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Plant Uptake Offsets Silica Release From a Large Arctic Tundra Wildfire

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Key Points:

- After the largest Arctic tundra fire in recent times, burned vegetation had 73% more silica in aboveground biomass, due to higher plant silica concentration in bryophytes and increased prevalence of silica-rich gramminoids in burned areas
- Wildfire redistributed peat silica stocks, with higher concentrations, but 29% lower total stocks due to shallower peat layer postburn
- Dissolved silica concentration in tributaries draining burned catchments did not differ from unburned catchments, indicating that accelerated vegetation uptake may limit lateral silica export during the first decade of post wildfire succession

Supporting Information:

- Supporting Information S1

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Abstract Rapid climate change at high latitudes is projected to increase wildfire extent in tundra ecosystems by up to fivefold by the end of the century. Tundra wildfire could alter terrestrial silica (SiO_2) cycling by restructuring surface vegetation and by deepening the seasonally thawed active layer. These changes could influence the availability of silica in terrestrial permafrost ecosystems and alter lateral exports to downstream marine waters, where silica is often a limiting nutrient. In this context, we investigated the effects of the largest Arctic tundra fire in recent times on plant and peat amorphous silica content and dissolved silica concentration in streams. Ten years after the fire, vegetation in burned areas had 73% more silica in aboveground biomass compared to adjacent, unburned areas. This increase in plant silica was attributable to significantly higher plant silica concentration in bryophytes and increased prevalence of silica-rich gramminoids in burned areas. Tundra fire redistributed peat silica, with burned areas containing significantly higher amorphous silica concentrations in the O-layer, but 29% less silica in peat overall due to shallower peat depth post burn. Despite these dramatic differences in terrestrial silica dynamics, dissolved silica concentration in tributaries draining burned catchments did not differ from unburned catchments, potentially due to the increased uptake by terrestrial vegetation. Together, these results suggest that tundra wildfire enhances terrestrial availability of silica via permafrost degradation and associated weathering, but that changes in lateral silica export may depend on vegetation uptake during the first decade of postwildfire succession.

Plain Language Summary Climate change in the Arctic is leading to more frequent and severe wildfire in Arctic tundra ecosystems. Studying the silica (SiO2) cycle in Arctic ecosystems is important because the amount of silica exported from land to sea can control uptake by marine primary producers in Arctic coastal waters. We investigated how tundra wildfire affects silica cycling by returning to a large Arctic wildfire 10 years after the burn to collect samples of stream water, vegetation, and peat. We found that plants growing on burned landscapes contained 73% more silica in their aboveground biomass compared to unburned areas nearby. While the fire thawed permafrost underneath it, we did not observe increased levels of silica in streams draining burned areas. This pattern indicates that elevated rates of silica uptake via plants may prevent increased silica export to marine waters following tundra wildfire. We conclude that the effect of tundra fire on silica cycling depends on the recovery trajectories of terrestrial and aquatic ecosystems in the Arctic.

1. Introduction

The permafrost zone, which contains half of Earth's soil organic matter (Hugelius et al., 2014), is warming approximately 6 times faster than the global mean (Huang et al., 2017). This rapid climate change at high latitudes is accelerating ecosystem disturbances, including permafrost collapse and wildfire (Jones et al., 2015; Rocha et al., 2012). Wildfire is a dominant disturbance type in the boreal forest (Kasischke & Turetsky, 2006), but until recently, it has been relatively rare in Arctic tundra because of cold and wet conditions. Increased temperature and evapotranspiration have increased tundra fire in some regions (Chipman et al., 2015; Hu et al., 2015, 2010; Rocha et al., 2012; Turetsky et al., 2011), and by the end of the century, tundra wildfire frequency and extent are projected to increase by 60% to 480% (Abbott et al., 2016; Flannigan et al., 2009; Kloster et al., 2012). Wildfire in the permafrost zone can dramatically alter fundamental ecosystem properties, such as surface albedo, plant community composition, net primary productivity, nutrient cycling, and lateral export (Goetz et al., 2005; Larouche et al., 2015; Loranty et al., 2018; Mack et al., 2011).

There is a growing understanding of how wildfire affects carbon and nitrogen dynamics in permafrost landscapes (Bret-Harte et al., 2013; Burd et al., 2018; Larouche et al., 2015; Mack et al., 2011), but little is known about how post wildfire succession affects the biogeochemical exchange of silica (SiO_2) between terrestrial and aquatic systems. Silica export from land to sea influences coastal primary productivity (Baines et al., 2012), where silica-requiring diatoms account for roughly half of marine primary productivity globally (Nelson et al., 1995; Rousseaux & Gregg, 2014) and >80% of high latitude marine primary productivity (Rousseaux & Gregg, 2014; Tremblay et al., 2012). Lithological weathering is the ultimate source of dissolved silica delivered to coastal waters, with geochemical factors, such as climate, runoff, and bedrock type exerting large controls on silica export rates from terrestrial systems at the global scale (Dürr et al., 2011; Gaillardet et al., 1999; Kump et al., 2000). However, terrestrial plants mediate this flux by incorporating large amounts of dissolved silica into their tissue, estimated at 84 ± 29 Tmol Si/year (Carey & Fulweiler, 2012b). At a planetary scale, this terrestrial silica pump is roughly a third the amount consumed each year by oceanic diatoms (Tréguer & De La Rocha, 2013). The magnitude of the terrestrial silica pump depends on vegetation type and phenology, as plant silica content varies substantially among plant species (Hodson et al., 2005). Consequently, changes in plant community composition and land cover alter terrestrial silica retention and lateral export to freshwater and marine ecosystems (Carey & Fulweiler, 2012a, 2012b; Chen et al., 2014; Conley et al., 2008; Struyf et al., 2010). The strength of the terrestrial silica pump in the Arctic is undetermined, representing an important unknown because the chemistry of Arctic Ocean is strongly influenced by terrestrial runoff, receiving ~10% of global land-derived runoff but containing only ~1% of total ocean volume (Opsahl et al., 1999).

Silica has often been considered relatively immune to disruption by human activities because geochemical drivers, such as bedrock lithology, hydrology, and climate, strongly influence its biogeochemistry (Abbott et al., 2018; Dürr et al., 2011). During the past few decades, a greater appreciation of the silica cycle's sensitivity to human perturbation has emerged, through recognition that silica export to the global oceans can be influenced by river damming (Humborg et al., 2000), nutrient overenrichment (Conley et al., 1993), permafrost thaw from climatic warming (Frey & McClelland, 2009; Guo et al., 2004; Smedberg et al., 2006), and recently, watershed land use (Carey & Fulweiler, 2012a, 2012b; Conley et al., 2008; Marçais et al., 2018; Struyf et al., 2010). Urbanization and agricultural land cover influence silica turnover and flux (Carey & Fulweiler, 2016; Clymans et al., 2011; Maguire & Fulweiler, 2016, 2019; Vandevenne et al., 2012), but little work has focused on wildfire as a disruptor of silica transfer between terrestrial and aquatic systems.

Wildfire could alter the Arctic terrestrial silica pump through three, nonexclusive mechanisms. First, combustion can increase reactive surfaces of soil material, increasing the solubility of silica in soils (Unzué-Belmonte et al., 2016) and the amount of silica available for plant uptake or lateral export post burn (Engle et al., 2008; Pereira et al., 2011). Second, fire removes surface organic soil layers and increases the depth of the seasonally thawed active layer (Rocha & Shaver, 2011a; Schuur et al., 2008; Zhou et al., 2019), exposing silica-rich mineral layers to chemical weathering. Permafrost thaw, be it from climatic warming or wildfire, increases infiltration rates and soil-water interactions, resulting in increased silica release from soils to aquatic systems (Frey & McClelland, 2009; Guo et al., 2004; Smedberg et al., 2006). Furthermore, warmer soil temperatures accelerate lithological weathering rates (Kump et al., 2000), further increasing silica mobilization with permafrost thaw and increased active layer depths (Millot et al., 2003; Smedberg et al., 2006). Third, fire alters plant community composition and aboveground primary productivity (Belsky, 1992; Melzer et al., 2010; Morrison et al., 1995). Because plant silica content varies by 2 orders of magnitude among plant species (Epstein, 2009), plant community composition can influence ecosystem-level silica retention (Carey & Fulweiler, 2012a, 2012b; Conley, 2002; Hodson et al., 2005). Plant-mediated differences in silica storage could be particularly pronounced in Arctic tundra because the relative prevalence of gramminoids (high silica accumulators) and dwarf shrubs (presumably lesser silica accumulators; Carey et al., 2017; Hodson et al., 2005) depends on disturbance type and history (Elmendorf et al., 2012; Pearson et al., 2013; Tape et al., 2006). Additionally, environmental stressors (e.g., desiccation, herbivory) can alter the mode of silica uptake by plants, shifting accumulation from being passive in nature (i.e., dissolved silica consumption from soil solution via transpiration) to active (i.e., active root uptake of dissolved silica against a concentration gradient) (Carey & Fulweiler, 2014; Cooke et al., 2016; Cooke & Leishman, 2011; Cornelis, Delvaux, et al., 2010; Cornelis, Ranger, et al., 2010; Raven, 2003).

In this context, we hypothesized that tundra wildfire would increase the amount of silica stored in plant biomass (the terrestrial silica pump), due to shifts in plant community and increased silica bioavailability. We also hypothesized that tundra wildfire would alter stream silica exports, either by increasing lateral losses due to deepening of active layer and hydrologic flowpaths, or by decreasing lateral losses due to increased silica retention in vegetation. To investigate these hypotheses, we measured plant silica concentrations and net accumulation in dominant plant species along a burn severity gradient at a large, 10-year-old Arctic tundra burn in northern Alaska. We compared dissolved silica concentration in streams draining burned and unburned catchments to assess the legacy effects of tundra wildfire on lateral silica export. Together, these data provide the first analysis of the effects of wildfire on silica cycling in tundra ecosystems.

2. Methods

2.1. Site Description

We collected samples on the North Slope of Alaska (United States) at the Anaktuvuk River fire scar (150.6385°W, 69.1352°N; Figure 1), the largest recorded fire on the North Slope in the past 50 years (Jones et al., 2009; Mack et al., 2011). The ~1,000 km^2 burn was ignited by lightning in July of 2007 and burned for nearly 3 months. Over 80% of the scar was classified as moderately to severely burned (Boelman et al., 2011). Continuous permafrost underlays this region, with bryophytes and tussock-forming sedges, consisting mostly of *Eriphorum vaginatum* and *Carex bigelowi* dominating the site (~70% cover) and dwarf shrub species (e.g., *Ledum palustre*, *Betula nana*, *Vaccinium vitus-idaea*, and *Salix pulchra*) constituting the rest of the species cover prior to the burn (Bret-Harte et al., 2013; Jones et al., 2009). Mean annual temperature is −10 °C and mean annual precipitation is 30 cm. The period leading up to the burn was marked by elevated temperature and extremely dry conditions (e.g., average snow depth during the 4-year period prior to the fire was 50% of normal and 2007 was the driest year in the prior 29-year record; Jones et al., 2009).

2.2. Plant and Soil Collection

In 2017, a decade after the fire, we measured total above and belowground biomass at unburned and severely burned locations near or within the fire scare (Figure 1). Following standard long-term ecological research (LTER) protocols (Bret-Harte et al., 2013), we collected biomass from 20 quadrats (10 × 40 cm) along 100 m transects at the severely and unburned sites in the eastern and western portion of the fire scar during the last week of July, which is the period of peak biomass (Rocha & Shaver, 2011a, 2011b). Harvested quadrats included all above and belowground vegetation and organic matter above the mineral soil layer. We collected material in large plastic bags in the field for transport to the laboratory. We measured organic and peat layer depths in situ along the four sides of each quadrat pit, and we collected soil bulk density from 10 profiles at each quadrat. From 2008 to 2017, thaw depth was measured twice a month at the plots via manual frost probing using a rigid metal rod (~1-cm diameter) from June through September. Following standard LTER protocols (Rocha & Shaver, 2011a, 2011b), we inserted the rod vertically into the peat and recorded the depth at which permafrost prevented further penetration.

During the first week of August 2017, we collected additional aboveground plant material for silica analysis. In total, we collected 67 samples from 11 plots that span the burn severity gradient: four severely burned plots, three moderately burned plots, and four unburned plots. We randomly chose these plots from a subset of existing plots previously studied at the burn scar (Table S1), for which burn severity was already defined using a severity index (Jandt et al., 2012). At each plot, we collected material from the six most prevalent plant species. We collected the entire aboveground portions of the bryophytes and gramminoids. We collected leaves of the shrub species, as transpiration termini (i.e., leaves rather than woody material) are the plant parts where the majority of plant silica is located (Epstein, 1994; Raven, 2003). Because plant silica concentration varies widely among individual plants (Carey & Fulweiler, 2014; Hodson et al., 2005), we collected material from five plants of each dominant species at each plot. Thus, each plot-level plant species silica value represents a composite sample of five individual plants of a given species.

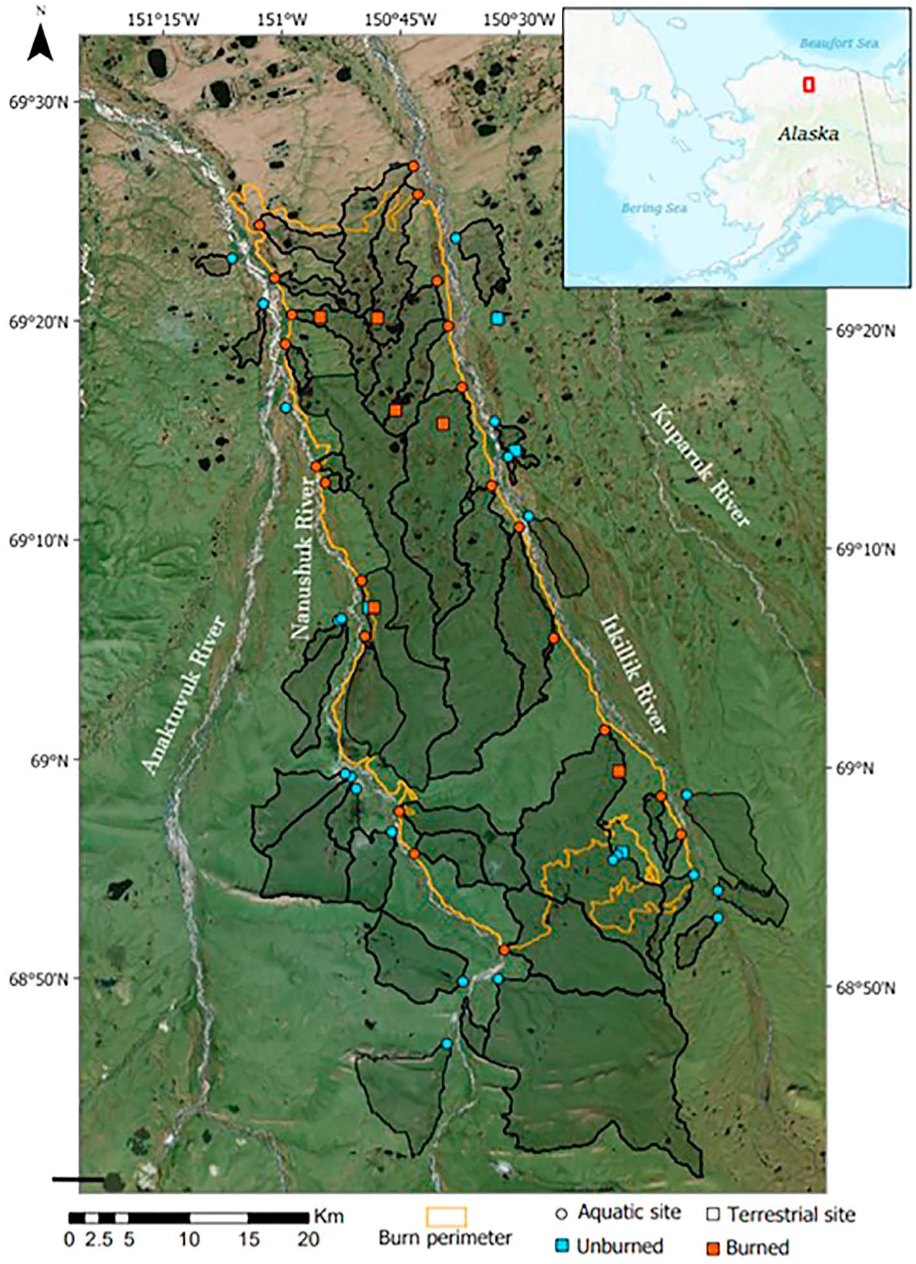

Figure 1. Map of the Anaktuvuk River Fire scar, terrestrial and aquatic sampling sites, and tributary catchment boundaries.

2.3. Stream Silica Concentration

To assess the legacy effects of tundra fire on lateral silica export, we collected water samples from streams draining 22 burned and 23 unburned catchments in early June, mid-July, and late August of 2017 (Figure 1). These sampling dates represented the early-season freshet (June), when the bulk of hydrological export occurs in many Arctic and Boreal catchments (McClelland et al., 2014), the peak growing season when plant-mediated changes in silica availability was most likely to be apparent (July), and the time of maximum thaw depth (August; Abbott et al., 2015), when geogenic silica release from degrading permafrost was most likely (Frey & McClelland, 2009). Due to the remoteness of the sites, we collected samples from a helicopter in prewashed high-density polyurethane bottles attached to a retractable pole. Immediately upon return to the lab, we filtered samples with a 0.2-μm cellulose acetate membrane filter and refrigerated in the dark until analysis (Figure 2).

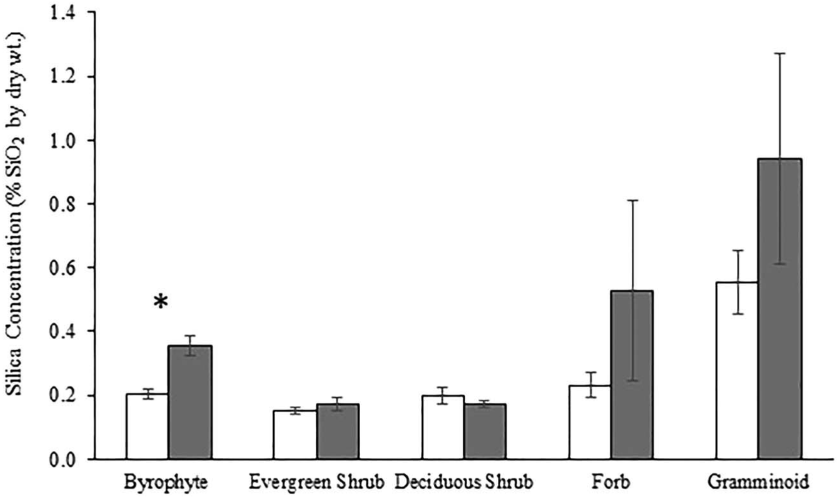

Figure 2. Plant silica concentrations in unburned (open bars) and burned (filled bars) plots, grouped by plant functional type. Asterisk indicates significant difference between burned versus unburned plot plant silica concentrations for a particular plant functional type.

For each stream, we extracted catchment areas and characteristics based on a 5-m digital elevation model. Catchment sizes ranged from 0.2 to 196 km^2 (24 ± 6 km^2, mean ± standard deviation, SD). We extracted characteristics for each delineated catchment from existing data layers using geospatial software (ESRI ArcMap 10.3). We classified stream catchments that fell within the burn perimeter as "burned," with most burned catchments consisting of >80% burned area. In addition to this binary classification, we also used two continuous variables to examine the relationship between catchment properties and stream chemistry: the Normalized Difference Vegetation Index (NDVI) as a proxy of primary productivity using National Aeronautics and Space Administration's 30-m Landsat Enhanced Thematic Mapper Plus moscaics from 2002 to 2012 (South Dakota State University, 2013) and differenced normalized burn ratio (dNBR) based on repeat NDVI measurements taken in 2006, 2008, and 2012 as a proxy of burn severity (Allen & Sorbel, 2008; Boelman et al., 2011). We regressed NDVI and dNBR against stream silica concentration using least squares regression (Figure S1 in the supporting information).

2.4. Laboratory Analysis

We separated harvested biomass from each of the 20 quadrats into new and old aboveground and belowground vegetation and litter to the species or plant functional type level. We assigned peat to O- or A-layers based on visually distinct changes in organic matter composition, bulk density, and color. We washed plant samples for silica analysis prior to drying. Material was dried at 60 °C for 2–3 days, at which point mass was recorded. To measure plant silica concentrations in plants and amorphous silica content of peat, we used the wet alkaline digestion technique. Plant and amorphous silica was extracted from 30 (±1) mg of homogenized, oven-dried material with 1% Na_2CO_3 solution (Conley & Schelske 2002; DeMaster, 1981). This material was digested in flat-bottom, polyethylene bottles in a hot water shaking bath (85 °C at 100 rpm). We digested plant samples for 4 hr and peat samples for 5 hr, with subsamples for mineral silica correction taken at hours 3 and 4. Analysis of an internal plant silica standard was always <6% of the expected value. We analyzed aliquots of dissolved silica from the alkaline extractions on a flow analyzer using the molybdenum blue colorimetric method, with sodium hexafluorosilicate (Na_2SiF_6) used as the silica standard. We used external dissolved silica standards (Hach) to ensure accuracy and these were always within 5% of the expected value. Stream silica samples were analyzed by inductively coupled plasma spectrometry (iCAP 7000 series, Thermo Scientific, Waltham, United States).

2.5. Standing Silica Stock Calculations

We estimated total plant silica in aboveground biomass by multiplying measured plant silica concentration with total biomass values. Based on our plant biomass harvest data, total woody biomass made up <10% of total aboveground biomass at unburned sites and <20% at burned sites; we used literature values of silica

Table 1
Total Average (±SE) Biomass in Aboveground Vegetation in Unburned and Burned Plots

	Total aboveground biomass (g/m^2)	
Plant functional type	Unburned	Burned
Byrophyte	352.1 (42.5)	122.0 (37)
Evergreen shrub	297.7 (28.4)	219.5 (42.4)
Deciduous shrub	84.3 (5.9)	181.5 (65.8)
Forb	34.8 (6.3)	40.6 (12.4)
Gramminoid	71.7 (17.2)	214.0 (51.6)
Lichen	85.9 (20.9)	0.0 (0.0)
Total	926.6 (58.5)	777.6 (101.6)

concentrations for woody material (0.02 ± 0.004 % SiO_2 by wt.; Clymans et al., 2016; Cornelis, Delvaux, et al., 2010; Cornelis, Ranger, et al., 2010), as we did not measure silica content of woody tissue because of its low plant silica content relative to leaves and minor component of total biomass. Indeed, our estimate was that woody silica constituted <1% of total plant silica at all plots. We represent plant and amorphous silica values as % SiO_2 of dry weight.

To compare responses between burned versus unburned plots, we used a two-tailed, one-way Student's t test. To compare differences in silica content between plant species and plant functional types, we used a one-way analysis of variance. We used a decision criterion of $\alpha = 0.05$ to determine statistical significance and all statistics were done in R (version 3.3.2).

3. Results

3.1. Aboveground Plant Biomass and Shifts in Plant Community Composition

Catchment NDVI was 38% lower in burned catchments in 2008 than in 2006, but by 2012, NDVI had recovered and was 5% higher than in 2006. In 2017, 10 years after the burn, total biomass was 777 ± 101 g/m^2 at the burned plots and 926 ± 59 g/m^2 at the unburned plots. Bryophyte biomass recovered less quickly than vascular plant biomass, meaning that burned plots had higher vascular plant biomass than unburned (Table 1). Differences in total aboveground biomass between burned and unburned plots was driven largely by shifts in community composition at the plant functional type level. For example, burned plots contained 3 times more gramminoid biomass (214 ± 52 versus 72 ± 17 g/m^2) and twice the biomass of deciduous shrubs (182 ± 66 versus 84 ± 6 g/m^2), compared to unburned plots, while moss biomass was three times higher at unburned plots. Moreover, lichen was not observed at any burned plots but was considerable (86 ± 21 g/m^2) at unburned plots (Table 1). In both unburned and burned areas, the bulk density of the O-layer was an order of magnitude lower than the A-layer (~0.05 and ~0.25 g/cm^3, respectively; Table 4), but bulk density was very similar in burned and unburned plots in both layers (Table 4).

3.2. Plant Silica Content

Plant silica concentration was not significantly different ($p = 0.27$, $n = 16$) between moderate and severely burned plots, so we combined data from these two categories in all subsequent analyses. As expected, silica concentration varied among plant species ($p = 0.007$, $n = 9$), with the highest concentration in gramminoids (*E. vaginatum* and *C. bigolowii)*, and the forb *Equisetum* spp. (Table 2). Grouping all samples together, mean plant silica concentration was higher at burned plots (0.49 ± 0.12 %) compared to unburned plots (0.28 ± 0.04%), though this difference was not significant ($p = 0.13$, $n = 67$; Table 2). Silica concentrations of individual species were not significantly different between burned and unburned plots in any case.

Table 2
Plant Silica Concentrations (%SiO_2 by Dry wt.) at Unburned and Burned Tundra

		Unburned			Burned		
Plant species	Plant functional type	Plant silica concentration	Standard error	n	Plant silica concentration	Standard error	n
Sphagnum spp.	Bryophyte	0.20	0.02	4	0.35	0.03	5
Carex bigelowii	Gramminoids	0.70	0.13	4	1.48	0.61	7
E. Vaginatum	Gramminoids	0.36	0.05	3	0.40	0.04	7
Rubus chamaemorus	Forb	0.23	0.04	4	0.25	0.05	4
Equisetum spp.	Forb	na	na	na	1.65	na	1
Letum palustre	Evergreen Shrub	0.15	0.01	3	0.18	0.02	6
Betula nana	Deciduous Shrub	0.17	0.01	3	0.17	0.02	7
Salix spp.	Deciduous Shrub	na	na	na	0.15	0.01	3
Petacites frigidus	Deciduous Shrub	0.27	na	1	0.16	na	1

Note. Burned samples include plants from both moderate and severely burned plots. Each sample (n) represents a composite of five individual plants, which were combined in the field.

Table 3
Average (±SE) Silica Stock in Aboveground Vegetation in Unburned and Burned Plots

	Total aboveground biogenic Si stock (g SiO2/m^2)	
Plant functional type	Unburned	Burned
Byrophyte	0.72 (0.09)	0.43 (0.13)
Evergreen Shrub	0.45 (0.04)	0.38 (0.07)
Deciduous Shrub	0.05 (0.02)	0.10 (0.03)
Forb	0.08 (0.01)	0.21 (0.07)
Gramminoid	0.40 (0.10)	2.01 (0.49)
Lichen	0.12 (0.03)	0.0 (0.0)
Total	1.81 (0.14)	3.14 (0.51)

Note. Lichen was not sampled during our field campaigns (no lichen was present at burned sites; Table 1), so lichen silica concentration at unburned plots is based on values from a nearby station on the North Slope (Carey et al., 2017). SE = standard error.

Although these differences across species were not significant, average silica concentrations were consistently higher from burned plots for all species, except in the case of *Petacites frigidus* (Table 2). At the plant functional type level, significant differences were only observed for the byrophytes, where silica concentrations were significantly higher at burned compared to unburned plots (0.35 and 0.20 %, respectively; $p = 0.006$, $n = 9$; Table 2). We note that we did not identify mosses to the species level and therefore, shifts in *sphagnum* species compositions after the burn could contribute to the observed shifts in moss silica concentrations post burn. Total plant silica in aboveground biomass was higher at burned plots compared to unburned plots (3.14 ± 0.51 and 1.81 ± 0.14 g SiO_2/m^2, respectively; Table 3). This large difference in standing plant silica stock was primarily driven by gramminoids, which had higher silica concentration and higher total biomass at the burned plots, resulting in five times more silica in gramminoids at burned plots compared to unburned plots (2.01 ± 0.48 and 0.40 ± 0.10 g SiO_2/m^2, respectively).

3.3. Peat Amorphous Silica Concentrations and Stocks

Mean peat loss was 6 cm across the burned area (Mack et al., 2011), consisting of the entire soil O-layer and part of the deeper peat (A-layer). Therefore, the O-layer samples from the burned plots consist entirely of material that accumulated since the fire. The O-layer, which is the top-most soil layer, consisted of 80 to 90% of dead moss material, as we removed all plant litter prior to analysis. This layer had extremely low density (~0.055 g/cm^3). Amorphous silica concentration in the O-layer was significantly higher in burned plots ($p = 0.03$, $n = 9$, 0.59 ± 0.07 and 0.33 ± 0.02% in the burned and unburned plots, respectively; Figure 3 and Table 4). The average depth of the O-layer at the burned plots was 1.7 cm (±0.35, $n = 31$), 73% less than the depth at unburned plots (Table 4). Therefore, despite the significantly higher silica concentrations and similar bulk density of the O-layer in burned plots, the shallower depth of the O-layer resulted in roughly half the amorphous silica in burned O-layers than in unburned O-layers (6.5 ± 0.01 and 12.3 ± 0.02 g SiO_2/m^2; Table 4).

Amorphous silica concentration in the A-layer peat (the layer between the O-layer and deeper mineral layer, consisting largely of organic material), was not significantly different between burned and unburned plots (Figure 3 and Table 4). Depth of the A-layer in burned plots was generally lower than unburned plots (4.5 and 6.9 cm, respectively), explaining the slightly lower total silica values (51 ± 0.15 and 69 ± 0.15 g SiO_2/m^2; Table 4).

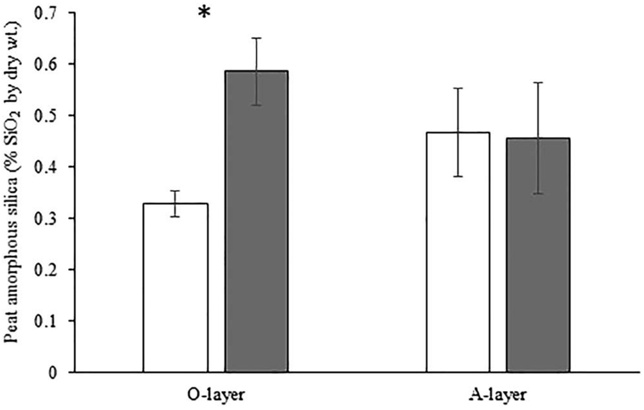

Figure 3. Amorphous silica concentration in O-layer and A-layer peat at unburned (open bars) and burned (filled bars) plots. O-layer silica concentrations were significantly ($p = 0.03$, $n = 9$) higher after fire disturbance, while no significant difference in A-layer peat was observed between treatments ($p = 0.95$, $n = 9$).

Maximum annual thaw depth (i.e., active layer depth) at burned plots was 30 ± 5.3 cm, which was 4.8 ± 0.92-cm deeper than the mean at unburned plots in 2017 ($n = 16$; Figure 4). Differences in active-layer depths in previous years were much greater than the last 2 years (Figure 4).

3.4. Stream Silica Concentration and Catchment Properties

Dissolved silica concentration ranged from 7.9 to 114 μM (mean 35 ± 2 μM, $n = 90$) across the entire sampling period (June–August 2017). Dissolved silica concentration behaved similarly in burned and unburned catchments, increasing through the sampling period, but with no significant differences for any of the months (Figure 5). Monthly or total stream silica concentration was not correlated with catchment NDVI or burn severity (R^2 consistently <0.17; Figure S1).

4. Discussion

We hypothesized that wildfire could alter plant silica uptake and stream silica exports from tundra ecosystems by increasing active

Table 4
Peat Properties at Unburned and Burned Plots

	Unburned				Burned			
	O-layer		A-layer		O-layer		A-layer	
Layer properties	Average	±SE	Average	±SE	Average	±SE	Average	±SE
Bulk density (g/cm^3; $n = 31$)	0.061	0.003	0.215	0.03	0.052	0.011	0.248	0.027
Layer depth (cm; $n = 31$)	6.21	0.63	6.9	0.75	1.66	0.35	4.54	0.76
Total mass (g/m^2; $n = 31$)	3763	384	14859	1613	1108	219	11245	1874
Amorphous silica (%SiO2 by wt.; $n = 18$)	0.33	0.02	0.47	0.09	0.59	0.07	0.46	0.11
Total ASi by mass (g SiO2/m^2; $n = 18$)	12.3	0.02	69.4	0.15	6.5	0.01	51.3	0.15

Note. SE = standard error.

layer depth, changing chemical structure of soils, and shifting plant community and growth. We found that 10 years after a large wildfire, the silica reservoir in Arctic tundra was nearly twice as large, surface peat amorphous silica stocks were 29% lower, but stream silica concentration was unchanged. Below, we discuss these changes in detail and address several mechanisms that explain the differing plant, peat, and stream silica responses to burning.

4.1. Differential Plant Silica Response to Wildfire

Bryophytes exhibited the most pronounced legacy effect of wildfire in terms of silica biogeochemistry, with both living bryophytes and O-layer peat (which consists of 80–90% dead bryophyte material) having significantly higher silica concentrations at burned plots. Bryophytes are often the first colonizers during secondary succession (Johnstone et al., 2010; Turetsky et al., 2010), and the O-layer is entirely newly formed since the burn. The higher concentration of silica in bryophytes following the burn may be because they grew directly on the A-layer, which is more silica-rich than the O-horizon in unburned plots (Figure 3). Higher silica availability could have also contributed to this difference because water-soluble silica, the form taken up by plants, has been shown to increase immediately after burning in laboratory (Unzué-Belmonte et al., 2016) and field studies (Pereira et al., 2011). While this is not always the case, especially in situations of elevated mineral content where crystallization may occur (Unzué-Belmonte et al., 2016), combustion increases reactive surfaces of soil material, often releasing water soluble silica to the surrounding environment.

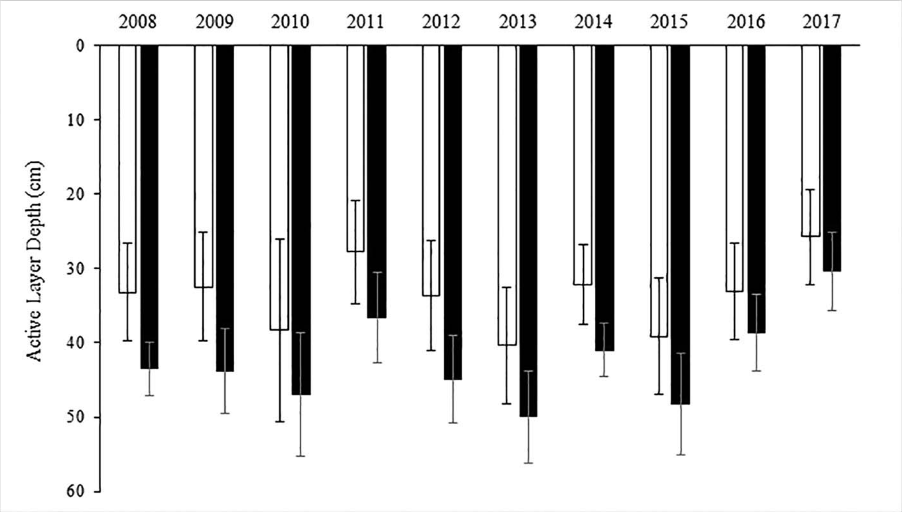

Figure 4. Average annual active layer depth (cm) in unburned (open bars) and burned (both severe and moderately burned; filled bars) plots. Error bars represent standard errors (each year of data represents an average of $n = 7$ and $n = 14$ for unburned and burned plots, respectively).

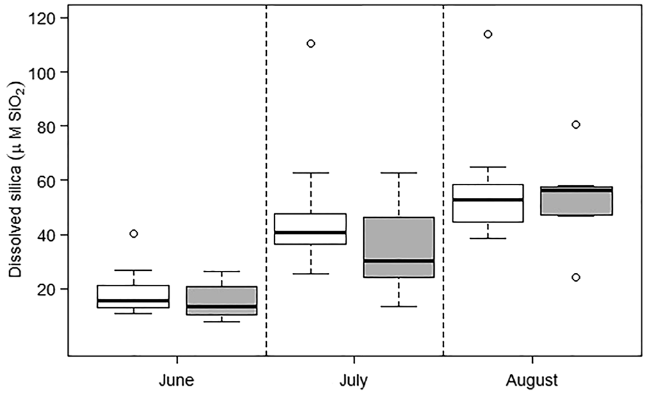

Figure 5. Box plots of stream dissolved silica concentrations (μM) in tributaries draining unburned (open white boxes) and burned (filled gray boxes) catchments during each month of sampling in 2017. Box plots represent median, quartiles, minimum, and maximum values within 1.5 times the interquartile range. Open points represent values beyond 1.5 times the interquartile range (mean *n* per box plot = 15).

Unlike the mosses, dwarf shrubs had similar plant silica concentration in burned and unburned sites, corresponding with the similar nature of silica in A-layer peat between the plots. Dwarf shrubs usually have relatively shallow rooting strategies, with their roots typically penetrating only into peat layers (Chapin et al., 1996; Hewitt et al., 2018; Wang et al., 2017). Conversely, gramminoids generally extend roots annually to the full depth of the active layer (Chapin et al., 1996; Hewitt et al., 2018), where they could likely access the deeper, silica-rich mineral layers (Carey et al., 2017). Although not significantly different, the elevated silica concentrations in gramminoids after burn disturbance (0.94 ± 0.33 versus 0.55 ± 0.1 in burned versus unburned plots; Table 2 and Figure 2) may be a result of higher silica concentration and availability after burning due to the significantly increased thaw depth (Figure 4), which increases water-soil interaction in space and time.

At the Anaktuvuk River fire scar, plant community composition shifted to favor gramminoids and deciduous shrubs at the expense of evergreen shrubs and byrophytes (Table 1). This shift corresponds to prior studies demonstrating altered plant community composition and rates of primary productivity following wildfire (Hu et al., 2010; Melzer et al., 2010). Thus, although we did not observe significant differences in plant silica concentrations between burned and unburned plots at the species level, the rapid biomass accumulation of relatively silica-rich gramminoids during burn recovery (Table 1) resulted in a near doubling of silica in terrestrial vegetation pool after the burn (3.14 ± 0.51 g SiO_2/m^2 versus 1.81 ± 0.14 g SiO_2/m^2 in unburned and burned plots; Table 3).

4.2. A diminished Terrestrial Silica Pool With Burning

Peat amorphous silica concentrations were low (range of 0.13–0.79%, $n = 18$), in agreement with values observed in temperate regions (Unzué-Belmonte et al., 2016) and elsewhere throughout the Arctic (Alfredsson et al., 2016). Amorphous silica concentrations of A-layer peat in burned versus unburned plots were strikingly similar, but the shallower nature of the peat layers that persist a decade into postfire succession (Table 4) resulted in 29% less amorphous silica stored in peat at burned plots, compared to unburned plots (58 versus 82 g SiO_2/m^2 in burned and unburned plots, respectively; Table 4). This peat data, in conjunction with the vegetation data, does not support the hypotheses that fire increases silica storage in terrestrial landscapes (Melzer et al., 2010); total plant and amorphous silica stocks in aboveground vegetation and peat were 27% lower in burned plots than unburned plots after 10 years of postfire succession (61 versus 84 g SiO_2/m^2 in burned and unburned plots, respectively; Tables 1, 3). However, these values do not include belowground vegetation silica stocks. We can estimate total belowground plant silica accumulation based on our total belowground biomass values (1,153 ± 260 and 1408 ± 202 g/m^2 at burned and unburned plots) and known concentrations in belowground tussock tundra vegetation from the region (0.40%; Carey et al., 2017). Including these estimates of the belowground silica reservoir (4.6 ± 1.0 and 5.6 ± 0.81 g SiO_2/m^2 in burned and unburned plots, respectively) into our calculations continues to demonstrate a 27% smaller plant and amorphous silica pool in burned plots 10 years after the burn.

4.3. Stream Silica Unchanged With Burning

The stream silica concentrations we observed were low compared to global average dissolved silica concentrations in rivers (~150 uM; Dürr et al., 2011; Tréguer & De La Rocha, 2013), but within the typical range of other North American Arctic rivers (Holmes et al., 2012). An important objective of this work was to determine how ecological processes occurring on the terrestrial landscape impact silica export to aquatic systems. In contrast to prior studies showing increased lateral silica exports with increased thaw depth (Frey & McClelland, 2009; Guo et al., 2004) and Engle et al. (2008), who observed elevated dissolved silica exports 9 years after a prescribed burn in a temperate North American Sequoia forest, we find no differences in stream silica concentrations in tributaries draining unburned versus burned plots 10 years after the tundra burn. Two potential explanations for this discrepancy are that our sampling 10 years after the burn missed a large pulse of silica released through streams or that terrestrial plant silica uptake offsets increases in postfire silica availability. First, it is possible that the fire resulted in an initial pulse of bioavailable silica directly after the burn, as the deepening of the active layer likely mobilized silica directly after the burn (Frey & McClelland, 2009), but this release may have occurred on timescales shorter than a decade. Thus, it is possible that stream silica chemistry has recovered from the burn in regards to silica exports. We see such signs of recovery in metrics of total biomass production and catchment greening (i.e., NDVI; Table 1 and Figure S1).

The second potential explanation for the lack of stream silica signal from the burn is the increased uptake by terrestrial vegetation during recovery, which may limit stream silica exports despite deeper thaw depths (~5 cm in 2017; Figure 4) following the burn. A deeper active layer should increase dissolved silica availability to the system due to increased weathering and soil water residence time (Frey & McClelland, 2009). However, additional plant silica uptake during postburn succession may be great enough to retain burn-released silica in the terrestrial landscape, resulting in no change in stream silica concentrations from burned catchments, despite deeper thaw depths. To determine if this mechanism for silica retention is reasonable, we compared the additional mass of silica taken up by plants during a decade of postburn succession to known lateral silica fluxes in the Arctic. To do this, we calculated the difference between plant silica in burned (3.14 g SiO_2/m^2) and unburned (1.81 g SiO_2/m^2) plots (Table 3, estimating that 1.3 g SiO_2/m^2 was taken up by plants during the 10-year period of postburn succession). We then compared this value to lateral fluxes measured in two large Arctic rivers in North America (Yukon and Mackenzie Rivers), which ranged from 0.72 to 1.81 g SiO_2 m^{-2} $year^{-1}$ on average from 1999 to 2008 (Homes et al., 2012). While differences in bedrock lithology across this large region may result in different baseline silica fluxes, this comparison indicates that each year of postburn recovery results in additional silica uptake by plants equal to 7–18% of average annual lateral silica fluxes from large North American Arctic rivers. From this, it appears that increased plant silica accumulation could indeed retain enough silica in terrestrial systems to limit increased stream exports from deeper thaw depths following a burn.

4.4. Complex and Persistent Effects of Wildfire on Tundra Silica

This study reveals that postwildfire succession has complex and persistent effects on biogeochemical cycling of silica in Arctic ecosystems, some of which are similar to the effects of other ecological disturbances on silica cycling in lower latitude ecosystems. For example, the magnitude of plant silica increase we observed following wildfire is similar to effects from CO_2 enrichment observed in a temperate forest, though those changed were associated with increased biomass production, rather than shifting species composition or plant silica concentrations (Fulweiler et al., 2015). Conversely, our observations of unchanged silica chemistry in small streams draining the tundra burn scar differ from deforestation treatments in a temperate hardwood forest where stream silica concentration remained elevated several decades after the disturbance (Conley et al., 2008). A likely explanation for the differing response of stream silica chemistry to these disturbances is the relatively low total stocks of biogenic and amorphous silica in the Arctic relative to lower latitudes (Alfredsson et al., 2016), especially in the soils where the majority of ecosystem amorphous silica is stored (Conley, 2002). For example, A-layer amorphous silica concentrations at our site (Table 4) are an order of magnitude lower than those observed from the Hubbard Brook Experimental Forest (United States; average 1.4 ± 0.37% SiO_2 by dry weight), where the long-term silica release was observed after deforestation (Conley et al., 2008). This reasoning aligns with several other studies showing no increased stream dissolved silica export following deforestation (Bäumler & Zech, 1999), where sandstone bedrock and associated vegetation composition prevented substantial soil amorphous silica accumulation (Conley et al., 2008; Saccone et al., 2007). It appears that the response of the silica cycle to disturbance depends on the amount and location of local soil silica stocks, the bedrock type, and the composition and abundance of the vegetation community.

These results add to the growing body of research documenting how ecological disturbances alter the global silica cycle. However, substantial uncertainties remain about how the silica cycle will respond to changes in wildfire in the tundra biome, as this is the first study on this subject, to our knowledge. Much of this uncertainty stems from the temporal limitations of our study. Our measurements are from a decade after the burn, and we do not know the impacts of wildfire on silica cycling immediately following the burn nor how they will evolve in the years and decades to come. Whether an initial lateral pulse of silica was exported following a burn, as well as the magnitude and duration of such a pulse, directly influences the mass balance of silica. Additionally, it remains unknown how long this newly accumulated reservoir of silica in terrestrial biomass will persist on site before dissolution or export to downstream systems occur; plant decomposition rates will likely differ with burn succession and shifting plant community composition (Barbe et al., 2019; Hobbie et al., 2000; Turetsky et al., 2010; Wickland et al., 2007), impacting lateral silica export rates from terrestrial systems over the long term.

Ten years after the largest known tundra fire, we observed a rapid increase in the size of the terrestrial vegetation silica reservoir, driven by increased plant silica concentrations and shifts in plant community composition. This is in contrast to the starkly diminished size of the peat amorphous silica pool, resulting in a cumulative loss of 27% in vegetation and nonmineral peat pools a decade after wildfire. Stream silica chemistry, which is similar regardless of catchment burn disturbance, appears resilient to such shifts in the size and structure of terrestrial silica pools. Our data suggest that a portion of the silica mobilized during postwildfire succession is retained in land plants, rather than being stored in peat or exported to downstream systems. The period preceding this unprecedented tundra fire was marked by extreme heat and record low precipitation, conditions likely to persist in the Arctic in the foreseeable future (Chapin, 2005; Jones et al., 2009). Continued examination of the role of fire on silica exchange in Arctic ecosystems is particularly important, as a shifting disturbance regime could alter rates of terrestrial silica retention and lateral export to aquatic ecosystems, with impacts to silica availability in coastal waters.

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