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Abstract

Background and aim Silicon is known to be able to substitute carbon in plant biomass, especially in cellulose, lignin and phenols. However, a more comprehensive picture regarding the effect of silicon accumulation on plant carbon quality (cellulose, lignin, phenol, wax, lipids, and free organic acids content) with regard to potential decomposability is still missing.

Methods Two different rice varieties (French brown and red rice cultivars) were cultivated under five different soil silicon availabilities. After maturity we harvested the plants and analyzed them regarding carbon quality by FTIR spectroscopy and regarding plant silicon concentrations.

Results Silicon accumulation was found to be dependent on silicon availability and on the specific rice cultivar. The lowering of carbon compounds content by silicon was found not to be restricted to cellulose, lignin and phenol. Silicon accumulation was able to decrease other carbon compounds such as fat, wax, lipids, and free organic acids, too.

Conclusions Consequently, silicon is important for the carbon quality of silicon accumulating plants. Furthermore, silicon accumulation in plants is interfering with a large range of different carbon compounds potentially altering the leaf economic spectra, decomposability, and thus potentially interfering with the whole performance of ecosystems dominated by silicon accumulating plant species.

Keywords: carbon compounds, carbon quality, rice pigmentation, rice plant tissues, silica, silicon

Introduction

Rice (*Oryza sativa* L.) is the main staple food for about half of the world's population (Zhu et al. 2008). Especially in poor regions of the world the daily energy consumption relies mainly on rice (Ninno and Dorosh 2001). Normal rice plant physiology requires silicon (Si) during plant growth (Broadley et al. 2012). Silicon is taken up from soil solution mainly as silicic acid [$Si(OH)_4$] (Ma et al. 2006), an uncharged monomeric molecule, whereas in aboveground biomass silicic acid polymerizes to different forms of amorphous silica with a higher condensation state (Schaller et al. 2013). The accumulation of Si by plants depends on soil Si availability ((Schaller et al. 2012b; Neu et al. 2017)), the specific plant cultivar (Li et al. 2014) and is closely related to plant transpiration (Ma and Takahashi 2002).

It was shown that Si content is negatively related to carbon contents in aboveground biomass of plants (Neu et al. 2017; Klotzbücher et al. 2018). It was also found that Si content affects the carbon quality of aboveground plant biomass. Silicon content seems to be negatively related to plant phenol content (Schaller et al. 2012a), is both either increasing or decreasing plant cellulose content (Schoelynck et al. 2010; Schaller et al. 2012a), depending on species, and has negative or no obvious effect on plant lignin content (Schoelynck et al. 2010; Schaller et al. 2012a; Klotzbücher et al. 2018).

As cellulose for example is built from sugar monomers or disaccharides (Richmond 2000), a decrease of cellulose formation due to increasing Si content may increase the sugar content of aboveground biomass or increase the amount of other carbon compounds, because these carbon compounds require sugars for their synthesis e.g. fatty acids (Rawsthorne 2002) as important compound for e.g. plant wax formation (Samuels et al. 2008). However, results of Si effects on a broader range of plant carbon compounds are still missing, yet.

To systematically evaluate effects of Si on plant carbon quality in rice, we thus grew two different rice varieties (the French red rice TamTam and one of the most commonly grown non-pigmented brown rice varieties in France (Arelate)) in climate-controlled chambers under different Si availabilities to examine differences between Si uptake and corresponding leaf carbon quality. We knew from preliminary screening that the red rice is accumulating more arsenic compared with the brown rice (Eberle 2015). We deduced from this information that the red rice may have higher requirements for Si compared with the brown rice, because under flooded growing conditions arsenic is present as arsenite which is taken up by plant root via the Si uptake pathway (Meharg and Meharg 2015). Our hypotheses were therefore that (i) Si accumulation will be lower for the brown rice compared to the red rice and (ii) Si content is affecting plant carbon quality in the rice aboveground biomass by reducing the concentration of specific carbon compounds such as phenols or cellulose by Si compounds. Thereby, plant carbon quality was assessed using Fourier-transformed infrared spectroscopy (FTIR) (Niemeyer et al. 1992; da Luz 2006). Additionally, we analyzed the Si transporter expression in rice seedlings in a separate experiment, to check whether potential differences in Si content between the used rice cultivars can be related to differences in expression of Si transporter.

Material and Methods

Seeds

Seeds for Si transporter gene expression analysis in hydroponic culture and the seeds for the rice cultivation experiment were obtained from the Centre Français du Riz (CFR) in Arles, France.

Si transporter gene expression analysis

To determine the expression of Si transporter genes, seedlings were cultivated hydroponically as described previously (Ma et al. 2002). All experiments were conducted in a greenhouse at 25 °C with natural light and a replication of three. Rice seedlings (18 days old) were exposed to a nutrient solution containing 0, 0.2 or 2 µM arsenite. Arsenite is an analog for silicic acid, both being uncharged and taken up via the same transport pathways, the LSi1 and LSi2 transport systems (Ma and Yamaji 2015). The solution was changed every two days. After 1-week exposure, the roots were sampled for RNA extraction. Total RNA was extracted from the roots using the RNeasy Plant Mini Kit (Qiagen). For conversion to cDNA, 0.5 µg of total RNA was used, following the protocol supplied by the manufacturers of SuperScript II (Invitrogen). Specific cDNAs were amplified by So Fast EvaGreen Supermix (Bio-Rad). Quantitative real-time PCR was performed with the primers shown in Supplementary Table 1. Actin was used as an internal standard.

Rice plant cultivation

For the rice cultivation experiments, the red cultivar TamTam and the brown cultivar Arelate were grown in phyto chambers (Thermotec, Weilburg, Germany) at a 12-hour day/night cycle (30 °C, 70 % RH, about 1000 µM m^2 s^{-1} light intensity from sodium vapor lamps at day and 18 °C, 80 % RH and zero light at the night) during germination. About 25 rice seeds were seeded on 3.5 kg homogenized soil (sieved to 2.5 mm, with 1.1 g $(NH_4)_2SO_4$ kg^{-1} soil, 0.44 g KH_2PO_4 kg^{-1} soil and 0.24 g KCl kg^{-1} soil added, in plastic containers) from Camargue (from the test fields at CFR). After germination the seedlings were reduced to 15 per pot. To measure dissolved and some of the exchangeable Si from soils we used a sodium acetate extraction according to Sauer et al. (2006), because this method was shown to correlate well with Si uptake by rice (Snyder 2001). In short, 5 g of soil were extracted with 50 mL sodium acetate, adjusted to pH = 4 for 5 h at 40 °C. The extracts were filtered (0.2 µm cellulose acetate) and analyzed for Si by inductively coupled plasma optical emission spectrometry (ICP-OES). Silicon was added to the soil as synthetic amorphous silica (Aerosil 300, Evonik Industries AG, Germany) at five concentrations, 0 (control), 1 (Si1), 5 (Si5), 10 (Si10) and 50 g amorphous silica

kg^{-1} soil (Si50), each in five replicates for both varieties, equaling 50 pots in total. The soils were pre-moistened with 1.5 L tap water (Bayreuth). Containers with red and brown rice plants were placed randomly in the chambers because cross-pollination was assumed to be low. During germination, the water levels were kept constant at 3 – 4 cm above the soil. After germination, the water levels were kept constant at 10 cm above the soil. Tap water was stored in plastic cans in the chambers to assure that the water temperature was appropriate for the plants. The Si concentration in tap water was ~3 mg L^{-1}. After germination, the climate was changed to a constant temperature and humidity of 21 °C and 80 % RH, respectively. We took pore water samples for the analysis of the available Si at six different time points over the whole growth period using suction samplers (Rhizon, Rhizosphere Research, Eijkelkamp, The Netherlands; see SI for details).

Harvest and post treatment

Plants were harvested at maturity (~150 days after seeding) when completely dried, 14 days after the last irrigation. Plants were cut off about 2 cm above the soil, separated into whole grain, husk, flag leaf, flag leaf sheath and leaf, weighed and dried at 75 °C for 3 days in paper bags. Flag leaves, flag leaf sheaths, leaves (all leaves other than the flag leaf), and husks were grinded in an ultra-centrifugal mill (Retsch, ZM1, 10000 r/min, 0.12 mm, Germany). All tissues were stored dark at room temperature until analysis.

Analysis

Si was extracted from plant samples by an alkaline digestion where 30 mg ± 1 mg of each sample were weighed into extraction vials, filled up with 30 mL 1 % Na_2CO_3 and treated 5 h at 85 °C in a heating block (DeMaster 1981; Meunier et al. 2014). Samples were filtered through 0.2 µm cellulose acetate filters and stored at room temperature until analysis with inductively coupled plasma optical emission spectrometry (ICP-OES).

FTIR analysis

FTIR spectra from leaves (all leaves other than the flag leaf) were obtained using a Cary 660 FTIR spectrometer (Agilent, Santa Clara, CA, USA). An amount of 2 mg of finely ground sample was mixed with 200 mg KBr (FTIR grade, Sigma Aldrich, St. Louis, MO, USA) and analyzed as a 13 mm pellet. A total of 32 scans were collected for each sample and averaged, a KBr background was subtracted, and a baseline correction was applied prior to further evaluation. Relative peak intensities and organic matter functional moieties were interpreted following existing studies (Niemeyer et al. 1992; da Luz 2006; Agethen and Knorr 2018; Hodgkins et al. 2018) and as listed in Table 1. We focused on wavenumbers indicative of aliphatics, waxes (2,850 to 2,920 cm^{-1}), of organic acids,

oxygenated compounds (~1,710 cm^{-1}), of aromatics, proteinaceous compounds (I) (1,650 cm^{-1}), of lignin, organic acids (1265, 1450, and 1515 cm^{-1}), and of proteinaceous compounds (II) (1550 cm^{-1}).

Table 1. Assignment of absorption bands assessed by Fourier-Transformed Infrared Spectroscopy (FTIR).

Wavenumber, cm-1	Assignment	Compound class	Reference
2920	Antisymmetric CH2	wax, lipid	(Niemeyer et al. 1992; Cocozza et al. 2003)
2850	Symmetric CH2	Wax, lipid	(Niemeyer et al. 1992; Cocozza et al. 2003)
1710	C=O stretch of COOH	Carboxylic acids	(Niemeyer et al. 1992)
1653	C=O of amides	Proteinaceous compounds	(Artz et al. 2008; Agethen and Knorr 2018)
1650 – 1600	Aromatic C=C stretching; C-O in COOH	Lignin and other aromatics, carboxylates	(Niemeyer et al. 1992)
1550	N-H in-plane vibration	Proteinaceous compounds	(Artz et al. 2008; Agethen and Knorr 2018)
1515	Aromatic C=C stretching	Lignin, phenolics, aromatics	(Niemeyer et al. 1992; Cocozza et al. 2003)
1450	-CH deformation and -CH bending	Lignin and aliphatics	(Niemeyer et al. 1992)
1265	C-O stretching of phenolic OH	Lignin	(Niemeyer et al. 1992)
1100	$[SiO_4]$ asymmetric stretching	(biogenic) silicates	(Meyer-Jacob et al. 2014; Vogel et al. 2016)
1080-1030	C-O stretching and O-H deformation	Polysaccharides	(Niemeyer et al. 1992)
<1000	Si-OH vibration	(biogenic) silicates	(Meyer-Jacob et al. 2014; Vogel et al. 2016)

Statistical analysis

An ANOVA was performed for comparison of the data followed by a Tukey-HSD *post hoc* test using SPSS (version 20.1).

Results

Silicon in soil, porewater and plant tissues

Initially plant-available (sodium acetate extractable) Si in the used soils was 64.5±3.2 mg Si kg^{-1} DW^{-1}. In the pore water, Si availability for the control, the Si-1, and the Si-5 treatment dropped remarkably after mid of July at the beginning of the reproductive phase for both varieties. Final concentrations in pore water were as low as 0.215 mg L^{-1} (Fig. S2). For the Si-50 treatment, concentrations were ≥25 mg L^{-1} over the whole growth period but the decrease during the reproductive phase was stronger for brown than red rice. At the end of July, Si concentrations re-increased to about 45 mg L^{-1} in brown rice, indicating a decreased uptake in brown rice at this stage. For red rice, the concentrations remained constantly high at about 40 mg L^{-1} irrespective of the growth stage, indicating an overall lower Si uptake.

The most striking result from the Si concentration data was that brown rice accumulated significantly (p<0.001, F=70,632, ANOVA) more Si in all tissues over all Si treatments compared with the red rice (Fig. 1). Tukey-HSD *post hoc* revealed significant differences between red and brown rice for the Si treatments (Fig. 1). The differences were most pronounced in the flag leaves (Si-50) (Fig. 1a), with around 100±12 and 50±17 mg g^{-1} DW^{-1} in brown rice and red rice, respectively. The same holds true for the husk, where brown rice accumulated about 50 % more Si in each treatment compared with red rice, including the control (Fig. 1d). Furthermore, the difference between red and brown rice husk Si concentrations was always roughly the same in absolute numbers for all Si treatments. There were no significant differences between red and brown rice in the flag leaf sheath (Fig. 1b) and the leaf (Fig. 1c). In all analyzed tissues, Si concentrations increased significantly (p<0.001, F=228,937, ANOVA) with Si treatments (except for Si-1) for both varieties (Fig. 1). Si concentrations in the grains were below the detection limit. In the other tissues, Si concentrations followed the decreasing order husk > flag leaf > flag leaf sheath > leaf.

Silicon transporter gene expression analysis

No significant differences were found between the pigmented red rice and the non-pigmented brown rice (LSi1 F 0.083, p=0.777; LSi2 F 0.085, p=0.775; LSi3 F 0.413, p=0.529; LSi6 F 0.339, p=0.529) regarding the expression levels of the different Si transporters for 14 day old plants (Fig. S1).

Silicon effects on leaf carbon quality

Silicon fertilization seemed to affect the quality of plant carbon in rice leaves as indicated by FTIR (Fig. 2, Table 1). With increasing Si availability (from control to Si-50) the absorbance at 2,850 to 2,920 cm^{-1} (aliphatics, waxes), at ~1,710 cm^{-1} (organic acids, oxygenated compounds), at 1,650 cm^{-1}

(aromatics, proteinaceous compounds), at 1265, 1450, and 1515 cm^{-1} (lignin, organic acids), and at 1550 cm^{-1} (proteinaceous compounds) was reduced compared to absorbance at 1090 cm^{-1}(Fig. 2, Fig. S3). This indicates a shift in carbon quality towards a relatively higher share of carbohydrates and relatively lower share of lignin, proteinaceous compounds, and waxes under Si fertilization; according to the higher Si uptake of brown rice, spectral changes were more pronounced for brown rice compared to red rice. Moreover, we found a broadening of the shoulder at 1,100 cm^{-1} and a more pronounced peak at around 800 cm^{-1}, presumably both indicative of higher biogenic silica contents at increased Si fertilization; again, these features were also more pronounced for brown rice, taking up more Si. Overall, we found no clear significant effect of the Si availability on the carbohydrate content (Fig. S4) for both the red (df=4, F=2.337, p=0.092) and the brown rice leaves (df=4, F=2.026, p=0.126). But we found a strong significant effect of the Si availability on the aromatics content (Fig. S4) for both the red (df=4, F=14.543, p<0.001) and the brown rice leaves (df=4, F=22.873, p<0.001). Variety (red or brown rice) had also a significant effect on both carbohydrate (df=1, F=4.118, p=0.049) and aromatics (df=1, F=25.059, p<0.001) content (Fig. S4).

Discussion

Our experiment revealed that Si fertilization led to a strong increase in the rice tissue Si content for brown as well as for red rice. This effect has been well documented for rice before (Bogdan and Schenk 2008) and also for other plants (Epstein 1999; Hodson et al. 2005; Schaller et al. 2012b; Neu et al. 2017) mainly from the family of the *Poaceae*. However, we found large differences between the pigmented red and the non-pigmented brown rice varieties with a Si content ranging between 0.45 and 5.99 % (lowest - highest Si availability) in red rice and 0.70 and 9.90 % in brown rice depending on the Si fertilization (p<0.001, F=70,632, ANOVA). This demonstrates the importance of the varieties for Si content. According to Dobermann and Fairhurst (2000), Si deficiency occurs at rice straw concentrations at maturity of less than 5 % DW^{-1} with an optimal range from 8-10 %. Because the flag leaf is a strong accumulator of Si we assumed that the concentrations in the whole straw were equal to the flag leaf concentrations or lower. Consequently, all plants (concentrations < 1 to ~ 3 % DW^{-1}), except those from the Si-50 treatment (concentrations ~ 4 to ~ 6 % DW^{-1}) might have suffered from Si deficiency. Our analysis showed that the gene expression of the respective transporters was the same in seedlings of red and brown rice, indicating similar uptake of Si. We tested the gene expression of Si transporters with arsenite, which is taken up via the same transporter. But, the physiological response of Si and arsenite are different as Si is known as beneficial element whereas arsenite is a toxicant. Hence, our gene expression data can provide only hints for Si uptake rates. Furthermore, the expression of the Si transporters may vary over the growth period (Yamaji and Ma 2007) with remarkably higher Si uptake during the reproductive phase (Ma et al. 1989). About 67 % of all Si is taken up during this phase due to the high biomass production during this period. In our experiment, the Si concentrations in the pore water of the control, Si-1 and Si-5 treatment were below 3 mg L^{-1} during this phase, which is considerably below the optimal range of ~20 mg L^{-1} for silicic acid (Savant

et al. 1996) and consequently the tissue Si concentrations were low due to insufficient supply. The assumption of different gene expression between red and brown rice is supported by the observation that the Si concentrations in the pore water dropped stronger for the brown rice, especially noticeable in the Si-50 treatment (Fig. S2) which might indicate a higher uptake. Additionally, our analysis revealed a significantly higher Si uptake of the brown rice compared to the red rice. These differences were most pronounced in the husk where Si concentrations were about 50 % higher in the brown husk compared to the red husk, even in the control. In this work, we could show that the Si concentrations in a non-pigmented brown rice variety were substantially higher than a in pigmented red rice variety.

At the FTIR-spectra around 1100, 1000 cm^{-1} and lower the plant biogenic silica may be seen in specific absorption features (Meyer-Jacob et al. 2014; Vogel et al. 2016). Indeed, for the samples with elevated Si content a more pronounced shoulder appeared at 1100 cm^{-1}. With increasing Si availability (from control to Si-50) the amounts of wax and lipids (2,850 to 2,920 cm^{-1}), free organic acids (~1,710 cm^{-1}), and lignin (1,650 cm^{-1}) were relatively reduced compared to carbohydrates, such as cellulose (Fig. 2). For references of the wave numbers for the different compounds see Table 1. This relative decrease in contribution of carbohydrates is not necessarily in contradiction with the reported reduction of absolute carbohydrate concentration due to increased Si content (Schoelynck et al. 2010; Schaller et al. 2012a; Klotzbücher et al. 2018). It was already suggested that Si accumulation leads to a decrease in cellulose, lignin and phenol concentrations in plants (Schoelynck et al. 2010; Schaller et al. 2012a; Klotzbücher et al. 2018). The dataset shown in this manuscript revealed that the Si effect on the content of carbon compounds is not restricted to cellulose, which was even relatively increased compared to other moieties. The effect seems much larger, leading also to a relative decreasing of other carbon compounds compared to carbohydrates, such as lignin, phenols, wax, lipids, and free organic acids.

Based on FTIR-spectra only changes in relative shares of compounds, not of absolute concentrations can be interpreted. A relative reduction in leaf wax content by increasing plant Si content would be in accordance with an earlier study showing the same reduction of wax content due to higher Si content (Agarie et al. 1998). The stronger Si effects on the amount of carbon compounds in brown compared with red rice seems to be related to the higher Si content in brown rice (Fig. 1 and 2).

Conclusions

Silicon accumulation is known to decrease the carbon content of the aboveground tissues of plants, especially grasses like rice. Hence, Si content in plants is interfering with a large spectra of different carbon compounds potentially altering the leaf economic spectra (Wright et al. 2004) in regard to carbon quality. As the carbon quality is determining both herbivory (Awmack and Leather 2002) and organic matter decomposition (Coûteaux et al. 1995) Si content is potentially interfering with the whole ecosystem performance of grassland systems, as suggested before (Schaller et al. 2017), by e.g. increasing decomposition rate, as shown before (Schaller et al. 2014). Additionally, the differences in Si content between the different cultivars may also affect the Si cycling in grass dominated ecosystems by changing Si release during straw decomposition or from straw derived products like biochars (Schaller et al. 2018; Li et al. 2019). Furthermore, carbon can be occluded in plant Si compounds (e.g. phytolith) in the range of 0.4 to 2.8 mg/g (Li et al. 2013; Song et al. 2017). The amount of carbon occluded in plant Si compounds is important for long term carbon storage in soils (Li et al. 2013; Song et al. 2017). However, in regard to the amount of carbon stored in rice plant biomass, the amount of carbon occluded in plant Si compounds is less important for the carbon storage in rice plant biomass as the carbon concentration of rice plant material is ~40% (Schaller et al. 2018).

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Figures

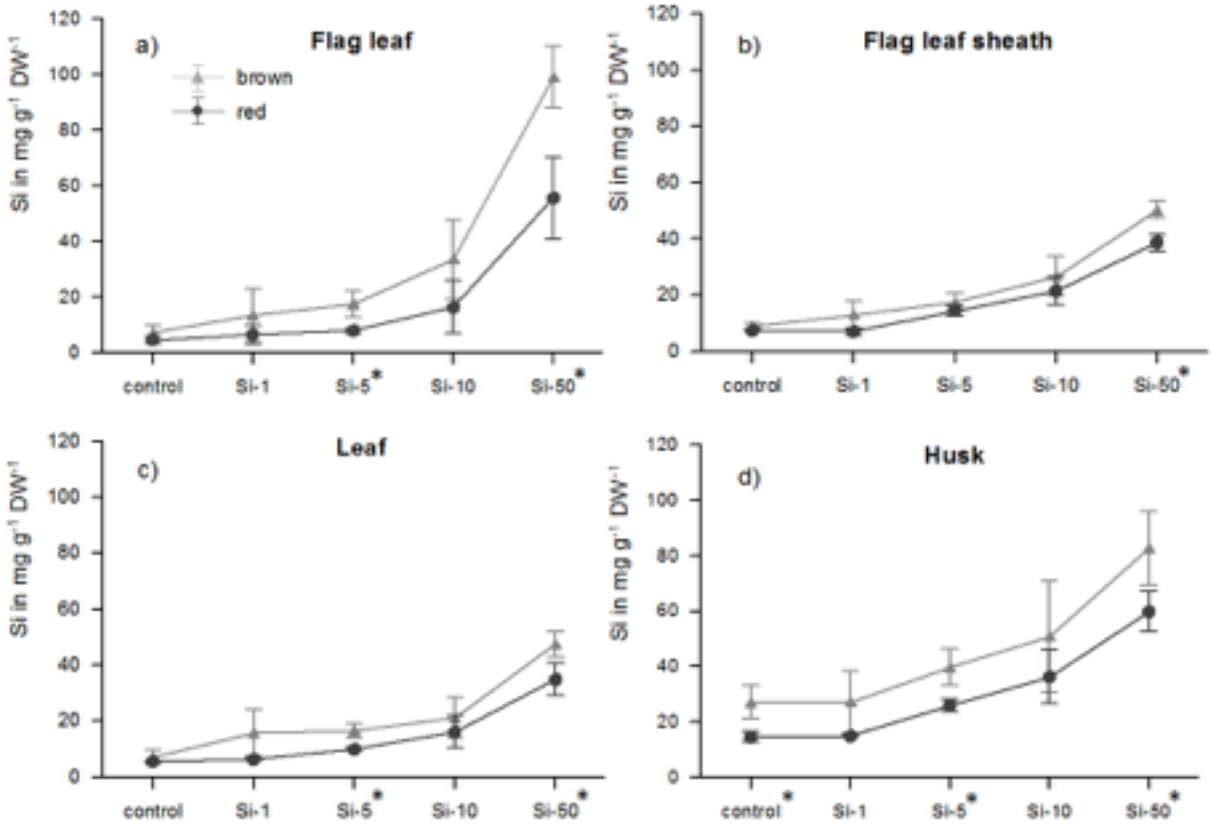

Figure 1: Mean±SD of Si concentration in different tissues of red and brown rice with different Si treatments and controls; * marks treatments with significant (p<0.05, Tukey-HSD post hoc) differences between red and brown rice; n = 4.

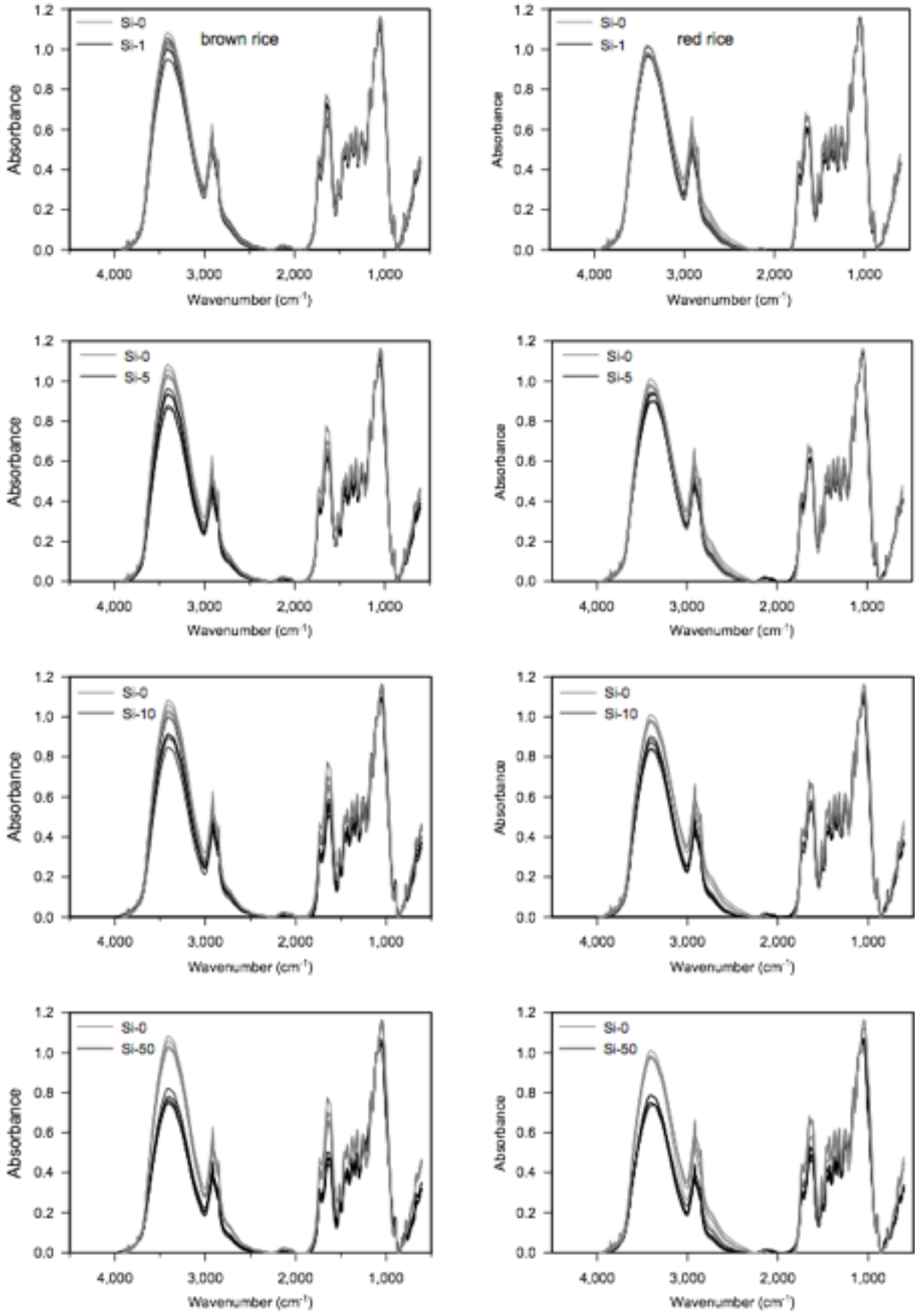

Figure 2: Magnitude of absorbance of different carbon compounds shown for red and brown rice varieties with different Si treatments and controls. n = 4.