Phylogenetic variation of phytolith carbon sequestration in bamboos

Beilei Li[1], Zhaoliang Song[1,2], Zimin Li[1,3], Hailong Wang[1], Renyi Gui[4] & Ruisheng Song[4]

[1]School of Environment and Resources, Zhejiang Agricultural and Forestry University, Lin'an, Zhejiang 311300, China, [2]State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guizhou, P.R. China, [3]Tea Research Institute of Chinese Academy of Agricultural Sciences and the Key Laboratory for Plant Biology and Resource Application of Tea, the Ministry of Agriculture, China, 310008, [4]School of Forestry and Bio-technology, Zhejiang Agricultural and Forestry University, Lin'an, Zhejiang 311300, China.

Phytoliths, the amorphous silica deposited in plant tissues, can occlude organic carbon (phytolith-occluded carbon, PhytOC) during their formation and play a significant role in the global carbon balance. This study explored phylogenetic variation of phytolith carbon sequestration in bamboos. The phytolith content in bamboo varied substantially from 4.28% to 16.42%, with the highest content in Sasa and the lowest in Chimonobambusa, Indocalamus and Acidosasa. The mean PhytOC production flux and rate in China's bamboo forests were 62.83 kg CO_2 ha^{-1} y^{-1} and 4.5 × 10^8 kg CO_2 y^{-1}, respectively. This implies that 1.4 × 10^9 kg CO_2 would be sequestered in world's bamboo phytoliths because the global bamboo distribution area is about three to four times higher than China's bamboo. Therefore, both increasing the bamboo area and selecting high phytolith-content bamboo species would increase the sequestration of atmospheric CO_2 within bamboo phytoliths.

Phytoliths are the amorphous silica deposited in plant tissues such as the cell wall, cell lumen and intercellular space during plant growth[1–3]. They are present in many plants, especially abundant in gramineous plants, e.g., bamboo[4–5]. A large amount of phytoliths are released in the topsoil through plant organic matter decomposition[6–7]. Importantly, phytoliths are very stable in some sediments[8] or even in harsh environments such as flood, earthquake and dust storms[9–11], due to their strong resistance to degradation[6,11,12]. Recent researches report that during the formation of phytoliths, 1%–6% organic carbon can be sequestered within the phytoliths, also called phytolith-occluded carbon (PhytOC)[6,13], which plays an important role in the global carbon cycle and climate change as a "safe" carbon sink[14,15].

Bamboo, a typical phytolith-accumulator[5,16], is predominantly distributed in the world tropical and subtropical regions, with a total area of 2.2 × 10^7 ha[17], occupying about 1% of the total global forest distribution area[18]. In China, bamboo is widely distributed with an total area of 7.2 × 10^6 ha, especially in Zhejiang, Fujian and Jiangxi Provinces[17]. Recently, Parr et al.[5] and Song et al.[19] estimated the global production of phytolith and PhytOC in bamboo. Furthermore, Song et al.[19] compared the production of PhytOC in bamboo with other forests in China. However, their studies were only based on a limited number of bamboo species (<11). The phylogenetic variation of phytolith in bamboo leaves has not been investigated. Therefore, this study selected 75 different bamboo species to explore the phylogenetic variation in phytolith composition and phytolith production of bamboo.

Results

The phytolith content in leaves of the 75 bamboo species ranged significantly from 4.28% to 16.42%, mostly within 8%–14% and with a mean of 9.59% (Table 1, Fig. 1). The highest phytolith content was in leaves of *Pleioblastus kongosanensis*, *Phyllostachys sulphurea viridisulcata*, *Phyllostachys ventricosa cv huangganlucao* and *Phyllostachys ventricosa cv. luganhuangcao*, with a mean of higher than 14%. The phytolith content in the leaves of *Chimonobambusa quadrangularis*, *Phyllostachys prominensa* and *Phyllostachys aureosulcata f. aureocaulis* was the lowest, with a mean of 4.28%, 4.52% and 4.84%, respectively. There was a significant variation in the phytolith content of bamboo leaves from different genera (Fig. 2A). The phytolith content was the highest in Sasa, while the lowest in Chimonobambusa, Indocalamus and Acidosasa (Table 1; Fig. 2A). There was no obvious variation in leaf phytolith content for bamboos belonging to different subtribes, bambuseaes and bambusataes (Fig. 2B–D). The C content of phytolith for bamboo varies slightly from 2.0% to 3.2%, with a median of 2.6% (Fig. 3).
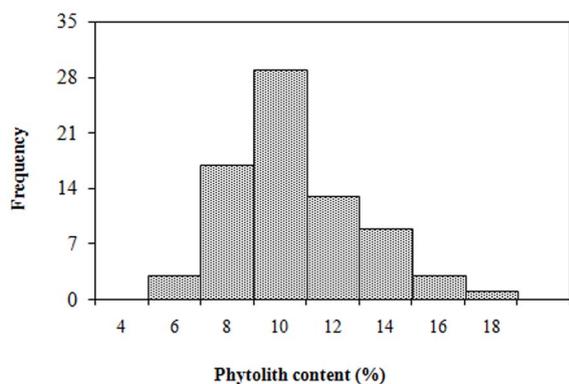
Figure 1 | Frequency distribution of phytolith content within 75 bamboo species.

Discussion

Recent studies indicate that the silicon (Si) content is higher in non-vascular plants and horsetails than in ferns, gymnosperms and angiosperms; higher in monocotyledons than in dicotyledons; and higher in gramineous plants and the Palmales than in other orders of plants[20,21]. Furthermore, the phylogenetic variation in Si content in different phyla is greater than that of the lower level classifications such as order and family[20,21]. Some researches show that there is a strong positive correlation between the phytolith and SiO_2 contents of biomass[5,15,19]. The above findings may have broad implications for phylogenetic variation in phytolith content of plants.

The dramatic variations of phytolith content within leaves of different bamboo species and genera may be due to different absorption capacities of Si[5,22,23]. Although the Si can be taken up by plant roots in the form of $Si(OH)_4$, through the transpiration stream[24–26], the ability of transpiration for Si may vary in bamboos of different genera or species[27]. So, the deposition of Si among different bamboo also differs significantly. The different origins of bamboo species may also influence the Si deposition within leaves[13,28,29]. For example, the different soil Si supply capacity from their original sites also leads to the different absorption capacity of Si in plants[13,28,29]. In addition, the hereditary variability of bamboo species could also affect the Si absorption capacity[30]. Although the mechanisms of Si absorption for some plants such as rice[28,29,31], wheat[32] and soybean[33] have been reported by many researchers, that mechanisms of Si absorption in bamboo and the influence of different levels of phylogenetic classification on bamboo phytolith accumulation remain to be revealed.

Recent researches have shown that PhytOC is much more stable than other organic carbon fractions in soils or some sediments, and can occupy up to 82% of the total carbon accumulation in a 2000 year old soil profile[8,13] suggesting that PhytOC accumulation has a crucial role in long-term terrestrial carbon sink and global climate change[2,3,5,15,34].

We have examined the relationship of PhytOC content of bamboo leaf and phytolith content (Fig. 4A) and carbon content of phytolith and phytolith content (Fig. 4B). In contrast with Parr et al.[5], the results show that there is no significantly negative relationship ($p > 0.05$) between phytolith content and carbon content of phytoliths but significantly positive relationship between the phytolith content and the PhytOC content in bamboo leaves. The results imply that increasing phytolith content is a potential measure to increase phytolith C accumulation.

Taking the C content in phytoliths of $3 \pm 1\%$ (Fig. 3; ref. 5 and 19) and net primary production for bamboo leaf litters of 5955 ± 1000 kg ha^{-1} yr^{-1} [19,35], we estimate that the phytolith carbon sequestration flux of bamboo is 28.04–107.55 kg CO_2 ha^{-1} yr^{-1}, with an average of 62.83 kg CO_2 ha^{-1} yr^{-1}. Taking China's current bamboo area of 7.2×10^6 ha and the mean bamboo PhytOC production flux of 62.83 kg CO_2 ha^{-1} yr^{-1}, we estimate that about 4.52×10^8 kg CO_2
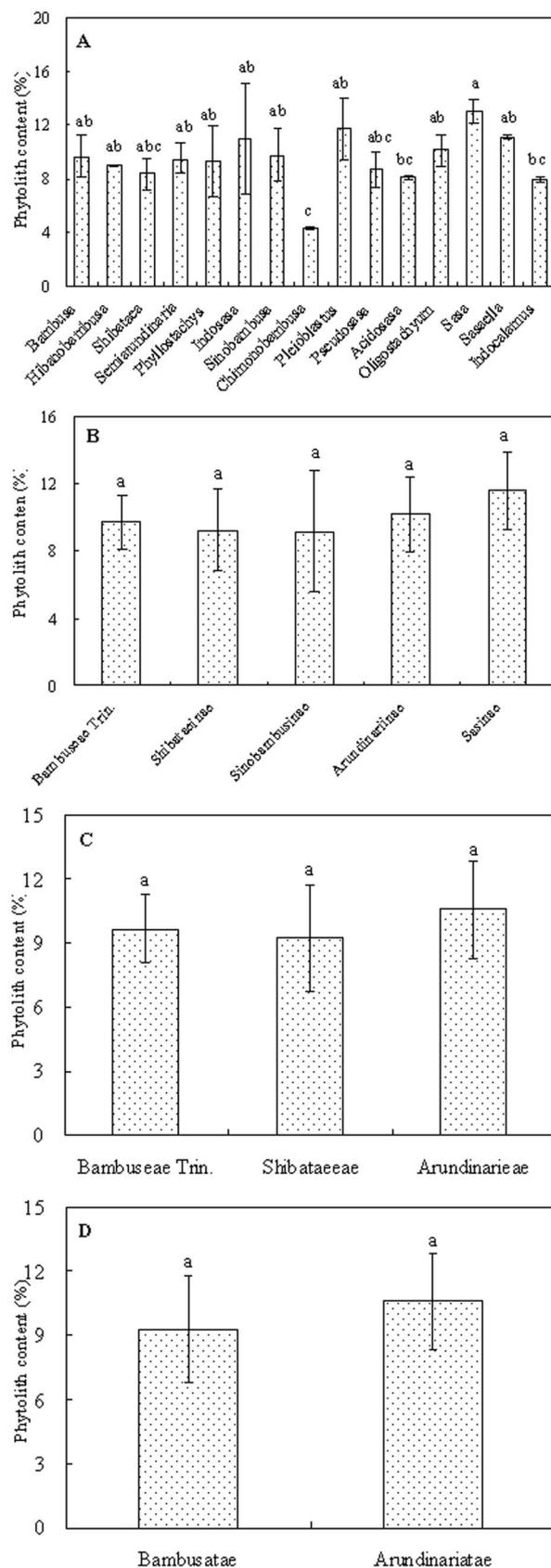

Figure 2 | Phytolith content in leaves for bamboo of: (A) different genera, (B) different subtribes, (C) different bambuseaes, (D) different bambusataes. Different letters above the error bars indicate significant difference among the different bamboo at $p < 0.05$ levels.
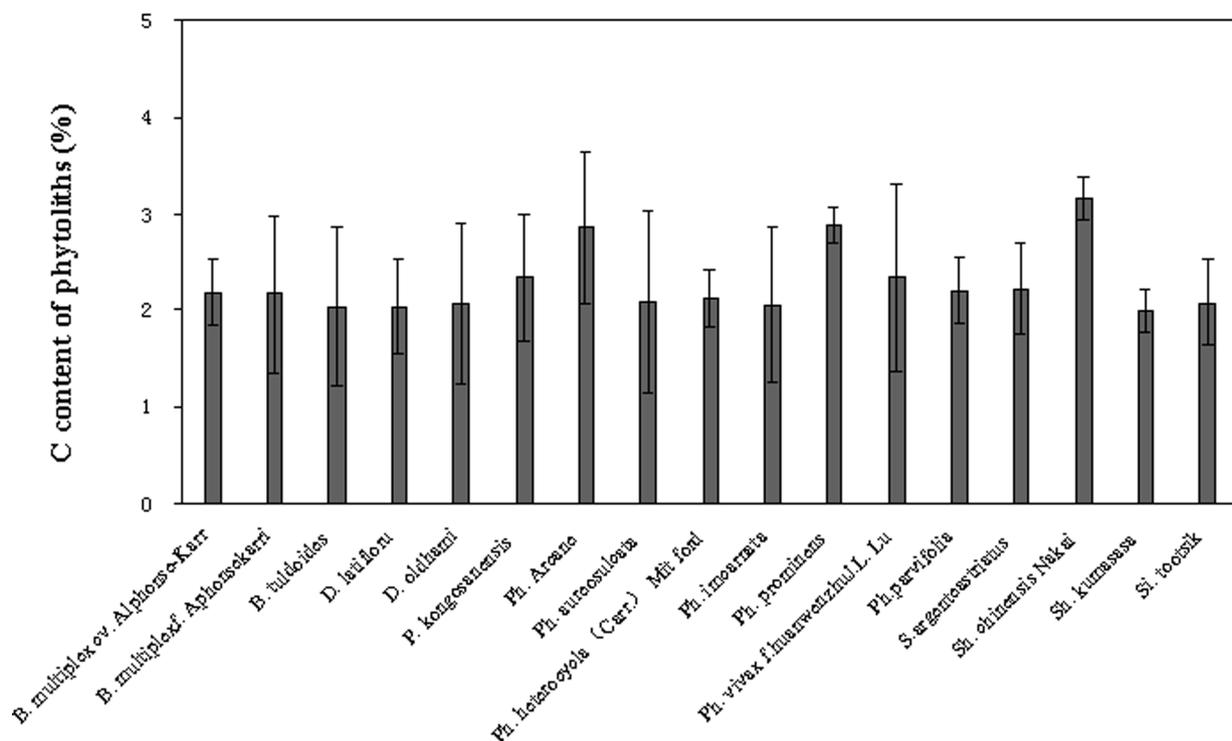
Figure 3 | The variation of the occluded C content of phytoliths in bamboo leaves. Different letters above the error bars indicate significant difference among bamboo bambuseaes at $p < 0.05$ levels.

yr^{-1} would be sequestered in phytoliths of Chinese bamboo forests. As shown in Table 1, it is possible to improve the production flux of PhytOC by selecting bamboo species (e.g., *Pleioblastus kongosanensis*, *Phyllostachys sulphurea viridisulcata*) with high phytolith content[5,15]. If those bamboo species could be widely planted in China, 7.2 $\times$ 10^8 kg CO_2 from the atmosphere would be captured within bamboo phytoliths.

The global bamboo distribution area is 2.2 $\times$ 10^7 ha, occupying about 1% of the global forests[17,18], and is mainly distributed in tropical and subtropical regions such as China, India, Thailand and Japan[17,18,36]. Taking the mean PhytOC production flux of 62.83 kg CO_2 ha^{-1} y^{-1}, we estimate that approximately 1.4 $\times$ 10^9 kg CO_2 would be sequestered in bamboo phytoliths globally each year. However, if the highest PhytOC production flux of 107.55 kg CO_2 ha^{-1} y^{-1} can be reached, atmospheric sequestration of 2.4 $\times$ 10^9 kg CO_2 each year through global bamboo phytolith is possible. Assuming an increase rate of bamboo area of 3% annually[37,38] and the mean PhytOC production flux in bamboo of 62.83 kg CO_2 ha^{-1} y^{-1}, then at least 2.8 $\times$ 10^9 kg CO_2 from the atmosphere would be sequestered in bamboo phytoliths globally by 2050. Taking the highest PhytOC production flux, 4.7 $\times$ 10^9 kg CO_2 would be sequestered in bamboo phytoliths globally.

Although the total forest area of the world has decreased significantly, the total area of bamboo forests has increased at a rate of 3% annually and will continue to increase in the next decades[19]. For example, it was estimated that an area of 27 $\times$ 10^7 ha may be available for afforestation in China and at least half of the land can be used for bamboo afforestation[18,19]. Furthermore, the world's bamboo may increase from 25 $\times$ 10^6 to 100 $\times$ 10^6 ha (approximately 3% of world's forests) by taking measures of bamboo afforestation/reforestation in the tropical and subtropical area of the world[18,19]. Therefore, it is possible to significantly increase phytolith carbon sink in bamboo forests by both increasing the bamboo area and selecting high phytolith-content bamboo species such as *Pleioblastus kongosanensis*, *Ph. Ventricosa cv. Luganhuangcao* and *Phyllostachys Ventricosa cv Huangganlucao*.
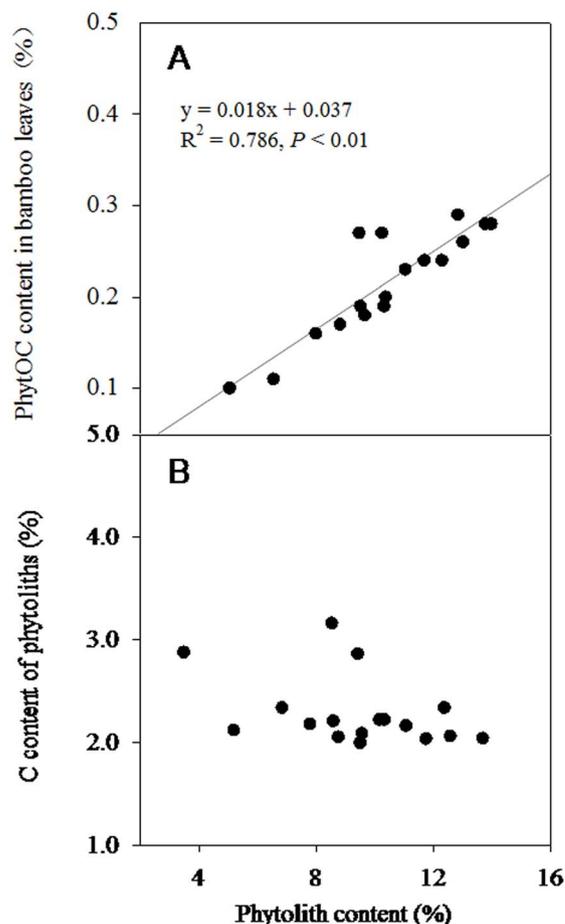

Figure 4 | The relationship between the phytolith content and the carbon content of phytoliths ($p > 0.05$) (A), and between the phytolith content and the PhytOC content in bamboo leaves (B).

Bambusatae	Bambuseae	Subtribe	Genus	Species	Phytolith (%)[a]
Bambusatae	Bambuseae Trin.	Bambuseae Trin.	Bambusa	B.rutila	10.41
				B. multiplex	11.92
				B. multiplex cv. Changye	10.02
				B.multiplex raeuschel	8.17
				B.alphonsekarri	10.12
				B.glaucescens	7.43
	Shibataeeae	Shibataeinae	Hibanobambusa	H.tranguillans.shiroshima	9.01
			Shibataea	Sh.kumasasa	9.74
				Sh. chinensis nakai	7.89
				Sh. chinensis nakai cv. jimao	7.52
			Semiarundinaria	S. yashadake f. kimmei	8.99
				S. yashadake makino	8.64
				S. yashadake f. ogon	10.83
			Phyllostachys	Ph.prominens	4.52
				Ph.vivax. huanwenzhu	6.59
				Ph.heterocycla taokiang	7.50
				Ph.heterocycla	6.82
				Ph.incarnata	7.82
				Ph. bambusoides	9.84
				Ph. bambusoides. cv. huayehuagan	11.24
				Ph.bambusoides.castillonis	8.96
				Ph. nigra	9.43
				Ph. nigra. cv. huaye	9.87
				Ph.aureosulcata.pekinensis	7.18
				Ph.aureosulcata	7.68
				Ph.aureosulcata.aureocaulis	4.84
				Ph.aureosulcata.spectabilis	8.30
				Ph.sulphurea.viridis	13.99
				Ph.sulphurea viridisulcata	15.63
				Ph. sulphurea	12.07
				Ph. houzeauana	8.99
				Ph. ventricosa	9.87
				Ph. ventricosa cv huangganlucao	16.42
				Ph. ventricosa cv. luganhuangcao	14.83
				Ph. ventricosa cv. huangjin	9.08
				Ph.arcana.luteosulcata	9.19
				Ph.propinqua	9.40
				Ph.vivax.aureocaulis	7.56
				Ph.heterocycla.gracilis	8.09
				Ph.nigra.henonis	8.59
				Ph.dulcis	10.02
				Ph.parvifolia	7.78
				Ph. violascens cv. xiye	9.48
				Ph. violascens cv. jianye	9.81
				Ph. violascens cv. viridisulcata	12.41
				Ph. violascens cv. flavistriatus	10.50
				Ph. violascens cv. panggan	10.32
				Ph. violascens cv. anhuiensis	7.81
				Ph. violascens cv. flavivaginis	7.52
				Ph. violascens cv. violascens	7.32
				Ph.bambussoides	8.50
				Ph.aureosulcata	6.52
				Ph. violascens cv. linanesis	10.38
		Sinobambusinae	Indosasa	I.acutiligulata	8.05
				I.sinica	13.92
			Sinobambusa	S. tootsik	11.15
				S. tootsik.cv. huaye	8.45
			Chimonobambusa	Ch.quadrangularis	4.28

Table 1 | Continued

Bambusatae	Bambuseae	Subtribe	Genus	Species	Phytolith (%)[a]
Arundinariatae	Arundinarieae	Arundin ariinae	Pleioblastus	*Pl. kongosanensis*	14.46
				Pl.hisauchii	8.96
				Pl.simonii.variegatus	9.98
				Pl.inearis	13.37
				Pl.chino.angustifoliu	12.11
			Pseudosasa	*P.amabilis*	6.73
				P. japonica	9.43
				P. japonica. tsutsumiana	9.34
				P. japonica cv. huaye	9.17
			Acidosasa	*A.gigantea*	8.08
			Oligostachyum	*O.sulcatum*	9.35
				O.ubricum	11.04
		Sasinae	Sasa	*S.argenteostriata*	12.02
				S.pygmaea	13.49
				S.auricoma	13.57
			Sasaella	*S.glabra.albo-striata*	11.05
			Indocalamus	*I.decorus*	7.94

[a]The data presented in this paper are the average of three replicates.

Methods

Experimental site. Fresh mature (two-year old) leaf samples were collected from 75 different bamboo species belonging to two bambusataes, three bambuseaes, five subtribes and 15 genera in the botanical garden at Zhejiang Agricultural and Forestry University (30°15′N, 119°43′E), Lin'an, Zhejiang, China. Lin'an is located in western Zhejiang and has a subtropical monsoon climate with an average elevation of 150 m above sea level. The distribution of precipitation is uneven, with an average of 1400 mm y^{-1}. The annual frost-free period is up to 234 d, and the annual average temperature is 16°C.

Experimental design and Analyses of the phytolith in samples. The leaves of the different bamboo species were used to examine the variability of phytolith production. Mature leaf samples were collected in May 2012, when they have higher phytolith content than that in younger leaves[5,39]. Each leaf sample was mixed, rinsed with ultrapure water, oven-dried at 75°C for 48 h to a constant mass and then cut into small pieces (<5 mm) for phytolith analysis. The phytoliths within bamboo leaves were extracted with a microwave digestion process[40] and Walkley–Black type digest[41]. The extracted phytoliths were oven-dried at 75°C to a constant weight. Dried phytoliths were weighed and recorded for phytolith content calculation. Occluded C content of phytoliths was determined with methods of ref. 15.

Data calculations and statistics. The data presented in this paper were the average of three replicates. Excel and SPSS were employed in the statistical analysis of data. One-way ANOVA and Duncan's Multiple Range Test ($p < 0.05$) were applied to examine the difference of data groups.

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Acknowledgments

Author contributions

B.L., R.G., R.S. and Z.S. carried out the sampling. B.L. and Z.L. performed the experimental work. B.L., H.W. and Z.S. analyzed the data. Z.S. designed the study and supervised the project. All authors discussed the results and contributed to the manuscript.

Additional information