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Plant silicon uptake increases active aluminum minerals in root-zone soil: Implications for plant influence on soil carbon

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ABSTRACT

Aluminum (Al) minerals form a strong complex with organic matter (OM) in soil, affecting the stability and degradability of OM and carbon (C) dynamics in soil. However, plant effects on the accumulation of Al minerals (particularly Al hydroxide minerals) that are not crystallized and actually or potentially associated with OM (active Al minerals) in soil have received little attention. Al also interacts with silicon (Si) in soil to form aluminosilicate minerals, and plants remove Si from soil through Si uptake. Plant Si uptake may thus lead to an increase in active Al minerals in soil because of a reduced influence of Si in soil and the resulting reduced formation of aluminosilicate minerals. To test whether plant Si uptake changes active Al minerals in root-zone soil, we performed two cultivation experiments using plants varying in Si uptake and compared changes in soil mineral indices during cultivation, including soil extractable Al concentrations in root-zone soils. In the first experiment, using five plant species varying in Si uptake, plant species with greater Si uptake, in particular grass species, showed higher pH (NaF) and $CuCl_2$-extractable Al in their root-zone soils, suggesting that plant Si uptake increases the amount of active Al in soil. This suggestion was supported by the second experiment, using two types of rice (*Oryza sativa*), a wild type and a mutant defective for a Si transporter. The results showed that pH (NaF) and extractable Al in root-zone soil decreased under the low-Si-uptake mutant, especially in the vicinity of their roots. These observations suggest that Si uptake by plant roots leads to an increase in active Al minerals, possibly enhancing OM retention and C accumulation in root-zone soil and may partly explain why grassland soils are often rich in C.

1. Introduction

Aluminum (Al) is the third most abundant element in the earth's crust and a major constituent of numerous minerals such as aluminosilicates. Al forms a strong association and complexation with organic matter (OM) in soil (Jardine et al., 1989; Kaiser et al., 1997; Kaiser et al., 2007; Parfitt et al., 1977), affecting the stability and degradability of the OM (Kaiser et al., 2007; Kögel-Knabner et al., 2008; Schneider et al., 2010; Sollins et al., 1996). Although the Al–OM relationship is actively formed on juvenile surfaces of Al hydrous oxides (Kaiser et al., 1997) and presumably promoted by carbonic acid regimes (Dahlgren et al., 2004), plant effects on its formation have been little investigated.

Plants can translocate soil minerals to their tissues via uptake, changing the chemical properties of soil minerals (Hinsinger et al., 2001; Kelly et al., 1998; Lucas, 2001; Schlesinger and Bernhardt, 2013). Silicon (Si) is a major component of many soil minerals, as is Al, and Si and Al together form aluminosilicate minerals. These two elements typically show contrasting translocation behaviors in plant–soil systems. Plants can enhance silicate weathering by the root exudation of protons and organic acids and acidification (Lucas, 2001; Song et al., 2012) and may destabilize silicate minerals through Si uptake (Alexandre et al., 1997; Drever, 1994). Plants absorb Si in the form of silicic acid [$Si(OH)_4$] (Lewin and Reimann, 1969; Takahashi and Hino, 1978) from root-zone soil up to 10% of their weight (Epstein, 1994),

Abbreviations: Si-c, $CuCl_2$-extractable Si; Si-p, phyrophosphate-extractable Si; Si-o, oxalate-extractable Si; Al-c, $CuCl_2$-extractable Al; Al-p, phyrophosphate-extractable Al; Al-o, oxalate-extractable Al; WT, wild-type.

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and this absorption can strongly affect soil Si status (Hinsinger et al., 2001; Kelly et al., 1998; Lucas, 2001). In contrast, plant Al uptake is mostly controlled because of Al toxicity to plant growth (Shew et al., 2007) and is smaller than Si uptake (Lucas, 2001). Preferential uptake of Si by plants would reduce Si in soil and mitigate the crystallization and stabilization of Al with Si, an action that might indirectly enhance association of Al with OM. This expectation is based on the assumption that OM and Si compete with each other to associate with Al, an assumption consistent with observations that the sequestration of Al with OM hinders the reaction of Al with Si (Huang and Violante, 1986) and prevents the formation of secondary aluminosilicates (Dahlgren and Ugolini, 1989). Plant Si uptake has received recent attention, particularly with respect to its direct effect on C sequestration through processes such as dynamics of phytolith and aggregates (Parr and Sullivan, 2005, 2011; Song et al., 2014), whereas the indirect effect of plant Si uptake on soil C retention by enhancing Al–OM association has not been investigated to the best of our knowledge.

To determine whether plant Si uptake influences active Al minerals (Al hydroxide minerals that are not crystallized and actually or potentially associated with OM) in root-zone soil, we performed two cultivation experiments. In the first experiment, we selected five plant species expected to have different Si uptake potentials because plants widely differ in ability to absorb Si (Epstein, 1994; Ma and Takahashi, 2002). After their cultivation, we compared the chemical characteristics of the plants and the root-zone soils among the plant species. In the second experiment, we used a rice mutant, *lsi1*, defective in Si uptake owing to the low silicon rice 1 (*lsi1*) gene (Ma et al., 2006) and compared the same chemical characteristics with those of wild-type rice to evaluate the effect of the plant Si-uptake function on soil Al. We discuss the results of the experiments using two different approaches with respect to the possible influence of plant Si uptake not only on Al forms but also on C sequestration in soil.

2. Materials and methods

2.1. First cultivation experiment

In the first experiment, we cultivated five plant species and analyzed the chemical properties of the plants and root-zone soils. We selected Japanese pampas grass (*Miscanthus sinensis*), rice (*Oryza sativa*), Japanese mugwort (*Artemisia indica* var. *maximowiczii*), clover (*Trifolium repens*), and tomato (*Solanum lycopersicum*). These plants were selected because they were suggested to have different Si uptake characteristics; for example, grass species are typical Si accumulators (Ma and Takahashi, 2002), and *Asteraceae*, tomato, and clover plants show intermediate to low Si contents (Jarvis and Jones, 1987; Ma and Takahashi, 2002). A kinetic study has shown that xylem loading of Si was mediated by a type of transporter in rice but by passive diffusion in tomato (Mitani and Ma, 2005).

We used a fresh volcanic ash soil for the cultivation experiments to shorten geological reactions in root-zone soils and the duration of the experiments because volcanic ash comprises fine particles and typically shows a vesicular nature (high surface area) and high weathering rate (Dahlgren et al., 2004; Saigusa et al., 1991). The fresh volcanic ash was sampled from the non-vegetated area at the edge of a scattered young pine (*Pinus thunbergii*) forest on an active volcanic island, Sakurajima (31°35′N 130°39′E), Japan, in November 2009. In the laboratory, the soil was sieved to <1 mm with a mesh screen, washed with tap water,

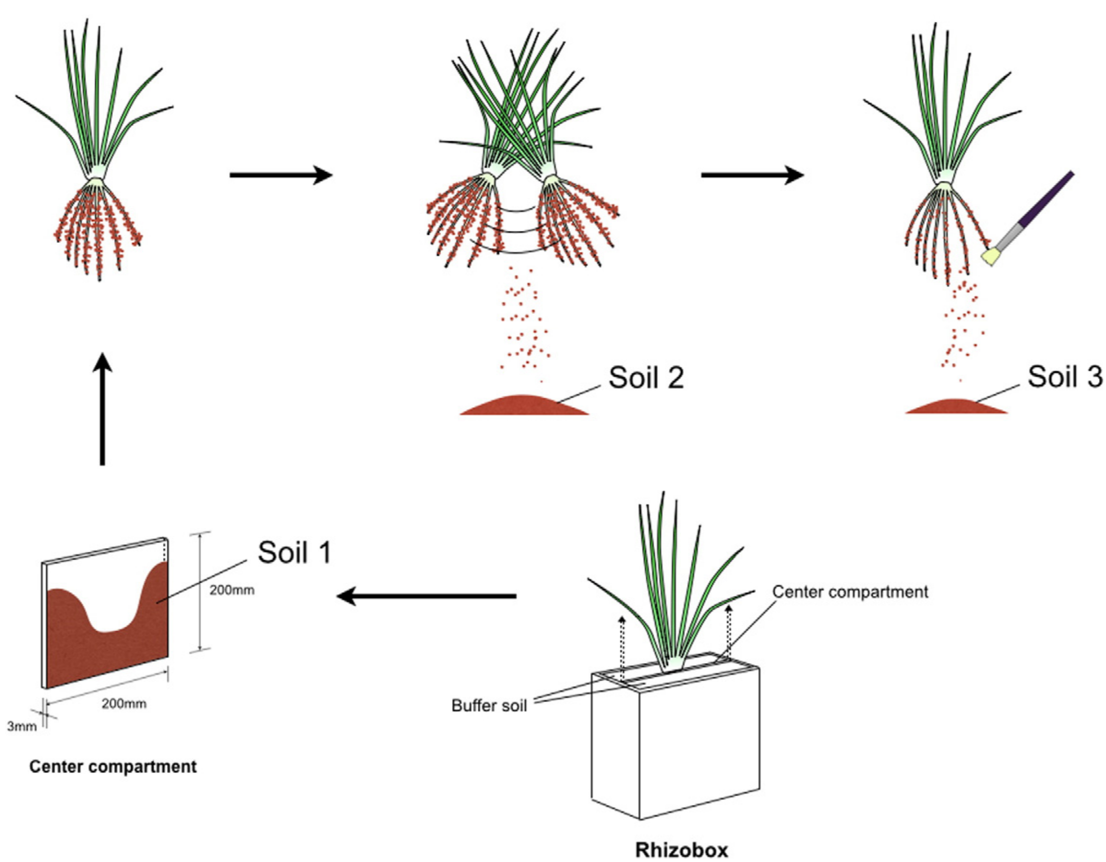

Fig. 1. The procedure for sampling root-zone soils in the second experiment. Soil in each rhizobox was separated into three after cultivation based on the status of its attachment to the plant roots: soil not attached to roots (soil freely removed from the root system without shaking) (soil 1), soil removed by shaking because it was loosely attached to the roots (soil 2) and soil that could not be removed by shaking because it was tightly attached to the roots (soil 3).