

Role of phytolith occluded carbon of crop plants for enhancing soil carbon sequestration in agro-ecosystems

S. Rajendiran*, M. Vassanda Coumar, S. Kundu, Ajay, M. L. Dotaniya and A. Subba Rao

Division of Environmental Soil Science, Indian Institute of Soil Science, Nabibagh, Bhopal 462 038, India

Phytolith occluded carbon (PhytOC) which is stable in the soil environment is considered to be an important fraction of soil organic carbon and substantially contributes to the terrestrial carbon sequestration for long periods (millennia). Phytoliths are silica bodies produced by plants as a result of biomineralization process. During this process, occlusion of carbon also takes place within the phytoliths. Some of the major agricultural crops like barley, maize, rice, sorghum, sugarcane and wheat are known to be prolific producers of phytolith and PhytOC. In India, an estimate indicates that these crops may annually contribute about 87 million tonnes (mt) of PhytOC. Hence, a great potential exists to enhance PhytOC accumulation in the soils of various agro-ecosystems. The rate of phytolith production and the carbon occluded in phytoliths vary among the plant community. In India, an estimate indicates that these crops may annually contribute about 87 mt of PhytOC and growing high PhytOC-yielding cultivars of these crops may additionally produce 1.05 mt of PhytOC. Therefore, selection of high PhytOC-yielding cultivars over low PhytOC-yielding cultivars for agricultural production under different agro-ecosystems offers an opportunity to enhance terrestrial carbon sequestration.

Keywords: Biomineralization, phytolith occluded carbon, soil organic carbon, terrestrial carbon sequestration.

GLOBAL warming and rapid increase in the concentration of atmospheric CO₂ have contributed to an increased awareness of carbon sequestration in the soil. Terrestrial carbon sequestration is fundamental to the global carbon cycle and is being utilized to counter increases in anthropogenic CO₂ emissions. So far several approaches are being adopted to mitigate global CO₂ emissions and to sequester carbon in the soil. However, these approaches restore C in the soil only for a short span of time. Long-term (decades to millennia) soil organic carbon sequestration is believed to be mainly by physical protection of chemically recalcitrant organic matter within organo-mineral complexes¹ and charcoal formation². These

mechanisms largely require and are dependant on existing forests and hardwood plantations. On the other hand, the land area available for woody plant production has become limited due to the increasing demand for agricultural production. Therefore, a more recent approach to improve phytolith occluded carbon (PhytOC) accumulation in plants and soils was demonstrated to increase the world carbon stocks of soils in various agro-ecosystems³⁻⁶.

PhytOC, an important fraction of soil organic carbon, is stable in the soil environment and substantially contributes to the terrestrial sequestration of carbon for a long period (millennia)^{7,8}. PhytOC fractions remain in the soil for a long period (millennia) that results in the reduction of CO₂ emission from agriculture, as against many other soil organic carbon fractions which may decompose over a much shorter time. PhytOC has been widely studied in archaeological, palaeobotanical, palaeoenvironmental and biogeochemical investigations⁹⁻¹². Morphotypes of silicophytoliths were used in the identification of taxonomical groups of plant species¹³⁻¹⁵. However, from the soil carbon sequestration point of view, there is little information available on the utilization of PhytOC of many agricultural crops³⁻⁶. Hence, an in-depth knowledge of PhytOC and its potential in long-term carbon sequestration is necessary. In recent years, many researchers have demonstrated that phytolith has a potential to sequester carbon in the soil as PhytOC for a long period^{3,6}. The objective of this article is to describe phytoliths, PhytOC and their importance, PhytOC content in plants, and the scope of carbon sequestration potential in agricultural systems across the world.

Phytoliths and their importance

Phytoliths (phyto means 'plant' and lithos means 'rocks' in Greek), also referred to as 'plant opal' or 'plant stone', are silica bodies produced by plants as a result of biomineralization. The soluble silica from the soil, particularly in the form of monosilicic acid (Si(OH)₄), is absorbed by the roots and carried to different plant parts through the vascular system. During the subsequent process, the silica is deposited in the intra- and extracellular structures of

*For correspondence. (e-mail: rajanselladurai@yahoo.co.in)

the leaf, stem and root systems¹⁶. Cell wall, cell lumen and intercellular spaces of the cortex are three sites where silica is mainly deposited in the plant tissues¹⁷. The amount of silica accumulated in the plant tissues ranges from 0.1% to 10% of the dry weight¹⁸. The size of the silica bodies that are deposited in the plant tissues mostly ranges between 10 and 30 μm and is occasionally up to 200 μm (ref. 19). The cell-wall deposits of silica often replicate the morphology of the living cells. During the biomineralization process, occlusion of carbon takes place within the phytoliths²⁰. These PhytOC are most likely the original cytoplasmic organic constituents⁷, simple carbohydrates¹² and cellulose²¹ depending upon the location of silicification.

Silica phytoliths in plants perform a variety of functions and provide structural rigidity and mechanical strength to the shoot^{22–25}. Silica phytoliths help the plants to survive many abiotic stresses such as salt, metal toxicity, nutrient imbalance, drought, radiation, high temperature, freezing and ultraviolet radiation²⁶ as well as reduce the impact of biotic stress such as insect pests and fungal diseases on plants.

Morphotypes of biomineralized silicophytoliths

In plants, accumulation of calcium carbonate, calcium oxalate and amorphous silica is a common biomineralization process. The study of plant biomineralization has become an important taxonomic approach as oxalate and carbonate crystals and phytoliths help in plant taxon identification^{13–15}. In particular, silicophytoliths are widely used as indicators of past plant communities and environmental conditions where these communities were evolved and developed^{27–29}. Biomineralization of silicophytoliths is considered to be an important process as it influences the earth carbon cycle by occlusion of carbon during the silicification process²². Morphotypes of biomineralized silicophytoliths have been widely studied and reported in aquatic plants³⁰, woody plants³¹, common grasses^{32,33}, wild and cultivated rice³⁴, foxtail millet (*Setaria italica*), common millet (*Panicum miliaceum*)³⁵ and even in some herbarium specimens³⁶. The morphological classes and distribution of grass phytoliths that occur in the sediments belong to a particular taxonomic group of Gramineae which falls under four main classes (Figure 1 and Table 1)¹³. The phytoliths extracted from inflorescence of *Triticum* sp. are papillae, trichome base and dendriform phytoliths (Figure 2)³⁷. Maize and domesticated squash mostly contain dendriform phytoliths in their leaves (Figure 3)³⁸.

Evidently, the presence of phytoliths in different plant families is well documented^{39,40}. Attempts have been made to distinguish phytoliths in cultivated crops from those of wild plants, especially wild relatives of crop plants^{38,41,42}. During the last two decades, phytoliths of 12

domesticated plants and their wild relatives have been widely studied⁴³. These domesticated plants include maize, squash and gourd, bottle gourd, cassabanana, arrowroot, rice, banana, ensets, barley, einkorn wheat, emmer wheat and bread wheat. In maize, eight distinct morphological variants of cross-body (quadralobate) phytoliths have been reported^{17,38}. This is used to differentiate maize and its wild species utilizing a combination of size and three-dimensional shape attributes. In rice genus *Oryza*, unique type of double-peaked hair-cell phytoliths is reported^{44,45}. Wave pattern of the long cell walls in the glumes of wheat and barley has been found useful in discriminating both taxa⁴⁶. Phytoliths of a bamboo genus, *Pleioblastus* have been recorded in parts of soils dated to the last interglacial period (130,000–74,000 BP) from Japan⁴⁷. Phytoliths can be used as palaeoenvironmental markers to understand the past environmental conditions. Such information is valuable in palaeoecological studies on monitoring climate change and reconstructing past vegetation^{47–49}.

Phytoliths, PhytOC content and their variability in plants

The rate of phytolith production and the amount of carbon occluded in phytoliths vary among the plant commu-

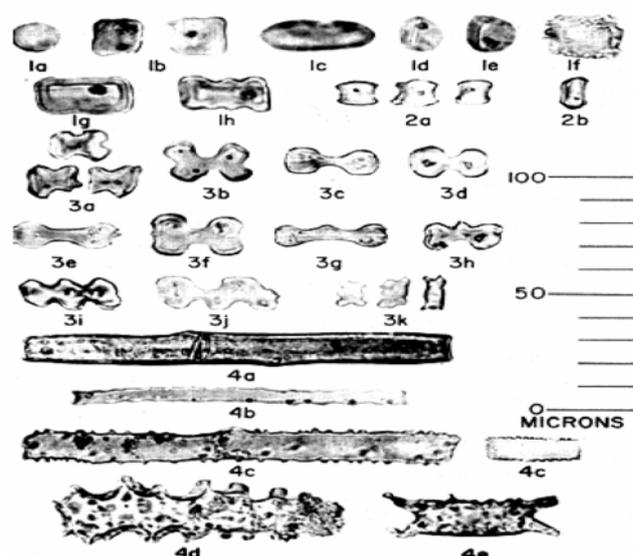


Figure 1. Morphological shapes of grass phytoliths¹³. 1. Festucoid class: 1a, Circular; 1b, Rectangular; 1c, Elliptical; 1d, Acicular, variable focus; 1e, Crescent, variable focus; 1f, Circular crenate; 1g, Oblong; 1h, Oblong, sinuous. 2. Chloridoid class: 2a, Chloridoid; 2b, Thin chloridoid. 3. Panicoid class: 3a, Cross, thick shank; 3b, Cross, thin shank; 3c, Dumbbell, long shank; 3d, Dumbbell, short shank; 3e, Dumbbell, long shank, straight or concave ends; 3f, Dumbbell, short shank, straight or concave ends; 3g, Dumbbell, nodular shank; 3h, Dumbbell, spiny shank; 3i, Regular, complex dumbbell; 3j, Irregular, complex dumbbell; 3k, Crenate. 4. Elongate class (no subfamily characteristics): 4a, Elongate, smooth; 4b, Elongate, sinuous; 4c, Elongate, spiny; 4d, Elongate, spiny with pavement; 4e, Elongate, concave ends.

Table 1. Distribution of phytoliths in common grasses of Gramineae¹³

Species of grass	Festucoid class 1								Chloridoid class 2		Panicoid class 3											Elongate class 4						
	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	g	h	i	j	k	a	b	c	d	e		
<i>Bromus inrrmis</i> leyss.	C	C	C				C	C	C																	A	A	
<i>Festuca elatior</i> L.	R	R	C	C	C																					A	A	
<i>Poa pratensis</i> L.	C	C	C	C	C	C	C																		A	A	R	
<i>Triticum aestivum</i> L.	C	C		C	C	C		C																	C	A	C	
<i>Aristida</i> sp. L.	C	C	C											C		C									C	A		
<i>Bouteloua curtipendula</i> (Michx.) Torr.									C	C															A	C	A	
<i>Bouteloua gracilis</i> (H. B. K.) Lag. and Steud.									C	C															A	A		
<i>Bouteloua hirsuta</i> Lag.									C	C															A	A		
<i>Buchloe dactyloides</i> (Nutt.) Engelm.									C	C															A	C	A	C
<i>Bambusa</i> sp.									C	C																A	A	
<i>Sorghum vulgare</i> Pers.																									A	C	A	C
<i>Panicum virgatum</i> L.											C	R	C	C		C	R	R	R						A	C	C	
<i>Andropogon gerardi</i> Vitman											C		C	C	C		R		R						A	A	A	
<i>Andropogon scoparius</i> Michx.											C		C	C	C	C	R	R	R	R	R				A	A	A	R
<i>Sorghastrum nutans</i> (L.) Zea mays L.											C	C	C	C	C										R	C	A	
<i>Zea mays</i> L.											C		C	C	C	C	R	R	R			R			C	C	A	
<i>Hilaria mutica</i> (Buckl.) Benth.											C			C					R	R						A	A	
	C	C									R			C	C	C												

A, Abundant; C, Common; R, Rare; No designation, None.

nities and also within the community. Many plant species are considered to be effective silica accumulators in the form of monosilicic acid, whereas other plant species can exclude effectively the uptake of monosilicic acid⁵⁰. Higher plants have been categorized into three groups according to their silicon content (SiO₂, expressed as a percentage of shoot dry weight): (1) members of Cyperaceae and wetland species of Gramineae (e.g., rice) with 10–15%, (2) dryland species of Gramineae (e.g., wheat, sugarcane) and a few dicotyledons with 1–3% and (3) most dicotyledons, especially legumes with less than 0.5% (ref. 50). Although silica occurs in many plants, some tree species and grasses such as Poaceae and Cyperaceae are generally considered as the most prolific producers of phytoliths^{51–56}. Most of the cell-wall deposits of silica contain occluded carbon and are generally found in herbaceous plants. The grasses are particularly good at occluding carbon via silica biomineralization processes⁶. As a result, long-term phytolith accumulation rates under grasslands are commonly 5–10 times greater than under forest land⁵⁷.

Many studies have been reported on phytolith content and its variability among different cultivars of agricultural crops like wheat, maize, sugarcane and rice, and even in some grasses like bamboo⁵. In rice, SiO₂ accumulation up to the level of 10% of shoot dry weight has been observed¹⁸. The SiO₂ content and its distribution in different plant parts of rice vary widely and 65.5% of silica is deposited in leaves compared to other plant parts of rice

(Table 2)⁵⁸. In wheat and sugarcane, phytolith content varies from 2.68% to 7.85% (ref. 4) and 1.3% to 2.6% (ref. 6) respectively.

The occluded carbon contents in phytoliths also vary widely. For example the carbon content in phytoliths extracted from oats varies from 5.0% to 5.8% (ref. 20) and in sugarcane⁶ from 3.88% to 19.26%. Significant variation was reported in PhytOC content of different varieties of sugarcane (Table 3)⁶. It is the efficiency by which carbon is encapsulated within silica, rather than the quantity of silica accumulated by the plant, which is an important factor in determining the relative PhytOC yields^{4,6}. The PhytOC yield of a sugarcane crop was 18.1 g C m⁻² yr⁻¹, an accumulation rate that is substantial over a long period (millennia) and yet comparable to the rates of carbon sequestration that are achievable (but only for a few decades) by land-use changes⁶. The rate of silica accumulation and carbon bio-sequestered within the silica phytoliths of the leaf and stem material of 53 wheat (*Triticum* sp.) cultivars sourced from 25 countries around the world was examined⁴, which showed that PhytOC content of wheat cultivars ranged from 0.06% to 0.60% of dry leaf and stem biomass. The phytolith carbon bio-sequestration potential of wheat cultivars is reported to be 0.246 t e-CO₂ ha⁻¹ yr⁻¹ (ref. 4). These phytolith carbon bio-sequestration rates indicate a substantial potential (~50 mt e-CO₂ yr⁻¹) for increasing the rate of carbon bio-sequestration in wheat (Table 4)⁴. Globally bamboo leaf litter has PhytOC yields of up to 0.7 t e-CO₂ ha⁻¹ yr⁻¹.

According to Parr *et al.*⁵, bamboo and sugarcane have a global potential to bio-sequester PhytOC of about ~1.5 billion t e-CO₂ yr⁻¹, which is equivalent to 11% of the current annual increase in atmospheric CO₂. Hence, this process offers the opportunity to use the plant species that yield high amounts of PhytOC to enhance terrestrial carbon sequestration. There are studies which demonstrate that simply growing high PhytOC-yielding cultivars over low PhytOC-yielding cultivars results in additional sequestration of carbon in the soil by ~0.25 t e-CO₂ yr⁻¹ ha⁻¹ for sugarcane⁶ and ~0.2 t e-CO₂ yr⁻¹ ha⁻¹ for wheat⁴ respectively.

PhytOC accumulation in soil

On a global scale organic carbon stored in the soil quantitatively dominates the carbon cycle, out-storing the possible carbon stored in the current vegetation cover by at least two-fold⁵⁹. It has the potential to assist in the mitigation of greenhouse gas emissions with appropriate management^{60,61}. The carbon occluded in the phytoliths has been demonstrated to be an important long-term terrestrial carbon fraction in the soil. For example, after 2000 years of *in situ* decomposition in Numundo sites of Australia, PhytOC was representing up to 82% of the total soil carbon in buried topsoils of up to 2 m depth, whereas the concentration of the total carbon fraction decreased markedly over this period (Figure 4)³. Although PhytOC was a relatively minor fraction of the soil carbon in the young Numundo topsoils (200 years), most of the other soil organic matter components were considerably decomposed in the older topsoils, resulting in PhytOC comprising a mean of 42% of the total carbon pool in these well-drained soils after 1000 years. Moreover, it has been demonstrated that relative to the soil organic carbon fraction that decomposes over shorter timescales, PhytOC is highly resistant against decomposition and persists in the soil environment for a long period^{3,7,8,62}. Radiocarbon dating of the phytoliths, extracted from palaeosols and peat sediments, indicated ages of at least 8,000 yrs BP (i.e. before 1950)³ to 13,300 ± 450 BP (ref. 9).

Phytoliths may experience a range of fates in terrestrial environments. For example, erosion, transportation by wind or water, loss due to burning in a forest fire, or biochemical changes while passing through the digestive systems of animals. Regardless of such fates, the potential of stability and persistence of phytoliths against such

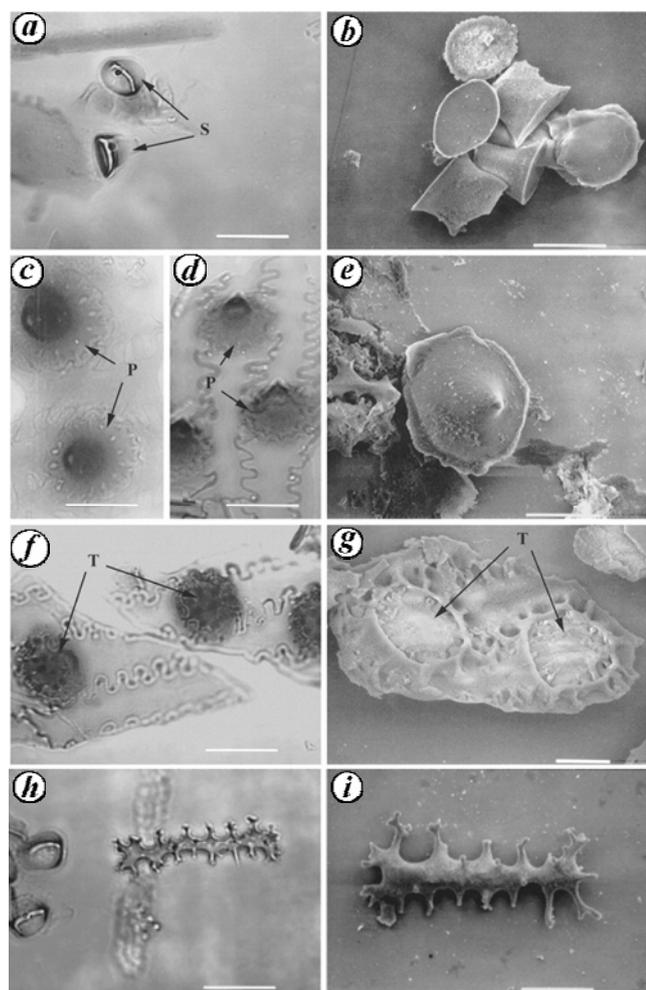


Figure 2. Phytoliths extracted from the inflorescence bracts of *Triticum* sp.³⁷. S, Silica cell phytoliths; P, Papillae phytoliths; T, Trichome base phytoliths. **a**, Light micrograph of silica cell phytoliths from *T. monococcum*; bar = 25 µm. **b**, Scanning electron micrograph of silica cell phytoliths from *T. aestivum*; bar = 10 µm. **c**, Light micrograph of papillae phytoliths from *T. aestivum*; bar = 25 µm. **d**, Light micrograph of papillae phytoliths from *T. monococcum*; bar = 25 µm. **e**, Scanning electron micrograph of papillae phytolith from *T. aestivum*; bar = 10 µm. **f**, Light micrograph of trichome base phytoliths from *T. monococcum*; bar = 25 µm. **g**, Scanning electron micrograph of trichome base phytoliths from *T. aestivum*; bar = 10 µm. **h**, Light micrograph of dendriform phytolith from *T. aestivum*; bar = 25 µm. **i**, Scanning electron micrograph of dendriform phytolith from *T. aestivum*; bar = 10 µm.

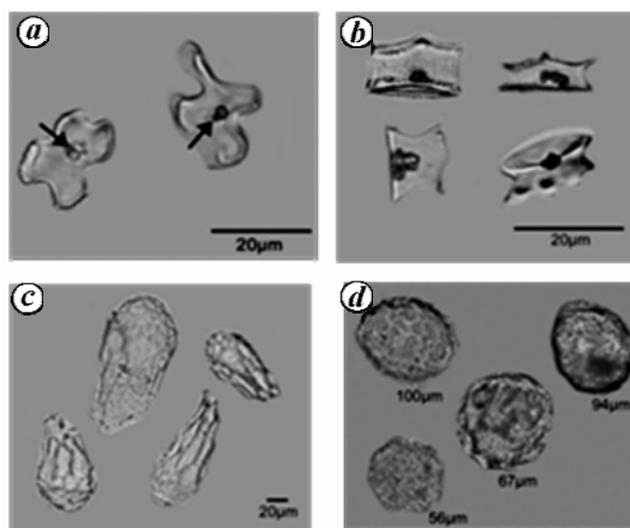


Figure 3. Light micrograph of dendriform phytolith from (a) maize leaves, (b) maize cobs, (c) domesticated squash species *Cucurbita moschata* and (d) *Cucurbita maxima*⁴³.

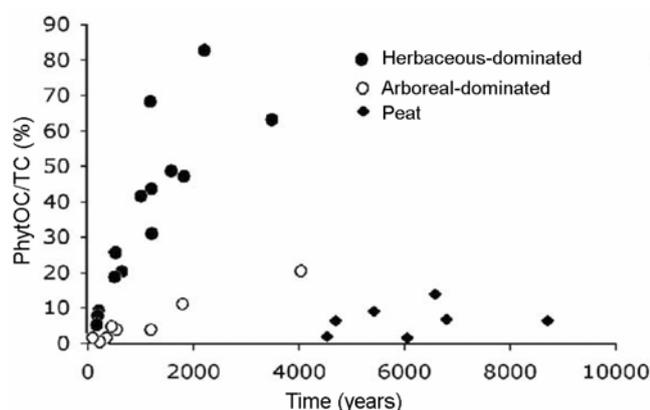
Table 2. SiO₂ concentration, accumulation and distribution in different plant parts of rice⁵⁸

Plant part	SiO ₂ concentration (% dry wt)	SiO ₂ accumulation (g per plant)	SiO ₂ distribution (% total silica)
Root	4.98 ± 0.84	0.171	3.41
Stem	8.30 ± 1.17	0.686	13.67
Leaf	21.61 ± 1.86	3.290	65.56
Husk	23.22 ± 0.29	0.863	17.20
Grain	0.11 ± 0.01	0.008	0.16

Table 3. Si-phytolith content, carbon content of phytolith, phytolith occluded carbon (PhytOC) content and yield of sugarcane varieties and PhytOC yield in carbon dioxide equivalents (e-CO₂) per hectare per year (for new (N) and ratoon (R) plantations)⁶

Sugarcane cultivar	Phytolith content of plant material (%)	Carbon content of isolated phytoliths (%)	PhytOC content of dry plant material (%)	PhytOC yield (kg ha ⁻¹ yr ⁻¹)	PhytOC yield* (t e-CO ₂ ha ⁻¹ yr ⁻¹)
N-1	1.6	12.35	0.198	79.04	0.290
N-2	2.6	6.06	0.158	63.02	0.231
R-3	1.9	8.51	0.162	64.68	0.237
R-4	2.2	3.88	0.085	34.14	0.125
N-5	2.5	9.56	0.239	95.60	0.350
R-6	1.9	11.81	0.224	89.76	0.329
R-7	1.5	11.21	0.168	67.26	0.247
N-8	2.0	11.66	0.233	93.28	0.342
R-9	1.3	19.26	0.250	100.15	0.368
N-10	2.2	8.40	0.185	73.92	0.271

*Assuming dry biomass production of sugarcane as 40 t ha⁻¹ yr⁻¹.

**Figure 4.** Phytolith occluded carbon (PhytOC) as a proportion of total carbon (TC) over a time for the Numundo (West New Britain) upland buried soils, and a peat wetland soil dominated by Restionaceae and Cyperaceae species³.

processes has been well documented^{63–73}. The rate of phytolith accumulation in the soil is also affected by factors other than plant species, including soil properties, climate and geomorphology⁵⁷. The quantity of phytoliths in the soil varies from several orders of magnitude at the regional scale⁵⁷ depending upon the type of phytolith containing above-ground biomass. For example, variations in opal yield in plants ranged from 10 kg ha⁻¹ yr⁻¹ in conifer forest of arid New Mexico⁷⁴ to 300 kg ha⁻¹ yr⁻¹ in prairie grassland of temperate Oregon⁷⁵. Although the concentration of phytoliths in the soil generally constitutes up to 3% on a total soil basis⁵⁷, some soil horizons,

particularly the upper layer (5–30 cm) of tropical podsoils of biogenic origin are almost completely composed of siliceous phytoliths⁷⁶.

Estimated annual PhytOC accumulation rates (0.72–0.88 g C m⁻² yr⁻¹) in the tropical and subtropical sites are reported to be similar³. In the case of temperate soils, the average PhytOC accumulation rate was 15 g m⁻² yr⁻¹ (ref. 9). But in similar soils in Ohio, the average carbon content of phytoliths was 2.40% and PhytOC accumulation rate was 0.36 g C m⁻² yr⁻¹ (ref. 9). PhytOC accumulation rates have contributed about 15% and 37% to the estimated global mean long-term soil carbon accumulation rate of 2.4 g C m⁻² yr⁻¹ over the last 10,000 years⁵⁹.

Potential and contribution of PhytOC from agricultural systems

Most of the economically important agricultural plant species, viz. barley, maize, rice, sorghum, sugarcane and wheat are considered to be producers of phytoliths^{77–79}. These agricultural crops contain a significant amount of PhytOC in their straws/stovers with considerable variation within cultivars^{4,6}. Generally, it is assumed that only about 30% of total non-grain biomass produced from these crops finally reaches the soil through residue incorporation, wastes after feeding the animals, animal excreta, farmyard manure in the form of compost and burnt ash.

Table 5 shows estimate of PhytOC contribution from some of the widely cultivated agricultural food crops like rice, wheat, maize, sorghum, barley and sugarcane

RESEARCH ARTICLE

Table 4. Country of origin, accession number, content of phytoliths in dry leaf and stem biomass, PhytOC content, PhytOC content in dry leaf and stem biomass, and estimated PhytOC yield per hectare in t CO₂ equivalents per hectare of wheat⁴

Country of origin	Australian accession number	Phytolith content (%)	PhytOC of phytoliths (%) (sd)	PhytOC of leaf and stem (%)	PhytOC yields t e-CO ₂ ha ⁻¹ yr ⁻¹
Afghanistan	13373	3.86	4.03 (0.33)	0.16	0.012–0.064
Australia	15688	6.06	3.58 (0.20)	0.22	0.017–0.089
Australia	1131	6.97	5.65 (0.77)	0.39	0.030–0.161
Australia	25607	4.76	1.63 (0.66)	0.08	0.006–0.032
Australia	10398	6.38	1.69 (0.05)	0.11	0.008–0.044
Australia	25271	4.17	4.07 (0.11)	0.17	0.013–0.070
Australia	1924	5.34	11.41 (0.61)	0.59	0.046–0.244
Australia	30434	3.68	3.85 (0.15)	0.14	0.011–0.058
Australia	93	6.39	3.01 (0.05)	0.19	0.015–0.079
Canada	7010	5.25	4.13 (0.23)	0.22	0.017–0.089
China	14011	5.37	4.16 (0.15)	0.22	0.017–0.092
China	13905	4.27	2.25 (0.32)	0.10	0.007–0.039
Croatia	4342	4.12	4.66 (0.17)	0.19	0.015–0.081
Ecuador	20775	5.69	1.80 (0.13)	0.10	0.008–0.042
Egypt	12957	7.85	2.53 (0.22)	0.20	0.015–0.081
Ethiopia	13085	5.29	6.51 (0.51)	0.34	0.026–0.141
Former Soviet Union	20438	7.67	1.29 (0.08)	0.10	0.008–0.04
Greece	4287	4.64	12.91 (0.31)	0.60	0.046–0.246
Iran	19143	3.96	2.68 (0.31)	0.11	0.008–0.044
Iran	19157	2.79	4.65 (0.04)	0.13	0.010–0.053
Iran	19161	3.8	4.41 (0.49)	0.16	0.012–0.064
Iraq	19133	4.19	3.17 (0.19)	0.13	0.010–0.054
Italy	483	5.24	6.97 (0.35)	0.37	0.028–0.150
Italy	12227	7.47	4.89 (0.06)	0.37	0.028–0.150
Japan	21846	4.45	2.03 (0.06)	0.09	0.007–0.037
Kenya	11996	5.49	2.84 (0.01)	0.16	0.012–0.064
Lebanon	4203	4.91	3.48 (0.17)	0.17	0.013–0.070
Lebanon	4205	5.41	3.06 (0.07)	0.17	0.013–0.068
Morocco	5080	5.29	3.88 (0.25)	0.21	0.016–0.084
Nepal	15006	7.63	2.12 (0.03)	0.16	0.012–0.066
Nepal	15028	4.83	5.47 (0.36)	0.26	0.020–0.108
Nepal	15022	5.24	3.32 (0.17)	0.17	0.013–0.071
Nepal	15005	6.72	4.42 (0.31)	0.30	0.023–0.122
Nepal	15025	5.24	3.91 (0.39)	0.20	0.016–0.084
Pakistan	17814	4.67	4.17 (0.38)	0.19	0.015–0.083
Pakistan	17737	3.9	5.17 (0.54)	0.20	0.015–0.083
Pakistan	17741	6.2	4.81 (0.28)	0.30	0.023–0.122
Portugal	3180	2.9	8.79 (1.69)	0.25	0.020–0.104
South Africa	7208	4.75	3.46 (0.25)	0.16	0.013–0.067
South Africa	1844	4.54	1.91 (0.00)	0.09	0.007–0.036
Spain	5639	6.44	4.03 (0.38)	0.26	0.020–0.106
Spain	12091	4.22	2.90 (0.24)	0.12	0.009–0.050
Spain	20103	4.37	2.11 (0.10)	0.09	0.007–0.038
Spain	2088	3.07	6.87 (0.53)	0.21	0.016–0.086
Syria	16132	3.41	4.67 (0.48)	0.16	0.012–0.065
Syria	19111	4.85	4.11 (0.25)	0.20	0.015–0.082
Syria	19114	3.68	2.73 (0.15)	0.10	0.008–0.041
Turkey	5567	3.8	3.87 (1.02)	0.15	0.011–0.060
Turkey	19103	2.68	7.28 (1.32)	0.20	0.015–0.080
Turkey	19189	3.08	1.82 (0.05)	0.06	0.004–0.023
Turkey	19182	3.95	4.53 (0.15)	0.18	0.014–0.073
Turkey	19193	4.29	1.90 (0.02)	0.08	0.006–0.033
The United States	130	4.95	4.41 (0.05)	0.22	0.017–0.089

Note: All the species were grown on the same paddock at the Biloela Agricultural Research Station, Queensland, Australia. Representative leaf and stem samples of the wheat cultivars were collected at a growth stage of 11.3 following Feeke's scale.

based on available data on area of cultivation⁸⁰. Phytolith content in the plant biomass and amount of PhytOC that reaches the soil were estimated based on the information

available in the literature^{4–6,38}. The estimate showed that the above-said crops globally produce PhytOC to the tune of 5.08–12.01 mt yr⁻¹, of which 1.52–3.60 mt

Table 5. Estimation of PhytOC production of some widely cultivated agricultural crops of the world

Crop	Area (m ha)	Straw/stover yield (t ha ⁻¹)	Total straw (mt yr ⁻¹)	Phytolith content of straw (%)		Phytolith production (mt yr ⁻¹)		*PhytOC production (mt yr ⁻¹)	
				Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
Rice	153	4.0	612	5.0	15.0	30.60	91.80	1.53	4.59
Wheat	218	3.5	763	3.5	6.0	26.70	45.78	1.33	2.29
Maize	145	6.0	870	2.0	7.0	17.40	60.90	0.87	3.05
Sorghum	44	5.0	220	9.0	12.0	19.80	26.40	0.99	1.32
Sugarcane	16	25.0	400	1.3	2.6	52.00	10.40	0.26	5.20
Barley	56	3.0	168	1.2	3.0	20.10	50.40	0.10	2.52

*Calculated taking average carbon content of phytoliths as 5% (refs 3–6).

Table 6. Estimation of total PhytOC production potential in India

Crop	Area (m ha)	Straw/stover yield (t ha ⁻¹)	Total straw (mt)	Phytolith content of straw (%)		Phytolith production (mt)		*PhytOC production (mt)	
				Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
Rice	44.0	3.0	132.0	5.0	15.0	6.60	19.80	0.330	0.990
Wheat	28.0	4.0	112.0	3.5	6.0	3.92	67.20	0.196	0.336
Maize	8.4	5.0	42.0	2.0	7.0	0.84	29.40	0.042	0.147
Sorghum	9.2	6.0	55.2	9.0	12.0	4.97	66.24	0.248	0.331
Sugarcane	4.3	20.0	86.0	1.3	2.6	1.12	22.36	0.056	0.112
Barley	0.8	4.0	3.2	1.2	3.0	0.04	0.10	0.002	0.005

*Calculated taking average carbon content of phytoliths as 5% (refs 3–6).

PhytOC accumulates in the soil every year. Further, inclusion of high PhytOC-yielding cultivars in agricultural systems may contribute about 2.08 mt C yr⁻¹ to the soil⁶. Thus, it contributes substantially to the soil carbon stock.

In India, the major cereal crops grown are rice, wheat, maize and sorghum, and in many parts of the country these crops are cultivated during two or three seasons in a year. The area under cultivation of rice, wheat, maize, sorghum, sugarcane and barley in India is 44, 28, 8.4, 9.2, 4.2 and 0.8 m ha respectively⁸¹. Considering the reported range of phytolith content and average 5% carbon content of phytolith, total phytolith and PhytOC yields for these crops are approximately 17.48 and 0.87 mt respectively (Table 6). At the same time if we take maximum phytolith content for these crops, the values are 38.41 mt of total phytoliths and 1.92 mt of PhytOC respectively (Table 6). Thus, by replacing low PhytOC yielding cultivars with high PhytOC yielding cultivars, 1.05 mt of additional PhytOC production can be enhanced annually.

Fate of PhytOC and its management in soil

PhytOC is a stable inert carbon fraction which remains in the soil for a long period. But it is transported to different places by wind, water, bioturbation and other mechanical means. However, the biochemical change of this fraction, particularly microbial oxidation, is very low or may not even take place. There are evidences that have revealed that PhytOC is not affected by forest fire, or biochemical

changes that occur in the intestine of mammals while it passes through an animal's stomach during digestion. There are many reports on the translocation of this carbon fraction within the soil. Alexandre *et al.*⁸² reported translocation to a depth of 2.2 m in a ferrallitic soil, with a slight accumulation in an impermeable clay layer at 1.3–1.4 m. Humphreys *et al.*⁸³ attributed the distribution pattern in Podzol mainly to translocation with percolating water. In contrast, Piperno⁴³ pointed out that the magnitude of transport is probably minimal because phytoliths occur commonly only in the upper part of recent soils and their concentration usually decreases in B horizons. The main factor which is responsible for the translocation of PhytOC is its size and shape. Larger sized fractions are mainly remains in the upper layer of the soil⁸⁴. Indeed, the diameter of phytoliths ranges between 5 and 50 µm (equal to the size of silt fractions in the soil). Although silt particles are less mobile than clay particles, the downward translocation of phytolith in the soil has been reported by several workers. Thus, PhytOC is relatively mobile in the soil.

Several soil processes and soil characteristics affect the phytolith distribution in a soil profile other than direct translocation mechanisms. These include the availability of macropore channels, the intensity of phytolith aggregation with clay particles, organic substances and oxides, and phytolith dissolution. A potential key determinant of phytolith transport is soil structure, in particular, continuity of macropore channels⁸⁵. Field experiment on phytolith transport provided direct evidence for significant

downward translocation in a loamy sand (Cambisol) and a silty loam (Luvisol) in southern Germany⁸⁶. The mean travel distance after one year was 3.99 ± 1.21 cm in the Cambisol and 3.86 ± 0.56 cm in the Luvisol. About 50% of the phytoliths were recovered below 5 cm depth in both soils⁸⁶. Transport in intact soil was significantly faster than in packed sand, indicating a crucial role of continuous macropores in transport efficiency.

It was estimated that conversion of cultivated agricultural land to either forest or grasslands contributes about $33.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ (ref. 1) and switching from conventional to no tillage practices resulted in additional carbon sequestered by $50.7 \text{ g C m}^{-2} \text{ yr}^{-1}$ (ref. 87). Carbon sequestration benefits provided by continuous cropping and changes in tillage practices can be further enhanced through PhytOC accumulation in the soil by growing high PhytOC-yielding cultivars.

Conclusions and future perspectives

To sum up, the opportunity exists to enhance both short- and long-term carbon sequestration by cultivation of high PhytOC-yielding plant species of agricultural crops. The carbon sequestration potential of sugarcane varieties ranged from 0.12 to $0.66 \text{ t e-CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$. Therefore, preference of high PhytOC-yielding variety over low PhytOC-yielding variety results in a net increase of $0.54 \text{ t e-CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ of carbon securely sequestered in phytoliths. Phytolith production may vary depending upon the cultivars, which in turn depend on environmental and management conditions. All the phytolith produced in plants may not reach the soil. There may be several factors that control phytolith accretion in the soil. They are crop factors like crop species and age, parts of the plant it accumulated, phytolith content, size and shape of the phytolith and amount of crop residue that reaches the soil, and soil factors like structure, particularly macropore channels, texture, clay content, soil water and microbial communities and its activity in the soil. Hence, PhytOC produced in the plants species under a specific environmental and management situation and the amount that reaches the soil should be quantified. The processes and properties that affect the stability and the losses of PhytOC from the soil need to be studied extensively. The potential of PhytOC fraction for increasing soil carbon sequestration in different crop production systems needs to be re-examined.

In future, studies should be mainly focused on the application of breeding and biotechnological tools for identification of the trait that would result in identification of crop cultivars with much greater PhytOC yields. Such a plant-breeding programme would provide growers with even greater opportunities to securely bio-sequester carbon in their crops than that exists at present. Enhancing the potential of PhytOC production and accumulation

in crop species through external application of silica needs to be explored.

1. Post, W. M. and Kwon, K. C., Soil carbon sequestration and land-use change: processes and potential. *Global Change Biol.*, 2000, **6**, 317–327.
2. Skjemstad, J. O., Clarke, P., Taylor, J. A., Oades, J. M. and McClure, S. G., The chemistry and nature of protected carbon in soil. *Aust. J. Soil Sci.*, 1996, **34**, 251–271.
3. Parr, J. F. and Sullivan, L. A., Soil carbon sequestration in phytoliths. *Soil Biol. Biochem.*, 2005, **37**, 117–124.
4. Parr, J. F. and Sullivan, L. A., Phytolith occluded carbon and silica variability in wheat cultivars. *Plant Soil*, 2011, **342**, 165–171.
5. Parr, J. F., Sullivan, L. A., Chen, B., Ye, G. and Zheng, W., Carbon bio-sequestration within the phytoliths of economic bamboo species. *Global Change Biol.*, 2010, **16**, 2661–2667.
6. Parr, J. F., Sullivan, L. A. and Quirk, R., Sugarcane phytoliths: encapsulation and sequestration of a long-lived carbon fraction. *Sugar Tech.*, 2009, **11**, 17–21.
7. Wilding, L. P., Brown, R. E. and Holowaychuk, N., Accessibility and properties of occluded carbon in biogenetic opal. *Soil Sci.*, 1967, **103**, 56–61.
8. Mulholland, S. C. and Prior, C. A., AMS radiocarbon dating of phytoliths. In *MASCA Research Papers in Science and Archaeology* (eds Pearsall, D. M. and Piperno, D. R.), University of Pennsylvania, Philadelphia, 1993, pp. 21–23.
9. Wilding, L. P., Radiocarbon dating of biogenetic opal. *Science*, 1967, **156**, 66–67.
10. Kelly, E. F., Amundson, R. G., Marino, B. D. and Deniro, M. J., Stable isotope ratios of carbon in phytoliths as a quantitative method of monitoring vegetation and climate change. *Quat. Res.*, 1991, **35**, 222–233.
11. Ding, Z. L. and Yang, S. L., C3/C4 vegetation evolution over the last 7.0 million years in the Chinese Loess Plateau: evidence from pedogenic carbonate ¹³C. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 2000, **160**, 291–299.
12. Krull, E. S., Skjemstad, J. O., Graetz, D., Grice, K., Dunning, W., Cook, G. D. and Parr, J. F., ¹³C-depleted charcoal from C3 and C4 grasses and the role of occluded carbon in phytoliths. *Org. Geochem.*, 2003, **34**, 1337–1352.
13. Twiss, P. C., Suess, E. and Smith, R. M., Morphological classification of grass phytoliths. *Soil Sci. Am. Proc.*, 1969, **33**, 109–115.
14. Ellis, R. P., A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. *Bothalia*, 1979, **12**, 641–671.
15. Nakata, P. A., Advances in our understanding of calcium oxalate crystal formation and function in plants. *Plant Sci.*, 2003, **164**, 901–909.
16. Siever, R. and Scott, R. A., Organic geochemistry of silica. In *Organic Geochemistry* (ed. Berger, I. A.), Pergamon Press, New York, 1963, pp. 579–595.
17. Piperno, D. R., *Phytolith Analysis: An Archaeological and Geological Perspective*, Academic Press, London, 1988.
18. Epstein, E., Silicon. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 1999, **50**, 641–664.
19. Wilding, L. P. and Drees, L. R., Biogenic opal in Ohio soils. *Soil Sci. Soc. Am. Proc.*, 1971, **35**, 1004–1010.
20. Jones, L. H. P. and Milne, A. A., Studies of silica in the oat plant. *Plant Soil*, 1963, **18**, 207–220.
21. Perry, C. C., Williams, R. J. P. and Fry, S. C., Cell wall biosynthesis during silicification of grass hairs. *J. Plant Physiol.*, 1987, **126**, 437–448.
22. Street-Perrott, F. A. and Barker, P. A., Biogenic silica: a neglected component of the coupled global continental biogeochemical cycles of carbon and silicon. *Earth Surf. Process. Landf.*, 2008, **33**, 1436–1457.

23. Kaufman, P. B., Takeoka, Y., Carlson, T. J., Bigelow, W. C., Jones, J. D., Moore, P. H. and Ghosheh, N. S., Studies on silica deposition in sugarcane (*Saccharum* spp.) using scanning electron microscopy, energy dispersive X-ray analysis, neutron activation analysis, and light microscopy. *Phytomorphology*, 1979, **29**, 185–193.
24. Ma, J. F. *et al.*, A silicon transporter in rice. *Nature*, 2006, **440**, 688–691.
25. Namaganda, M., Lye, K. A., Friebe, B. and Heun, M., Leaf anatomical characteristics of Ugandan species of *Festuca* L. (Poaceae). *S. Afr. J. Bot.*, 2009, **75**, 52–59.
26. Ma, J. F. and Yamaji, N., Silicon uptake and accumulation in higher plants. *Trends Plant Sci.*, 2006, **11**, 392–397.
27. Rovner, I., Potential of opal phytoliths for the use of palaeoecological reconstruction. *Quat. Res.*, 1971, **1**, 343–359.
28. Alexandre, A., Meunier, J., Colin, F. and Koud, J., Plant impact on the biogeochemical cycle of silicon and related weathering processes. *Geochim. Cosmochim. Acta*, 1997, **61**, 677–682.
29. Barboni, D., Bonnefille, R., Alexandre, A. and Meunier, J. D., Phytoliths as palaeoenvironmental indicators, West Side Middle Awash Valley, Ethiopia. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 1999, **152**, 87–100.
30. Borrelli, N., Honaine, M. F., Altamirano, S. M. and Osterrietha, M., Calcium and silica biomineralization in leaves of eleven aquatic species of the Pampean Plain, Argentina. *Aquat. Bot.*, 2011, **94**, 29–36.
31. Ge, Y., Jie, D. M., Sun, Y. L. and Liu, H. M., Phytoliths in woody plants from the northern slope of the Changbai Mountain (North-east China), and their implication. *Plant Syst. Evol.*, 2011, **295**, 55–62.
32. Lu, H. and Liu, K., Phytoliths of common grasses in the coastal environments of southeastern USA. *Estuarine Coastal Shelf Sci.*, 2003, **58**, 587–600.
33. Fahmy, A. G., Diversity of lobate phytoliths in grass leaves from the Sahel region, West Tropical Africa: Tribe Paniceae. *Plant Syst. Evol.*, 2008, **270**, 1–23.
34. Saxena, A., Prasad, V., Singh, I. B., Chauhan, M. S. and Hasan, R., On the Holocene record of phytoliths of wild and cultivated rice from Ganga Plain: evidence for rice based agriculture. *Curr. Sci.*, 2006, **90**, 1547–1552.
35. Lu, H., Zhang, J., Wu, N., Liu, K., Xu, D. and Li, Q., Phytoliths analysis for the discrimination of foxtail millet and common millet. *PLoS One*, 2009, **4**, e.4448.
36. Parr, J. F., Dolic, V., Lancaster, G. and Boyd, W. E., A microwave digestion method for the extraction of phytoliths from herbarium specimens. *Rev. Palaeobot. Palynol.*, 2001, **116**, 203–212.
37. Ball, T. B., Gardner, J. S. and Anderson, N., Identifying inflorescence phytoliths from selected species of wheat (*Triticum monococcum*, *T. dicoccon*, *T. dicoccoides* and *T. aestivum*) and barley (*Hordeum vulgare* and *H. spontaneum*) (Gramineae). *Am. J. Bot.*, 1999, **86**, 1615–1623.
38. Piperno, D. R., A comparison and differentiation of phytoliths from maize and wild grasses: use of morphological criteria. *Am. Antiquity*, 1984, **49**, 361–383.
39. Geis, J. W., Biogenic silica in selected species of deciduous angiosperms. *Soil Sci.*, 1973, **116**, 113–130.
40. Runge, R., Opal phytolithe in Pflanzen aus dem humiden und semi-ariden Osten Afrikas und ihre Bedeutung für die Klima- und Vegetationsgeschichte. *Bot. Jahrb. Syst.*, 1996, **118**, 303–363.
41. Pearsall, D., Chandler-Ezell, K. and Chandler Ezell, A., Maize can still be identified using phytoliths: response to Rovner. *J. Archaeol. Sci.*, 2004, **31**, 1029–1038.
42. Pearsall, D., Chandler-Ezell, K. and Chandler-Ezell, A., Identifying maize in neotropical sediments and soils using cob phytoliths. *J. Archaeol. Sci.*, 2003, **30**, 611–627.
43. Piperno, D. R., *Phytoliths: A Comprehensive Guide for an Archaeologists and Paleoecologists*, AltaMira, New York, 2006.
44. Pearsall, D. M., Piperno, D. R., Dinan, E. H., Umlauf, M., Zhao, Z. and Benfer Jr, R. A., Distinguishing rice (*Oryza sativa* Poaceae) from wild *Oryza* species through phytoliths analysis. I: Results of preliminary research. *Econ. Bot.*, 1995, **49**, 183–196.
45. Zhao, Z., Pearsall, D. M., Benfer Jr, R. A. and Piperno, D. R., Distinguishing rice (*Oryza sativa* Poaceae) from wild *Oryza* species through phytoliths analysis. II: Finalized method. *Econ. Bot.*, 1998, **52**, 134–145.
46. Rosen, A. M., Preliminary identification of silica skeletons from Near Eastern archaeological sites: an anatomical approach. In *Phytolith Systematics: Advances in Archaeological and Museum Science* (eds Rapp Jr, G. and Mulholland, S. C.), Plenum Press, New York, 1992, pp. 129–147.
47. Sase, T. and Hosono, M., Phytolith record in soils interstratified with late Quaternary Tephra overlying the eastern region of Towada volcano, Japan. In *Phytoliths: Applications in Earth Sciences and Human History* (eds Meunier, J. D. and Colin, F.), Balkema Publisher, The Netherlands, 2001, pp. 57–71.
48. Iriarte, J., Assessing the feasibility of identifying maize through the analysis of cross-shape size and three-dimensional morphology of phytoliths in the grasslands of southeastern South America. *J. Archaeol. Sci.*, 2003, **30**, 1085–1094.
49. Iriarte, J., Holst, I., Marozzi, O., Listopad, C., Alonso, E., Rinderknecht, A. and Montana, J., Evidence of cultivar adoption and emerging complexity during the Mid-Holocene in La Plata Basin, Uruguay. *Nature*, 2004, **432**, 614–617.
50. Marschner, H., *Mineral Nutrition of Higher Plants*, Academic Press, London, 1995, 2nd edn, p. 889.
51. Sharma, M. and Rao, K. R., Investigations into the occurrence of silica in Indian timbers. *Indian For.*, 1970, **96**, 740–754.
52. Ter Welle, B. J. H., Silica grains in woody plants of the neotropics, especially Surinam. *Leiden Bot. Ser.*, 1976, **3**, 107–142.
53. Bozarth, S. R., Classification of opal phytoliths formed in selected dicotyledons native to the Great Plains. In *Phytolith Systematics: Emerging Issues* (eds Rapp Jr, G. and Mulholland, S. C.), Society for Archaeological Sciences, New York, 1992, pp. 193–214.
54. Brown, D. A., Prospects and limits of a phytolith key for grasses in the central United States. *J. Archaeol. Sci.*, 1984, **11**, 345–368.
55. Krishnan, S., Samson, N. P., Ravichandran, P., Narasimhan, D. and Dayanandan, P., Phytoliths of Indian grasses and their potential use in identification. *Bot. J. Linn. Soc.*, 2000, **132**, 241–252.
56. Mehra, P. N. and Sharma, O. P., Epidermal silica cells in the Cyperaceae. *Bot. Gaz.*, 1965, **126**, 53–58.
57. Drees, L. R., Wilding, L. P., Smeck, N. E. and Senkayi, A. L., Silica in soils: quartz and disordered silica polymorphs. In *Minerals in Soil Environments* (eds Dixon, J. B. and Weed, S. B.), Soil Society of America, Madison, Wisconsin, 1989, pp. 471–552.
58. Sun, L., Wu, L. H., Ding, T. P. and Tain, S. H., Silicon isotope fraction in rice plants, an experimental study on rice growth under hydroponic conditions. *Plant Soil*, 2008, **304**, 291–300.
59. Schlesinger, W. H., Evidence from chronosequence studies for a low carbon storage potential of soils. *Nature*, 1990, **348**, 232–234.
60. Chan, K. Y., Cowie, A., Kelly, G., Singh, B. and Slavich, P., Scoping paper: soil organic carbon sequestration potential for agriculture in NSW. NSW DPI Science and Research Technical Paper, Dept Primary Industries, NSW, 2008, pp. 1–28.
61. Walcott, J., Bruce, S. and Simms, J., Soil carbon for carbon sequestration and trading: a review of issues for agriculture and forestry. Bureau of Rural Sciences, Fisheries and Forestry, Canberra, Australian Government, 2009, pp. 1–33.
62. Wilding, L. P. and Drees, L. R., Contributions of forest opal and associated crystalline phases to fine silt and clay fractions of soils. *Clay Miner.*, 1974, **22**, 295–306.
63. Baker, G., A contrast in the opal phytolith assemblages of two Victorian soils. *Aust. J. Bot.*, 1959, **1**, 88–96.

64. Baker, G., Opal phytoliths and adventitious mineral particles in Wheat dust. Commonwealth Scientific and Industrial Research Organization, Melbourne, 1961.
65. Baker, G., Jones, L. H. P. and Wardrop, I. D., Opal phytoliths and mineral particles in the rumen of sheep. *Aust. J. Agric. Res.*, 1961, **12**, 462–471.
66. Bowdery, D., Phytolith analysis: sheep, diet and fecal material at Ambathala Pastoral Station, Queensland, Australia. In *Plant, People and Places – Recent Studies in Phytolith Analysis* (eds Madella, M. and Débora, Z.), Oxbow, Oxford, 2007.
67. Hart, D. M. and Humphreys, G. S., Plant opal phytoliths: an Australian perspective. *Quat. Australias.*, 1997, **15**, 17–25.
68. Humphreys, G. S., Bioturbation, biofabrics and the biomantle: an example from the Sydney Basin. In *Soil Micromorphology: Studies in Management and Genesis* (eds Ringrose-Voase, A. J. and Humphreys, G. S.), Elsevier, New York, 1994, pp. 421–436.
69. Jones, L. and Handreck, K., Silica in soils, plants and animals. *Adv. Agron.*, 1967, **19**, 107–149.
70. Rovner, I., Downward percolation of phytoliths in stable soils: a non-issue. In *Plant Opal Phytolith Analysis in Archaeology and Palaeoecology* (ed. Rovner, I.), The Phytolitharian, Occasional Papers, Raleigh, 1986, pp. 23–28.
71. Sangster, A. G. and Parry, D. W., Ultrastructure of silica deposits in higher plants. In *Silicon and Siliceous Structures in Biological Systems* (eds Simpson, T. L. and Volcani, B. E.), Springer, New York, 1981, pp. 383–407.
72. Parr, J. F., Effect of fire on phytolith coloration. *Geoarchaeology*, 2006, **21**, 171–185.
73. Pearsall, D. M., *Paleoethnobotany: A Handbook of Procedures*, Academic Press, London, 1989.
74. Norgren, A., Opal phytoliths as indicators of soil age and vegetative history. *Abstr. Int.*, 1973, **33**, 3421B.
75. Pease, D. S. and Anderson, J. U., Opal phytoliths in *Bouteloua eriopoda* Torr. roots and soils. *Soil Sci. Soc. Am. Proc.*, 1969, **33**, 321–322.
76. Riquier, J., Les phytoliths de certains sols Tropicaux et des podzols. In 7th Trans International Congress of Soil Science, Madison, Wisconsin, 1960, vol. 4, pp. 425–431.
77. Lanning, F. C., Hopkins, T. L. and Loera, J. C., Silica and ash content and depositional patterns in tissues of mature *Zea mays* L. plants. *Ann. Bot.*, 1980, **45**, 549–554.
78. Piperno, D. and Pearsall, D., Phytoliths in the reproductive structures of maize and teosinte: implications for the study of maize evolution. *J. Archaeol. Sci.*, 1993, **20**, 337–362.
79. Yeo, A. R., Flowers, S. A., Rao, G., Welfare, K., Senanayake, N. and Flowers, T. J., Silicon reduces sodium uptake in rice (*Oryza sativa* L.) in saline conditions and this is accounted for by a reduction in the transpirational bypass flow. *Plant Cell Environ.*, 1999, **22**, 559.
80. FAO datasets on land use, land-use change, agriculture and forestry and their applicability for national greenhouse gas reporting. Food and Agriculture Organization of the United Nations, 2007; <http://faostat.fao.org/site/567/default.aspx>
81. Annual Report, Department of Agriculture and Co-operation, Ministry of Agriculture, Government of India, 2011, p. 107.
82. Alexandre, A., Meunier, J. D., Lézine, A. M., Vincens, A. and Schwartz, D., Phytoliths: indicators of grassland dynamics during the late Holocene in intertropical Africa. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 1997, **136**, 213–229.
83. Humphreys, G. S., Hart, D. M., Simons, N. A. and Field, R. J., Phytoliths as indicator of process in soils. In *Phytolith and Starch Research in the Australian–Pacific–Asian Regions: The State of the Art* (eds Hart, D. M. and Wallis, L. A.). *Terra Australas.*, 2003, **19**, 93–104.
84. Fisher, R. F., Newell Bourne, C. and Fisher, W. F., Opal phytoliths as an indicator of the floristics of prehistoric grasslands. *Geoderma*, 1995, **68**, 243–255.
85. Jiang, G., Noonan, M. J., Buchan, G. D. and Smith, N. P., Transport and deposition of *Bacillus subtilis* through an intact soil column. *Aust. J. Soil Res.*, 2005, **43**, 695–703.
86. Fishkis, O., Ingwersen, J., Lamers, M., Denysenko, D. and Streck, T., Phytolith transport in soil: a field study using fluorescent labeling. *Geoderma*, 2010, **157**, 27–36.
87. West, T. O. and Post, W. M., Soil organic carbon sequestration by tillage and crop rotation: a global data analysis. *Soil Sci. Soc. Am. J.*, 2002, **66**, 1930–1946.

Received 25 July 2011; revised accepted 21 August 2012