



# Plant impact on the coupled terrestrial biogeochemical cycles of silicon and carbon: Implications for biogeochemical carbon sequestration

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## ABSTRACT

The coupled terrestrial biogeochemical cycles of silicon (Si) and carbon (C) that are driven by plant action play a crucial role in the regulation of atmospheric CO<sub>2</sub>. Generally, the processes involved in the coupled cycles of Si and C include plant-enhanced silicate weathering, phytolith formation and solubilization, secondary aluminosilicate accumulation, phytolith occlusion of C as well as physico-chemical protection of organic C in soils. There is increasing evidence of biological pumping of Si in terrestrial ecosystems, suggesting that complex feedbacks exist amongst the processes within the coupled Si and C cycles. Recent advances in the coupled Si and C cycles offer promising new possibilities for enhancing atmospheric CO<sub>2</sub> sequestration. Organic mulching, rock powder amendment, cultivating Si-accumulating plants and partial plant harvesting are potential measures that may allow for long-term manipulation and biogeochemical sequestration of atmospheric CO<sub>2</sub> in soil–plant systems.

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Abbreviations: SOC, soil organic C; PhytOC, phytolith-occluded C; SAS, secondary aluminosilicates; PPOC, physico-chemically protected organic C; BSi, biogenic Si; DSi, dissolved Si; ANPP, aboveground net primary productivity.

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## 1. Introduction

The rapid increase in atmospheric CO<sub>2</sub> and global surface temperature since the advent of the Industrial Revolution has motivated much scientific research into the relationship between the terrestrial C cycle and other geochemical cycles (Richter et al., 1999; Falkowski et al., 2000; Luyssaert et al., 2008; Street-Perrott and Barker, 2008; Janssens and Luyssaert, 2009; Smith and Fang, 2010). Silicon (Si), the second-most abundant element of the Earth's surface, is usually coupled with C in many terrestrial geochemical processes that occur at different time-scales. It therefore has a crucial role in the regulation of atmospheric CO<sub>2</sub> (Street-Perrott and Barker, 2008; Li et al., 2011). The physical and chemical protection of organic C by newly-formed secondary aluminosilicate minerals within soil profiles is an example of the coupling of the terrestrial geochemical cycles of C and Si in terms of a glacial-interglacial time-scale (Torn et al., 1997). In geological time-scales ( $\geq 10^6$  years) the cycles are coupled by other mechanisms, which include the drawdown of atmospheric CO<sub>2</sub> with chemical weathering of Ca and Mg-silicate minerals in continental rocks (Gaillardet et al., 1999).

Dissolved silicon (DSi) within the soil environment, that is in the form of H<sub>4</sub>SiO<sub>4</sub> or Si(OH)<sub>4</sub>, is readily taken up by plants and plays an important role in plant growth, mineral nutrition, mechanical strength and improves resistance to fungal disease, herbivory and adverse environmental conditions (Epstein, 1994; Marschner, 1995). The manner in which plants are involved in Si and C use makes them major components of the global Si and C cycles (Serna and Fenoll, 2003). A large amount of research has focused on understanding the exact role of terrestrial plants in the coupled terrestrial biogeochemical Si and C cycles (Serna and Fenoll, 2003) and some studies have provided evidence of plants accelerating silicate weathering and CO<sub>2</sub> consumption (Alexandre et al., 1997; Kelly et al., 1998; Moulton et al., 2000; Hinsinger et al., 2001; Song et al., 2011). Recent studies have emphasized the importance of phytolith-occluded C (PhytOC) in the coupled terrestrial biogeochemical cycles of C and Si. Opal phytoliths are formed within tissues of Si-accumulating plants as a result of amorphous hydrated silica deposition. Silicon-accumulating plants, such as grasses, sedges, palms, certain temperate deciduous trees and conifers, may contain up to 5.8% PhytOC (Parr and Sullivan, 2005; Street-Perrott and Barker, 2008; Parr et al., 2010; Zuo and Lü, 2011). Other studies have revealed that plant activity enriches the upper part of soil profiles with inorganic elements used during growth (e.g., Si, K, Ca, Mg). The phenomenon has been termed “nutrient uplift”, “element translocation” or “biological pumping” (Jobbágy and Jackson, 2001; Lucas, 2001; Barré et al., 2009). It may counteract the leaching of these elements from surface soils and also promote the stability or formation of secondary aluminosilicate minerals in upper soil horizons (Barré et al., 2009), thereby increasing the physical and chemical protection capacities of organic C (Torn et al., 1997).

Notwithstanding these significant advances, the complete mechanisms and significance of the coupling between the terrestrial biogeochemical cycles of C and Si on various time-scales is still largely unrecognized (Street-Perrott and Barker, 2008). In this paper, we summarize and review the existing knowledge that couples the biogeochemical Si and C cycles in terrestrial ecosystems at different time scales. In contrast to other reviews mainly concerned with the biogeochemical Si cycle and silicate weathering (e.g., Lucas, 2001; Street-Perrott and Barker, 2008), our specific focus is on plant Si uptake, impact of land use on the Si cycle, and the role that plants play in long-term biogeochemical sequestration of atmospheric CO<sub>2</sub> through coupling with the Si cycle. As weathering and subsequent Si cycling in ecosystems are the two main controlling processes of coupled biogeochemical Si and C cycles (Alexandre et al., 1997; Street-Perrott and Barker, 2008; Song et al., 2011), we first consider the overall role of plants in enhancing Si release and atmospheric CO<sub>2</sub> consumption during silicate weathering. Then, we briefly review the effects of plants

on dynamics of phytolith formation and the occlusion of C within these phytoliths, and also discuss plant impact on secondary aluminosilicate (SAS) accumulation and physico-chemical protected organic C (PPOC) in soils. In addition, we investigate how integrating these mechanisms within the context of terrestrial ecosystems suggests that specific manipulations may promote long-term biogeochemical sequestration of atmospheric CO<sub>2</sub> through the Si cycle. To conclude, we introduce new tools for studying the biogeochemical Si cycle.

## 2. Plant Si uptake and impact of land use on Si cycle

Plants take up Si from soil solution as uncharged monosilicic acid in the form of H<sub>4</sub>SiO<sub>4</sub> or Si(OH)<sub>4</sub> (Epstein, 1994; Marschner, 1995). However, the uptake varies significantly between plant species and the Si content may vary from 0.1% to more than 10% of the dry matter (Epstein, 1994). Generally, Si accumulation is greater in monocotyledons than in dicotyledons (Epstein, 1994). Silicon accumulation is high in Poaceae, Equisetaceae and Cyperaceae (4%), moderate in Cucurbitales, Urticales and Commelinaceae (2 to 4%) and low in most other species (Epstein, 1994). This strongly suggests that differences in plant types and related recent changes in land use/land cover (LULC) significantly influence the relative contribution of different coupling mechanisms of Si and C due to its effects on plant uptake of Si.

### 2.1. Active vs. passive uptake of Si in plants

Silicon uptake by plants may be either passive or active. A passive mechanism corresponds to a Si uptake that is proportional to mass flow. For a passive Si uptake, under the same Si concentration in soil solution, variations in Si accumulation between plant species is a function of transpiration rates (Ding et al., 2005, 2008; Cornelis et al., 2011). However, an anomaly does occur with passive Si uptake, as the Si content in xylem is frequently higher than that found in the soil solution (Meunier et al., 2008).

By contrast, the Si content is larger than that predicted by mass flow when an active Si uptake mechanism is utilized (Casey et al., 2003; Rains et al., 2006; Cornelis et al., 2011). Ma et al. (2006, 2007) have described various external influx (LSi1) and internal efflux (LSi2) Si transporters in rice roots. Their location within rice roots allows for effective uptake and transcellular transport of Si in rice roots. Other transporters (LSi6—in the leaf sheath and leaf blades) are responsible for the transport of Si out of the xylem and affect leaf Si distribution in rice shoots (Yamaji et al., 2008). Differences in Si accumulation among plants with an active Si uptake usually results from density differences of Si transporters in the plant roots (low-Si genes: Lsi1 and Lsi2) and shoots (Lsi6) (Mitani and Ma, 2005; Ma et al., 2006, 2007; Yamaji et al., 2008).

Although the passive vs. active uptake mechanism of Si is well studied in rice, further research into the mechanisms of Si transport within other plant types is still necessary. Furthermore, at a global scale, it remains unclear whether plants that actively pump Si through their root systems are more important than other more widely distributed plants in the terrestrial Si biogeochemical cycle.

### 2.2. Impact of land use on Si cycle

Changes in LULC on both regional and global scales are significant threats to biodiversity, nutrient cycles, water resources and ecosystem services (Foster and Aber, 2004; Foley et al., 2005; Onderka et al., 2012). Only 21% of indigenous forests remain due to the increase in human population and changes in LULC since the Industrial Revolution (Conley et al., 2008). Considering changes in LULC and the control that terrestrial plants exert on the Si cycle due to differing rates of Si uptake (Fulweiler and Nixon, 2005; Struyf et al., 2010; Vandevenne et al., 2010; Carey and Fulweiler, 2011; Clymans et al., 2011), it is likely that LULC also alters the flux of Si from land to aquatic ecosystems. However, the impact of LULC on Si export from terrestrial to aquatic ecosystems

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