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Fire and grazing impacts on silica production and storage in grass dominated ecosystems

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Abstract Grassland ecosystems are an important terrestrial component of the global biogeochemical silicon cycle. Although the structure and ecological functioning of grasslands are strongly influenced by fire and grazing, the role of these key ecological drivers in the production and storage of silicon represents a significant knowledge gap, particularly since they are being altered worldwide by human activities. We evaluated the effects of fire and grazing on the range and variability of plant derived biogenic silica stored in plant biomass and soils by sampling plants and soils from long-term experimental plots with known fire and grazing histories. Overall, plants and soils from grazed sites in the South African ecosystems had up to 76 and 54% greater biogenic silica totals (kg ha^{-1}), respectively, than grazed North American sites. In North American soils, the combination of grazing and annual fire resulted in the greatest abundance of biogenic silica, whereas South African soils had the highest biogenic silica content where grazed regardless of burn frequency. These results as well as those that show greater Si concentrations in grazed South African plants indicate that South African plants and soils responded somewhat differently to fire and grazing with respect to silicon cycling, which may be linked to differences in the evolutionary history and in the grazer diversity and grazing intensity of these ecosystems. We conclude that although fire and grazing (as interactive and/or independent factors) do not affect the concentration of Si taken up by plants, they do promote increased silicon storage in aboveground biomass and soil as a result of directly affecting other site factors such as aboveground net primary productivity. Therefore, as management practices, fire and grazing have important implications for assessing global change impacts on the terrestrial biogeochemical cycling of silicon.

Keywords Biogenic silica · North American grasslands · Soil · South African savannas · Terrestrial plants

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Abbreviations

AB	Annually burned
ANOVA	Analysis of variance
ANPP	Aboveground net primary productivity
BSi	Biogenic silica
BNPP	Belowground net primary productivity
G	Grazed
IB	Intermediate burned
LTER	Long Term Ecological Research
SOC	Soil organic carbon
UB	Unburned
UG	Ungrazed
WRB	World Reference Base

Introduction

Silicon is the second most abundant element in the Earth's crust after oxygen and its biogeochemical coupling with the global carbon cycle makes knowledge of Si cycling particularly important (Treguer et al. 1995; Ragueneau et al. 2000; Treguer and Pondaven 2000; Yool and Tyrell 2003; Struyf and Conley 2008). The weathering of primary silicate minerals (e.g. anorthite) to secondary forms (e.g. kaolinite) is a process whereby carbon dioxide reacts with silicate minerals in the presence of water to yield bicarbonate. In other cases the weathering of primary and secondary minerals also yields silicic acid. Such chemical weathering reactions play an important role in C sequestration as CO_2 is consumed. Additionally, these weathering processes are an important Si source for marine diatoms that remove silicic acid from estuaries and oceans for long term storage as skeletal biogenic silica (BSi) sediments (Berner and Berner 1996; DeMaster 2002; Yool and Tyrell 2003). Diatoms are important in uptake of atmospheric CO_2 and are Si-limited in some ocean basins, linking Si availability to CO_2 regulation (Dugdale et al. 1995). Together, mineral weathering and diatom production processes link not only the Si and C cycles, but also the terrestrial and oceanic biogeochemical systems.

Terrestrial land plants are key contributors to this continental-to-oceanic relationship through the production of weathering agents (Kelly et al. 1998) and by mobilizing Si through plant uptake from the soil (Conley 2002; Blecker et al. 2006). Similar to diatoms in aquatic ecosystems, terrestrial plants also transform silicic acid into BSi (Raven 1983; Datnoff et al. 2001). Grasses, in particular, take up monosilicic acid ($Si(OH)_4$) from the soil solution and deposit it as BSi, or phytoliths on cell walls, in luminas and in intercellular spaces (Siever and Scott 1963; Raven 1983; Epstein 1999). When plants die, their BSi is returned to the soil where its amorphous form is more soluble than quartz and less soluble than other siliceous crystalline minerals (Lindsay 1979). These solubility differences distinguish various Si pools (Fig. 1) that determine the release of Si from the soil environment and into riverine and oceanic systems. For example, the higher solubility of BSi relative to quartz makes Si more readily available for cycling into the soil water pool where it is either available for biotic uptake or leached from the system.

Recent estimates have shown that rivers transport approximately 5 Tmol Si year^{-1} globally or 80% of the total annual flux from continents to oceans (Treguer et al. 1995; Conley 2002). Although silicate mineral weathering is a primary source of this flux, the terrestrial production of BSi also controls Si mobility, and its role has been largely underestimated in Si export models (Berner and Berner 1996). The underestimation of this important biogenic component

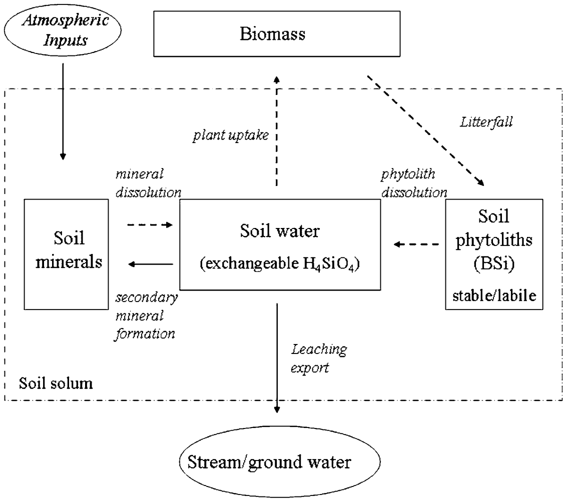


Fig. 1 Conceptual model of the terrestrial silica cycle used in this study. *Boxes* represent pools and *arrows* represent fluxes. *Dashed arrows* emphasize the area of the cycle that was of particular interest for measurements in this study (Adapted from Blecker et al. 2006)

(BSi) is particularly apparent in grassland systems where recent estimates indicate that North American grasslands alone yield 0.3 Tmol Si in aboveground biomass and 130 Tmol Si in the soil (Blecker et al. 2006). Thus, the BSi stored in the soils of temperate grassland ecosystems alone rivals the estimated storage in global biomass determined by Conley (2002) to be at 60–200 Tmol Si year^{-1}. In addition, Blecker et al. (2006) suggested that the geochemical behavior as well as the variability of BSi within grassland ecosystems is linked closely to climate and ANPP. However, other ecological processes, namely fire and grazing, have not been assessed with regard to their impact on the production and cycling of silica.

Fire and grazing, whether natural or managed, play an important role in the structure and function of grassland and savanna ecosystems worldwide (Hulbert 1969; Old 1969; Vogl 1974; Axelrod 1985). Fire and grazing in grass dominated systems prevent the invasion of woody species and strongly impact plant species composition (Bragg and Hulbert 1976; Knapp et al. 1999; Uys et al. 2004; Briggs et al. 2005). The mesic grasslands of North America and the savannas of South Africa are two examples of ecosystems where both fire and grazing play a key role in virtually all ecological processes (Knapp et al. 1998; Du Toit 2003).

Although frequently used as management tools (Tainton 1999), fire and grazing are considered to be “natural disturbances” to grassland ecosystems as they remove biomass and alter resource availability (Pickett and White 1985). The frequency at which an ecosystem experiences burning can strongly influence the plant community (Freeman 1998; Lunt and Morgan 2002) and can alter the chemical composition (Gillon 1983; Cass et al. 1984; Gill et al. 1990) and development of the soil (Powers et al. 1990; Huggett 1998; Neary et al. 1999). Given that precipitation, fire, and grazing regimes are being impacted directly and indirectly by human activities in grasslands and savannas worldwide, an understanding of the influence of fire and grazing on BSi production and storage is needed, particularly with the potential link between Si and C cycles.

In a bioclimatic study across the Great Plains, Blecker et al. (2006) found productivity to be an important control over Si storage as BSi content in aboveground biomass increased with increased precipitation. Their results suggest that fire and grazing, two additional drivers of productivity are thus, likely to be important. Indeed, the turnover time of grasses and the release of BSi into the soil may be largely controlled by fire and grazing. Buis (2009) found that ANPP intermittently responded positively to fire alone and was affected strongly by soil depth and N availability post fire. Based on these regional-scale observations, a study was conducted with the following objectives: (1) to evaluate the range and variability of BSi accumulation in aboveground biomass and storage in grassland and savanna soils as a function of fire frequency and grazing treatments (2) to determine whether the older soils of South African savannas exhibit similar patterns in Si production and storage as the younger soils of North American grasslands under similar fire regimes and grazing treatments.

Methods

Study areas

Research was conducted within the framework of three long-term field experiments in North America and South Africa to specifically examine the effects of fire and grazing on BSi (Table 1). The North American and two South African sites allow for comparative studies because of similarities in key aspects of their experimental design. Like the North American grasslands, the South African savannas are dominated by C_4 grass species such as red grass (*Themeda triandra*). According to Sage et al. (1999), the grasslands of southern Australia, the steppe of south-east Asia, the pampas of South America and the tallgrass prairie of North America are all structurally analogous to the grasslands of South Africa.

The North American site is located on the 3,487 ha Konza Prairie Biological Station (Konza) which lies in the northern Flint Hills region of northeastern Kansas and has been a participant in the Long Term Ecological Research (LTER) network since the program’s inception in 1981 (Callahan 1984). The majority of the North American Great Plains grassland ecosystem has been strongly influenced by Pleistocene glaciation (Axelrod 1985); however, the localities presented in this study lie just beyond the limit of the last glacial extent. The silty clay loam- to clay loam soil textures at Konza are derived from parent materials of cherty limestone and shale (Jantz

Table 1 Climatic and site property data of three grassland fire treatments

Site properties	Konza			Satara			Ukulinga		
	Burn treatment								
	UB	IB	AB	UB	IB	AB	UB	IB	AB
ANPP (SE), g m^{-2} [a]									
Grazed	270 (19)	235 (14)	285 (18)	478 (45)	523 (59)	496 (43)			
Ungrazed	296 (9)	286 (17)	285 (30)				511 (65)	464 (28)	537 (46)
MAP (mm)	835[b]			544[c]			844[c]		
MAT (°C)	12.7[b]			21.2–23.3[c]			17.6[c]		
MMT (°C)	−2.7 to 26.6[d]			16–28[c]			13.2–21.4[c]		
Latitude/longitude	39° 05.48 N/96° 34.12 W			23–25°S/30-31°E			29°40′S/30°20′E		
Elevation range (m)	320–444			240–320			840		
Underlying geology	Cherty limestone and shale			Basalt			Marine shales and dolerite colluvium		
Soil type	Udic argiustolls			Rhodic nitisols, Haplic luvisols, Leptic phaeozems			Dystric leptosols, Chromic luvisols, Haplic plinthisols		
Vegetation type	Tall grass			Mixed lowveld bushveld			Tall grassveld		
Biome type	Mesic grassland, temperate			Savanna, subtropical			Savanna, subtropical		

UB unburned, *IB* intermediately burned, *AB* annually burned, *ANPP* annual aboveground net primary productivity, *MAP* mean annual precipitation, *MAT* mean annual temperature, *MMT* mean monthly temperature range

[a] Data from Buis (2009)

[b] Data from Bark (1987)

[c] Data from Mills and Fey (2004a)

[d] Data from Hayden (1998)

et al. 1975; Ransom et al. 1998). Morphologically the soils are typical of North American grassland Mollisols with high concentrations of organic carbon in the surface A horizons and high base saturation (Blecker et al. 2006). Konza is a tallgrass prairie dominated by native perennial C_4 grasses such as big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*) (Knapp et al. 1998). The climate is continental with mean monthly temperature ranges from −2.7°C in January to 26.6°C in July (Hayden 1998). Annual precipitation averages 835 mm with 75% falling during the growing season between April and September (Bark 1987).

Konza is divided into 60 experimental units where the unit of study is the watershed. Each watershed is associated with a fire treatment where prescribed fire treatments are replicated with burning intervals of 1-, 2-, 4-, 10- and 20-years. Additionally, bison are present in a subset of the watersheds to address the role of native grazers and fire-grazing interactions (Knapp et al. 1999; Johnson and Matchett 2001). Data for this study are from plots (ca. 250 m^2) in watersheds that are grazed by bison or ungrazed and burned annually (AB), quadrennially, or every 20 years and considered unburned (UB).

One of the two South African sites was located near Satara in the approximately 2 million ha Kruger National Park of north-eastern South Africa. The fine textured soils at Satara are derived from basalt and are classified as rhodic nitisols, haplic luvisols and leptic phaeozems (WRB) (Mills and Fey 2004a, b). Vegetation at the site consists of a mixture of scattered marula (*Sclerocarya birrea*) and knobthorn (*Acacia nigrescens*) trees (Mills and Fey 2004a, b) and grasses (Table 2). The climate is semi-arid with mean monthly temperature ranges from 16 to 28°C (Mills and Fey 2004a) and with a mean annual precipitation of 544 mm (Govender et al. 2006). The experimental fire plots at Satara are approximately 7 ha each, with fire return intervals similar to Konza, including AB, triennially burned, or left unburned (UB). A diverse suite of large grazers have unrestricted access to the plots at Satara.

The second South African site is on the Ukulinga Research Farm (Ukulinga) located in KwaZulu-Natal within the Coast Hinterland Bushveld (Low and Rebelo 1996). The clay loam to sandy clay loam textured soils at Ukulinga are derived from parent materials of shales and dolerite and are classified as chromic luvisols and haplic plinthosols (WRB) (Mills and Fey 2004a). Although characterized as savanna where the dominant non-graminoid species is *Asteraceae* (Mills and Fey 2004a), the regular burning at Ukulinga has maintained it as an open grassland (Tainton and Mentis 1983; Table 2). The climate is sub-humid with mean monthly temperature ranges

Table 2 Satara and Ukulinga dominant grass species across burn frequency

Site	Burn frequency		
	AB	IB	UB
Satara	*Bothriochloa radicans* *Eragrostis nindensis* *Panicum coloratum* *Urochloa mosambicensis*	*Bothriochloa radicans* *Panicum coloratum* *Themeda triandra* *Urochloa mosambicensis*	*Bothriochloa radicans* *Chloris virgata* *Digitaria eriantha* *Panicum coloratum* *Panicum maximum* *Themeda triandra*
Ukulinga	*Cymbopogon validus* *Diheteropogon amplectens* *Heteropogon contortus* *Hyparrhenia hirta* *Themeda triandra* *Tristachya leucothrix*	*Aristida junciformis* *Cymbopogon excavatus* *Eragrostis curvula* *Tristachya leucothrix*	*Aristida junciformis* *Cymbopogon excavatus* *Eragrostis curvula* *Panicum maximum*

UB unburned, *IB* intermediately burned, *AB* annually burned from 13.2 to 21.4°C (Mills and Fey 2004a) and with a mean annual precipitation of 710 mm (Tainton 1981).

The experimental fire plots at Ukulinga are approximately 14 × 18 m each, and the burning treatments include AB, triennially burned, or left unburned (UB). There are no large grazers at Ukulinga. Thus, in South Africa, the effects of varying fire frequency alone (Ukulinga) or of varying fire frequency combined with grazing (Satara) can be assessed, but assessing interactions between fire and grazing at the same site is not possible. In contrast, the fully factorial design at Konza allows for assessment of the main and interactive effects of fire and grazing.

Field sampling

The sampling scheme and terminology used in this study and applied to the Konza, Satara and Ukulinga sites are defined as follows. The plot is the smallest unit that is experimentally burned at each site. The treatments are the fire frequency prescribed to each plot. For the remainder of this paper, the Konza quadrennially burned plots and the Satara and Ukulinga triennially burned plots will be referred to as intermediate (IB) burned plots. For each site, each treatment was replicated three times. Soil in each replicate plot was sampled at two depth intervals, 0–10 cm and 10–20 cm using a tile spade shovel. These depths were sampled because there is generally a sharp decline in soil phytolith accumulation with depth where the highest amounts are typically in the A horizon and less abundant in other genetic horizons. Konza plots were sampled in both ungrazed and bison grazed watersheds subjected to the different burn treatments. This allowed us to compare the Konza plots to both the Satara plots, which are grazed by large herbivores and the Ukulinga plots, which are ungrazed. A total of 108 soil samples in both North America and South Africa were collected at each depth; 54 samples are from Konza (3 plots × 3 fire regimes × 2 grazing treatments × 3 replicates), 27 samples are from Satara (3 plots × 3 grazed fire regimes × 3 replicates) and 27 samples are from Ukulinga (3 plots × 3 ungrazed fire regimes × 3 replicates). The samples from all sites were returned to the laboratory in plastic bags kept in coolers, air dried and then sieved. Replicate samples from each site at each depth were kept separate throughout all analytical procedures. For tissue silica, we focused on the 3–4 dominant grass species in replicate plots that were actively grazed or ungrazed. Individual plants of each species were sampled adjacent to the soil sampling area and combined for analyses. Estimates of productivity (g m^{-2} $year^{-1}$) for all sites (including *historically* grazed/ungrazed sites from exclosures) were made by harvesting aboveground biomass at the end of the growing season, drying the biomass, and determining the mass of current year's production (Buis 2009). Although scattered trees and shrubs were found at most sites, particularly in unburned plots, these were not sampled for BSi or included in productivity estimates.

Analytical methods

Soil samples were air dried, sieved through a 2 mm (#10 mesh) sieve, ground in a ball mill and oven dried in preparation to be analyzed for carbon and nitrogen. Total carbon and total nitrogen were analyzed on a LECO-TruSpec CN analyzer. Subsamples of prepared oven dried soils were also analyzed for inorganic carbon by pressure transducer (Harris et al. 2001). Percent organic carbon was determined by taking the difference of the results found from each carbon analysis (total C − inorganic C = organic C). Soil pH on air-dried soil using the soil:water (1:1) method was measured with an Orion Model 420A pH meter.

Due to the inability to acquire soil clods from the organic rich upper 20 cm of the Konza and Ukulinga soils, bulk density was calculated empirically from particle size and organic matter content (organic matter is determined from organic carbon, LECO data) (Adams 1973; Rawls 1983). Bulk density for the Satara soils was determined using the Blake and Hartge (1986) clod method in which natural soil peds were coated in paraffin wax and weighed first in air and then again in water.

Biogenic silica

Biogenic silica was recovered from dominant plant species using a gravimetric approach (Blecker et al. 2006) adapted from Piperno (1988), Kelly (1990), and Parr et al. (2001) in which samples were washed, ashed, chemically treated, filtered and weighed. Approximately 10 g of 2–3 cm length oven dried plant material were cleaned with a solution of 5%

sodium hexametaphosphate, 10% HCl and de-ionized water (DI) in a 1:1:8 ratio respectively. Samples were then thoroughly rinsed with DI, treated with 80°C, 70% ethanol to strip them from their waxy coatings, and rinsed with DI water again. They were dried at 65°C in preparation for dry ashing. Pre-weighed subsamples of washed and dried plant material were placed in ceramic crucibles and ashed for 2 h in a muffle furnace at 500°C after which they were allowed to cool in a desiccator and weighed. The resultant ash was then treated with 10% HCl at a temperature of 65°C, filtered through pre-weighed 0.2 μm polycarbonate membranes, treated with 30% H_2O_2 at a temperature of 65°C and filtered again through pre-weighed 0.2 μm polycarbonate membranes. Finally, samples were rinsed thoroughly with DI water then oven dried at 60°C and weighed.

The alkaline wet chemical dissolution method using the weak base Na_2CO_3 was used to analyze for BSi in soils. Although this Na_2CO_3 method has been primarily used by aquatic scientists studying aquatic systems (DeMaster 1981; Conley 1998), we along with our colleagues found it suitable for recovery of BSi from soils of terrestrial ecosystems (Saccone et al. 2006, 2007; Sauer et al. 2006).

Approximately 30 (±0.05) mg of freeze-dried soil were hand- instead of machine- ground to reduce artificially high BSi values from increased surface area and solubility. Soil was measured into 60 mL polypropylene round flat-bottom bottles with 40.0 mL of 1% Na_2CO_3. Bottles were placed in an 85°C shaking water bath for a total of 3, 4 and 5 h at which times 1.0 mL aliquots were removed for analysis. Analysis for dissolved Si was conducted using the molybdate blue spectrophotometric method where the spectrophotometer was set at 812 nm (Mortock and Froelich 1989), a modification from the reduced molybdosilicic acid spectrophotometric method (Strickland and Parsons 1968; Fanning and Pilson 1973). The solubility differences between BSi and mineral Si cause them to go into solution (of Na_2CO_3) at different rates. Dissolution of BSi occurs within the initial 2 h, whereas mineral Si (specifically clay minerals) dissolves at a constant rate for a much longer period of time (DeMaster 1981; Koning et al. 2002; Saccone et al. 2006). Thus, BSi is calculated from the intercept of the linear portion of the mineral Si dissolution curve (DeMaster 1981; Koning et al. 2002).

Statistics

Data were analyzed by an analysis of variance (ANOVA) in SAS (version 9.1) (Cary, NC). A two-way ANOVA was used at Konza with main effects for fire treatment (UB, IB, AB) and grazing treatment (G, UG) and a one-way ANOVA was used at Satara and Ukulinga with only fire treatment as a main effect. Comparisons were also made across continents (North America and South Africa) where fire treatment, grazing and continent were main effects. Sites were analyzed separately as a randomized complete block design. Replicate samples were averaged for each treatment site. Depth (0–10 cm and 10–20 cm) were added together and not considered as a separate effect as the focus of the study was on the total amount of BSi and not its depth distribution. Additionally, the two depth intervals were combined as no significant differences in phytolith abundance was observed between these intervals. Pairwise comparisons were made using the Bonferroni adjustment method with an $\alpha = 0.05$.

Results

Plant biogenic silica

Using the amount of BSi in the dominant grasses of Konza and aboveground productivity data, we estimated that BSi in the vegetation aboveground ranged from 87 to 140 kg ha^{-1} (3.2–5.0 wt.% in the grasses) in grazed plots and 124 to 215 kg ha^{-1} (4.2–6.4 wt.% in the grasses) in ungrazed plots. The greatest BSi values across all fire and grazing treatments were from ungrazed and unburned sites. However, under grazed treatments alone, the greatest BSi values were from annually burned sites. There were no significant ($P < 0.05$) fire or grazing effects (Fig. 2).

Dominant grasses of the grazed Satara and ungrazed Ukulinga sites (Table 2) yielded BSi values ranging from 305 to 552 kg ha^{-1} (5.8–10.6 wt.% in the grasses) and 98 to 363 kg ha^{-1} (2.1–6.8 wt.% in the grasses), respectively. Although the greatest BSi values from both Satara and Ukulinga were from burned sites, the fire effect at the grazed Satara sites is not statistically significant. Biogenic silica content (kg ha^{-1}) in the dominant grasses was significantly greater ($P < 0.05$) in annually burned treatments as

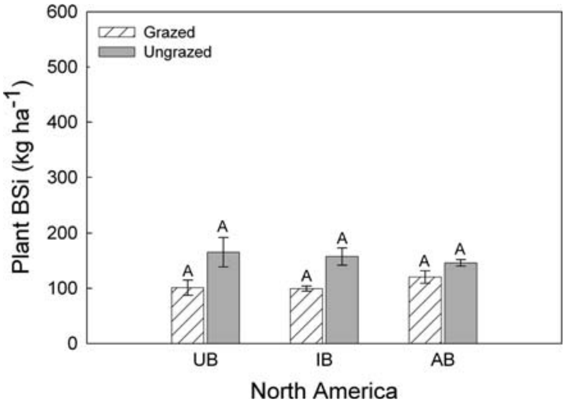


Fig. 2 Mean plant biogenic silica (BSi) amounts (kg ha^{-1}) (± 1 standard error of the mean) for the dominant grass species at unburned (UB), intermediately burned (IB), and annually burned (AB) plots that are grazed or ungrazed in North America (Konza). A *letter change* indicates significant differences in means across grazed-ungrazed paired plots and across fire treatments at $\alpha = 0.05$. Main effects were for fire treatment ($P < 0.05$), grazing ($P < 0.05$), and fire treatment × grazing ($P < 0.05$)

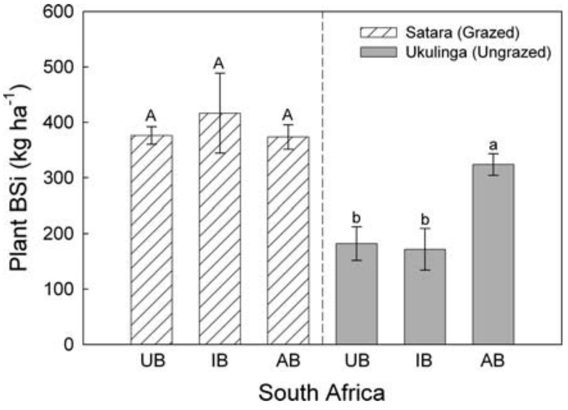


Fig. 3 Mean plant biogenic silica (BSi) amounts (kg ha^{-1}) (± 1 standard error of the mean) for the dominant grass species at unburned (UB), intermediately burned (IB), and annually burned (AB) plots that are grazed (Satara) or ungrazed (Ukulinga) in South Africa. *Capital-* and *lower-case* letters are designated for grazed (Satara) and ungrazed (Ukulinga) plots respectively. A *letter change* indicates significant differences in means across fire treatments at $\alpha = 0.05$. Main effects were for fire treatment ($P < 0.05$)

compared to unburned and intermediately burned treatments at the ungrazed Ukulinga sites (Fig. 3). Biogenic silica content (kg ha^{-1}) in the grasses at grazed Satara sites was significantly greater ($P < 0.05$) in unburned (by 52%) and intermediately burned (by 59%) plots than in ungrazed Ukulinga counterparts.

A continental comparison between North American (Fig. 2) and South African (Fig. 3) grasses revealed that the South African sites had significantly greater ($P < 0.05$) BSi content (kg ha^{-1}) (by 73% in UB, 76% in IB and 68% in AB plots) than the North American sites in all fire treatments when grazers were present (i.e., Konza vs. Satara). The North American and South African sites with the highest BSi content (kg ha^{-1}) were those with the highest ANPP (Table 1).

Plant analyses were also conducted across grazed and ungrazed burn treatments using BSi *concentration* data (in contrast to total BSi amounts in kg ha^{-1}) to address the question of whether uptake and storage of BSi was a direct response to fire and grazing or whether total BSi content was a direct reflection of ANPP and thus, an indirect response to fire and grazing. Results suggest that there was no significant ($P < 0.05$) fire or grazing effect at Konza (Fig. 4), Satara, or Ukulinga (Fig. 5) sites in plant BSi concentrations. However, under grazed treatments South African sites had significantly greater ($P < 0.05$) BSi concentrations than North American sites.

In summary, the total BSi amounts (kg ha^{-1}) in vegetation were not affected by grazing or fire in

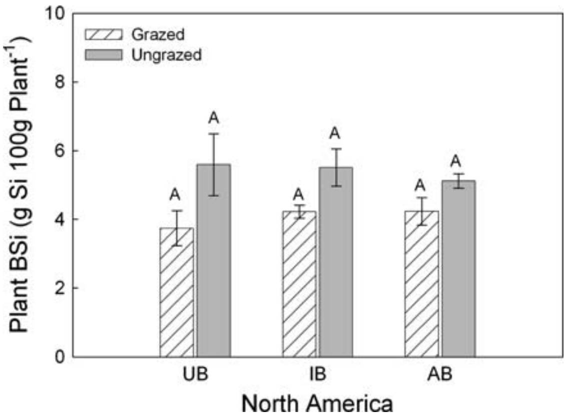


Fig. 4 Mean plant biogenic silica (BSi) concentrations (g Si 100 g Plant^{-1}) (± 1 standard error of the mean) for the dominant grass species at unburned (UB), intermediately burned (IB), and annually burned (AB) plots that are grazed or ungrazed in North America (Konza). A *letter change* indicates significant differences in means across grazed-ungrazed paired plots and across fire treatments at $\alpha = 0.05$. Main effects were for fire treatment ($P < 0.05$), grazing ($P < 0.05$), and fire treatment × grazing ($P < 0.05$)

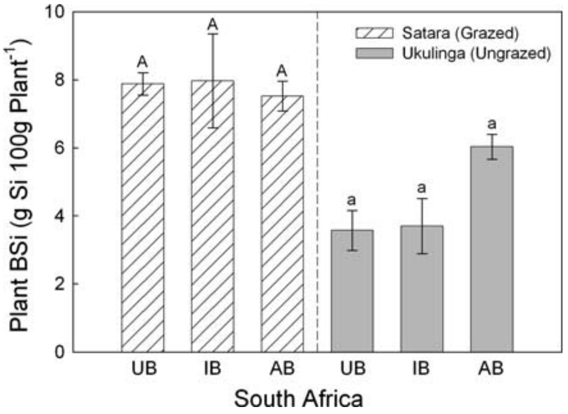


Fig. 5 Mean plant biogenic silica (BSi) concentrations (g Si 100 g Plant^{-1}) (± 1 standard error of the mean) for the dominant grass species at unburned (UB), intermediately burned (IB), and annually burned (AB) plots that are grazed (Satara) or ungrazed (Ukulinga) in South Africa. *Capital*- and *lower-case* letters are designated for grazed (Satara) and ungrazed (Ukulinga) plots respectively. A *letter change* indicates significant differences in means across fire treatments at $\alpha = 0.05$. Main effects were for fire treatment ($P < 0.05$)

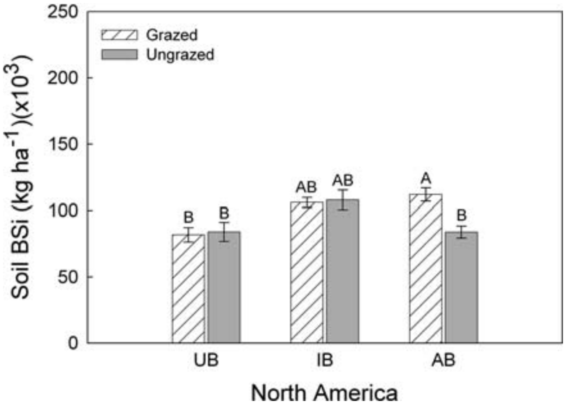


Fig. 6 Mean soil biogenic silica (BSi) amounts (kg ha^{-1}) (× 10^{3}) (± 1 standard error of the mean) at depths up to 20 cm at unburned (UB), intermediately burned (IB), and annually burned (AB) plots that are grazed or ungrazed in North America (Konza). A *letter change* indicates significant differences in means across grazed-ungrazed paired plots and across fire treatments at $\alpha = 0.05$. Main effects were for fire treatment ($P < 0.05$), grazing ($P < 0.05$), and fire treatment × grazing ($P < 0.05$)

North America, but were affected by annual fire in ungrazed South Africa. Biogenic silica concentrations in the vegetation in North America and South Africa were not affected by grazing or fire. The largest differences were found when comparing North America and South Africa where South African grazed sites had the greatest total BSi amounts (kg ha^{-1}) and concentrations across fire treatments.

Soil biogenic silica

The amount of BSi (kg ha^{-1}) in the soil (0–20 cm) was three orders of magnitude greater than ecosystem level plant BSi (kg ha^{-1}), a ratio similar to other terrestrial grassland systems (Blecker et al. 2006). Biogenic silica amounts within the top 20 cm of the soil surface at Konza ranged from 22,000 to 78,100 kg ha^{-1} (2.0–7.1 wt.%) at grazed sites and 18,700 to 81,400 kg ha^{-1} (1.7–7.4 wt.%) at ungrazed sites. Biogenic silica content (kg ha^{-1}) was significantly greater ($P < 0.05$) in burned treatments compared to unburned treatments in the presence of grazers (Fig. 6). Biogenic silica content (kg ha^{-1}) in grazed Konza sites was significantly greater (by 25%) in annually burned plots than in ungrazed counterparts. There was no significant fire effect on soil BSi in ungrazed sites.

Biogenic silica content within the top 20 cm of the soil surface at the grazed Satara and ungrazed Ukulinga sites ranged from 22,400 to 176,400 kg ha^{-1} (1.6–12.6 wt.%) and 24,000 to 88,800 kg ha^{-1} (2.0–7.4 wt.%), respectively. The greatest BSi content (kg ha^{-1}) at Satara were from unburned treatment plots and the greatest BSi content (kg ha^{-1}) at Ukulinga were from annually burned treatment plots (Fig. 7). Biogenic silica content (kg ha^{-1}) was significantly greater in unburned and annually burned treatments as compared to intermediately burned treatments at Satara sites. Biogenic silica content (kg ha^{-1}) at grazed Satara was significantly greater in unburned (by 52%) and annually burned (by 34%) plots than in ungrazed Ukulinga counterparts.

A continental comparison between North America (Fig. 6) and South Africa (Fig. 7) revealed that under grazed treatments, South African soils had significantly greater BSi content (kg ha^{-1}) than North American soils in unburned (by 54%) and annually burned (by 34%) treatment plots and in annually burned (by 26%) plots where ungrazed.

In summary, the total BSi amounts (kg ha^{-1}) in soil were only affected by grazing with annual fire in North America and only affected by fire when grazed in South Africa. Similar to the findings for vegetation, the greatest differences in total BSi amounts in soil

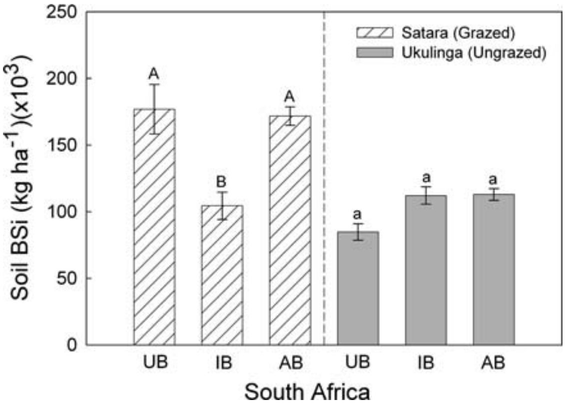


Fig. 7 Mean soil biogenic silica (BSi) amounts (kg ha^{-1}) ($\times$ 10^3) ($\pm$ 1 standard error of the mean) at depths up to 20 cm at unburned (UB), intermediately burned (IB), and annually burned (AB) plots that are grazed (Satara) or ungrazed (Ukulinga) in South Africa. *Capital-* and *lower-case* letters are designated for grazed (Satara) and ungrazed (Ukulinga) plots respectively. A *letter change* indicates significant differences in means across fire treatments at $\alpha = 0.05$. Main effects were for fire treatment ($P < 0.05$)

were found when comparing North America and South Africa where South African grazed sites had the greatest BSi totals (kg ha^{-1}).

Soil to plant BSi ratios

Soil to plant ratios of BSi were calculated to gain information about Si cycling between the plants and soils (to a depth of 20 cm). Across all treatments and on both continents the ratio was on the same order of magnitude, and on the basis of kg ha^{-1} ranged from 251:1 at Satara intermediately burned sites to 930:1 at Konza annually burned and grazed sites. Soil and plant concentration data yielded soil:plant BSi ratios ranging from 1:1 to 3:1 with most sites having a ratio of 2:1 (Fig. 8). Approximately 50% of the variance in soil BSi was explained by plant BSi. A continental comparison, however, showed that, when analyzed separately, South African sites contributed most to this positive correlation as approximately 75% of the variance in soil BSi was explained by plant BSi in South African sites alone.

Both soil BSi and soil organic carbon (SOC) are plant mediated and thus data were regressed against each other to determine whether SOC content could be used as a general predictor of BSi content. A general relationship ($r^2 = 0.65$) existed between SOC and soil BSi across North American sites (Fig. 9a). The North American burned and grazed sites contributed most, and the unburned ungrazed sites least, to this positive correlation. A similar trend was not evident ($r^2 = 0.30$) for South African samples (Fig. 9b).

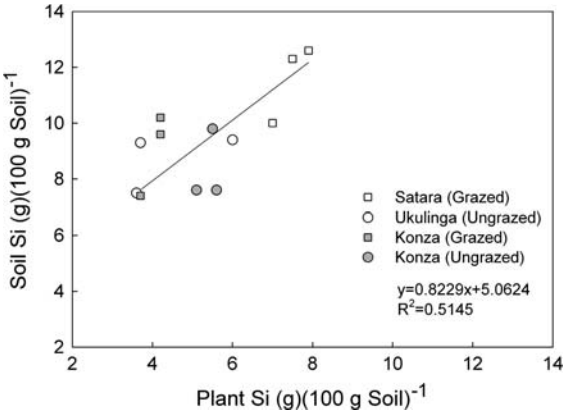
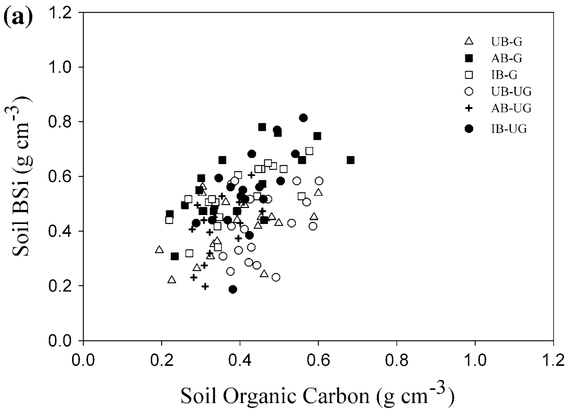


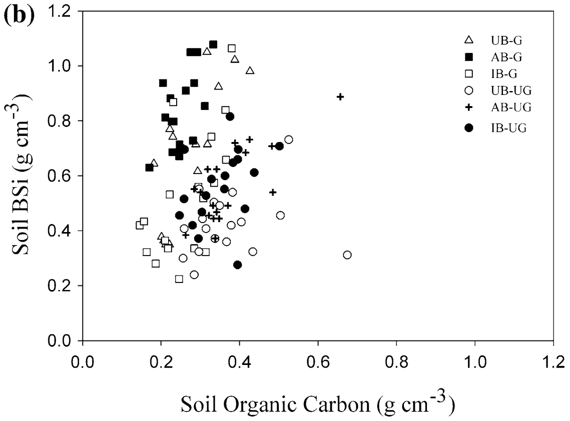
Fig. 8 Relationship between plant and soil biogenic silica (BSi) wt.% at grazed and ungrazed North American (Konza) and South African (Satara and Ukulinga) sites, regardless of burn treatment

Discussion

This study contrasted the response of ecosystem level BSi in plants and soils under different fire frequencies and in the presence or absence of grazers in North American grasslands and South African savannas. Globally, grasslands share a common reliance upon fire and grazing to maintain community structure and function (Collins 1992; Fuhlendorf and Smeins 1999; Veen et al. 2008). Fire and grazing influence vegetation composition, annual aboveground net primary productivity (ANPP) and nutrient cycling. However, grasslands may respond differently to fire and grazing depending on the limitations of above- and belowground resources and the feedbacks between plant and soil systems. For example, although higher rates of precipitation are largely responsible for the gradients in ANPP across the Great Plains, ANPP is not necessarily correlated with precipitation variability in the tallgrass prairie, where other factors such as availability of light and N are often limiting under different fire frequencies (Blair 1997; Knapp et al. 1998).



North America



South Africa

Fig. 9 Relationship between two biologically mediated soil constituents, soil organic carbon and biogenic silica (BSi), across interactive burning and grazing regimes in **a** North American grasslands (Konza), **b** South African savannas (Satara and Ukulinga). Unburned (UB), intermediately burned (IB), and annually burned (AB) treatments make up the fire regime, and grazed (G) and ungrazed (UG) treatments make up the grazing regime

The effects of fire and grazing have been more thoroughly examined in the Great Plains of North America than in other regions. A relatively consistent ecological response to greater fire frequency has been greater ANPP (Briggs and Knapp 2001; Knapp et al. 1998) and belowground net primary productivity (BNPP) (Johnson and Matchett 2001) in the North American tallgrass prairie. Frequent fire results in enhanced light availability following removal of deritus and greater N limitation, enhancing growth of the dominant C_4 grasses that, in turn, dominate over forbs in abundance and diversity (Collins et al. 1998; Briggs and Knapp 2001). Grazing has also been shown to have positive effects on ANPP in some North American grasslands (Frank et al. 2002).

The relationship of ANPP to BSi is important as previous studies show that ecosystem level plant BSi (kg ha^{-1}) distribution across North American grasslands is largely driven by differences in ANPP (Blecker et al. 2006). They found that the plant BSi content (kg ha^{-1}) increases with increasing ANPP along a bioclimosequence. Fire may indirectly affect ecosystem level plant BSi (kg ha^{-1}) by directly stimulating ANPP. However, Buis (2009) speculates on other potential factors that may alter the effects of fire and grazing on grasslands and they include dormant season climate, diversity of large herbivores, soil fertility, and evolutionary history. We hypothesized that fire would have a negative effect on soil BSi content (kg ha^{-1}) as a direct physical vector of loss by wind driven removal of ash after fire (Vermeire et al. 2005); therefore we expected to see less soil BSi accumulation from burned plots. Grazing was hypothesized to have a positive effect on soil BSi content (kg ha^{-1}) because grasses were expected to take up greater amounts of BSi at higher concentrations as a response to, and protection against, herbivory (Cid et al. 1990; Pondaven et al. 2006). Consumption of Si rich grasses by grazers was expected to increase turnover and return of Si back into soil through deposition of fecal material. We therefore expected to see more BSi accumulation in these grazed soils.

In the present study, ecosystem level plant and soil BSi (kg ha^{-1}) from Konza exhibited similar *general* responses to fire and grazing: both plant and soil BSi contents (kg ha^{-1}) were, (1) greater in grazed burned versus unburned treatments and (2) less in grazed versus ungrazed sites across treatments with exception of the annually burned soils. More significant, however, are the interactive effects of fire and grazing on soil BSi content (kg ha^{-1}), where soils from annually burned grazed sites had greater storage of Si than unburned grazed sites.

Our results did not support our hypothesis regarding the direct loss of soil BSi content after fire. We suspect that fire may positively influence ANPP by removing detritus and enhancing light penetration (Knapp and Seastedt 1986) thereby indirectly affecting BSi accumulation in ecosystem level BSi storage in plants and in soil. The decrease in forb abundance and the increase in grasses at frequently burned sites likely resulted in greater ecosystem level BSi storage because, according to Blecker et al. (2006), forbs take up less Si on a dry weight basis. Specifically, forbs at Konza only averaged 0.29 ± 0.07% Si (Blecker et al. 2006). Buis (2009) does not show a strong significant relationship between fire and ANPP alone and attributes the variability to other site factors, in particular, greater soil depth and water availability. Similarly, ecosystem level BSi storage in plants is not only dependent on ANPP, but also on soil factors such as mineral dissolution (bedrock type) and the weathering environment (climate). Storage of BSi in soil is in turn dependent on plant storage and turnover rates and the soil weathering environment.

We found that although many ecological variables respond in contrasting ways to grazing and fire, together they promoted Si storage by influencing ANPP among other site factors. The effects of fire and grazing as interactive factors have been minimally studied; however, Archibald et al. (2005) found that fire affects grazing by altering large-scale foraging patterns and suggested that the new growth after fire attracts grazers onto frequently burned sites. Additionally, they found that grazers affect fire by reducing fuel loads and altering fire spread in a landscape which may ultimately reduce the amount of material susceptible to fire derived wind erosion.

Although the interactions between fire and grazing cannot be assessed directly in South Africa, we can speculate about potential interactions based on the independent effects of fire and grazing and on comparisons to effects of fire and grazing at Konza. Like the plants and soils at grazed Konza sites, those from Satara and Ukulinga exhibited similar general relationships to fire in that burned sites had greater BSi amounts (kg ha^{-1}) in plants and soils (with the exception of Satara soils) than unburned sites. Unlike the Konza sites, the grazed Satara sites had greater ecosystem level plant and soil BSi amounts (kg ha^{-1}) than the ungrazed Ukulinga sites; however, this difference may be attributed to other site factors (i.e., plant species identity and differences in climate, parent material and overall weathering potential) and not directly a grazing effect. In the plants and soils of Satara and Ukulinga, the effects of fire and grazing on Si storage appear to have been independent. Biogenic silica content (kg ha^{-1}) in plants at the ungrazed Ukulinga sites was greater when burned annually, but BSi was predominantly greater at the grazed Satara sites in plants and soils.

South African plants and soils store significantly greater ($P < 0.05$) amounts of BSi (kg ha^{-1}) than North American plants and soils when compared in the end-member fire treatments with grazing, indicating that North American and South African systems respond differently to the combined effects of the key ecological drivers, with respect to Si storage. From an ecological perspective, this difference in BSi storage between North American and South African sites is likely linked to differences in the evolutionary history and in the grazer diversity and grazing intensity of these ecosystems. However, the biogeochemistry of Si at the ecosystem scale is also dependent on parent material (the primary source of Si), stage of soil development and the consequent mineralogical composition of the soil. Along with climate, these additional factors regulate the solubility of Si and its availability for plant uptake. For example, the basalt and shale bedrock of Satara and Ukulinga in South Africa is more likely to yield more silica than the cherty limestone bedrock of Konza in North America. Although there is more silica in chert as quartz, basalt yields more silica because of its high chemical instability relative to other silicates (Goldich 1938). Also, it is probable that not enough time has elapsed for the quartz in the Konza cherts to be a significant contributor of Si in solution especially when the temperatures are much colder than those in South Africa.

Importantly, the Si concentration results are also significantly greater at grazed South African compared to North American sites and suggest that the dominant South African grasses sampled may have developed a defense mechanism against herbivory (by taking up more Si) in response to its long history of grazing. Although both North American and South African grasslands have a long evolutionary history of grazing, the South African grasslands are considered to be much older (Bond et al. 2003) with a longer presence of large fauna. Grazing activity often enhances the cycling of other nutrients (McNaughton 1983) and may increase Si concentrations in grasses (McNaughton et al. 1985; Gali-Muhtasib et al. 1992).

Although our BSi concentration data suggest that there is not a requirement of plants to uptake greater concentrations of Si in response to fire or grazing, we did not sample identical plant species across sites. Changes in species composition as a result of fire or grazing may indeed cause differences in overall BSi storage as different species take up different concentrations of Si; however, this direct physiological response needs to be addressed in subsequent studies. We suggest that mass (kg ha^{-1}) differences of BSi in plants among treatments result from differences in ANPP (and potentially plant species composition) and are indirectly affected by fire and grazing in their individual instances.

Soil to plant BSi ratios imply that South African plant BSi values are better predictors of BSi soil storage than North American plants. Generalized soil storage estimations may be made from plant BSi data using our predictive model (Fig. 8); however, this model was best suited for South African sites and only considered plant and soil components of the Si cycle. The other approximate 50% of the variability in soil BSi concentration that was not accounted for by plant BSi concentration may be influenced by primary mineral dissolution, secondary mineral formation, atmospheric deposition, and leaching outputs (Fig. 1). South African soils may stockpile greater proportions of BSi in the soil from what is provided by plant decomposition than North American systems. However, this relationship is dependent on the dominant factors driving the soil system, climate and parent material. The difference in the timing and amount of precipitation and its effect on the parent material creates the weathering environment and determines the soil chemistry, leaching and uptake potential, and soil BSi pools for these systems. Differences in the cause of the dormant season (low temperature in North America and drought in South Africa) for example can affect the chemical weathering potential of the soil as well as plant-soil interactions.

Unlike the North American soils, the South African soils did not show a trend between soil BSi and soil organic carbon (SOC). The soils of South Africa receive greater amounts of precipitation than the soils of North America and therefore experience higher rates of decomposition which may function to cycle soil BSi more rapidly. Parent material also influences organic matter accumulation through its effect on soil texture and fertility where soil organic matter tends to increase as clay content increases and accumulate with abundant vegetative growth where soils are more fertile. Silicon from mineral/nonbiogenic pools may be an additional and perhaps a greater Si source in South Africa than in North America. The combination of Si supplied from biogenic and nonbiogenic sources would diminish the direct correlation with SOC because it is biologically mediated. Evolutionarily, the North American plants may not have adapted the need for additional Si uptake and their Si source may be solely from the soil BSi pool. Future work on ecosystem scale Si biogeochemistry would benefit from focusing on Si mass balance and the importance of parent material and other geologic controls on the mobilization of BSi.

Summary and conclusions

This study suggests that quantities (kg ha^{-1}) of BSi aboveground are coupled to quantities found in the soil, suggesting that fire and grazing do not negatively affect the total BSi pool size in these grassland systems. Leaching of BSi was not considered a major vector of loss because in water limited ecosystems such as grassland and savanna environments silica precipitates in the soil and leaching losses are probably more important over pedogenic scales (Schaetzl and Anderson 2005). Plant and soil BSi values appear to be influenced directly by ANPP and thus, indirectly by fire and grazing. However, on a mass per area basis, BSi cycling between South African plants and soils may be more responsive to grazing than North American sites, and may promote Si release via chemical weathering as Si supplied by soil labile BSi reservoirs are transported. The additional source of Si from mineral dissolution may make South African sites less correlative with SOC and biologic turnover compared to North American sites.

Grassland ecosystems make up 40% of terrestrial earth and, based on estimates of BSi production and storage, are one of the largest repositories of this labile form of Si. The alterations of grasslands by fire and grazing management practices in differing continental grasslands may have potential implications on BSi totals and BSi cycling, and the future of global grasslands in the presence of a changing climate. Perhaps the most significant results are those comparing North American and South African grazed sites. Biogenic silica pool sizes are much larger in South African plants and soils in grazed sites irrespective of fire regime. This may be as a response to variation in ANPP or to differences in species composition; the latter of which needs to be addressed. Estimating BSi in plants and soils of similar grassland systems, but with differing evolutionary histories, has allowed us to define a range of variability as to the effects that ecological drivers such as fire and grazing have on BSi production and storage in sensitive and easily manipulated grassland ecosystems.

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