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ARTICLE

Phytolith-occluded organic carbon in intensively managed Lei bamboo (*Phyllostachys praecox*) stands and implications for carbon sequestration

Zhangting Huang, Yongfu Li, Scott X. Chang, Peikun Jiang, Cifu Meng, Jiasen Wu, and Yan Zhang

Abstract: Phytolith-occluded organic carbon (PhytOC) is an important long-term (up to several thousand years) terrestrial carbon (C) fraction in forest ecosystems. The objectives of this study were to (*i*) investigate the spatial distribution of PhytOC in Lei bamboo (*Phyllostachys praecox* C.D. Chu & C.S. Chao.) forests under intensive management (mulching and fertilization) and (*ii*) assess the role of PhytOC in C sequestration in a Lei bamboo stand and across subtropical China. Phytolith concentrations in Lei bamboo plant components were ($P < 0.05$) in the following order: rhizome ≈ stump > leaf ≈ branch > culm. The distribution of PhytOC in bamboo leaves, branches, culms, rhizomes, and stumps was 22.2%, 12.1%, 16.1%, 15.9%, and 33.7%, respectively. The PhytOC stock was in the following order ($P < 0.05$): soil (9361 kg C·ha^{-1}) > mulching materials (197.5 kg C·ha^{-1}) > belowground plant parts (13.0 kg C·ha^{-1}) ≈ aboveground plant parts (12.8 kg C·ha^{-1}) ≈ litterfall (11.3 kg C·ha^{-1}). The PhytOC accretion rate in the vegetation in the Lei bamboo stand was 19.4 kg C·ha^{-1}·year^{-1}, equivalent to 71 kg CO_2-eq·ha^{-1}·year^{-1}. The soil PhytOC stock decreased markedly with depth and had an accretion rate of 325 kg C·ha^{-1}·year^{-1} for the 0–60 cm soil layer. Based on a PhytOC accretion rate of 0.795 Mg CO_2-eq·ha^{-1}·year^{-1}, PhytOC accretion rate in the 2.62×10^6 ha of Lei bamboo stands in southern China is estimated to be 2.08×10^6 Mg CO_2-eq·year^{-1}. In conclusion, intensively managed Lei bamboo stands have a large potential in long-term C sequestration in the form of PhytOC, and the PhytOC stock belowground should not be ignored due to its contribution to the ecosystem level PhytOC stock.

Key words: spatial distribution, biogeochemical carbon sequestration, Lei bamboo (*Phyllostachys praecox*), phytolith, phytolith-occluded organic carbon (PhytOC).

Résumé : Le carbone organique occlus dans les phytolithes (PhytOC) représente une fraction importante à long terme (jusqu'à plusieurs milliers d'années) du carbone (C) terrestre dans les écosystèmes forestiers. Les objectifs de cette étude étaient (*i*) d'étudier la répartition spatiale des PhytOC dans les forêts de bambou Lei (*Phyllostachys praecox* C.D.Chu & C.S.Chao.) sous aménagement intensif (paillage et fertilisation) et (*ii*) d'évaluer le rôle des PhytOC dans la séquestration du C dans un peuplement de bambou Lei et à travers la Chine subtropicale. La concentration des phytolithes parmi les composantes des plants de bambou Lei décroissait dans l'ordre suivant ($P < 0,05$) : rhizome ≈ souche > feuilles ≈ branches > chaume. La proportion de PhytOC dans les feuilles, les branches, le chaume, les rhizomes et les souches de bambou était respectivement de 22,2 %, 12,1 %, 16,1 %, 15,9 % et 33,7 %. L'importance des stocks de PhytOC décroissait dans l'ordre suivant ($P < 0,05$) : sol (9361,0 kg C·ha^{-1}) > matériaux utilisés pour le paillage (197,5 kg C·ha^{-1}) > parties souterraines des plantes (13,0 kg C·ha^{-1}) ≈ parties aériennes des plantes (12,8 kg C·ha^{-1}) ≈ chute de litière (11,3 kg C·ha^{-1}). Les PhytOC s'accumulaient dans la végétation du peuplement de bambou Lei à raison de 19,4 kg C·ha^{-1}·an^{-1}, correspondant à 71 kg éq. CO_2·ha^{-1}·an^{-1}. Les stocks de PhytOC dans le sol diminuaient de façon marquée avec la profondeur et avaient un taux d'accumulation de 325 kg C·ha^{-1}·an^{-1} dans la couche de 0–60 cm. Sur la base d'un taux d'accumulation des PhytOC de 0,795 Mg éq. CO_2·ha^{-1}·an^{-1}, on estime à $2,08 \times 10^6$ Mg éq. CO_2·an^{-1} le taux d'accumulation des PhytOC dans les $2,62 \times 10^6$ ha occupés par des peuplements de bambou Lei dans le sud de la Chine. En conclusion, les peuplements de bambou Lei sous aménagement intensif ont un potentiel énorme de séquestration à long terme du C sous forme de PhytOC et les stocks souterrains de PhytOC ne devraient pas être ignorés étant donné leur contribution au stock de PhytOC à l'échelle de l'écosystème. [Traduit par la Rédaction]

Mots-clés : répartition spatiale, séquestration biogéochimique du carbone, bambou Lei (*Phyllostachys praecox*), phytolithe, carbone occlus dans les phytolithes (PhytOC).

1. Introduction

The carbon dioxide (CO_2) concentration in the atmosphere has been estimated to be increasing at the annual rate of 0.5% since the 1850s, mainly due to fossil fuel combustion and land-use conversion (Intergovernmental Panel on Climate Change (IPCC) 2007). The increasing CO_2 emission rate markedly influences the global climate. Over recent decades, global warming induced by the rapidly increasing atmospheric CO_2 concentration has increased the interest for C sequestration in forest ecosystems (Parr and Sullivan 2005), because C sequestration by growing forests is a cost-effective option for mitigating CO_2 emissions, and forests contain up to 80% of the total aboveground carbon (C) and 40% of belowground C in terrestrial ecosystems (Dixon et al. 1994). Increasing forest land area and selecting tree species with a high

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Table 1. Selected chemical and physical properties of the soil in the Lei bamboo stand.

Soil depth (cm)	Total porosity (%)	Soil bulk density (g·cm^{-3})	pH (H_2O)	Organic matter (g·kg^{-1})	Total N (g·kg^{-1})	Available Si (g·kg^{-1})	Hydrolyzable N (mg·kg^{-1})	Available P (mg·kg^{-1})	Available K (mg·kg^{-1})
0–20	52.8	1.25	5.03	38.42	1.71	0.18	254	76.6	96
20–40	56.4	1.16	5.24	30.82	1.53	0.19	159	24.2	150
40–60	53.8	1.22	6.05	21.11	0.98	0.24	76	1.6	70

Note: N, nitrogen; Si, silicon; P, phosphorus; K, potassium.

CO_2-fixation capacity are considered to be important approaches for increasing C sequestration in forests (Zhou et al. 2009; Schulp et al. 2008). However, the land area available for growing woody plants has become limited due to the increasing demand for agricultural production and other competing land uses. Moreover, these approaches store C in the biomass or in the soil only for a short period of time, as the trees get harvested and soil organic C (SOC) becomes mineralized. Therefore, methods that allow long-term storage of C in a stable form would be desirable.

Recent research showed that organic C is occluded in phytoliths (Parr and Sullivan 2005), which are formed as amorphous silicon dioxide minerals in living plants through silicification of cell walls, cell lumina, or intercellular spaces (Wang and Lü 1992; Piperno 2006). After litter decomposition, phytoliths and the occluded C are released and become mineral constituents in soils. Recent studies revealed that phytoliths contain 0.2%–5.8% of phytolith-occluded organic carbon (PhytOC) (Parr and Sullivan 2011; Parr et al. 2010; Zuo and Lü 2011). The PhytOC is highly resistant against decomposition and may accumulate in soils with pH values that range from 3.5 to 9.8 for several thousand years (Wilding et al. 1967; Parr and Sullivan 2005). Accumulation of PhytOC in plants and soils has been demonstrated to be a promising approach for increasing long-term organic C storage (Parr et al. 2009, 2010; Song et al. 2011). As PhytOC accumulates in the soil over the long term, this would effectively mitigate CO_2 emission from anthropogenic sources (Parr et al. 2009). However, because this is a new area of research, data on PhytOC concentrations in different plant species and soils are quite limited, and such data are urgently needed for us to better understand the potential for C sequestration through PhytOC production and accumulation.

Bamboo forests are an important forest type in subtropical and tropical regions. Bamboo includes about 1200 species belonging to over 70 genera, distributed in about 22.0×10^6 ha and accounting for about 0.5% of the total forested area in the world (Guo et al. 2005). With a long history of production and utilization of bamboo, China is one of the countries with the richest bamboo resources and the largest area under bamboo forests (Song et al. 2011). Bamboo is widely distributed and is a fast-growing, high-yielding renewable natural resource (Fu 2001), with a very high biomass C sequestration rate (6–22 Mg C·ha^{-1}·year^{-1}) (Wang et al. 2013). Bamboo has also been found to perform ecological and environmental functions such as soil erosion control, water conservation, and land rehabilitation (Zhou et al. 2005; Song et al. 2011). Recent studies have demonstrated that bamboo, known as an effective silica accumulator, has a high PhytOC production capacity (Parr and Sullivan 2005; Parr et al. 2010) and has considerable potential for the biosequestration of C in the form of PhytOC in soils (Parr et al. 2010).

Lei bamboo (*Phyllostachys praecox* C.D. Chu & C.S. Chao.) is a bamboo species widely used for producing edible bamboo shoots, and its growth characteristics and management are quite different from that of other bamboo species. One of the unique management techniques is the heavy mulching of Lei bamboo stands in early winter, which functions to increase soil temperature in the winter and early spring and preserve soil moisture to increase the early production of bamboo shoots and fetch a much higher price (Jiang et al. 2006). Because of the great economic incentive, many growers frequently convert paddy fields to Lei bamboo stands. As a gramineous plant, Lei bamboo has a substantial potential for PhytOC production. Moreover, mulching materials used in Lei bamboo systems may also be a source for PhytOC sequestration.

Current studies on C biosequestration potential by bamboo stands only involve PhytOC production rates of leaf litter of 10 bamboo species (Parr et al. 2010). PhytOC production rates of leaf litter of bamboo species make up a part of PhytOC production rates in bamboo forests and do not fully reflect the potential for C biosequestration within the phytoliths of bamboo species. In light of the above, this experiment was conducted to (*i*) investigate the spatial distribution of PhytOC in Lei bamboo forests, and (*ii*) estimate C sequestration potential in the form of PhytOC in Lei bamboo stands in subtropical China.

2. Materials and methods

2.1. Sampling site

The study site was located in Sankou Township, Lin'an County (30°14′N, 119°42′E), Zhejiang Province, in southeastern China. This area has a central–subtropical climate, with a mean annual precipitation of 1422 mm and a mean annual temperature of 15.8 °C based on climatic data available between 2000 and 2009, with minimum and maximum temperatures of –13.3 °C and 41.7 °C, respectively. The annual mean number of sunshine hours and frost-free days between 2000 and 2009 were 1946 h and 239 days, respectively. The sampling site had a slope of 8° to ~10° and was 100–150 m above sea level. The soils in the experimental area were derived from a siltstone and classified as Ultisols in *Soil Taxonomy* (Soil Survey Staff 1999). The basic physicochemical properties of the soil are listed in Table 1.

2.2. Bamboo forest management

The Lei bamboo stand used in this experiment was established in 2002, and it had 20 450 plants·ha^{-1}, with an mean diameter at breast height (1.3 m) of 3.9 cm. The bamboo stands were established on former paddy fields; farmers in the region had frequently converted paddy fields to bamboo plantations in the last several decades due to the greater economic value of bamboo shoot production (Jiang et al. 2006). An intensive management regime was applied to the stand. This management regime includes the application of a thick layer of organic material (mulching) to the soil surface in late November to raise the soil temperature and maintain soil water content in the winter season. In the mulching process, about a 10 cm thick layer of rice straw is usually applied on the soil surface and then a 20 cm thick layer of bamboo leaf is placed on the rice straw. In this study, the rice straw and bamboo leaves were applied at 7.5 and 75 Mg·ha^{-1}·year^{-1}, respectively. The mulching practice could increase soil temperature at the 10 cm depth by 7–9 °C, which could result in the early emergence of bamboo shoots (Cao et al. 1995). Fertilizer was applied three times in the year: mid-May, late September, and mid-December, applying 35%, 30%, and 35%, respectively, of the total annual fertilizer application that included 1.125 Mg·ha^{-1} of urea and 2.25 Mg·ha^{-1} of a compound fertilizer (N:P_2O_5:K_2O = 15:15:15). To reduce the density in Lei bamboo stands and improve the economic return, growers usually harvest all 4-year-old bamboo plants every year as well.

2.3. Plant and soil sampling

Four sampling plots (10 m × 10 m) were established in the experimental stand in June 2012. The height and diameter of all bamboo plants in the sampling plots were measured. Three bamboo plants were randomly selected and harvested for each of 1-, 2-, 3- and 4-year-old plants from each sampling plot, and the biomass of leaves, branches, culms, and stump was determined. At the same time, four 1 m × 1 m subplots were randomly set up in each sampling plot, and the rhizomes in the subplots were dug up. Fresh masses of each component of bamboo plants were determined, and about 1000 g of fresh sample was collected for each component for further analysis. Four 1 m × 1 m subplots were set up in each sampling plot, and all the litterfall in each of the subplots was collected every month from February to September (litterfall was negligible in the other months under Lei bamboo stands) using a litter trap and weighed. At the same time, samples of rice straw and bamboo leaves used as mulching material were collected from the soil surface every month. About 100 g of those plant samples was washed in deionized water using an ultrasonic vibrating machine for 1 min, dried at 105 °C for 20 min, and then dried at 70 °C for 48 h in a forced-air oven. The dry mass of each sample was determined to calculate the moisture content in the plant samples. The plant samples were then ground to pass through a 0.25 mm mesh for chemical analysis.

Soil samples (2.0 kg) were collected from seven points per plot at 0–20, 20–40, and 40–60 cm depths and mixed to form a composite sample, air-dried, and divided into two parts. One part was ground to pass through a 0.5 mm screen and used for silicon (Si) and phytolith analysis, and the other part was passed through a 2 mm screen and used for other soil chemical analyses. Soil bulk density samples were collected in all three layers using a bulk density corer with a volume of 200 cm^3. The paddy soil samples were collected from seven points per plot at 0–20, 20–40, and 40–60 cm depths in June 2002 before the bamboo stands were established.

2.4. Plant and soil analysis

Total nitrogen (N) of the soil was measured using the semimicro-Kjeldahl method. Available N, phosphorus (P), and potassium (K) were determined by the diffusion absorption method (soil samples were reacted with 1 $mol \cdot L^{-1}$ NaOH solution, and the released NH_3 was absorbed by 0.3 $mol \cdot L^{-1}$ H_3BO_3 solution), Bray-1 method (soil samples were extracted with a mixed solution of 0.025 $mol \cdot L^{-1}$ HCl and 0.03 $mol \cdot L^{-1}$ NH_4F), and the NH_4OAc extraction-flame photometric method, respectively. Soil pH was determined by a pH electrode on a 1:5 (*m*:*v*) soil to water extract ratio. Organic C concentrations in plant and soil samples were determined by the $K_2Cr_2O_7$ + H_2SO_4 digestion method. The total Si concentrations in plant and soil samples were determined by an Optima 7000 DV ICP-OES (PerkinElmer, Inc., Waltham, Massachusetts) after pretreatment with the lithium metaborate melting method. The available Si in soil samples were determined by the citric acid extraction spectrophotometric method (Soil Science Society of China (SSSC) 2000). Samples were also collected from each plot using a bulk density corer with a 200 cm^3 volume to measure bulk density. All of the aforementioned methods followed Soil Science Society of China (SSSC) (2000).

A microwave digestion method described by Parr et al. (2001) and Parr (2002) was used in this study to isolate phytoliths from plant and soil samples. Duplicates were analyzed for each plant and soil sample. This process was followed by a Walkley–Black type digestion (Walkley and Black 1934) to ensure that the extracted phytoliths were free of extraneous organic material. The extracted phytoliths were oven-dried at 75 °C for 24 h and then weighed. Finally, each sample was further checked on an optical microscope (Olympus CX31, Olympus Corporation, Japan) to confirm that all extraneous organic materials on the surface of the phytoliths were thoroughly removed. The C concentration in the phytolith was then analyzed by a Flash EA 1112 CHNS/O Elemental Analyzer (Thermo Finnigan). Soil (GBW07405) and plant (GBW07602) standards were analyzed along with the samples for quality control; in cases that the relative error was greater than 5%, all samples in the batch were re-analyzed.

2.5. Calculations

The storage of PhytOC in the plant and soil was calculated using the following equations:

$$(1)\ \text{PhytOC stock in the plant}\ (\text{kg C}\cdot\text{ha}^{-1}) = \sum \left[\begin{array}{r} \text{PhytOC concentration in each plant component}\ (\text{kg}\cdot\text{Mg}^{-1}) \\ \times\ \text{biomass of each plant component}\ (\text{Mg}\cdot\text{ha}^{-1}) \end{array} \right]$$

$$(2)\ \text{PhytOC stock in the soil}\ (\text{kg C}\cdot\text{ha}^{-1}) = \sum \left[\begin{array}{r} 10000\ \text{m}^2 \times \text{thickness of soil layer (m)} \times \text{bulk density}\ (\text{Mg}\cdot\text{m}^{-3}) \\ \times\ \text{PhytOC concentration}\ (\text{kg C}\cdot\text{Mg}^{-1}\ \text{soil}) \end{array} \right]$$

The PhytOC stock in the soil before and after the conversion from paddy field to Lei bamboo forest was calculated, and the PhytOC accretion rate ($kg \cdot ha^{-1} \cdot year^{-1}$) in the soil was calculated as the difference between the two divided by the time since land use conversion (10 years).

2.6. Statistical analyses

A one-way analysis of variance (ANOVA) and the least significant difference (LSD) test were used to test the significant difference of parameters among different tissues. Unless otherwise mentioned, an α level of 0.05 was used in all statistical analyses. Linear regression analyses were conducted to determine the relationships between phytolith concentration and SiO_2 concentration, between SiO_2 concentration and C concentration of phytolith, between C density and C concentration of phytolith, and between phytolith concentration and C concentration in phytolith. All statistical analyses in this study were performed using the SPSS software (SPSS 13.0 for Windows, SPSS Inc., Chicago, Illinois).

3. Results

3.1. PhytOC in different Lei bamboo tissues

The total biomass of the Lei bamboo stand was 35 163 $kg \cdot ha^{-1}$. The biomass of the different tissues were in the following order ($P < 0.05$): culm (16 938 $kg \cdot ha^{-1}$) > stump (6705 $kg \cdot ha^{-1}$) > rhizome (3991 $kg \cdot ha^{-1}$) ≈ leaf (3788 $kg \cdot ha^{-1}$) ≈ branch (3742 $kg \cdot ha^{-1}$) (Table 2). The SiO_2, phytolith, and PhytOC concentrations were variable among Lei bamboo plant tissues (Table 2). The mean phytolith concentration in the Lei bamboo plant tissues tended to increase with age and had the following order ($P < 0.05$): rhizome (34.58 $g \cdot kg^{-1}$) ≈ stump (32.28 $g \cdot kg^{-1}$) > leaf (26.03 $g \cdot kg^{-1}$) ≈ branch (24.77 $g \cdot kg^{-1}$) > culm (3.82 $g \cdot kg^{-1}$). The concentrations of SiO_2 and PhytOC in different bamboo tissues followed a similar pattern among the different tissues (Table 2).

The PhytOC concentration in the phytolith ranged from 2.65% to 6.98%, whereas the PhytOC concentrations in different Lei bamboo tissues ranged from 0.12 to 2.12 $g \cdot kg^{-1}$ (Table 2). The amounts of PhytOC stored in leaves, branches, culms, rhizomes, and stumps in

Table 2. Biomass, concentration of silicon dioxide (SiO_2), phytolith concentration, concentration of PhytOC in phytolith (PhytOC/Phytolith), PhytOC concentration, and PhytOC stock in the Lei bamboo stand with different-aged bamboo plants.

Component	Bamboo age (year(s))	Biomass ($kg·ha^{-1}$)	SiO_2 ($g·kg^{-1}$)	Phytolith concentration ($g·kg^{-1}$)	PhytOC/ phytolith (%)	PhytOC concentration ($g·kg^{-1}$)	PhytOC stock (kg $C·ha^{-1}$)
Leaf	1	60d	10.67c	9.91d	6.00ab	0.60de	0.04e
	2	2089c	19.07b	21.58c	5.60bc	1.21b	2.52a
	3	940cd	26.94ab	31.29b	5.73bc	1.79a	1.69bc
	4	698cd	31.56a	41.33a	5.12c	2.12a	1.48bc
	Mean	947	22.06	26.03	5.61	1.43	1.43
Branch	1	326d	9.41cd	7.00d	3.64d	0.25e	0.08de
	2	1640cd	28.08ab	26.59bc	3.16d	0.84bc	1.38bc
	3	1012cd	28.78ab	31.75b	3.00d	0.95bc	0.96bcd
	4	764cd	30.47ab	33.75ab	2.65d	0.89bc	0.69cde
	Mean	936	24.19	24.77	3.11	0.74	0.78
Culm	1	2168c	1.88d	2.15d	6.98a	0.15e	0.33de
	2	6135a	4.46cd	1.88d	6.22ab	0.12e	0.72cde
	3	3939bc	5.83cd	5.32d	6.62a	0.35de	1.39c
	4	4696b	10.52c	5.92d	6.20ab	0.37de	1.72b
	Mean	4235	5.67	3.82	6.51	0.25	1.04
Rhizome	Mean	3991	35.21	34.58	2.98	1.03	4.11
Stump	1	963cd	17.43a	16.04c	3.95d	0.63d	0.61e
	2	2412c	25.49a	26.19bc	3.97d	1.04bc	2.51d
	3	1544cd	38.89a	40.05ab	3.88d	1.55ab	2.40d
	4	1786cd	45.40a	46.85a	3.80d	1.78a	3.18c
	Mean	1676	31.80	32.28	3.90	1.25	2.17
Total	—	35163	—	—	—	—	25.81

Note: Means with different lowercase letters in a column indicate a significant difference at $P = 0.05$ based on the least significant difference (LSD) test. For the rhizome component, we cannot calculate the amount of bamboo rhizome in different bamboo ages, as the bamboo rhizomes of different bamboo ages were connected with each other. PhytOC, phytolith-occluded organic carbon.

different-aged bamboo plants were 5.73, 3.11, 4.16, 4.11, and 8.70 kg $C·ha^{-1}$, respectively (Table 2), accounting for 22.2%, 12.1%, 16.1%, 15.9%, and 33.7% of the total PhytOC, respectively. Lei bamboo leaves had a higher PhytOC concentration (1.43 g $C·kg^{-1}$) and lower biomass (3.79 $Mg·ha^{-1}$) than other bamboo tissues, resulting in a low PhytOC stock (5.73 kg $C·ha^{-1}$). Lei bamboo stump had higher PhytOC concentration (1.25 g $C·kg^{-1}$) and biomass (6.71 $Mg·ha^{-1}$) than other tissues, resulting in the highest PhytOC stock (8.70 kg $C·ha^{-1}$) (Table 2). The PhytOC stock (12.8 kg $C·ha^{-1}$) in the belowground plant component (including bamboo rhizomes and stumps) accounted for 49.6% of the total PhytOC stock in the vegetation.

The amount of bamboo leaf litter (3.48 $Mg·ha^{-1}·year^{-1}$) produced was lower than living leaves on bamboo plants (3.79 $Mg·ha^{-1}·year^{-1}$) (Tables 2 and 3). Mean phytolith (74.69 $g·kg^{-1}$) and PhytOC (2.87 g $C·kg^{-1}$) concentrations in the leaf litter were greater than that in the living leaves of bamboo plants (26.03 and 1.43 $g·kg^{-1}$, respectively). Thus, the PhytOC production rate by leaf litter (11.30 kg $C·ha^{-1}·year^{-1}$) (Table 3) was 97% greater than that by the living leaves (5.73 kg $C·ha^{-1}·year^{-1}$) (Table 2). The phytolith concentration was much greater in bamboo leaf litter (74.69 $g·kg^{-1}$) than in the bamboo leaves used as the mulching material (48.48 $g·kg^{-1}$). The PhytOC production in bamboo leaf and rice straw through the mulching practice were 189.23 and 8.31 kg $C·ha^{-1}·year^{-1}$, which was equivalent to 693.9 and 30.5 kg CO_2-eq$·ha^{-1}·year^{-1}$, respectively (Table 3).

3.2. Soil phytolith and PhytOC in Lei bamboo and paddy sites

Both soil phytolith and PhytOC concentrations were much greater in Lei bamboo stands than in paddy sites. The PhytOC stock in Lei bamboo and paddy soils decreased with depth. The PhytOC stock in the 0–20 cm soil layer in the Lei bamboo stand and paddy field were 60.5% and 68.3%, respectively, of those in the 0–60 cm soil layer (Table 4). Total PhytOC stock in the 0–60 cm soil layer in the Lei bamboo stand (9361 kg $C·ha^{-1}$) was 53.2% greater than that in the paddy field. The PhytOC accretion rate in the Lei bamboo soil was estimated to be 325 kg $C·ha^{-1}·year^{-1}$ in the 0–60 cm soil layer (Table 4).

3.3. Distribution of PhytOC in the Lei bamboo stand

The PhytOC stock in the Lei bamboo stand had the following order ($P < 0.05$): soil (9361 kg $C·ha^{-1}$) > mulching materials (197.5 kg $C·ha^{-1}$) > aboveground vegetation (13.0 kg $C·ha^{-1}$) ≈ belowground plant tissues (12.8 kg $C·ha^{-1}$) ≈ litterfall (11.3 kg $C·ha^{-1}$), in which the PhytOC stock in the 0–60 cm soil layer accounted for 97.6% of the total stock in the Lei bamboo stand (Table 5).

3.4. Relationships between Si or C concentrations and PhytOC concentrations in the Lei bamboo stand

The phytolith and Si concentrations in Lei bamboo plant components were significantly positively correlated ($R^2 = 0.96$, $P < 0.01$) (Fig. 1*a*), whereas the Si and PhytOC concentrations were significantly negatively correlated ($R^2 = 0.53$, $P < 0.01$) (Fig. 1*b*). A significantly positive correlation ($R^2 = 0.21$, $P < 0.05$) was found between C concentrations in the tissues and C concentrations of the phytolith in the leaves, branches, culms, rhizome, and stump of Lei bamboo plants (Fig. 1*c*). There was a relatively strong negative correlation ($R^2 = 0.44$, $P < 0.01$) between C concentrations of phytolith and phytolith concentrations in the tissues of bamboo plants (Fig. 1*d*).

4. Discussion

4.1. PhytOC in Lei bamboo plantation soils

The PhytOC accretion rate in the soil is affected by the composition and age of plant species, forest management practices, soil structure, soil water availability, and the composition and activity

Table 3. Phytolith concentrations and PhytOC concentrations and fluxes in litterfall and mulching materials (bamboo leaf and rice straw) in Lei bamboo stands.

Organic input type	Amount of organic input (Mg·ha^{-1})	Phytolith concentration (g·kg^{-1})	PhytOC/ phytolith (%)	PhytOC concentration (g·kg^{-1})	PhytOC content (kg·ha^{-1})	PhytOC fluxes (kg CO_2-eq·ha^{-1}·year^{-1})
Bamboo leaf litter	3.48±0.41	74.69±6.92	3.89±0.14	2.87±0.21	11.30±2.54	41.45±9.32
Bamboo leaf	75.0±9.7	48.48±6.43	4.69±0.55	2.52±0.16	189.23±22.8	693.9±55.2
Rice straw	7.5±1.9	43.11±5.12	4.11±0.44	1.11±0.28	8.31±1.24	30.5±3.9

Note: All values are mean ± standard error. The bamboo leaf litter is the cumulative amount from February to September. The phytolith-occluded organic carbon (PhytOC) content of bamboo leaf litter = sum of PhytOC concentration´ mass of litterfall in each month.

Table 4. Distribution of phytolith and PhytOC with soil depth in the Lei bamboo stand and paddy sites.

Soil depth (cm)	Organic C (g·kg^{-1})	Phytolith concentration (g·kg^{-1})	PhytOC/ phytolith (%)	PhytOC concentration (g·kg^{-1})	Soil PhytOC/soil TOC (%)	PhytOC stock (kg C·ha^{-1})	PhytOC accretion rate (kg C·ha^{-1}·year^{-1})
Lei bamboo stand (2012)							
0–20	22.28±2.54	42.46±5.56	5.34±0.58	2.27±0.34	10.18±1.3	5668±489	149±13
20–40	17.52±1.53	24.61±1.68	4.97±0.48	1.22±0.21	5.78±0.7	2837±272	135±9
40–60	12.24±1.18	7.34±1.48	4.79±0.35	0.35±0.06	1.76±0.3	856±84	41±3
Total	—	—	—	—	—	9361±632	325±27
Paddy sites (2002)							
0–20	12.57±2.21	30.07±1.19	5.04±0.41	1.61±0.26	12.85±1.3	4176±398	—
20–40	10.14±1.41	10.68±2.85	4.87±0.38	0.53±0.08	5.23±0.7	1487±146	—
40–60	8.23±1.01	4.72±0.63	4.39±0.34	0.17±0.05	2.02±0.2	448±64	—
Total	—	—	—	—	—	6111±596	—

Note: All values are mean ± standard error. PhytOC, phytolith-occluded organic carbon; TOC, total organic carbon.

Table 5. PhytOC concentration and stock in various components in the Lei bamboo stand.

Component	Phytolith concentration (g·kg^{-1})	PhytOC/ phytolith (%)	PhytOC concentration (g·kg^{-1})	PhytOC stock	
				kg C·ha^{-1}	%
Aboveground	16.21±2.89	6.37±0.79	0.80±0.53	13.0±0.52	0.14
Belowground	34.98±6.34	6.19±0.81	2.17±0.77	12.8±1.84	0.13
Litterfall	74.69±6.92	3.89±0.14	2.87±0.21	11.3±2.54	0.12
Mulching material	48.00±6.53	4.64±1.01	2.39±0.65	197.5±31.9	2.06
0–60 cm soil layer	24.80±3.78	5.03±0.75	1.28±0.45	9361±632	97.6
Total	—	—	—	9595.6	100.0

Note: All values are mean ± standard error. PhytOC, phytolith-occluded organic carbon.

of microbial communities in the soil (Parr and Sullivan 2005). Generally, only about 30% of total nongrain biomass produced from crops reaches the soil through the incorporation of crop residue, wastes from animal feedlots, and farmyard manure or compost. For Lei bamboo stands, the PhytOC in the soil comes mainly from plant litterfall and the mulching material and organic fertilizers applied. In the Lei bamboo stands studied, 97.6% of the total PhytOC stock was in the soil (9361 kg C·ha^{-1}), indicating that the soil was the main reservoir for PhytOC storage in the ecosystem (Table 5).

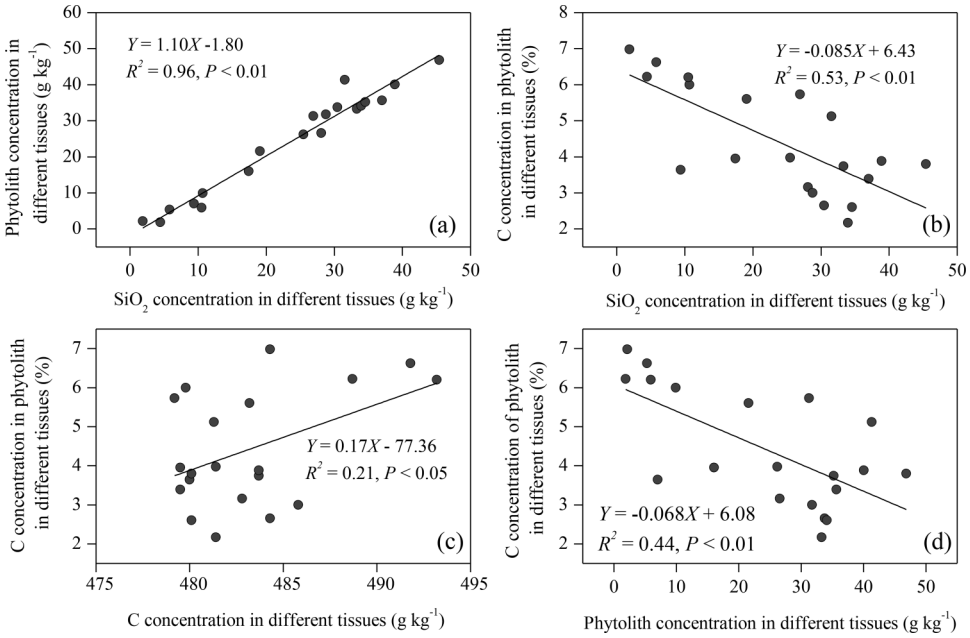
The PhytOC accretion rate in the soil (325 kg·ha^{-1}·year^{-1}) was greater than that in the mulching material and litterfall (209 kg·ha^{-1}·year^{-1}) in the studied Lei bamboo stand, which was contributed by the application of large amounts of organic manure and mulching materials in Lei bamboo production (Jiang et al. 2009). Intensive management including winter mulching and heavy application of organic manure has been extensively used in Lei bamboo stands, resulting in rapid accumulation of SOC (Meng et al. 2011; Jiang et al. 2009; Sun et al. 2009; Xu et al. 2010). Moreover, the accumulation of SOC in Lei bamboo stands was accelerated over time. The concentration of SOC in the 0–10 cm soil depth was up to 45.96 g C·kg^{-1} and SOC accretion rates in 2001–2006 in the 0–10, 10–20, and 20–40 cm soil depths were 6.69, 3.05, and 1.38 Mg C·ha^{-1}·year^{-1}, respectively (Cai et al. 2007). The high accumulation rate of SOC in Lei bamboo stands has resulted in a rapid increase in the PhytOC in the soils.

The results of this study provided direct evidence for significant downward translocation of PhytOC in the soils. The PhytOC stock in 0–20, 20–40, and 40–60 cm soil under the Lei bamboo stand was increased by 1492, 1350, and 408 kg C·ha^{-1}, respectively, as compared with the baseline in the paddy soil before establishing the Lei bamboo stand (Table 4). The accumulation of PhytOC in the deeper soil layers can be attributed to mechanical mixing caused by deep tillage after fertilization and down growth of bamboo roots and rhizomes. Large amounts of the PhytOC formed from mulching materials and organic manure applied to the soil provide a source of material for downward translocation of PhytOC in the soil, whereas macropores created by root channels provide the passage for the translocation of PhytOC in the soil.

4.2. PhytOC sequestration potential in Lei bamboo stands

There was considerable variation ($P < 0.05$) in the mean concentrations of phytolith and PhytOC among various bamboo tissues. Significant differences in phytolith concentrations among various bamboo tissues contributed to significant differences in Si concentrations, whereas significant differences in PhytOC concentrations among various bamboo tissues contributed to significant differences in C concentrations (Fig. 1). The same trend in the change

Fig. 1. Relationships between (*a*) SiO_2 concentration in different tissues and phytolith concentration in different tissues, (*b*) SiO_2 concentration in different tissues and C concentration in phytolith in different tissues, (*c*) C concentration in different tissues and C concentration in phytolith in different tissues, and (*d*) phytolith concentration in different tissues and C concentration of phytolith in different tissues . Tissues include the leaves, branches, culms, bamboo rhizome, and bamboo stump of Lei bamboo plants.



in concentrations of SiO_2 and PhytOC in different bamboo tissues resulted in a strong linear relationship between them (Fig. 1). The mean phytolith concentrations in Lei bamboo plant tissues tended to increase with age (Table 2) as a result of the ageing of bamboo tissues (Jiang et al. 2009).

The Phytolith production rate and the phytolith C sink in bamboo ecosystems have been calculated based on their concentrations in the leaf tissue. However, statistically significant differences of PhytOC contents and biomass were found in different tissues of bamboo plants in this study; therefore, it is necessary to measure PhytOC content in every part of bamboo plants for an accurate estimation. The PhytOC stock (12.8 kg C·ha^{-1}) in belowground plant components (including bamboo rhizomes and stumps) accounted for 49.6% of the total in the vegetation, suggesting that belowground components are a very important component for C biosequestration in bamboo stands.

Estimation of the annual net primary production (ANPP) in a plant ecosystem is vitally important for estimation of PhytOC production rates of forest. The growth habit of Lei bamboo is quite different from that of other forests. Therefore, estimation of ANPP for Lei bamboo stands is also different from that of other forests. For Lei bamboo stands, all of the 4-year-old bamboo plants are harvested every year. We consider that the ANPP of Lei bamboo stands consists of the biomass of 4-year-old bamboo plants, total current vegetation biomass divided by cultivation ages, and the litterfall under stands.

In this study, litterfall production rate and current biomass in vegetation store in the Lei bamboo ecosystem were 3.48 Mg·ha^{-1}·year^{-1} (Table 3) and 35.16 Mg·ha^{-1} (Table 2), respectively. According to the calculation of Parr et al. (2010), the 22 million ha of bamboo forests could biosequester 15.6 × 10^6 Mg·year^{-1} of stable C if they are managed under an optimum regime. We considered that the C biosequestration rate was greatly overestimated, because it was estimated according to PhytOC production rate of 0.709 Mg CO_2-eq·ha^{-1}·year^{-1}, which was based on the production of 37 Mg bamboo litter·ha^{-1}·year^{-1}. Kleinhenz and Midmore (2001) reported 37.0 Mg·ha^{-1}·year^{-1} of bamboo leaf biomass was in the living leaves of *Sphaerobambos philippinensis* (Gamble) S.Dransf. instead of reporting the leaf-litter production rate. We are not able to found a reference in which the leaf-litter biomass of bamboo stands exceeds 8 Mg·ha^{-1}·year^{-1}.

The PhytOC accretion rate in the vegetation of the Lei bamboo stand in this study included biomass of 4- year-old bamboo plants (8.1 kg·ha^{-1}·year^{-1}) (Table 2) and annual litter fall (11.3 kg·ha^{-1}·year^{-1}) (Table 5). Thus, the PhytOC accretion rate in the vegetation of Lei bamboo stand was 19.4 kg·ha^{-1}·year^{-1}, which was equivalent to 71 kg CO_2-eq·ha^{-1}·year^{-1} and far less than the value of 0.709 Mg CO_2-eq·ha^{-1} reported by Parr et al. (2010). The possible explanation would be that Parr et al. (2010) greatly overestimated the C biosequestration rate of bamboo ecosystems, because our result was directly calculated by the data obtained through the site investigation, whereas that of Parr et al. (2010) was estimated by the PhytOC concentration in leaf samples. Another possibility for those large differences could be related to the spatial variation that is associated with soil C sequestration estimates.

If we consider that the total photosynthate roughly equals the amount of biomass produced in the studied bamboo forests, the percentage of C sequestered in the form of PhytOC in the Lei bamboo forests represents about 1%–2% of the photosynthate (Table 5). The PhytOC accretion rate by Lei bamboo stand in this study consisted of vegetation (0.071 Mg CO_2-eq·ha^{-1}), bamboo leaves as mulching material (0.694 Mg CO_2-eq·ha^{-1}), and rice straw as mulching material (0.030 Mg CO_2-eq·ha^{-1}), for a total 0.795 Mg CO_2-eq·ha^{-1}·year^{-1}. Based on that rate and the area planted to Lei bamboo in southern China (2.62 × 10^6 ha; Jiang et al. 2009), the PhytOC accretion rate in Lei bamboo stands in China is estimated to be 2.08 × 10^6 Mg CO_2-eq·year^{-1}.

4.3. Relationships between SiO_2 and phytolith or PhytOC concentrations

The SiO_2 concentrations in bamboo plants increased with bamboo age (Table 1), because the accumulation of silica was found to be greater in plants near maturity than in juvenile plants (Norris and Hackney 1999; Motomura et al. 2002).

As the phytolith contains more than 90% of silica in a plant (Wang 1998), the phytolith concentration in the plants was signif-

icantly positively correlated with SiO_2 concentration in plants (Song et al. 2012; Li et al. 2013), which was also found in our study. Therefore, the phytolith concentration can be estimated from the silica concentration in plants (Song et al. 2012; Li et al. 2013). A significantly positive correlation between C concentrations in the tissues of bamboo plants and C concentrations in phytolith in the tissues of bamboo plants (Fig. 1*c*), whereas a negative correlation was observed between the C concentration in the phytolith and the SiO_2 concentration in tissues (Fig. 1*b*). The latter was attributed to the dilution effect, because the increase in SiO_2 concentration in phytolith was much greater than that in C concentration. The aforementioned results suggest that the PhytOC yield in plant tissues would be largely dependent on the nature of silica deposition and the efficiency of PhytOC formation (Parr et al. 2010) rather than the quantity of silica taken up by roots.

5. Conclusions

We conclude that there was a large variation in PhytOC concentrations among different bamboo plant tissues, and therefore, it would be necessary to measure the PhytOC concentrations of different tissues in Lei bamboo forests to accurately estimate the PhytOC stock in this forest system. The PhytOC stock of belowground components accounted for 49.6% of the total PhytOC stock, suggesting that the contribution of belowground plant components to the ecosystem-level PhytOC stock should not be ignored. The PhytOC stock of Lei bamboo system studied was mainly concentrated in the 0–60 cm of soil depth (9361 kg C·ha^{-1}), accounting for 97.56% of total PhytOC stock. The intensively managed Lei bamboo system showed great potential in long-term C sequestration through the formation of PhytOC, which might be related to winter mulching, an intensive management practice aimed at increasing bamboo shoot production. By increasing the application rate of mulching materials or adding mulching materials with a high PhytOC concentration, soil PhytOC stock in Lei bamboo forests could be further increased. About 2.08×10^6 Mg CO_2 could be sequestered in the form of PhytOC annually based on a PhytOC accretion rate of 0.795 Mg CO_2-eq·ha^{-1}·year^{-1} and Lei bamboo area of 2.62×10^6 ha in southern China. Future research should be conducted to improve our understanding of mechanisms related to the response of PhytOC production rate of different plantation systems to different management practices.

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