Impacts of silicon on biogeochemical cycles of carbon and nutrients in croplands

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Abstract
Crop harvesting and residue removal from croplands often result in imbalanced biogeochemical cycles of carbon and nutrients in croplands, putting forward an austere challenge to sustainable agricultural production. As a beneficial element, silicon (Si) has multiple eco-physiological functions, which could help crops to acclimatize their unfavorable habitats. Although many studies have reported that the application of Si can alleviate multiple abiotic and biotic stresses and increase biomass accumulation, the effects of Si on carbon immobilization and nutrients uptake into plants in croplands have not yet been explored. This review focused on Si-associated regulation of plant carbon accumulation, lignin biosynthesis, and nutrients uptake, which are important for biogeochemical cycles of carbon and nutrients in croplands. The tradeoff analysis indicates that the supply of bioavailable Si can enhance plant net photosynthetic rate and biomass carbon production (especially root biomass input to soil organic carbon pool), but reduce shoot lignin biosynthesis. Besides, the application of Si could improve uptake of most nutrients under deficient conditions, but restricts excess uptake when they are supplied in surplus amounts. Nevertheless, Si application to crops may enhance the uptake of nitrogen and iron when they are supplied in deficient to luxurious amounts, while potassium uptake enhanced by Si application is often involved in alleviating salt stress and inhibiting excess sodium uptake in plants. More importantly, the amount of Si accumulated in plant positively correlates with nutrients release during the decay of crop biomass, but negatively correlates with straw decomposability due to the reduced lignin synthesis. The Si-mediated plant growth and litter decomposition collectively suggest that Si cycling...
in croplands plays important roles in biogeochemical cycles of carbon and nutrients. Hence, scientific Si management in croplands will be helpful for maintaining sustainable development of agriculture.

**Keywords:** silicon, cropland, biogeochemical cycle, biomass carbon, nutrient

1. Introduction

The land-use conversion of natural ecosystems to croplands usually depletes soil organic carbon pool (Lal 2004), and contributes to approximately 17% of global carbon emission (IPCC 2013). The depletion of soil organic carbon pool in croplands usually causes soil degradation, such as the reduction of water- and nutrient-holding capacity, and thereby adversely impacts crop productivity and global food security (Lal 2004; Canellas et al. 2010). Therefore, carbon cycling in croplands plays crucial roles in influencing climate change and maintaining soil fertility. In order to maintain and sustain agricultural productivity, it is critical to preserve and enhance soil organic carbon storage in croplands, especially in less fertile areas.

Even though not considered as a plant essential element, Si can accumulate in plants and has multiple eco-physiological functions, which helps plant to acclimatize their unfavorable habitats (Ma et al. 2001; Etesami and Jeong 2018). The beneficial effects of Si on plant growth usually play important roles in biogeochemical cycles of carbon and nutrients. For example, Si cycling in plant–soil system often promotes carbon accumulation in plant biomass along with greater gain in crop yield (Detmann et al. 2012; Kang et al. 2016; Marxen et al. 2016; Song et al. 2016a), and affects the components of secondary cell wall by restraining lignin biosynthesis (Hashemi et al. 2010; Suzuki et al. 2012; Yamamoto et al. 2012). The application of Si also mediates nutritional stress by improving nutrient use efficiency and inhibiting excessive nutrient uptake (Ma and Takahashi 1990; Deren 1997; Ma et al. 2001; Cartes et al. 2015).

In addition, increasing Si supply to rice can promote plant nitrate uptake from soils and thus decrease denitrification potential (Song et al. 2017). Therefore, Si management is essential in simultaneously regulating biogeochemical cycles of carbon and nutrients in croplands.

Multiple beneficial effects of Si on plant growth, such as abiotic stress alleviation and biotic stress resistance, have been widely reviewed (Ma 2004; Liang et al. 2007; Zhu and Gong 2014). However, the impacts of Si on biogeochemical cycles of carbon and nutrients have been rarely systematically explored. This review compiles data from peer-reviewed publications to portray recent advances in Si-associated impacts on biogeochemical cycles of carbon and nutrients in croplands. The references the compiled data collected from are listed in Appendix A. Also, implications for Si management in croplands are discussed for sustainable development of agriculture.

2. Biogeochemical silicon cycle in croplands

Silicon constitutes 28.8% of the Earth’s crust by weight and Si content varies from 19.3% in most ultra-basic to 46.5% in acidic rocks (Epstein 1999; Monger and Kelly 2002; Anderson 2007). By contrast, Si content in soils ranges from 0.56% in Histosols and up to 45% in very old Podzols (Skjemstad et al. 1992; Steinmann and Shotyk 1997). Only a small portion of Si in earth system participates in biogeochemical cycles (Conley 2002). The migration of Si from terrestrial solid phases to oceans and organisms mainly occurs in aqueous solution via hydrologic cycles around the planet. The concentration of Si in aqueous solution saturates at 1.67 mmol L$^{-1}$ (in the prevailing form of monosilicic acid at pH below 9.0) and is usually between 0.1 and 0.6 mmol L$^{-1}$ in most soil solutions (Epstein 1994; Cooke and Leishman 2016). The dominant form of Si in soil solutions is monosilicic acid, whose concentration varies with the retention time of capillary water, soil types, and seasons in croplands (Farmer 2005; Sommer et al. 2006). Since hydrothermal conditions across different climate zones have an important influence on weathering intensity and Si availability (Sommer et al. 2006), and the ability of plants in accumulating Si varies widely among plant species (Epstein 1999), the biogeochemical cycles of Si would be considerably divergent and typical across different climate zones and crop types.

The availability of monosilicic acid in soils and the amount of Si accumulated in crops are the predominant factors in biogeochemical Si cycle, because monosilicic acid is the only known form of Si that can be absorbed by and accumulated in plants (Exley 1998). In natural ecosystem, Si cycling in plant–soil system is driven by biological processes, such as root absorption and earthworm ingestion (Bityutskii et al. 2016; Cornelis and Delvaux 2016). Plants constitute a large part of the biogenic Si pool, which is considered as central importance to biogeochemical Si cycle (Bartoli 1985; Liang et al. 2015). Crop harvesting substantially interrupts the replenishment of biogenic Si pool and thus severely interferes in Si cycling in croplands (Vandevenne et al. 2016).
2012; Haynes 2017). For example, it is reported that rice harvest of one growing season could remove averagely 0.62 and 0.25 Mg Si per hectare in the Philippines and Vietnam, respectively (Klotzbücher et al. 2016). It is expected that repeated cropping Si accumulating crops such as rice and sugarcane would deplete the availability of Si for further plant growth in a near future (Ma and Yamaji 2006). Hence, it is necessary to supplement Si to the croplands where soils are Si-deficient in order to sustain agricultural production.

3. Silicon modifies carbon biogeochemical cycle

Although the phytolith-occluded carbon and immobilized CO₂ during silicate weathering are inactive in carbon cycle in croplands (Song et al. 2012, 2016b), carbon immobilized in plant biomass and preserved in soil can be coupled to or influenced by Si cycle in agricultural ecosystems (Song et al. 2014a; Marxen et al. 2016). By contrast, Si-mediated increases of biomass production and straw decomposability (Schaller and Struyf 2013; Marxen et al. 2016) indicate that Si cycling in croplands plays an important role in biogeochemical cycle of carbon. Therefore, elucidating the impacts of Si on plant growth and biomass carbon accumulation is crucial for scientific management of Si in croplands.

3.1. Stimulation of net photosynthetic rate and carbohydrate metabolism

Plant growth and biomass carbon accumulation depend largely on photosynthesis and carbon assimilation. Improvement of Si application in net photosynthesis rate and water use efficiency has been widely confirmed (Song et al. 2006; Detmann et al. 2012; Zhu et al. 2016), while the expression of some key genes related to photosynthesis (e.g., photosynthesis pigment) is increased with exogenous Si application even under unstressed conditions (Song et al. 2014b; Ashfaqe et al. 2017). The feedforward stimulation of Si on net CO₂ assimilation rate fundamentally associates with the enhanced mesophyll conductance, which leads to higher chloroplastic CO₂ concentration and maximum rate of carboxylation (Detmann et al. 2012). In summary, Si accumulation in crops can stimulate and enhance photosynthesis pigments and net photosynthetic rate (Fig. 1). Taken together, Si application in croplands imposes a positive effect on immobilization of atmospheric CO₂ into photo assimilates.

In addition, Si application to crops can promote orchestrating carbohydrate and amino acid remobilization in shoots and roots (Detmann et al. 2012; Zhu et al. 2016). For example, after the application of Si, the content of soluble carbohydrates in leaf of tomato and cucumber is reduced under both drought and salt stresses (Silva et al. 2012; Zhu et al. 2016). In addition, Detmann et al. (2012) found that the contents of sucrose, fructose and glucose in flag leaves of low-silicon mutant rice decreased in response to Si application, while those of several amino acids in flag leaves of wild type rice decreased as well. Many studies have reported that higher silicon accumulation in crops is usually associated with increases in plant biomass and crop yield (Anderson 1991; Kaya et al. 2006; Tuna et al. 2008; Song et al. 2016a). Thus, Si accumulation in crops can stimulate higher rates of photo-assimilates translocation, consequently enhancing carbon sink strength. Therefore, Si accumulation in crops exerts a feedforward effect on carbon immobilization in plant biomass.

3.2. Modulation of lignin biosynthesis

Plant growth under salt stress usually lead to dwarf
phenotype due to excessive lignin biosynthesis (Sánchez-Aguayo et al. 2004; Ortega et al. 2006). Comparatively, Si application to alleviate salt stress can reduce tissue lignification (Hashemi et al. 2010). It is also reported that Si mediation of mechanical stress could reduce the biosynthesis of lignin in tobacco leaves (Hajiboland et al. 2017), while Si deficiency stimulates lignin accumulation in rice (Suzuki et al. 2012; Yamamoto et al. 2012). The concentrations of Si are reported to be negatively correlated with lignin-derived phenols in rice straw and wetland species (Schoelynck et al. 2010; Klotzbücher et al. 2018). Concurrently, the components of organic macromolecule in plant litter, especially cellulose and lignin, are intrinsic factors in plant litter decomposition by contrast with the environmental and biological controls (Schmidt et al. 2011; Wang et al. 2017). These findings indicate that variable Si accumulation in crops affects carbon cycling in croplands by controlling lignin biosynthesis. However, crops differ in their abilities to absorb Si and bioavailable Si varies across different croplands, reflecting heterogeneous effects of Si on lignin biosynthesis and biogeochemical cycle of carbon.

Currently, research on Si-modulated lignin biosynthesis not only spotlights on grass family such as rice (Oryza sativa) and wheat (Triticum aestivum), but also focuses on dicot such as canola (Brassica napus) and tobacco (Nicotiana rustica). Both monocots and dicots show negative correlations between the concentrations of Si and those of lignin in crop straw and leaves, especially under stress conditions (Hashemi et al. 2010; Murozuka et al. 2014; Hajiboland et al. 2017; Klotzbücher et al. 2018). However, the impacts of plant Si fluxes on plant lignification and soil carbon cycle across different crops, soil types, and climate zones have not yet been comprehensively studied. Therefore, Si-modulated lignin contents in crop residue, notably in crop roots, and their contribution to biogeochemical cycle of carbon in croplands need to be clarified in the years to come.

### 3.3. Enhancement of plant biomass carbon accumulation

The application of Si to crops can enhance plant biomass accumulation, including aboveground and belowground biomass and crop yield, especially under stressful conditions (Fig. 2; Tuna et al. 2008; Chen et al. 2011; Li et al. 2018). Compared to the control, Si application averagely increases the whole-plant biomass, shoot biomass, root biomass, and crop yield by 36, 34, 35, and 21%, respectively. Because

![Figure 2](image-url)
Si application enhances Si accumulation in plant biomass, studies on the tradeoff between biomass carbon reduction and Si accumulation indicate that an increase in Si content of plant by 1% averagely causes a reduction of biomass carbon by less than 1% (Neu et al. 2017; Klotzbücher et al. 2018). According to the compiled data set (Appendix B), the mass proportion of the increased Si ranges from 0.01 to 5.87%, with an average of 1.26%. It is suggested that Si application averagely causes a biomass carbon reduction of less than 1.26% in mass proportion of biomass carbon reduction, with a maximum of 5.87%. Because carbon content of biomass is approximately 45% (Schlesinger 1991; Neu et al. 2017; Klotzbücher et al. 2018), Si application averagely increases plant biomass carbon, shoot biomass carbon, and root biomass carbon by 35, 33, and 34% (with a minimum increase of 31, 29, and 30%), respectively. However, these results are mainly derived from pot and hydroponic cultivation. The contribution of Si-mediated biomass increment to plant biomass carbon accumulation in the field conditions needs to be readjusted in the future.

It can be further extrapolated that biogeochemical Si cycles in croplands not only enhance carbon stock in aboveground biomass, but also promote carbon immobilization in belowground biomass. The tradeoff analysis from the compiled data set indicates that Si-mediated increase in shoot biomass carbon and root biomass carbon is unbiased (P>0.05). In addition, it is reported that root biomass contributes more organic carbon to soil organic carbon pool than shoot biomass (Rasse et al. 2005; Jafari 2013). This suggests that enhanced Si supply in soils can increase crop biomass carbon, especially root biomass carbon input to soil organic carbon pool. Therefore, the biogeochemical cycle of Si generally exerts a positive impact on biogeochemical cycle of carbon in croplands, especially under abiotic and biotic stress conditions.

4. Silicon regulates biogeochemical cycles of nutrients

4.1. Regulation of biogeochemical nitrogen cycle

Excessive nitrogen (N) supply to crops often increases pathogen infection and lodging susceptibility (Savary et al. 1995; Wu et al. 2012), because high N accumulated in crops usually elevates the concentration of low molecular weight organic N compounds in leaves (Osuna-Canizalez et al. 1991; Huber et al. 2012). It is reported that Si can counteract the negative effects of excessive N supply on leaf erectness and rice lodging (Idris et al. 1975; Broadley et al. 2012). The beneficial effects of Si on counteracting excessive N supply to crops are probably because high Si accumulation in shoots can suppress N uptake (Islam and Saha 1969; Deren 1997). In addition, Si accumulation in crops can accelerate the transformation of low molecular weight carbohydrates and organic N compounds into high molecular weight compounds (e.g., proteins, starch, and cellulose) (Detmann et al. 2012; Zhu et al. 2016). Hence, the counterweight of Si to the negative effects of excessive N supply is probably through the suppressing of excessive N uptake and decreasing the levels of soluble sugar and organic N compounds in leaves and stems.

More importantly, deficient N supply to crops often results in crop failure, while Si application to crops also can enhance N uptake into the shoots and increase crop yield under deficient and even luxurious soil N conditions (Shen et al. 1992; Guo et al. 2004; Ren et al. 2012). Although N content in the shoots sometimes decreases after Si application (Marxen et al. 2016; Barreto et al. 2017), the reduction of N content mainly attributes to the dilution from Si-mediated enhancement of plant biomass accumulation. However, the contribution of Si-mediated enhancement to crop N uptake and crop yield is far lower than that of application of N fertilizer (Shen et al. 1992; Li and Ren 2001). Besides, the beneficial effects of Si on enhancing crop N uptake is restricted by low phosphorus supply levels (Zhang et al. 2017). Song et al. (2017) recently have reported that high Si supply to rice could promote nitrate uptake into plant, thereby decreasing N₂O emission and soil potential denitrification. Therefore, high Si accumulation in crops can promote biogeochemical cycle of N (such as the transport of N from soil to plant) in croplands.

It is clear that the beneficial effect of Si application on the suppression of excessive N uptake coexists with the improvement of crop N uptake under deficient and luxurious N conditions. On the whole, the observation frequency of Si-mediated increase in crop N content is approximately 70% across the compiled data set (Fig. 3-A), while the observation frequency of Si-mediated improvement of N uptake in the shoots is roughly 90% (Fig. 3-B). Nevertheless, the demanded quantity of nitrogen across various crops (e.g., gramineae and dicots) is extremely discrepant (Gastal and Lemaire 2002). Hence, the suppression of excessive N uptake is not, as a rule, observed with high concentration of N in aboveground and belowground biomass of crops. Because N deficiency and enough N supply are more prevalent than excessive N supply in croplands (Liu et al. 2010), the improvement of Si application plays more important roles in accelerating soil N turnover rate than in protecting crops from the negative effects of excessive N supply.

4.2. Regulation of phosphorus biogeochemical cycle

The application of Si to a hydroponic rice experiment
indicates that high Si supply can decrease plant phosphorus (P) uptake at both medium and high P levels (Ma and Takahashi 1990). In addition, the phenomenon that high Si accumulation in crops can suppress excessive P uptake and decrease shoot P concentrations was also observed recently in field (Hu et al. 2017; Zhang et al. 2017). However, many studies reported that Si application to crops could also increase plant P uptake, especially under P deficient soil conditions (Shi et al. 1996; Marxen et al. 2016; Kostic et al. 2017; Zhang et al. 2017). Predictably, the application of Si to crops can suppress P uptake into the crop shoots under luxurious and excessive P levels but improve plant P absorption under P deficient soil conditions (Fig. 4). Nevertheless, the demanded quantity of P varies largely from gramineous crops to dicotyledonous crops (Otani and Ae 1996; Hua et al. 2016). This may be the reason why Si-mediated suppression and improvement of P uptake coexists at low and medium shoot P concentration levels.

Recently, Hu et al. (2017) have investigated into the mechanisms by which Si suppresses the uptake of excessive P, and found that high Si accumulation in rice shoots can decrease plant P uptake by down-regulating inorganic P transporter gene in the roots. Under P deficient soil conditions, application of Si can enhance plant P uptake by increasing organic acids exudation from roots to activate inorganic P in the rhizosphere and up-regulating inorganic P transporter gene in the roots (Kostic et al. 2017). In addition, increased Si concentration in soils has almost negligible effects on P sorption at the similar sites, especially on organo-mineral surfaces in soils (Cartes et al. 2015). The beneficial effects of Si on modulation of P uptake suggest that the biogeochemical cycle of Si in croplands strongly impacts the biogeochemical cycle of P by regulating plant

![Fig. 3](image-url) The effect of Si application on nitrogen concentration in plant biomass (A) and the frequency distribution of Si-mediated enhancement of nitrogen uptake in the shoots (B). The subscripts of “control” and “+Si” are experimental treatments without and with Si application, respectively. Data are from Appendix A.

![Fig. 4](image-url) The effect of Si application on phosphorus concentration in plant biomass (A) and the frequency distribution of Si-mediated enhancement of phosphorus uptake in the shoots (B). The subscripts of “control” and “+Si” are experimental treatment without and with Si application, respectively. Data are from Appendix A.
4.3. Regulation of potassium biogeochemical cycle

Many studies reported that Si application can enhance plant potassium (K) uptake, especially under salt stress (Tuna et al. 2008; Ashraf et al. 2010; Mehrabanjoubani et al. 2015; Guong et al. 2017). A few studies reported that the application of Si can decrease K concentration in the shoots (Chen et al. 2011; Gao et al. 2011). Such discrepancies indicate that the impact of Si on plant K uptake is not unilateral enhancement from low K concentration to high levels (Fig. 5). Nevertheless, the Si-mediated increases in K uptake are observed much more commonly than Si-mediated decreases in K uptake.

Under K deficient soil conditions, organic acid exudation from roots enhanced by high Si level in plants may be the reason for Si-mediated enhancement of plant K absorption (Kostic et al. 2017). In addition, high Si accumulation in the shoots can enhance the root aquaporin activity and activate K⁺ translocation from root cortex cells to the xylem (Chen et al. 2016). The hydraulic conductance from crop roots to shoots, which is enhanced by the increased K⁺ concentration and the decreased osmotic potential in the xylem, can further alleviate K deficient induction of plant dehydration (Chen et al. 2016). Excluding the dilution effect, the reason for Si-mediated decrease in plant K uptake remains unclear. Nevertheless, Si-mediated enhancement of K uptake will accelerate the turnover rate of soil K pool in croplands, while the suppression of Si on K uptake will improve K use efficiency (Neu et al. 2017; Etesami and Jeong 2018). In conclusion, biogeochemical Si cycle may impose a positive effect on biogeochemical cycle of K in croplands.

4.4. Regulation of biogeochemical cycles of other nutrients

The effects of Si application on nutrients uptake demonstrate parallel results for other nutrients, including calcium (Ca), magnesium (Mg), manganese (Mn), copper (Cu), zinc (Zn), boron (B), and chlorine (Cl). The application of Si can elevate the concentration of these nutrients in crop biomass at low concentration levels but decrease it at high concentration levels (Fig. 6). However, the application of Si can increase the concentration of iron (Fe) in crop biomass even at high concentration levels but somewhat lead to a decrease in iron concentration of crop biomass at medium and low concentration levels. Plant-specific absorption capacities of Fe among different crops and the dilution effect may be the reason for Si-associated Fe increase at a high concentration level (Gonzalo et al. 2013). In total, Si-regulated nutrient absorption for plant elemental homeostasis plays important roles in improving nutritional use efficiency of these nutrients.

Ma and Takahashi (2002) noted that Si accumulating plants often hold low Ca concentrations in plant biomass, and vice versa. In the compiled data set, the application of Si shows a weak and fluctuated influence on the regulation of Ca concentration in crop biomass. Mechanisms of Si-mediated Mg uptake may be similar to Si-mediated Ca uptake by crops. Horst and Marschner (1978) found that the application of Si could increase manganese tolerance of Phaseolus vulgaris through preventing the Mn accumulation in leaf tissues. The concentrations of Mn were slightly suppressed in the bean plant leaves, but considerably suppressed in stems and roots at high Mn levels. By contrast, the application of Si could alleviate Cu toxicity through suppressing Cu concentration in leaves, stems

Fig. 5 The effect of Si application on potassium concentration in plant biomass (A) and the frequency distribution of Si-mediated enhancement of potassium uptake in the shoots (B). The subscripts of “control” and “+Si” are experimental treatments without and with Si application, respectively. Data are from Appendix A.
and roots (Ali et al. 2016). However, the mechanism of Si-mediated B absorption in plant may be similar to Si-mediated regulation of phosphorus uptake. Plant Cl uptake that is mediated by high Si supply may be due to Si-mediated regulation of Cl transporter gene in the roots (Shi et al. 2013). For plant Fe uptake, high Si supply may interact with insoluble iron to form soluble Fe (III)-silica complexes (Pokrovski et al. 2003; Pavlovic et al. 2013), which in turn, can inhibit Fe polymerization in plants and further enhance Fe mobility from rhizosphere to roots. The application of Si to alleviate Zn deficiency is similar to the case of Fe deficiency in soybean (Pascual et al. 2016). Nevertheless, the application of Si to alleviate Mn and Cu deficiency and Zn toxicity needs to be further studied in the future.

![Graphs showing the effects of Si application on calcium, magnesium, iron, manganese, copper, zinc, boron, and chlorine concentration in plant biomass.](image)

Fig. 6 The effects of Si application on calcium, magnesium, iron, manganese, copper, zinc, boron, and chlorine concentration in plant biomass. The subscripts of “control” and “+Si” are experimental treatments without and with Si application, respectively. Data are from Appendix A.
conclusion, the compiled data sets collected from the peer-reviewed publications indicate that biogeochemical Si cycle in croplands plays an important role in regulating macro- and micro-nutrient uptake into crops. This, in turn, exerts multiple impacts on biogeochemical cycles of nutrients in croplands.

5. Implications for silicon management in croplands

In croplands, repeated cropping and continuous application of chemical fertilizer have depleted bioavailable Si in soils (Ma and Yamaji 2006). The deficiency of Si is especially severe in soils where cultivate Si accumulating crops such as rice and sugarcane are grown. As a result, Si fertilizer has been regularly applied to croplands under Si deficient soil conditions to maintain sustainable crop yields. Although plant nutrient use strategy varies with the ability of plant to adsorb Si (Fig. 7), more Si supply can also help crops to resist multiple abiotic and biotic stresses, consequently resulting in enhancing plants growth (Detmann et al. 2012; Li

![Fig. 7](image-url) The relationship between Si and nutrients in plants. Data contain both the control and Si treatments. Data are from Appendix A.
Therefore, the application of Si to crops can not only enhance plant resistance to abiotic and biotic stresses (Tuna et al. 2008; Zhu and Gong 2014; Song et al. 2016a), but also promote plant biomass accumulation and regulate element uptake into the roots (Adrees et al. 2015; Etesami and Jeong 2018). The multiple beneficial effects of Si on crop growth indicate that Si management in croplands will be a crucial part for sustainable agriculture.

In addition, the shoot biomass and root biomass are equivalently enhanced by Si application (Fig. 2). Because the aboveground biomass is substantially harvested and removed from croplands, the increased root biomass contributes the major input to soil organic carbon pool. Hence, the application of Si exerts a positive effect on soil organic carbon turnover, which in turn, fosters soil nutrient pool in croplands (Fig. 8). Besides, different amount of Si accumulation in plants usually results alteration of nutrient content and modifies nutrient use efficiency (Schaller et al. 2012; Neu et al. 2017). Furthermore, Si-poor litter is more susceptible to nutrient release than Si-rich litter due to Si-mediated alteration of nutrient content and stoichiometry, whereas Si-rich litter decays faster (Schaller and Struyf 2013; Marxen et al. 2016). The alteration of Si-associated nutrient released from straw decomposition will potentially change the biological transformation (e.g., denitrification) and migration of the nutrients from soils to water bodies. Therefore, high Si accumulation in crops can modify the biogeochemical cycles of carbon and nutrients in croplands for sustainable agriculture.

However, the amount of bioavailable Si pool that varies in different croplands exerts distinct impacts on Si-associated biogeochemical cycles of carbon and nutrients. Because the ability to accumulate Si varies widely among different crops, ranging from 0.1 to 10% (Ma and Takahashi 2002), the efficiency of Si application to different crops varies considerably due to diverse competitive strategies against nutrient limitation (Massey et al. 2007). Besides, soil fertility and resource-availability in different croplands also impose an impact on Si application to the same crop. Therefore, biogeochemical cycle of Si across different types of cropland, soil types and climatic zones should be comprehensively considered when Si fertilization is considered in the future.

6. Conclusion and perspective

Based on the multiple regulation of Si on plant biomass carbon accumulation, lignin synthesis, and nutrients adsorption, this review highlighted the impacts of Si on the biogeochemical cycles of carbon and nutrients in croplands. The increased biomass production and straw decomposability (due to the reduced lignin synthesis) can increase root biomass input to soil organic carbon pool and accelerate the turnover rate of soil organic carbon. Besides, high Si accumulation in crops usually decreases the release rate of nutrients during the biomass decay. The alteration of Si-associated nutrients uptake will potentially change the biological transformation (e.g., denitrification) and migration of the nutrients from soils to water bodies. In total, Si accumulation in plants has multiple impacts on biogeochemical cycles of carbon and nutrients in croplands.
croplands. And, there are some areas needing to be further investigated:

1. Biogeochemical cycle of Si and the amount of Si accumulation in above-ground biomass across various croplands should be investigated to make Si management possible in croplands.

2. Tradeoff analyses for reduction of carbon and lignin concentration versus increase of Si and biomass production in response to Si accumulation need to be further investigated to ascertain the comprehensive impacts of Si on biogeochemical carbon cycle in croplands.

3. The effect of Si on lignin synthesis in crop roots should be elucidated to evaluate the contribution of the increased root biomass to soil organic carbon turnover.

4. The mechanisms of Si-mediated regulation of plant nutrient uptake across different nutrients and crops, and the effects on their biogeochemical processes need to be further explored.

Acknowledgements

We acknowledge the supports from the National Natural Science Foundation of China (41522207, 4157130042, 31572191 and 31772387) and the National Key R&D Program of China (2016YFA0601002).

Appendices associated with this paper can be available on http://www.ChinaAgrSci.com/V2/En/appendix.htm

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Section editor ZHANG Wei-li
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