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Silicon's organic pool and biological cycle in moso bamboo community of Wuyishan Biosphere Reserve*

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Abstract: Biomineralization of Si by plants into phytolith formation and precipitation of Si into clays during weathering are two important processes of silicon's biogeochemical cycle. As a silicon-accumulating plant, the widely distributed and woody *Phyllostachys heterocycla* var. *pubescens* (moso bamboo) contributes to storing silicon by biomineralization and, thus, prevents eutrophication of nearby waterbodies through silicon's erosion of soil particles.

A study on the organic pool and biological cycle of silicon (Si) of the moso bamboo community was conducted in Wuyishan Biosphere Reserve, China. The results showed that: (1) the standing crop of the moso bamboo community was 13355.4 g/m^2, of which 53.61%, 45.82% and 0.56% are represented by the aboveground and belowground parts of moso bamboos, and the understory plants, respectively; (2) the annual net primary production of the community was 2887.1 g/(m^2·a), among which the aboveground part, belowground part, litterfalls, and other fractions, accounted for 55.86%, 35.30%, 4.50% and 4.34%, respectively; (3) silicon concentration in stem, branch, leaf, base of stem, root, whip of bamboos, and other plants was 0.15%, 0.79%, 3.10%, 4.40%, 7.32%, 1.52% and 1.01%, respectively; (4) the total Si accumulated in the standing crop of moso bamboo community was 448.91 g/m^2, with 99.83% of Si of the total community stored in moso bamboo populations; (5) within moso bamboo community, the annual uptake, retention, and return of Si were 95.75, 68.43, 27.32 g/(m^2·a), respectively; (6) the turnover time of Si, which is the time an average atom of Si remains in the soil before it is recycled into the trees or shrubs, was 16.4 years; (7) the enrichment ratio of Si in the moso bamboo community, which is the ratio of the mean concentration of nutrients in the net primary production to the mean concentration of nutrients in the biomass of a community, was 0.64; and lastly, (8) moso bamboo plants stored about 1.26×10^{10} kg of silicon in the organic pool made up by the moso bamboo forests in the subtropical area of China.

Key words: *Phyllostachys heterocycla* var. *pubescens*, Moso bamboo community, Silicon-accumulating, Silicon biological cycle, Wuyishan Biosphere Reserve
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INTRODUCTION

Silicon (Si), the element in many plant biologists' minds, as we come into an age of research '*in silico*', still is an enigma when it comes to its nutritional role in the higher land plants (Raven, 2003). The element occurs in the soil solution at 0.1~0.6 mol/m^3 as $Si(OH)_4$ (two orders of magnitude higher than the macronutrient phosphorus ($H_2PO_4^-/HPO_4^{2-}$)) (Epstein, 1999). Although silicon is not an essential element for higher plants, it is an important nutrient for phytoplankton and is easily absorbed by terrestrial plants, especially gramineous plants (Li and Lin, 1995; Liu, 1996; Alexandre *et al*., 1997; Raven, 2003; Basile-Doelsch *et al*., 2005). Silicon can improve efficiency of water use and decrease both biotic and abiotic stresses in plants (Epstein, 1994; Liang, 1999; Gao *et al*., 2004), and can also enhance plant tolerance of drought; this is attributed to increased selectivity in ion uptake by plant cells (Liang, 1999). Also Si can help plants recover from wound (Pereira and Felcman, 1998) and can also assist in the fixation and removal of carbon dioxide from the atmosphere

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through its weathering (Berner, 1997; Liese, 2001; Graetz and Skjemstad, 2003; Derry *et al*., 2005). But the continental cycle of silicon is not well known and the attempts to associate Si with metabolic or physiological activities have been inconclusive (Epstein, 1994; Liang, 1999; Basile-Doelsch *et al*., 2005).

Basile-Doelsch *et al*.(2005) suggested that the re-precipitation of quartz plays an important role in the biogeochemical cycle of silicon. Traditionally, two processes that fractionate Si isotopes have been suspected: biomineralization of Si by plants into phytolith formation and precipitation of Si into clays during weathering (Basile-Doelsch *et al*., 2005). Among different plants, the gramineous plants have been classified as silicon-accumulators (Takahashi and Miyake, 1976; Li and Lin, 1995; de Bakker *et al*., 1999). *Phyllostachys heterocycla* (Carr.) Matsum. var. *pubescens* (Mazet) Owhi (moso bamboo), a typical silicon-accumulating plant, is widely distributed in China.

Moso bamboo community is an important forest type dominated by woody and silicon-rich bamboos (Poaceae) and is distributed widely from Taiwan in the east to Sichuan in the west, from Guangdong in the south to Henan in the north, and from plain to mountain (Wu, 1980; Chen, 1984). We proposed that the moso bamboo community is an important organic silicon pool in terrestrial ecosystem. Here we focus on it with case study conducted at one of the central areas of its overall distribution range—Wuyishan Biosphere Reserve.

SITE DESCRIPTION

Wuyishan Biosphere Reserve locates in the northern part of the subtropical province of Fujian in China, covers a total area of 56527 hm^2 (Fig.1). The reserve has been well known for its ecosystem diversity and also its species and genetic richness for plants, insects, birds and reptiles (Li *et al*., 2004). It became a national nature reserve in China in 1979, and was accepted as a MAB Reserve by UNESCO in 1987. Because of its lofty peaks and deep gorges, this area provided habitats for many vegetation types and is characterized by abundant biodiversity (Lin and Ye, 1993).

The study site (27°42′ N, 117°41′ E), Dazhulan in Wuyishan Biosphere Reserve, has mountainous topography, southeast-facing slope of 20°, and altitude of 1100 m (Fig.1). Evergreen broadleaved and moso bamboo forests dominated the natural areas at low altitudes in this subtropical region (Wu, 1980; Lin, 1986).

The moso bamboo (*Phyllostachys heterocycla* var. *pubescens*) community is a natural vegetation dominated by mature moso bamboo plants (i.e., 14~20 cm dbh (diameter breast high), 17.5 m in mean height) with density of 1900 individuals/hm^2. The understory is fairly open, consisting of *Eurya nitida*, *Lindera aggregata*, *Liriope platyphylla*, *Dryopteris fuscipes*, *Alpinia japonica*, *Lonicera japonica*, *Millettia dielsiana*, and the seedlings of *Castanopsis eyrei*, *Cunninghamia lanceolata*, and *Cyclobalanopsis glauca*.

The underlying bedrock is volcanic lava. Soil is

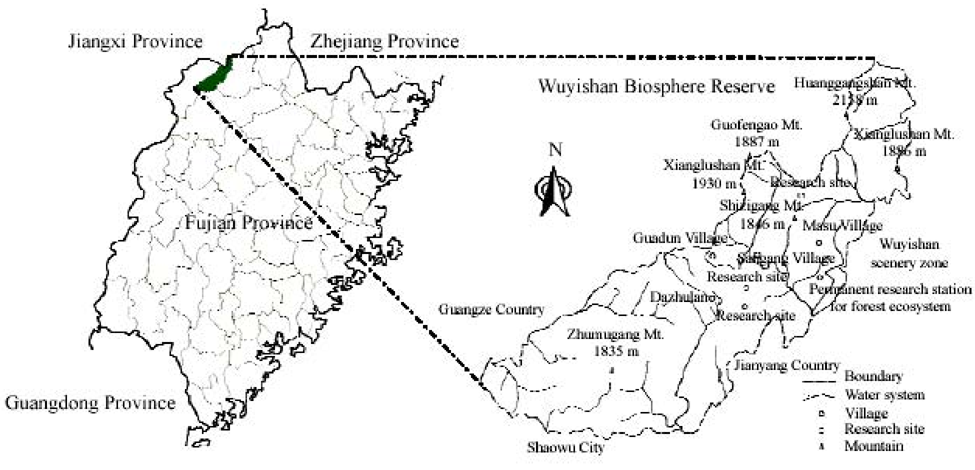

Fig.1 Location of research sites in Wuyishan Biosphere Reserve

characterized as mountain yellow earth, 50~110 cm in depth, and covered with a litter layer of 5 cm consisting of 4.52%~6.43% of soil organic matters with pH of 4.5~5.5.

The climate at the study site is monsoonal and subtropical maritime, with mean annual temperature of 12.8 °C; the monthly averages ranging from 5.6 °C in January to 21.7 °C in July. The annual relative humidity and rainfall are 86.6% and 2678.8 mm. The highest precipitation occurs in June (average of 1143 mm). Solar duration is 1434.3 h and the annual mean wind speed is 0.91 m/s (Li *et al*., 2000).

MATERIALS AND METHODS

Sampling methods

1. Aboveground bamboo biomass

Aboveground bamboo biomass was calculated using forest inventory and regression techniques (Li *et al*., 1993). We established four 10 m×10 m plots at each site and measured the diameter breast high (dbh) of all bamboos and other woody trees that were greater than 2.5 cm in diameter. A total of 8 bamboo trees, i.e., two pieces each of one year growth, three years growth and five years growth with 12 cm (dbh), and one piece of bamboo tree with 10 cm and 14 cm each, were harvested for biomass measurement and for Si measurement in stems, branches, leaves, base of stem, root and whip. These measurements were converted to biomass using bamboo-specific equations derived from our studies in southern Fujian (Li *et al*., 1993). Understory plants and litter were sampled in another four plots measuring 5 m×5 m. Subsamples were collected from homogenized component samples to determine the total dry mass at 70 °C.

2. Root biomass

Root and whip biomass were collected at every 10 cm interval of soil layer within a total depth of 110 cm in four random plots measuring 1 m×1 m in each sampling plot (Li *et al*., 1993). Soil and root weights were measured as the subsamples were collected. Root materials were separated and washed. All roots and whips samples measuring <2 mm, 2~5 mm, >5 mm diameter were collected and separated into live and dead fractions based on visual identification.

3. Net primary productivity (NPP)

We calculated NPP by the increases in biomass plus the litter production, sheaths, production of understory plants and dead shoots (Li *et al*., 1993).

The increment of living bamboo plant biomass was converted to NPP using bamboo-specific equations derived from our studies in south Fujian (Li *et al*., 1993).

Litterfall was collected at 10 d intervals in 20 traps that measured 1 m×1 m in size, randomly placed on the forest floor. The biomass increment for bamboo and the understory plants was calculated with species-specific equations (Li *et al*., 1993). The weight of masses of living and dead roots was taken from the core samples of soil removed from the four plots at every 10 cm interval.

Measurements of dead shoots were obtained in April from four random 5 m×5 m plots. These samples were oven dried at 70 °C to obtain a consistent dry weight. Biomass of the understory plants was estimated by harvesting seasonally also from another 4 random plots measuring 5 m×5 m.

4. Si content measurement

Each sample obtained for Si measurement was made up of about 250 g of composite plant materials consisting of the harvested uniform bamboos, litterfall, dead shoots and understory plants. All samples were dried at 70 °C and weighed to determine the mass per area (MA). Si content was measured by gravimetric method (Nayar *et al*., 1977).

Calculation

The calculation of turnover time, which is the average time the nutrient remains in the soil before it is recycled into the trees or shrubs, was achieved by the rate of the nutrients accumulating in the standing crop of a community and the mass of nutrients by annual return (Woodwell *et al*., 1975).

The enrichment ratio of nutrients refers to the ratio of the mean concentration of nutrients in the net primary production to the mean concentration of nutrients in the biomass of a community (Woodwell *et al*., 1975).

RESULTS

Biomass and productivity in moso bamboo community

1. Biomass and standing crop of moso bamboo

community

The standing crop of the moso bamboo community was 13355.4 g/m^2, of which, the aboveground part of the moso bamboo biomass was 7160 g/m^2, representing 53.61%; the underground part of moso bamboo was 6120 g/m^2, representing 45.82%; and understory plants was 75.4 g/m^2, representing only 0.56% (Fig.2).

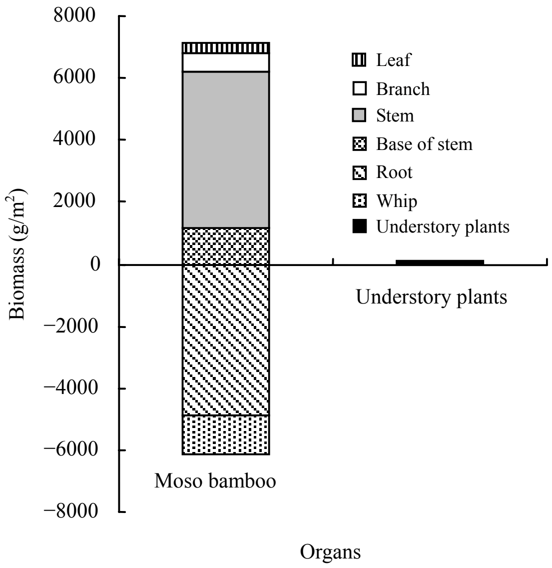

Fig.2 Biomass of moso bamboo community in Wuyishan Biosphere Reserve

2. Productivity of moso bamboo community

The annual net primary production of the moso bamboo community was calculated to be 2887.1 g/(m^2·a), in which, the aboveground part of moso bamboo plants contributed 55.86%, the belowground part, 35.30%, litterfalls, 4.50%, and other fractions, 4.34% (Table 1).

Silicon content and storage in moso bamboo community

1. Silicon content in the biomass

The silicon concentration in stem, branch, leaf, base of stem, root, and whip of bamboos and other plants were calculated to be 0.15%, 0.79%, 3.10%, 4.40%, 7.32%, 1.52% and 1.01% respectively (Fig.3).

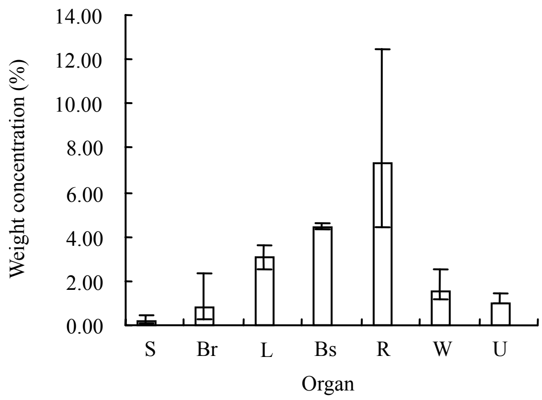

Fig.3 Concentration of silicon in different organs of moso bamboo community in Wuyishan Biosphere Reserve
S: Stem; Br: Branch; L: Leaf; Bs: Base of stem; R: Root; W: Whip; U: Understory plants

2. Silicon storage in moso bamboo community

Silicon mainly stored in roots compared to other organs of bamboos (Fig.4). The amount of Si stored in bamboos accounted for 99.83% of the total silicon accumulated to 448.91 g/m^2 in the moso bamboo community. In the bamboo plants, 79.41% is stored in root, and 11.08% in stem.

Retention, return and uptake of silicon in moso bamboo community

In the moso bamboo community, silicon

Table 1 Annual net primary production of moso bamboo community in Wuyishan Biosphere Reserve

Fraction	Annual net primary production (g/(m^2·a))	Percentage to total (%)
Aboveground part of moso bamboo	1612.81	55.86
Underground part of moso bamboo	1079.25	35.30
Understory plants	75.40	2.61
Litterfalls of moso bamboo	129.89	4.50
Dead bamboo shoots	20.15	0.70
Sheaths of bamboo shoots	29.60	1.03
Total annual net primary production	2887.10	100.00

retention was 68.43 g/(m^2·a) (Table 2), return was 27.32 g/(m^2·a) (Table 3) and uptake was 95.75 g/(m^2·a).

As indicated in Tables 2 and 3, 27.32 g/(m^2·a) (33.37% of silicon absorbed by moso bamboo community) are returned to the soil.

Turnover time and enrichment ratio of Si in moso bamboo community

For the Si element in moso bamboo community of Wuyishan Biosphere Reserve, the turnover time was 16.4 years, and the enrichment ratio was 0.640. This means that Si does not accumulate long in the moso bamboo community.

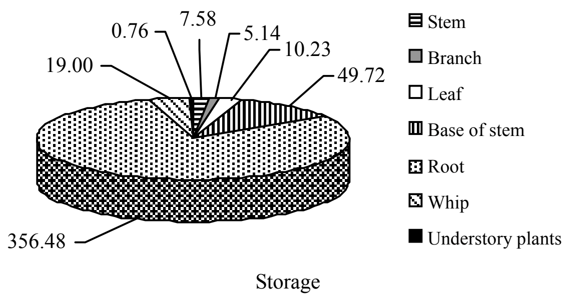

Fig.4 The storage (g/m^2) of silicon in different organs of moso bamboo in Wuyishan Biosphere Reserve

DISCUSSION

Biomass and productivity of moso bamboo community

Comparing the biomass and NPP of moso bamboo communities obtained from different areas in China (Table 4), we can notice that the biomass changes significantly in different places due to the management and temperature factors. The higher standing crop calculation at Yixing, Jiangsu (Zhou, 1987), Fenghua, Zhejiang (Wen, 1990) and Chishui, Guizhou (Wu, 1983) is due to better management. At the center of the distribution range of moso bamboo communities, the amount of biomass changed from 12012 to 18240 g/m^2 due to good management practices (Huang *et al*., 1993). In the periphery of its

Table 2 Annual retention of Si in moso bamboo community

Item	Stem	Branch	Leaf	Base of stem	Whip	Root	Understory plants	Total
Production (g/(m^2·a))	1794.34	250.18	355.29	410.29	344.14	575.72	75.40	3805.36
Concentration of Si (%)	0.15	0.79	3.10	4.40	7.32	1.52	1.01	–
Si-accumulating (g/(m^2·a))	2.69	1.98	11.01	18.05	25.19	8.75	0.76	68.43

Table 3 Annual return of Si in moso bamboo community

Item	Leaf	Branch	Understory plants	Dead shoots	Bamboo sheaths	Dead root	Cut bamboo	Total
Production (g/(m^2·a))	111.97	7.01	10.91	20.15	29.60	181.23	2124.90	2485.77
Concentration of Si (%)	7.36	0.79	1.01	1.09	9.37	4.52	0.36	–
Si-accumulating (g/(m^2·a))	8.25	0.06	0.11	0.22	2.77	8.19	7.72	27.32

Table 4 Biomass and primary productivity of moso bamboo communities in different places in China

Site	Location	Biomass (g/m^2)	NPP (g/(m^2·a))	Cited
Yixing, Jiangsu	31°19′ N, 119°38′ E	27051	–	Zhou, 1987
Fuyang, Zhejiang	30°4′ N, 119°55′ E	18240	2252	Huang *et al*., 1993
Fenghua, Zhejiang	29°37′ N, 121°20′ E	21609	2701.5	Wen, 1990
Chishui, Guizhou	28°33′ N, 105°43′ E	26538	–	Wu, 1983
Wuyishan, Fujian	27°42′ N, 117°41′ E	13355.4	2887.1	This paper
Yongchun, Fujian	25°27′ N, 117°40′ E	6475	–	Peng *et al*., 2002
Hubeliao, Fujian	24°56′ N, 117°14′ E	8289	2146.7	Li *et al*., 1993
Chiton, Taiwan	23°39′ N, 120°48′ E	5545 (aboveground)	1110 (aboveground)	Wang, 1981
Mean*	–	17365	2499	–

*Not including the data from Taiwan

distribution, the calculated standing crop was as low as 6475~8289 g/m^2 (Peng *et al*., 2002; Li *et al*., 1993) due to the temperature, or other factors.

Moso bamboo is a widely distributed plant in China. Other works on this plant community conducted in Guangxi, Hubei and other areas focus on its structure or nutrition diagnosis (Nie, 1992; Chen *et al*., 2004). The productivity of the moso bamboo community varied from 2146 to 2887 g/(m^2·a) in northern area. We think that this is affected mainly by temperature.

The annual productivity of moso bamboo community of Wuyishan Biosphere Reserve was higher than some bamboo communities occurring elsewhere, but due to the relatively poor management, the biomass measurement is still lower than that reported from areas such as Yixing in Jiangsu Province, and Fenghua in Zhejiang Province. This means that in northern Fujian, there is a potential to improve on the management and enhance its biomass production.

In comparison, the moso bamboo community productivity is still higher than that reported for the evergreen broadleaved community (about 1382~1922 g/(m^2·a)) in the same subtropical zone (Dang and Wu, 1994; Lin *et al*., 1996; Sun, 2005). This means that the moso bamboo community is a good sustainable forest to have in the China countryside.

Concentration and storage of Si in moso bamboo community

The results of our study showed that the silicon concentration in organs of moso bamboo plants ranges from 0.15% to 7.32%. In a similar study on moso bamboo community in Asia, the silicon concentration ranges from 0.10% to 7.6% in various organs of moso bamboo plants (Takahashi *et al*., 1981; Huang, 1983; Chen, 1984; Lux *et al*., 2003). In the organs of other bamboo plants, *Pleioblastus amarus* and *Phyllostachys praecox* f. *preveynalis*, it ranges from 1.10% to 6.43% (Jiang and Yu, 2000; Liu *et al*., 2004). In the stem of *Spartina anglica*, the silicon concentration ranges between 0.35% and 1.17% (de Bakker *et al*., 1999). Most researchers agree that the content of silicon is higher in gramineous plants than in non-gramineous plants.

Our study showed further that the amount of silicon stored in the moso bamboo community of the Wuyishan Biosphere Reserve reaches to 448.15 g/m^2. This may explain why the growth of moso bamboo community is better here in the central area of the range of this type of community when compared to the same bamboo community growing at the southern periphery of the range where the silicon contents of the bamboo community is a low 70.03 g/m^2 (Li and Lin, 1995).

Usually, silicon concentration in non-gramineous plants is lower than 2% (Lu and Wu, 1991; de Bakker *et al*., 1999). Silicon is an important nutrient for gramineous pasture plants, gramineous crops and bamboo plants. Abundant supply of SiO_2 can increase therefore the production of these plants substantially, and increase also their resistance to injury by diseases (Winslow *et al*., 1997; Li *et al*., 1998a; Xu *et al*., 2004).

This research showed that Si is important in moso bamboo community. Its concentration and deposition in the bamboos is much higher than those of other nutrient elements. The Ca storage in some tropical forests are reported to be as high as 6.8~11.3 g/m^2 in the aboveground part (Jiang and Lu, 1991), and in some subtropical evergreen broadleaved forests, it is reported to be as high as 103.0~201.9 g/m^2 (Li *et al*., 1998b; Liu e*t al*., 1995), but in moso bamboo community the amount of Ca storage is as low as 5.84~9.83 g/m^2. According to the findings above, we propose, in addition, that in gramineous pasture plants, gramineous crops and bamboo plants, Si may serve as substitute for Ca in some ways.

Biogeochemical cycle of Si in moso bamboo community

Biogeochemical cycle refers to natural processes that recycle nutrients in various chemical forms from the nonliving environment to living organisms, and then back to the nonliving environment (Miller, 2001).

The uptake of silicon in moso bamboo community was shown in this study to be 95.75 g/(m^2·a). The figures are much higher than those reported for N (9.46 g/(m^2·a)), P (0.43 g/(m^2·a)) (Lin *et al*., 1997), Na (0.178 g/(m^2·a)) (Lin *et al*., 1998), Mg (1.87 g/(m^2·a)) (Li *et al*., 1998b), Ca (4.66~19.94 g/(m^2·a)), K (1.80~14.49 g/(m^2·a)) (Sun, 2005) in broadleaved forests in the same subtropical zone. In the case of silicon, 74.98% of which is shown to be retained in the bamboo plants, while the remaining portion in its organic form is returned to the soil. This means that moso bamboo community can efficiently take up and accumulate silicon from arid soil and use it to support its growth in height; thus, the moso bamboo community contributes to prevent silicon erosion greatly.

Our study also showed that silicon was not recycled and accumulated further in the moso bamboo community of Wuyishan Biosphere Reserve, probably because the community is located inside the nature reserve and is being protected; so the old individual bamboo trees are not harvested. In other moso bamboo communities elsewhere, it is advisable to continue to remove the old bamboo trees in order to help recycle this element by absorbing it from the soil.

Estimation of Si accumulation in organic pool by moso bamboo community in China

Si accumulated in leaves and roots represents a huge biological pool of Si in area covered with bamboo vegetation. It has been demonstrated that a mat of fine roots developed by the bamboo community serves as an efficient nutrient recovery mechanism by minimizing the loss brought about by leaching to the subsoil in tropical forests (Stark and Jordan, 1978). Moreover, deeply penetrated bamboo roots (up to a depth of 75 cm) are thought to constitute a 'nutrient pump' that recovers nutrients from the lower part of the soil horizon (Christanty *et al.*, 1997; Hu *et al.*, 1994).

According to this research, at the center of the range of moso bamboo forests, 3754.8 kg of biogenic Si is present in soil per hm^2. Take the whole distribution of bamboo forests in China, the moso bamboo forests, with coverage area of over 2.8×10^6 hm^2 throughout the subtropical region (Huang and Zhang, 1992), can store about 1.26×10^{10} kg silicon in the organic pool. This shows that the moso bamboo plants contribute greatly to the storing of silicon by the biomineralization process. This may prevent eutrophication of nearby waterbodies through the growth of diatoms brought by soil erosion.

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