the MNT site fell within the range observed at the MAT sites ($18.9 \pm 0.7\%$, $0.0027 \pm 0.0003\%$, $0.051 \pm 0.006\%$ respectively). Inter-tussock elemental ratios showed a large range, which were driven mainly by differences in BSi content (Table 2). Inter-tussock Si:C ratios ranged from 0.0011 to 0.016, whereas Si:N ratios ranged from 0.023 to 0.72.

Our calculations indicate that roughly 0.48 ± 0.07 g SiO₂ m⁻² is stored in above-ground graminoid biomass in the WST. In the MAT, we estimate that across plant functional types, bryophytes contained the most BSi per unit area (0.63 ± 0.11 g SiO₂ m⁻²), roughly double that of graminoids (0.34 ± 0.07 g SiO₂ m⁻²) and more than an order of magnitude more than that of deciduous (0.047 ± 0.01 g SiO₂ m⁻²) and evergreen (0.082 ± 0.01 g SiO₂ m⁻²) shrubs (Table 3). These differences in quantity of BSi stored above-ground were driven mostly by differences in total biomass rather than in BSi concentrations, as bryophytes have more than double the biomass of graminoids per unit area in the MAT (248 g/m² vs. 110 g/m²) (Shaver & Chapin, 1991). Summing these values for tussock tundra as a whole, we estimate that $1.1 (\pm 0.2)$ g SiO₂ m⁻² is stored in above-ground vascular and non-vascular biomass early in the growing season (Table 3).

3.3 | Concentrations of BSi in below-ground tissue

BSi concentrations in below-ground biomass, which includes both live and dead below-ground material, ranged from <0.001 to 4.5% BSi. We did not observe any trends in below-ground biomass BSi concentrations with depth (Figures 3 and 4), so for purposes of analysis, we report values as averages across all sample depths.

TABLE 2 Percent BSi concentration and elemental ratios of dominant plant functional types and species across all sites

		BSi (% SiO ₂)		C:N		Si:C		Si:N		
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	n
Wet sedge (<i>Carex</i> and <i>Eriophorum</i> spp.)										
Toolik	Live	0.55	0.07	16.92	0.64	0.0153	0.0022	0.1011	0.0115	3
	Dead	1.44	0.15	36.89	2.43	0.0184	0.0025	0.5830	0.0594	3
Tussock species (<i>E. vaginatum</i>)										
Coldfoot	Live	0.26	0.01	23.26	1.73	0.0027	0.0001	0.0626	0.0055	5
	Dead	0.37	0.02	82.21	13.67	0.0039	0.0002	0.3220	0.0576	5
Toolik (MNT)	Live	0.28	0.03	18.69	0.67	0.0027	0.0003	0.0512	0.0057	3
	Dead	0.52	0.07	59.47	6.12	0.0056	0.0007	0.3245	0.0244	3
Toolik (MAT)	Live	0.31	0.02	18.44	0.98	0.0079	0.0007	0.0034	0.0004	3
	Dead	0.37	0.05	55.18	3.73	0.0034	0.0006	0.0043	0.0005	3
Sagvvon	Live	0.25	0.02	18.98	1.35	0.0026	0.0002	0.0481	0.0025	3
	Dead	0.42	0.05	62.91	3.54	0.0044	0.0005	0.2764	0.0292	3
Inter-tussock species (All live tissue)										
Toolik MNT	<i>Cassiope tetragona</i>	1.38	na	46.72	na	0.0155	na	0.7249	na	1
	<i>Equisetwn</i> spp.	0.18	0.03	17.48	5.76	0.0020	0.0002	0.0353	0.0147	2
	<i>Sphagnum</i> spp.	0.40	0.21	41.50	7.62	0.0022	0.0004	0.0792	0.0031	3
	<i>Salix</i> spp.	0.62	0.43	29.59	17.30	0.0073	0.0049	0.3012	0.2717	2
	<i>Vaccinium uliginosum</i>	0.14	na	55.82	na	0.0013	na	0.0702	na	1
Toolik MAT	<i>Betula nana</i>	0.13	0.01	18.77	0.76	0.0013	0.0001	0.0240	0.0014	3
	<i>Carex bigelowii</i>	0.48	0.06	13.68	0.61	0.0051	0.0007	0.0706	0.0059	3
	<i>Sphagnum</i> spp.	0.28	0.01	44.65	1.00	0.0031	0.0005	0.1357	0.0036	3
	<i>Vaccinium vitis-idaea</i>	0.15	na	43.80	na	0.0015	na	0.0654	na	1
Sagwon	<i>Andromeda polifolia</i>	0.16	0.01	30.89	2.12	0.0016	<0.0000	0.0483	0.0044	2
	<i>Betula nana</i>	0.17	0.02	17.61	1.90	0.0017	0.0002	0.0304	0.0067	3
	<i>Carex bigelowii</i>	0.41	0.07	18.35	3.62	0.0043	0.0007	0.0807	0.0277	2
	<i>Cassiope tetragona</i>	0.22	0.02	53.68	2.60	0.0020	0.0001	0.1071	0.0047	3
	<i>Sphagnum</i> spp.	0.30	0.04	55.22	12.46	0.0034	0.0005	0.1806	0.0263	3
	<i>Salix</i> spp.	0.18	na	18.40	na	0.0018	na	0.0337	na	1
	<i>Vaccinium xitis-idaea</i>	0.18	0.01	54.64	1.73	0.0018	0.0001	0.0974	0.0026	2
Coldfoot	<i>Andromeda polifolia</i>	0.14	0.01	40.72	5.56	0.0013	0.0001	0.0539	0.0089	3
	<i>Lichen</i>	0.14	na	90.17	na	0.0016	na	0.1438	na	1
	<i>Sphagnum</i> spp.	0.19	0.03	68.96	16.60	0.0021	0.0005	0.1322	0.0284	3
	<i>Vaccinium uliginosum</i>	0.21	na	72.15	na	0.0021	na	0.1518	na	1
	<i>Vaccinium vitis-idaea</i>	0.12	<0.00	39.50	5.52	0.0011	0.0000	0.0446	0.0049	3

Below-ground BSi concentrations were significantly ($p < .01$) different across the three tundra types, with the MNT having the lowest concentrations and WST having the highest concentrations (Figure 3). As was the case for above-ground BSi, the WST contained an order of magnitude more BSi below-ground ($1.42 \pm 0.23\%$ by wt) compared to the tussock and inter-tussock portions of the MAT and MNT ($p < .001$) (Figure 3). BSi concentrations in below-ground WST closely matched those observed in dead above-ground biomass at this site ($1.44 \pm 0.15\%$ BSi).

Across the three MAT field sites, BSi concentrations in below-ground tussock vegetation were significantly ($p < .01$) different, with

Coldfoot having the most BSi ($0.47 \pm 0.05\%$ BSi), and Sagwon having the least ($0.28 \pm 0.04\%$ BSi) (Figure 4). On the other hand, inter-tussock BSi concentrations were not significantly different across the three MAT sites ($0.36 \pm 0.02\%$ BSi). Unlike the WST and MNT, the MAT displayed similar BSi concentrations in above and below-ground vegetation. Below-ground MAT biomass of tussocks contained $0.37 \pm 0.03\%$ BSi by wt. compared to $0.33 \pm 0.03\%$ BSi in above-ground tissue (average of live and dead tissue from these three sites).

Significant differences between below-ground BSi concentrations of tussock versus inter-tussock portions of the tundra were observed

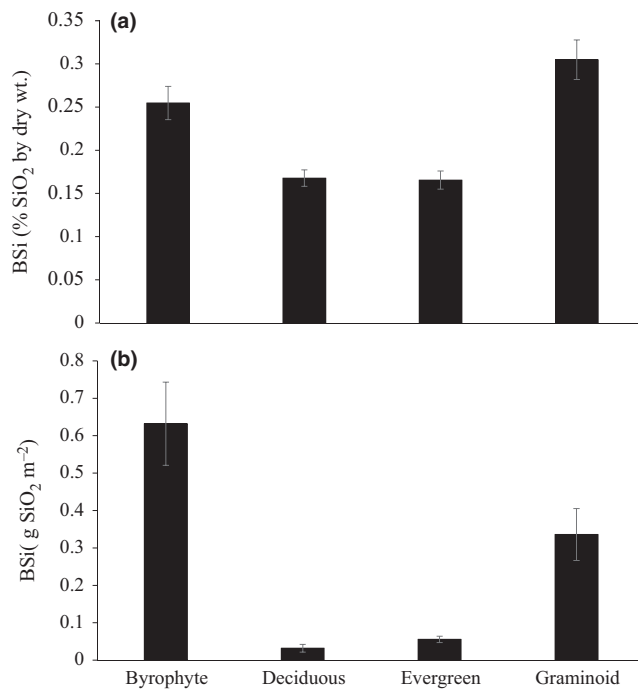


FIGURE 2 Mean ($\pm$ SE) above-ground biogenic silica (BSi) (a) concentration and (b) mass by plant functional type across the three moist acidic tundra (MAT) sites. Shrub (both deciduous and evergreen) data represents leaves only

at the MNT ($p < .01$) and the MAT Toolik ($p < .04$) sites (Figure 4). However, the relative differences between tussock and inter-tussock below-ground BSi storage at these two sites were in opposition, as tussock BSi concentrations were higher than those of the inter-tussock in the MNT ($0.20 \pm 0.02\%$ vs. $0.14 \pm 0.006\%$ in the tussock and inter-tussock sites respectively), whereas inter-tussock BSi concentrations were higher than the tussock portions of the MAT at Toolik ($0.36 \pm 0.01\%$ vs. $0.43 \pm 0.01\%$ in the tussock and inter-tussock sites respectively). No significant differences between these two portions of the tundra were observed in the below-ground biomass at the other two MAT sites (i.e. Sagwon and Coldfoot) (Figure 4).

4 | DISCUSSION

4.1 | Arctic tundra vegetation contains less BSi than previously thought

Our measured values are lower than those reported in a recent global estimate of silica accumulation in Arctic tundra vegetation (Carey & Fulweiler, 2012a), as well as being lower than those of many other graminoid species, such as temperate wetland or agricultural crops (Carey & Fulweiler, 2012a, 2013; Keller, Guntzer, Barboni, Labreuche, & Meunier, 2012; Struyf & Conley, 2009). Correspondingly, Si:C ratios of our live graminoid samples are an order of magnitude lower than those reported by Carey and Fulweiler (2012a) (Table 2), due to dramatically lower BSi content in our plants. The relatively high concentrations (1.38% BSi by dry wt.) that we observed in *C. tetragona* at the

MNT is likely due to the presence of older leaves, which can remain active for up to 10 years, as this is a non-deciduous shrub (Molau, 1997). However, the low sample size for this shrub, which was observed only in one inter-tussock plot, makes it difficult to draw conclusions about this particular species.

Our sample collection coincided with an uncharacteristically early period of peak biomass for 2015 (days 180–200) (Parker et al., *in revision*). Thus, we believe our BSi values present values of maximum BSi for these plant species during the growing season. We also have additional evidence that the timing of our sample collection cannot explain the relatively low concentrations we observe here, as *E. vaginatum* collected just prior to senescence in 2016 at Toolik Field Station contained concentrations that were extremely similar to the values reported here ($0.27 \pm 0.02\%$ BSi, $n = 4$) (Carey, unpubl. data). Thus, it appears that Arctic plants are not particularly large accumulators of BSi, especially when compared to graminoid species found in lower latitude regions. We hypothesise that this may be due to limited access of plant roots to mineral soils, as these soil layers are only accessible during the few summer months when the active layer is deepest (see below for extended discussion). In addition, lower BSi concentrations in Arctic plants may be due to the relatively lower temperatures and shorter duration of the growing season in the Arctic, which limit soil weathering rates, plant transpiration rates, and overall plant productivity, factors which often correlate to plant BSi accumulation (Carey & Fulweiler, 2013; Cornelis, Delvaux, & Titeux, 2010).

4.2 | Shifts in land cover will alter the size of BSi reservoir in terrestrial Arctic plants

We find significant differences in BSi concentrations with plant functional type in the MAT, with graminoid species containing higher concentrations of BSi compared to moss, shrub, and tree species. We hypothesise that these differences could be due to (1) different plant silica accumulation strategies or (2) different below-ground rooting strategies (Iversen et al., 2015). The uptake of silica by plants is typically categorised by the mode of accumulation (Ma, Miyake, & Takahashi, 2001; Ma & Yamaji, 2015; Raven, 2003), with three possible modes of silica uptake: (1) active accumulation, where plants take up more silica than they would through transpiration alone, (2) passive accumulation, where plants have similar rates of silica and water uptake, and (3) rejective or excluder accumulation, where silica is taken up in smaller proportions than water (Takahashi, Ma, & Miyake, 1990). While it is possible to estimate the mode of silica accumulation based on plant BSi concentrations (Street-Perrott & Barker, 2008; Takahashi et al., 1990), this technique ignores differences in plant transpiration rates or in situ DSi availability, which can greatly influence BSi concentrations (Carey & Fulweiler, 2014; Raven, 2003). In turn, it is difficult to estimate the mode of silica accumulation at our sites based on our dataset, although further analysis of soil amorphous silica (ASi, which includes the pedogenic and biogenic forms of silica), as well as DSi in the soil solution, at these sites could shed light on this issue.

Differences in BSi concentrations with plant functional type could also be due to different plant rooting strategies. Shrubs tend to have

TABLE 3 Mass of BSi stored in wet sedge, tussock, and shrub tundra landscape covers

Tundra type	Plant functional type	BSi concentration (% SiO ₂)		Biomass (g/m ²)		Mass (g SiO ₂ m ⁻²)	
		Mean	SE	Mean	SE	Mean	SE
Wet sedge tundra							
	Graminoid	0.550	0.069	86.6	7.5	0.477	0.072
Tussock tundra							
	Byrophyte	0.255	0.024	248.0	36.8	0.632	0.111
	Deciduous						
	Leaves	0.168	0.009	19.0	4.0	0.032	0.007
	Woody tissue	0.020	0.004	76.1	16.2	0.015	0.004
	Evergreen						
	Leaves	0.165	0.010	33.6	3.2	0.056	0.006
	Woody tissue	0.020	0.004	134.3	12.9	0.027	0.006
	Graminoid	0.305	0.026	110.2	20.7	0.336	0.069
	Total			621.2		1.10	0.20
Shrub tundra							
	Byrophyte	0.255	0.024	477.4	291.0	1.216	0.750
	Deciduous						
	Leaves	0.168	0.009	178.1	10.5	0.299	0.024
	Woody tissue	0.020	0.004	712.6	42.1	0.143	0.030
	Evergreen						
	Leaves	0.165	0.010	0.12	0.12	0.0002	0.0002
	Woody tissue	0.020	0.004	0.48	0.48	0.0001	0.0001
	Graminoid	0.305	0.026	20.2	6.8	0.062	0.021
	Total			1388.9		1.72	0.83

BSi concentrations of woody shrub tissue based on bark and wood data from six tree species (*Acer saccharum*, *Betula alleghaniensis*, *Pseudotsuga menziesii*, *Picea abies*, *Pinus nigra*, *Quercus sessiliflora*) (Clymans et al., 2016; Cornelis, Ranger, et al., 2010).

shallow rooting strategies, which isolate their roots to the organic soil layer. Similarly, mosses are also abundant in the organic soil layers, with little to no access to the mineral horizon. Conversely, the roots of *E. vaginatum* penetrate down to the mineral soil horizons, where DSi concentrations in the soil solution are likely higher due to weathering of mineral silicates. Thus, disparate plant root strategies and access to variable soil horizons could be driving the differences in silica accumulation that we observe for different plant functional types. However, rooting strategies may not be a driving mechanism in the plant BSi patterns we observed here, as the organic soil layer could in fact have elevated DSi concentrations for several reasons. First, BSi likely accumulates in the organic layer; the more soluble nature of BSi compared to mineral silicates could lead to higher DSi concentrations in the top layer compared to deeper soil horizons. Moreover, relatively high concentrations of low molecular weight organic acids in the rhizosphere should drive down soil pH, which would also result in elevated DSi concentrations in top soil layers (Alfredsson, Clymans, Hugelius, Kuhry, & Conley, 2016; Cornelis & Delvaux, 2016; Drever, 1994).

The changing climate in the Arctic has implications for the variation in BSi storage with vegetation type. Climatic warming is resulting in shifts in land cover in many parts of the Arctic, with increasing shrub

abundance and growth (Forbes, Fauria, & Zetterberg, 2010; Tape, Sturm, & Racine, 2006). Experimental warming of the tundra indicates that graminoids and mosses will be at a competitive disadvantage to faster growing deciduous shrubs (Elmendorf et al., 2012; Sistla et al., 2013). At a first glance, the lower concentrations of BSi in shrubs indicate that shrub expansion with a concurrent decrease in graminoid coverage may result in less BSi storage within the Arctic vegetation pool. This idea aligns with that of Alfredsson et al. (2015) who suggest that shrub expansion into regions currently occupied by graminoid species will reduce storage of biologically fixed Si. However, climatic warming is likely to result in higher overall rates of biomass production in northern Arctic latitudes (Goetz et al., 2005; Tape et al., 2006). As growing season length increases in response to climate change, the resulting increase in biomass could be up to 75 g C m⁻² by 2100 (Euskirchen et al., 2006). Considering that total plant BSi accumulation is a direct function of total plant biomass (Fulweiler, Maguire, Carey, & Finzi, 2015), expansion of larger plants onto the Arctic tundra (Pearson et al., 2013) has the potential to offset decreases in BSi storage associated with plant types that have lower BSi concentrations.

To examine this further, we used biomass values for dominant plant functional types (Shaver & Chapin, 1991) to compare

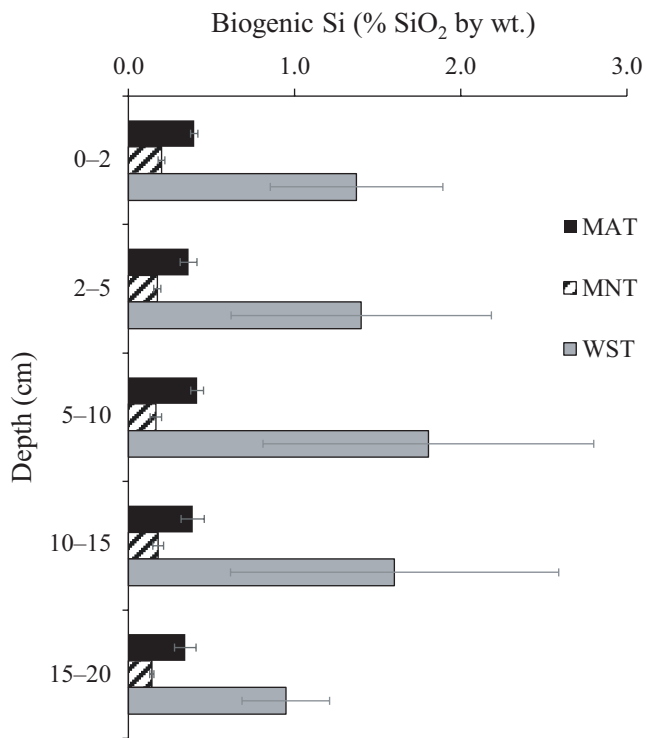


FIGURE 3 Profiles of below-ground root and rhizome BSi concentrations across three tundra types at Toolik Lake LTER Station. MAT, Moist acidic tundra; MNT, Moist non-acidic tundra; WST, Wet sedge tundra. Values represent mean $\pm$ SE

above-ground BSi storage in Arctic shrub versus tussock tundra cover. Our calculations indicate that shrub tundra contains $1.72 (\pm 0.83) \text{ g SiO}_2 \text{ m}^{-2}$, while tussock tundra contains $1.1 (\pm 0.2) \text{ g SiO}_2 \text{ m}^{-2}$ (Table 3). Thus, despite dramatically lower BSi concentrations in shrubs (both leaves and woody material) compared to graminoids, shrub tundra contains ~45% more BSi per unit area than tussock tundra due to higher total biomass in shrub tundra. These calculations indicate that as Arctic shrub biomass continues to increase in response to warming (Pearson et al., 2013),

above-ground BSi storage in Arctic biomass will also continue to increase (Figure 5).

To fully understand how terrestrial vegetation impacts net silica retention on land, we must consider not only plant BSi accumulation, but also rates of BSi mineralisation. Variable rates of decay for different species will directly affect how expansion of Arctic shrubs will alter the strength of the ecosystem silica filter (Clymans et al., 2016; Struyf & Conley, 2012). Differences in litter quality of *E. vaginatum* compared to shrubs will alter the timing of BSi recycling in the terrestrial landscape. C:N ratios of *E. vaginatum* (18–23) are lower than shrub species (18–72) (Table 2), suggesting that tussock tundra vegetation is more labile compared to shrub tundra. Accordingly, we hypothesise that the slower remineralisation rates associated with shrub tundra may further increase BSi retention on terrestrial landscapes, thereby decreasing net exports to aquatic systems.

The relationship between herbivore populations (e.g. invertebrates, voles, birds) and plant BSi content remains uncertain, but is likely another factor to consider with shifting plant functional types. Changes in the amount of silica stored in terrestrial biomass may also impact herbivore-plant interactions, as BSi has been shown to be a strong deterrent of plant herbivory in lower latitudes (Epstein, 1994; Frew, Powell, Sallam, Allsopp, & Johnson, 2016). Plant silica contents are sometimes positively related to grazing activity, indicating intricate interactions between grazers and plant silica behavior (McNaughton, Tarrants, McNaughton, & Davis, 1985). Just as shifts in the quantity and quality of plant litter can be directly related to herbivores and decomposer activity (Gough, Moore, Shaver, Simpson, & Johnson, 2012; Wookey et al., 2009), shifts in vegetation BSi content may likely be an additional driver of plant-consumer feedbacks.

The future of BSi storage in below-ground tundra appears less predictable than that for the above-ground components. Just as BSi storage in plant tissue scales with plant biomass, soil BSi content scales with soil organic matter (Alfredsson et al., 2016). While some Earth system models predict an increase in soil C as vegetation biomass increases (Qian, Renu, & Ning, 2010), a recent empirical study demonstrated large decreases in soil C with experimental

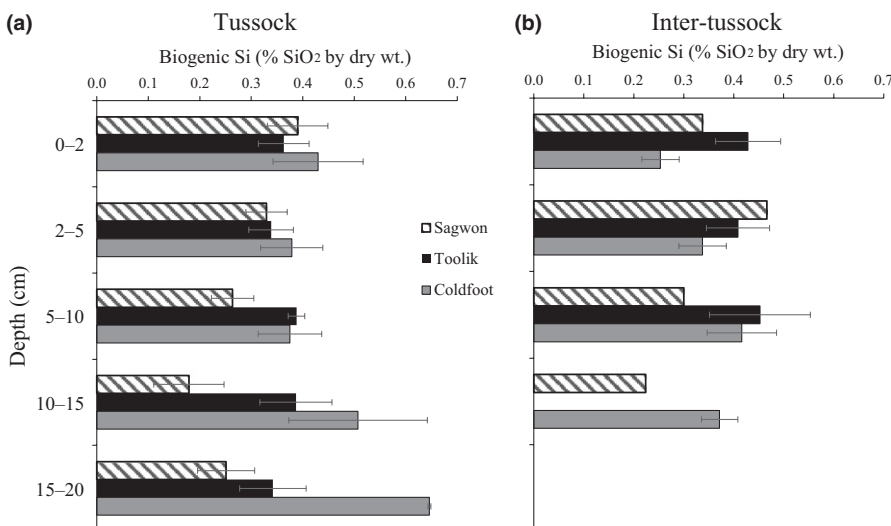


FIGURE 4 Profiles of below-ground BSi concentrations across three MAT sites in both the tussock (a) and inter-tussock (b) portions of the tundra. The depth of active layer was shallower at the inter-tussock site during our sampling period. Values represent mean $\pm$ SE. No significant differences with depth were observed; grouping all depths together for each site we find no significant differences between sites in the inter-tussock, whereas significant differences were observed under the tussocks (Sagwon was different than Toolik and Coldfoot, but Toolik and Coldfoot were not different from each other)

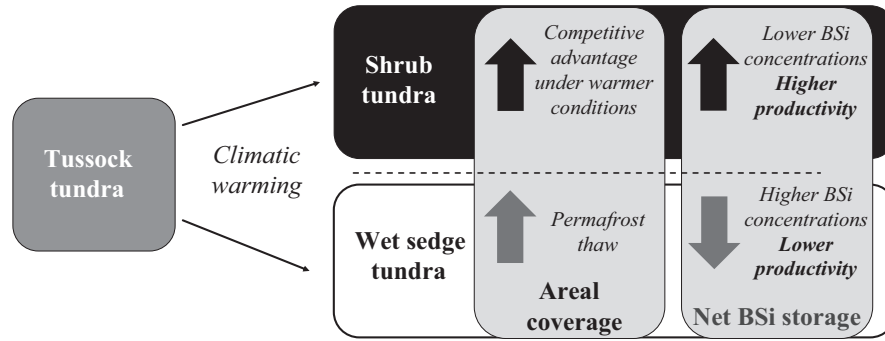


FIGURE 5 Conceptual model of how warming is altering net biogenic silica (BSi) storage in above-ground biomass. Although shrubs contain lower BSi concentrations compared to tussock species (specifically *Eriophorum vaginatum*), the higher biomass associated with shrub tundra will result in increased net BSi storage. Conversely, although wet sedge tundra species contained the highest BSi concentrations in our study, the lower biomass associated with this tundra type will result in decreased BSi storage if tussock tundra converts to wetland area as a result of permafrost thaw

warming, particularly in high latitude systems (Crowther et al., 2016). Furthermore, more productive Arctic ecosystems typically store the least soil organic matter, with plant functional type playing a key role in determining long-term storage of C in the ecosystem (Parker, Subke, & Wookey, 2015). The same may be true for net below-ground BSi storage under shrub expansion; increased biomass production may result in increased below-ground BSi storage over short time scales, while faster decomposition rates under warmer temperatures may increase BSi remineralisation rates in the long term. What is more, shifts in below-ground biomass production, specifically root growth, will alter organic acid production in the rhizosphere. Over the long term, such shifts will have direct implications for weathering rates and thus, DSi availability and export rates (Cornelis & Delvaux, 2016; Drever, 1994; Landeweert, Hoffland, Finlay, Kuyper, & van Breemen, 2001).

4.3 | Arctic wetlands as 'hot spots' for BSi accumulation?

Compared to other plant functional types, we find significantly higher above and below-ground BSi concentrations in WST vegetation compared to other non-wetland tundra types. Relatively high silica accumulation in wetland plants likely depends on several factors, such as elevated transpiration rates or the active mode of silica accumulation, which could be a mechanism to thrive in high-stress environments (Cooke & Leishman, 2011). In addition, elevated plant BSi concentrations could result from the passive accumulation of elevated concentrations of DSi in the soil solution in wetlands, as wetlands in general (Struyf & Conley, 2009), and boreal wetlands in particular (Struyf, Mörtz, Humborg, & Conley, 2010) have been shown to be hot spots for ASi accumulation, which is often coupled to concentrations of DSi in the soil solution (Carey & Fulweiler, 2013, 2014).

Our values of above-ground WST plant silica concentrations fall within the range observed in a suite of North American temperate saltmarshes during peak biomass (0.45%–0.96% BSi) (Carey & Fulweiler, 2014). However, because total above-ground biomass production of WST is less than that of lower latitude wetlands (Shaver & Chapin, 1991; Valiela, Teal, & Persson, 1976), total BSi storage in WST

is correspondingly lower than in lower latitude wetlands. For example, our estimates of total BSi storage in WST ($0.48 \pm 0.07 \text{ g SiO}_2 \text{ m}^{-2}$) are four to 13 times lower than BSi storage in a relatively undisturbed, low nutrient North American saltmarsh during the summer (Carey & Fulweiler, 2013).

Permafrost thaw is resulting in increased wetland area in some regions of the Arctic (Mitra, Wassmann, & Vlek, 2005). A cursory view of concentration data may indicate that increasing wetland coverage would thereby increase the amount of BSi stored in Arctic vegetation. However, total vascular and non-vascular above-ground biomass is almost four-fold lower in WST versus tussock tundra (Shaver & Chapin, 1991). Our estimates point to roughly half the mass of BSi storage in above-ground WST versus tussock tundra (0.48 g vs. $1.1 \text{ g SiO}_2 \text{ m}^{-2}$) (Table 3). These data indicate that the conversion of tussock to WST via permafrost thaw in the northern Arctic will decrease the size of the Arctic terrestrial silica pump, resulting in less BSi retention in above-ground terrestrial vegetation (Figure 5).

4.4 | Implications

Clearly, competing factors, such as plant type, primary production rates, water availability, and permafrost thaw influence total plant BSi accumulation in the Arctic, although often in disparate ways. Our data indicate that conversion of tussock to shrub tundra via warming will increase the size of the pool of BSi in Arctic terrestrial vegetation, whereas wetland expansion via permafrost thaw would likely have the opposite effect. Our investigation of the controls on silica dynamics in the Arctic is in its infancy, but obtaining a more holistic understanding of how plants interact with silica is essential for study of the changing Arctic. The differences in BSi content observed across plant functional and tundra types presented here indicate that land cover change will alter silica retention in vegetated Arctic landscapes. Shifts in the amount of BSi stored within the terrestrial landscape will alter the rates and amounts of silica delivery to coastal receiving waters, with direct implications for diatom production and marine carbon dynamics (Conley, Schelske, & Stoemer, 1993; Ittekkot, Humborg, & Schafer, 2000; Justić, Rabalais, Turner, & Dortch, 1995).

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AUTHORS' CONTRIBUTIONS

J.C.C and J.T. conceived the ideas and designed methodology; J.C.C. and T.P. collected the data; J.C.C. analysed the data; J.C.C. and N.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.98c6c> (Carey, Parker, Fetcher, & Tang, 2017).

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