



Phytolith carbon sequestration in global terrestrial biomes



Zhaoliang Song^{a,*}, Hongyan Liu^{b,*}, Caroline A.E. Strömberg^{c,*}, Xiaomin Yang^a, Xiaodong Zhang^a

^a Institute of the Surface-Earth System Science, Tianjin University, Tianjin 300072, China

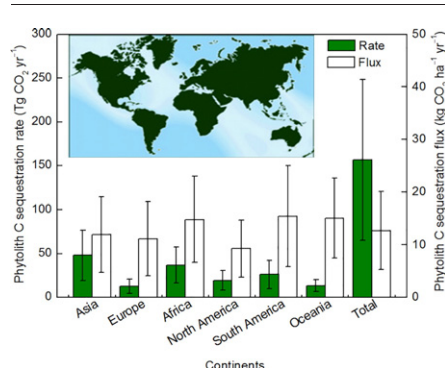
^b College of Urban and Environmental Sciences, Peking University, Peking 100871, China

^c Department of Biology and Burke Museum of Natural History and Culture, University of Washington, Seattle, WA 98195, USA

HIGHLIGHTS

- Carbon occluded within phytolith is a stable bio-geochemical C sink mechanism.
- Phytolith C sequestration in global terrestrial biomes is $156.7 \pm 91.6 \text{ Tg CO}_2 \text{ yr}^{-1}$.
- The main contributors are Asia (31%), Africa (24%), and South America (17%).
- Appropriate practices could theoretically double the phytolith C sink in global terrestrial biomes.

GRAPHICAL ABSTRACT



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ABSTRACT

Terrestrial biogeochemical carbon (C) sequestration is coupled with the biogeochemical silicon (Si) cycle through mechanisms such as phytolith C sequestration, but the size and distribution of the phytolith C sink remain unclear. Here, we estimate phytolith C sequestration in global terrestrial biomes. We used biome data including productivity, phytolith and silica contents, and the phytolith stability factor to preliminarily determine the size and distribution of the phytolith C sink in global terrestrial biomes. Total phytolith C sequestration in global terrestrial biomes is $156.7 \pm 91.6 \text{ Tg CO}_2 \text{ yr}^{-1}$. Grassland (40%), cropland (35%), and forest (20%) biomes are the dominant producers of phytolith-based carbon; geographically, the main contributors are Asia (31%), Africa (24%), and South America (17%). Practices such as bamboo afforestation/reforestation and grassland recovery for economic and ecological purposes could theoretically double the above phytolith C sink. The potential terrestrial phytolith C sequestration during 2000–2099 under such practices would be 15.7–40.5 Pg CO_2 , equivalent in magnitude to the C sequestration of oceanic diatoms in sediments and through silicate weathering. Phytolith C sequestration contributes vitally to the global C cycle, hence, it is essential to incorporate plant-soil silica cycling in biogeochemical C cycle models.

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1. Introduction

Motivated by rapid increases in global emissions of carbon dioxide (CO_2), many scientists have recently focused on terrestrial carbon (C) sequestration (Heimann and Reichstein, 2008; Pan et al., 2011; Peters et al., 2013; Taylor et al., 2016). Phytoliths are microscopic silica bodies

* Corresponding authors at: Institute of the Surface-Earth System Science Research, Tianjin University, No. 92, Weijin Road, Tianjin 300072, China.

E-mail addresses: zhaoliang.song@tju.edu.cn (Z. Song), lhy@urban.pku.edu.cn (H. Liu), caestrom@u.washington.edu (C.A.E. Strömberg).

that form inside tissues in living plants and, in doing so, occlude carbon into the silica lattice (Piperno, 2006; Alexandre et al., 2015). Although accumulation of phytolith-occluded carbon (PhytOC) in soils is slow on an annual-decadal scale, it may contribute ~15–37% of the global mean long-term (10,000 years) soil carbon sequestration rate (Parr and Sullivan, 2005). Based on these calculations, it has been suggested that occlusion of C within phytoliths is an important biogeochemical carbon sequestration mechanism (Parr and Sullivan, 2005; Parr et al., 2010; Song et al., 2012a, 2012b).

A wide range of vascular land plants produce phytoliths that occlude carbon (Smith and White, 2004; Strömberg et al., 2016). Soils contain 400–1000 times more PhytOC than the aboveground biomass for most ecosystems, demonstrating that PhytOC is highly resistant to decomposition and may accumulate in soils and sediment for several hundreds or thousands of years (Meunier et al., 1999; Parr and Sullivan, 2005; Blecker et al., 2006)—if not millions of years (Prasad et al., 2005; Strömberg, 2011). Previous work has estimated the amount of PhytOC produced from leaf litters within grassland (Song et al., 2012a), forest (Parr et al., 2010; Song et al., 2013a) and cropland (Zuo and Lü, 2011) ecosystems of a country (China), within different ecosystems of a region (the Chinese Loess Plateau) (Zuo et al., 2014), and within cropland ecosystems across the world (Parr and Sullivan, 2011; Rajendiran et al., 2012; Song et al., 2013b). However, the magnitude and potential of phytolith C sequestration at a global scale and relative to C sequestration as a whole, and how it varies among continents remain unknown.

Here, we present estimates of how much C is sequestered in plant silica within the world's terrestrial biomes based on data of aboveground net primary production (ANPP) of silicon (Si)-rich tissues, phytolith content of vegetation on average in biomes, C contents of phytoliths, and the PhytOC stability factor for terrestrial ecosystems within 100 years (PSF_{100}) estimated from phytolith turnover time ($PSF_{100} = 1 - 100 / \text{phytolith turnover time}$) (Materials and methods). Because phytoliths are mainly produced from the aboveground parts of the biomes (Parr et al., 2010; Parr and Sullivan, 2011) and we are mainly interested in potential storage of phytoliths (and hence PhytOC) in soils well beyond the life of the plants, we have only included PhytOC input from aboveground litterfall and subsequent accumulation in soils or sediments. To account for variation among biomes in phytolith C sequestration estimates due to differential vegetation distribution and phytolith production in relevant plant types, we divided each continent into forest (including bamboo), grassland, wetland, cropland, tundra, and desert. We then used the relative areal extent and average phytolith production of each biome type when

preliminarily calculating continental phytolith C sequestration (for more details see Appendix A).

2. Materials and methods

2.1. Productivity, phytolith and silica content data

From relevant published papers, we obtained ANPP data of herb and/or tree litter (hereafter referred to as Si-rich tissues) for forests (Feng et al., 1999; Parr et al., 2010; Song et al., 2013a), grasslands (Blecker et al., 2006; Ma et al., 2010; Melzer et al., 2010; Alexandre et al., 2011), and other biomes (Li et al., 2013a, 2013b, 2013c; Song et al., 2013b) (Table 1). Forest ANPP in the form of wood and bark for evergreen and deciduous trees was excluded because the Si contribution to the soil pool from wood/bark is negligible compared to leaf biomass (Bartoli, 1983; Li et al., 2006); although note that because tropical woods often contain a lot of silica (Amos, 1952; Welle, 1976), our estimates for tropical regions are conservative. Phytolith and silica content data were obtained from published monographs (Hou, 1982; Xu et al., 1998) and papers (Ding et al., 2008; Parr and Sullivan, 2011; Li et al., 2013a, 2013b, 2013c; Song et al., 2012a, 2013a, 2013b).

2.2. Estimation of phytolith and PhytOC contents

Because the ratio of phytolith/silica for most plants is approximately 1 (Song et al., 2012a, 2013a, 2013b), the phytolith content of plant biomass was estimated from silica content (weight % of plant dry biomass) (Table 2). As most ecosystems contain different plant functional types and even more species, we arrived at one phytolith content value per ecosystem using different phytolith content for different plant functional types within those ecosystems and then averaged those based on estimated relative ANPP for each plant functional type. Based on our own measurements and data from 22 published papers (up to 199 data points, for more details see Appendix B), the C content of phytoliths mainly extracted by a microwave digestion method varies from 0.1% to >10%. Therefore, we used the average occluded C content in phytoliths of these relevant plants for each ecosystem as a preliminary estimation due to the difficult and extremely labor-intensive measuring of the PhytOC for all plants in different biomes. Based on the analysis of these data, we approximated the average PhytOC content as 2.36% for (sub-) tropical forest, 2.37% for temperate forest, 3.06% for boreal forest, 1.85% for grassland (including tropical savanna and temperate steppe), 1.59% for wetland, 4.21% for cropland, 2.67% for shrubland, and 1.5% for

Table 1
General information on global terrestrial biomes.

| Biomes | Area (10 ⁶ ha) | Above ground Si-rich tissues | ANPP of Si-rich tissues (t ha ⁻¹ yr ⁻¹) ^c | References |
|-------------------------------|---------------------------|--|---|------------|
| Forest | | | | |
| (Sub)tropical forest | 1949 | Tree leaf litter and herb litter | 6.95 | 1 |
| Temperate forest | 810 | Tree leaf litter and herb litter | 6.09 | 1 |
| Boreal forest | 1304 | Tree leaf litter and herb litter | 5.19 | 1 |
| Total or average ^a | 4063 | | 6.21 | |
| Grassland | | | | |
| Tropical savanna | 2250 | Herb litter | 6.89 | 2–4 |
| Temperate steppe | 1250 | Herb litter | 2.06 | 2, 3, 5, 6 |
| Total or average ^b | 3500 | | 5.17 | |
| Wetland | 330 | Herb litter | 6.50 | 7, 8 |
| Cropland | 1533 | Crop straw including sheath, stem and leaf | 5.28 | 9 |
| Shrubland | 250 | Shrub leaf litter and herb litter | 3.20 | 2, 10 |
| Tundra | 743 | Shrub leaf litter, herb litter and moss litter | 0.89 | 2, 10 |
| Desert | 1925 | Shrub leaf litter and herb litter | 0.42 | 2, 10 |
| Total or average ^b | 12,344 | | 4.52 | |

1 Song et al., 2013a; 2 Atjay et al., 1979; 3 Melzer et al., 2010; 4 Alexandre et al., 2011; 5 Blecker et al., 2006; 6 Song et al., 2012b; 7 Guo et al., 2008; 8 Zong et al., 2011; 9 Song et al., 2013b; 10 Olson et al., 2001.

^a Area for different biomes based on Atjay et al. (1979), Costanza et al. (1997) and Pan et al. (2011).

^b Average weighted by area, calculated from total biome ANPP of Si-rich tissues and total biome area.

^c ANPP of Si-rich tissues in Shrubland, Tundra, and Desert was estimated from their NPP data by multiplying an ANPP/NPP ratio of 0.4 (Olson et al., 2001).

Table 2

Phytolith content, PhytOC production flux of Si-rich tissues and stability factor of phytoliths in global terrestrial biomes.

| Biomes | Phytolith content (% of dry opal weight) | | Carbon in phytoliths ^d (%) | PhytOC production flux (kg CO ₂ ha ⁻¹ yr ⁻¹) ^b | | PSF ₁₀₀ ^c | Data sources of phytolith content |
|-------------------------------|---|------|---------------------------------------|--|-------|---------------------------------|--------------------------------------|
| | Mean | SE | | Mean | SE | | |
| Forest | | | | | | | |
| (Sub)tropical forest | 2.48 | 0.58 | 2.36 | 14.93 | 9.83 | 0.6 | 1, 2 |
| Temperate forest | 1.28 | 0.29 | 2.37 | 6.79 | 4.41 | 0.7 | 1, 2 |
| Boreal forest | 1.32 | 0.24 | 3.06 | 7.69 | 3.91 | 0.9 | 1, 2 |
| Weighted average ^a | 2.03 | 0.37 | | 10.98 | 6.85 | | |
| Grassland | | | | | | | |
| Tropical savanna | 7.74 | 2.63 | 1.85 | 36.17 | 12.27 | 0.7 | 3, 4 |
| Temperate steppe | 5.60 | 0.70 | 1.85 | 7.83 | 0.97 | 0.9 | 1, 5, 6 |
| Weighted average ^a | 7.43 | 2.35 | | 26.05 | 8.23 | | |
| Wetland | 3.55 | 0.81 | 1.59 | 13.45 | 3.07 | 0.6 | 1, 7, 8 |
| Cropland | 5.52 | 2.99 | 4.21 | 44.98 | 24.37 | 0.8 | 9 |
| Shrubland | 1.79 | 0.22 | 2.67 | 5.61 | 0.69 | 0.9 | 1 |
| Tundra | 2.29 | | 1.50 | 1.12 | 0.75 | 0.9 | 10 |
| Desert | 1.83 | 0.60 | 1.50 | 0.42 | 0.14 | 0.9 | 1 |
| Weighted average ^a | 3.94 | 1.78 | | 17.19 | 7.78 | | |

1 Hou, 1982; 2 Song et al., 2013a; 3 Melzer et al., 2010; 4 Alexandre et al., 2011; 5 Blecker et al., 2006; 6 Song et al., 2012b; 7, 8 Li et al., 2013a, 2013b; 9 Song et al., 2013b; 10 Carey and Fulweiler, 2012.

^a Average weighted by biomass, calculated from total biome phytolith C sequestration rate and total biome area.

^b C content in phytoliths was used to estimate PhytOC production flux with Eq. (1).

^c PSF₁₀₀ was estimated based on phytolith turnover time studies of Bartoli (1983), Alexandre et al. (1997), Meunier et al. (1999), Parr and Sullivan (2005) and Blecker et al. (2006) using Eq. (2).

^d For more details see Appendix B.

tundra and desert (Table 2). Note that whereas some studies reported that the C content in phytolith dry weight extracted using rapid H₂SO₄/H₂O₂ digestion mainly ranges from 0.1% to 0.5% of phytolith dry weight (Santos and Alexandre, 2017), the study of Parr and Sullivan (2014) demonstrated that the C content in phytoliths extracted through modified microwave digestion is at least one order of magnitude higher. Light microscopy and scanning electron microscopy (SEM) examination demonstrate that this variation is not due to insufficient decomposition of non-PhytOC fractions when using the modified microwave digestion method but is more likely caused by the shattering of phytoliths after rapid H₂SO₄/H₂O₂ digestion (Parr and Sullivan, 2014). For this reason, the PhytOC content values obtained from phytoliths extracted via the modified microwave digestion method should be considered more reliable.

2.3. Calculation of PhytOC production flux and rate

The PhytOC production flux, that is, the weight per area and time unit of the carbon (in the form of CO₂) sequestered as PhytOC (kg CO₂ ha⁻¹ yr⁻¹) (Table 2), can be calculated (Song et al., 2013a) as:

$$\text{PhytOC production flux} = \text{PhytOC content} \times \text{ANPP of Si-rich tissues} \times 44/12 \quad (1)$$

where PhytOC content is the PhytOC concentration in the Si-rich tissues of plants (% of dry weight), ANPP of Si-rich tissues is the dry-weight Aboveground Net Primary Production of Si-rich tissues per unit area (kg ha⁻¹ yr⁻¹) (Table 1), and 44/12 is the mass transfer coefficient of CO₂/C. Note that uncertainty estimates of PhytOC production flux account for uncertainties of phytolith content of plant biomass and carbon content of phytoliths. See below for discussion.

2.4. Estimation of phytolith stability factor

Although a considerable percentage of biomass (10–50%) may be harvested or consumed so that not all plant phytoliths return to the soil, studies of biomes such as tropical forest (Alexandre et al., 1997; Meunier et al., 1999), temperate forest (Bartoli, 1983) and temperate grassland (Blecker et al., 2006) show that soils contain 300–1300 times more phytoliths than the aboveground biomass. These values

imply that most (ca. 80%) phytoliths have relatively intact surfaces and can be preserved in soils and sediments for 400 to 3000 years (Alexandre et al., 1997; Meunier et al., 1999; Blecker et al., 2006), though a subset of small or flat phytolith particles may be preferentially dissolved due to their high specific surface area (Meunier et al., 1999; Parr and Sullivan, 2005). While it is possible that some C from cell wall phytoliths may be quite labile and easily lost at an annual–decadal scale compared to C trapped in lumen phytoliths, which are likely to be much more stable at a centennial–millennial scale (Perry et al., 1987), the stability of PhytOC should overall track the stability of the phytoliths in which it is contained. Therefore, we hypothesize that the stability and turnover time of PhytOC equal to those of phytoliths. The phytolith or PhytOC stability factor (PSF₁₀₀) can thus be estimated from phytolith turnover time, which has been shown to increase with decreasing humidity and temperature (Blecker et al., 2006) for a terrestrial biome over 100 years (the time span of greatest concern in studies of C sink prediction for our immediate future; Sitch et al., 2008), as:

$$\text{PSF}_{100} = 1 - 100/\text{PhytOC turnover time} \\ = 1 - 100/\text{phytolith turnover time} \quad (2)$$

where phytolith turnover time (yr) is calculated as soil phytolith storage (g m⁻²) divided by plant phytolith production flux (g m⁻² yr⁻¹), assuming near steady state of the soil system.

2.5. Calculation of phytolith C sink flux and rate

The phytolith C sink flux, that is, how much C occluded in phytoliths is stored in the soil (kg CO₂ ha⁻¹ yr⁻¹), can be estimated from PSF₁₀₀ and PhytOC production flux (Song et al., 2013a, 2013b):

$$\text{Phytolith C sink flux} = \text{PSF}_{100} \times \text{PhytOC production flux} \quad (3)$$

where the PSF₁₀₀ is given by Eq. (2) and PhytOC production flux is given by Eq. (1).

Phytolith C sink flux and terrestrial biome area can be used to calculate the phytolith C sink rate and the total annual phytolith C sink of a terrestrial biome (Tg CO₂ yr⁻¹) (Song et al., 2013a):

$$\text{Phytolith C sink rate} = \text{Phytolith C sink flux} \times \text{area}/1000 \quad (4)$$

where phytolith C sink flux ($\text{kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$) is given by Eq. (3) and the area is expressed as 10^6 ha .

3. Results

3.1. Phytolith production in terrestrial biomes

Phytolith content in above ground Si-rich tissues varies greatly among biomes (1.00–10.37% of dry opal weight) (Table 2). The phytolith content in grassland (weighted average $7.43 \pm 2.35\%$) is 1.3 to 5.8 times higher than that of other biomes. The phytolith content of grassland and forest in the tropical zone is generally higher than that in other climatic zones (Table 2). Based on the weighted average phytolith content ($3.94 \pm 1.78\%$) and ANPP ($4.52 \text{ t ha}^{-1} \text{ yr}^{-1}$) of global terrestrial biomes (for more details see Tables 1, 2), the total phytolith production rate in global terrestrial biomes ($12,344 \times 10^6 \text{ ha}$) is estimated to be $2198 \pm 993 \text{ Tg yr}^{-1}$ (dry opal weight).

3.2. Production and stability of PhytOC in terrestrial biomes

The average PhytOC production flux for the seven biomes is $17.19 \pm 7.78 \text{ kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ (Table 2). The PhytOC production flux of cropland is 3 to 100 times higher than that of (sub)tropical forest and other biomes (Table 2). The stability of PhytOC (PSF₁₀₀) ranges from 0.9 in dry grasslands to 0.6 in tropical rainforest (Table 2). In particular, large differences are observed among biomes that vary in temperature and humidity. For example, generally, PhytOC from biomes with low temperature and/or humidity such as tundra and desert is more stable than that from other biomes.

3.3. Phytolith C sequestration in terrestrial biomes

The phytolith C sequestration flux varies from $0.4 \pm 0.2 \text{ kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ for desert to $36.0 \pm 24.0 \text{ kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ for cropland, with an average of $12.7 \pm 7.4 \text{ kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ (Table 3). According to Eq. (3) and the total distribution area of all global terrestrial biomes, the total phytolith C sequestration rate of global terrestrial ecosystems is $156.7 \pm 91.6 \text{ Tg CO}_2 \text{ yr}^{-1}$ (Table 3). Grassland (40%), cropland (35%), and forest (20%) are the dominant contributing biomes to this phytolith C sequestration. Among continents, the largest phytolith C sequestration rates occur in Asia ($48.0 \pm 28.8 \text{ Tg CO}_2 \text{ yr}^{-1}$), Africa ($36.9 \pm 20.4 \text{ Tg CO}_2 \text{ yr}^{-1}$) and South America ($26.2 \pm 16.3 \text{ Tg CO}_2 \text{ yr}^{-1}$),

which account for 31%, 24%, and 17% of the total global terrestrial PhytOC storage, respectively (Fig. 1).

4. Discussion

4.1. Global phytolith C sink estimation and uncertainties

Our total phytolith production rate in global terrestrial biomes ($2198 \pm 993 \text{ Tg yr}^{-1}$ dry opal weight) is lower than $84 \pm 29 \text{ Tmol Si yr}^{-1}$ (equivalent to $5040 \pm 1740 \text{ Tg yr}^{-1}$ dry opal weight) estimated by Conley and Carey (2015). The difference arises in part because, unlike these authors, we assume no phytolith production in plant tissues with low Si content such as roots, trunks, and branches of trees. In fact, these tissues may also produce some amount of phytoliths in many tree taxa. For example, bark and wood of Douglas fir (*Pseudotsuga menziesii*), Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and Oak (*Quercus sessiliflora*) may produce, respectively, 0.05%, 0.11%, 0.39% and 0.03% phytoliths per dry weight, though most biogenic Si (SiO_2) are accumulated in the leaves/needles (1.13%, 0.97%, 1.59 and 1.17, respectively) (Cornelis et al., 2010). For (sub)tropical forest, especially bamboo forest, the stem tissues (e.g., wood, bark) of trees often contain a lot of silica (Amos, 1952; Welle, 1976; Yang et al., 2015a). Because we did not consider these additional reservoir of silica in this study, our estimation is conservative, particularly in (sub)tropical regions. Furthermore, Conley and Carey (2015) presumed a Si content of all primary production in terrestrial ecosystems of 1–3% of dry weight, which may be an overestimate (Epstein, 1994; Conley, 2002). In comparison, Hodson et al. (2005) compiled Si content of 735 plant species from 125 published studies and found an average value of only 0.92%. Recently, Yang et al. (2015b) also reported that the average Si content of 108 plant species in forests of North China was only 0.42%. In addition, plants generally accumulate more silica as they get older (Motomura et al., 2002; Cornelis et al., 2010), a phenomenon that may also cause the observed difference. If the contribution of belowground (e.g., root, rhizome) and wood phytolith deposition is also considered, our values for phytolith C sequestration in soils would be higher—although not likely as high as Conley and Carey (2015).

Our phytolith C sink estimate is also associated with a higher uncertainty than that of Conley and Carey (2015) (48% and 34% of the estimate, respectively). Beyond uncertainty in the phytolith content of plant biomass, the inexactness of our estimation stems from uncertainties in ANPP data of Si-rich tissues, C content of phytoliths and phytolith turnover time. As outlined above, our uncertainty calculations for

Table 3
Estimated current phytolith C sequestration in global terrestrial biomes.^a

| Biomes | Area (10^6 ha) | Phytolith C sequestration flux ($\text{kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$) | | Phytolith C sequestration rate ($\text{Tg CO}_2 \text{ yr}^{-1}$) | |
|---|----------------------------|--|------|--|------|
| | | mean | SE | mean | SE |
| Forest | | | | | |
| (Sub)tropical forest | 1949 | 9.0 | 7.4 | 17.5 | 14.4 |
| Temperate forest | 810 | 4.8 | 3.8 | 3.9 | 3.1 |
| Boreal forest | 1304 | 6.9 | 4.3 | 9.0 | 5.6 |
| Weighted average or subtotal ^b | 4063 | 7.5 | 5.7 | 30.3 | 23.0 |
| Grassland | | | | | |
| Tropical savanna | 2250 | 25.3 | 12.2 | 57.0 | 27.5 |
| Temperate steppe | 1250 | 7.0 | 1.7 | 8.8 | 2.1 |
| Weighted average or subtotal ^b | 3500 | 18.8 | 8.4 | 65.8 | 29.5 |
| Wetland | 330 | 8.1 | 3.2 | 2.7 | 1.1 |
| Cropland | 1533 | 36.0 | 24.0 | 55.2 | 36.8 |
| Shrubland | 250 | 5.0 | 1.2 | 1.3 | 0.3 |
| Tundra | 743 | 1.0 | 0.8 | 0.7 | 0.6 |
| Desert | 1925 | 0.4 | 0.2 | 0.7 | 0.3 |
| Total weighted average ^b | 12,344 | 12.7 | 7.4 | 156.7 | 91.6 |

^a Phytolith C sequestration contributed from belowground parts or wood is not considered in this study because phytoliths are considered to be mainly produced from the aboveground, photosynthetic parts of the biomes (Parr et al., 2010; Parr and Sullivan, 2011). The ANPP data for Si-rich tissues and PhytOC content for phytolith C sequestration estimation and comparison among different biomes are listed in Tables 1 and 2, respectively.

^b Average weighted by biomass, calculated from total biome phytolith C sequestration rate and total biome area.

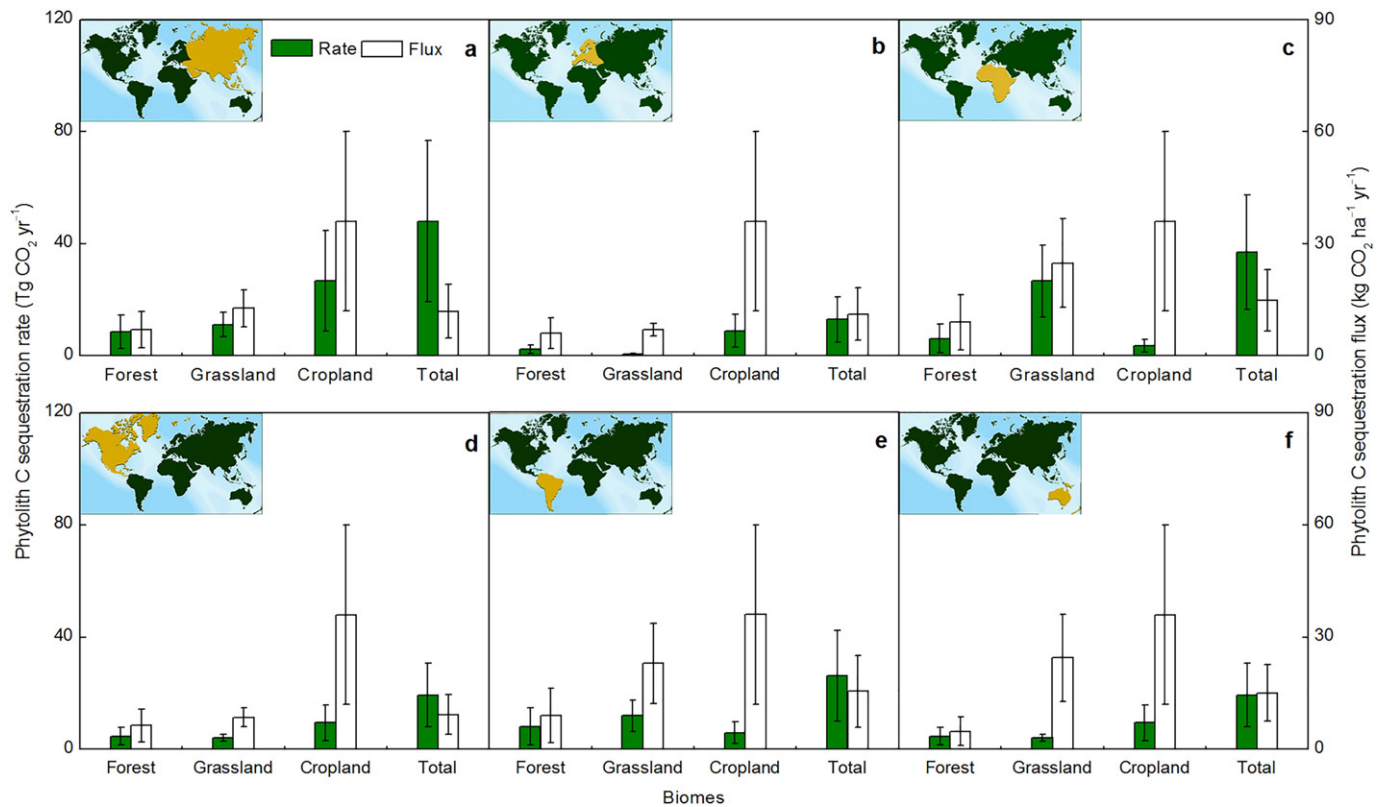


Fig. 1. Phytolith C sink rate and flux in terrestrial ecosystems from different continents. a: Asia, b: Europe, c: Africa, d: North America, e: South America, f: Oceania.

PhytOC production flux account for uncertainties of phytolith content of plant biomass and C content of phytoliths, but do not include uncertainty in the estimates of ANPP of Si-rich tissues for global terrestrial biomes. Furthermore, we consider variation of phytolith turnover time across different climates, but do not consider difference of soil chemistry, which is considered a less important factor at a global or regional scale than climate (Dove, 1995; Dove et al., 2008). A more realistic evaluation of uncertainties would therefore be slightly larger than what we report, but not substantially larger. Notwithstanding these uncertainties, our study presents the first, relatively realistic approximation of phytolith C sink in global terrestrial biomes.

Future work should focus on improving estimates of ANPP of Si-rich tissues for global terrestrial biomes, phytolith content in roots, rhizomes, and wood as well as phytolith turnover time under different soil conditions to better constrain global phytolith C sink.

4.2. Contribution of different ecosystems to global phytolith C sink

At a global scale, the chief portion of phytolith C sequestration occurs in grasslands, as a result of both the large global area and high phytolith C sequestration flux of this biome (Tables 1, 3; Blecker et al., 2006; Melzer et al., 2010; Song et al., 2012a). In contrast, the contributions from forest and cropland are mainly a result of, respectively, large area (Song et al., 2013a) and high phytolith C sequestration flux (Parr and Sullivan, 2011; Song et al., 2013b) (Tables 1, 3). We also found large variation among different ecosystems within each major biome type (Table 3). For example, tropical savanna ($57.0 \text{ Tg CO}_2 \text{ yr}^{-1}$) is responsible for approximately 85% of the grassland phytolith C sequestration, and tropical/subtropical forest ($17.5 \text{ Tg CO}_2 \text{ yr}^{-1}$) contributes >55% of phytolith C sequestration in forests overall, mainly due to high phytolith C sequestration flux in these ecosystems (e.g. $25.3 \text{ kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ for tropical savanna in grassland biome type and $9.0 \text{ kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ for (sub)tropical forest in forest biome type). We hypothesize that the

large amounts of PhyOC stored in tropical savannas is the result of high ANPP in many of these humid, fire-adapted ecosystems and high phytolith content of tropical grasses (Bond, 2008; Quigley and Anderson, 2014), despite higher rates of dissolution of phytoliths in wetter grassland soils compared to drier soils (Blecker et al., 2006). Similarly, the high contribution of tropical/subtropical forests to forest phytolith C sequestration may be related to rapid plant growth (higher ANPP) and generally higher aboveground Si storage (Blecker et al., 2006). In particular, tropical/subtropical forests with abundant bamboo have much-elevated PhyOC flux because of the very high phytolith production and rapid growth of these plants (leaf litter PhyOC production flux for bamboo is 3–80 times higher than for other forests; Song et al., 2013a).

4.3. Factors controlling continental difference of phytolith C sink

Africa has the highest PhyOC sequestration rate of all continents, despite having 2/3 of the area of Asia. This pattern is almost entirely linked to exceptionally high phytolith C storage flux in tropical savanna, where both the overwhelming dominance of grasses (Poaceae) and sedges (Cyperaceae) and the rapid growth and high ANPP of, above all, savanna grasses promote high phytolith input into the soils (Melzer et al., 2010). The relatively high phytolith C sequestration rate in South America is similarly associated with high PhyOC fluxes in savanna and tropical forest (Blecker et al., 2006; Fig. 1). In contrast, Asia has a relatively low area-weighted PhyOC flux (Fig. 1), likely tied to the large areal fraction of temperate and boreal forests (Pan et al., 2011; Song et al., 2012a), as well as temperate steppes (Song et al., 2013b), all of which have relatively low flux values (Song et al., 2012a, 2013a; Yang et al., 2015b). Its large phytolith C storage results mainly from its overall vast area, which also includes biomes with high phytolith C sequestration fluxes (e.g., bamboo-dominated forests; Parr et al., 2010).

4.4. Significance and potential of global phytolith C sequestration

The carbon in phytoliths is highly resistant to decomposition and may accumulate in soil profiles for several thousands of years (Parr and Sullivan, 2005), and, in buried soil profiles, for millions of years (e.g., Strömberg, 2011). The accumulation of PhytOC in soils is slow on an annual–decadal scale, but is prominent at a centennial–millennial scale (Fig. 3). The large C sequestration in the global pool of phytoliths indicated by our analysis therefore supports the idea that the biogeochemical silica cycle contributes vitally to the global carbon cycle (see also Conley and Carey, 2015).

Furthermore, because phytoliths are formed in plants and subsequently incorporated into the soil, it seems possible that vegetation management such as rational fertilization could not only recover degraded ecosystems but also substantially increase the size of the global C sink; this in turn would help to offset increases in atmospheric CO₂ (Song et al., 2013a, 2013b; Zhao et al., 2015). Our calculations indicate that phytolith C sequestration in global terrestrial ecosystems, contributed mainly from grassland, forest and cropland, could be roughly doubled from the current 156.7 ± 91.6 Tg CO₂ yr⁻¹ by the end of the 21st century through strategic management plans for these ecosystems (Fig. 2; Tables 3, 4).

In forests, economically-driven management practices such as carefully managed afforestation/reforestation and regular harvesting of bamboos with elevated leaf litter PhytOC production flux (e.g., *Phyllostachys pubescens*, Zhou et al., 2011) may significantly augment phytolith C sequestration (Song et al., 2013a). It has been suggested that the area currently covered by bamboo globally could increase from 25×10^6 ha to 100×10^6 ha (~3% of world's forests) in the next few decades (Zhou et al., 2011; Song et al., 2013a), a change that could significantly boost the PhytOC fluxes for subtropical forests on several continents. These practices in combination with other measures for increasing bamboo shoot production such as input of external Si from silicate rock powder amendment and organic mulching (Huang et al., 2014) may further boost bamboo PhytOC production flux from 81.6 ± 7.1 to >300 kg CO₂ ha⁻¹ yr⁻¹ (Parr et al., 2010; Song et al., 2013a). Using a median PhytOC production flux of bamboo (300 kg CO₂ ha⁻¹ yr⁻¹) (Parr et al., 2010), a hypothesized expansion of the world's bamboo area from 25×10^6 to 100×10^6 ha over the next few decades (Zhou et al., 2011; Song et al., 2013a), and a PSF₁₀₀ of 0.6 ± 0.1 (Table 2), the phytolith C sink in global bamboo forests can be preliminarily estimated at 18.6 ± 4.0 Tg CO₂yr⁻¹. These

calculations suggest that, with the appropriate management, the phytolith carbon sink in forests globally could theoretically increase from 30.3 ± 23.0 to 47.1 ± 27.0 Tg CO₂ yr⁻¹ by the end of the 21st century (Fig. 2).

Similarly, sustainable grassland management such as controlled grazing and fire could significantly increase biomass production and Si uptake, thus enhance phytolith C sequestration in the prominently phytolith-producing grasses and sedges that dominate these ecosystems (Song et al., 2012a). Indeed, Melzer et al. (2010) estimated that expanded grazing and more frequent fires could enhance grass biomass production/phytolith production by as much as 50–100% in tropical grasslands. Furthermore, practices for recovery of degraded grasslands under drought stress such as N and Si fertilization (Eneji et al., 2008; Zhao et al., 2015) may increase biomass production and/or Si content. For example, it has been reported that Si fertilization may have augmented biomass yields by 205% for Rhodes grass under deficient irrigation conditions (Eneji et al., 2008). Combined, these approaches could be expected to roughly double phytolith C sequestration in grasslands by the end of the 21st century (Fig. 2).

Finally, global croplands have a high potential for storing more PhytOC. The phytolith C sequestration in global cropland has tripled since 1961 mainly as a result of cropland expansion, fertilization, and irrigation (Song et al., 2013b). Measures designed to increase food production, such as enhancement of cereal area and percentage in croplands, more rotation of crops, and reasonable fertilization and irrigation would likely also increase overall biomass production and, linked to that, Si uptake by plants. Given that cereals such as rice, wheat, and corn have higher PhytOC production fluxes than other crops (Parr and Sullivan, 2011; Song et al., 2013b), such practices would therefore enhance cropland phytolith C sequestration. Ongoing work to facilitate crop adaptation to biotic and abiotic stresses such as genetic engineering (Jansson et al., 2010) and Si fertilization (Liu et al., 2014), could also significantly augment the cropland phytolith C sink. For example, it has been estimated that the global phytolith C sequestration in croplands could reach approximately 2600 Tg CO₂ yr⁻¹ through increased phytolith production if all crops in the world were genetically engineered (Jansson et al., 2010). Although it constitutes an extreme case, this assessment implies that, even if only 1–2% of crops were genetically engineered, in combination with other measures, an additional 52 Tg CO₂ yr⁻¹ could with certainty be sequestered in cropland phytoliths. Therefore, through scientific management, phytolith C sequestration in croplands globally could be expected to increase from 55.2 ± 36.8 to 165.5 ± 110.3 Tg CO₂ yr⁻¹ by the end of the 21st century (Fig. 2).

Taking the present and potential global terrestrial phytolith C sequestration rates to be, respectively, 156.7 ± 91.6 Tg CO₂ yr⁻¹ and 349.5 ± 198.7 Tg CO₂ yr⁻¹ (Fig. 2), we preliminarily estimate the total terrestrial phytolith C sequestration during 2000–2099 to 15.7 – 35.0 Pg CO₂, which corresponds to 25–110% of conservative estimate of total land uptake or 1–5% of average estimate of total land uptake (Sitch et al., 2008) (Fig. 3). As large uncertainties of total land uptake estimate are associated with complex responses of vegetation to changing soil moisture status and elevated temperatures (Sitch et al., 2008) and selection of different models and future CO₂ emission scenarios, we think that the preliminary estimate is reasonable.

4.5. Implications

The projected global terrestrial phytolith C sequestration is equivalent in magnitude to the burial of diatom–Si bound carbon (Tréguer et al., 1995; Montagnes and Franklin, 2001) and CO₂ consumption through silicate weathering (Gaillardet et al., 1999; Taylor et al., 2016; Fig. 3). Therefore, the phytolith C sink and other mechanisms related to the coupled biogeochemical cycles of Si and C, such as diatom C sequestration and CO₂ consumption during silicate weathering could be explored in tandem as complementary means to stably sequester atmospheric

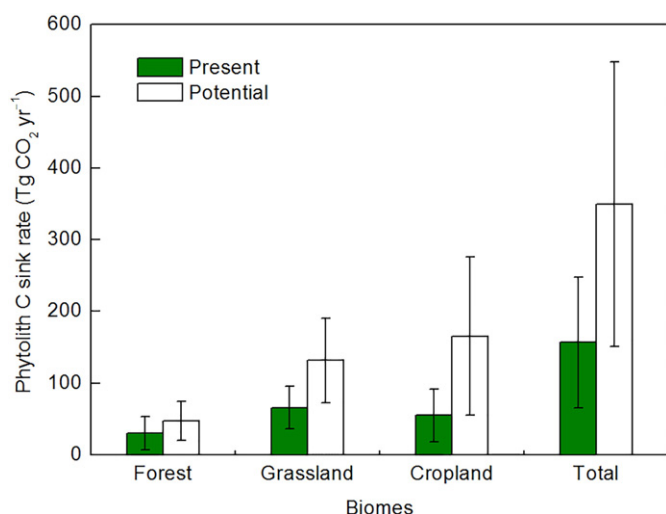


Fig. 2. The present and potential phytolith C sequestration in global terrestrial biomes. The increase in potential relative to current phytolith C sequestration in global terrestrial biomes is the result of application of strategic management of forest, grassland, and cropland biomes (Table 4).

Table 4
Potential measures to enhance phytolith C sink in terrestrial biomes.

| Enhancing potential (Tg CO ₂ yr ⁻¹) | Measures | Mechanisms | Potential application |
|---|---|---|----------------------------------|
| Forest (17 ± 4) | Bamboo afforestation/reforestation | Enhancing bamboo area and phytolith content | Tropical and subtropical regions |
| | Silicate rock powder amendment | Enhancing phytolith content | Bamboo forests |
| Grassland (66 ± 30) | Si input from organic mulching | | |
| | Increasing the proportion of Poaceae and Cyperaceae | Enhancing phytolith content | Savanna and temperate grasslands |
| | Silicate rock powder amendment | | |
| | Silicon fertilization | | |
| | Restoration of degraded and desertified soils | | |
| Cropland (110 ± 74) | Rational grazing, enhanced fertilization and irrigation | Enhancing grass growth | |
| | Enhancement of cereal area and percentage in croplands | Enhancing crop output and phytolith content | Most croplands |
| | Organic mulching | | |
| | Silicon fertilization | | Cereal production |
| | Silicate rock powder amendment | | |
| | Genetic engineering of high PhytOC production crop | | |
| | Enhancement of multi-cropping index | Enhancing crop output | Most croplands |
| | Reasonable chemical fertilization | | |

For more details see the text.

CO₂ in the future. Furthermore, ecosystem-level feedback mechanisms in the Si cycle and phytolith C sequestration in response to different management practices (e.g., fire, grazing, or Si fertilization), and in particular how these responses might depend on climatic and soil conditions are not fully understood and need to be further researched before strategic management of biogeochemical C sequestration can be implemented.

5. Conclusions

We estimate that the total phytolith C sequestration in global terrestrial biomes is 156.7 ± 91.6 Tg CO₂ yr⁻¹, with grassland, forest, and cropland as the dominant producers of phytolith-based C. Practices such as bamboo afforestation/reforestation and grassland recovery for

economic and ecological purposes could theoretically double the above phytolith C sink, which is equivalent in magnitude to the C sequestration of oceanic diatoms in sediments and through silicate weathering. Studies using terrestrial biogeochemical models should seek to more explicitly incorporate plant-soil Si-C cycling modules to better constrain global biogeochemical C sequestration.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.scitotenv.2017.06.107>.

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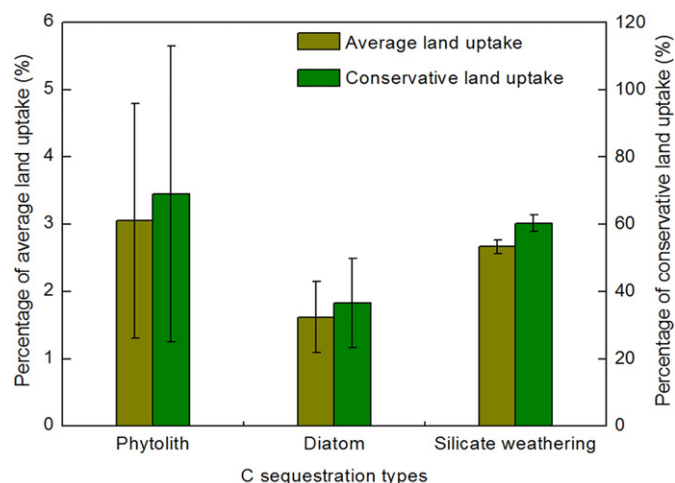


Fig. 3. A comparison of cumulative phytolith, diatom and silicate weathering C uptake indicated as a percentage of average and conservative estimate of total land uptake during 2000–2099. Land uptakes are the average and minimum net cumulative organic C sequestration in plants and soils for this time period estimated by Sitch et al. (2008). For total global terrestrial phytolith C sequestration estimation during 2000–2099, the average of the present and potential global terrestrial phytolith C sequestration fluxes (Fig. 2) was used. Diatom C uptake here refers only of burial of diatom-Si bound C on century time scales excluding short-term biological C pump of diatoms as the carbon storage in living diatoms is similar to carbon storage in phytoliths in living plant tissue and that is not what we're considering in this study. Oceanic diatom C uptake was estimated from the net diatom burial flux of 6.1 ± 2.0 Tmol yr⁻¹ (Tréguer et al., 1995) and average C content in diatoms of 10% (Montagnes and Franklin, 2001). CO₂ consumption from Ca-Mg silicate weathering on the continents is based on Meybeck (1987) and Gaillardet et al. (1999).

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