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Silicon Accumulation and Distribution in Petunia and Sunflower Grown in a Rice Hull-amended Substrate

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Abstract*. Silicon (Si) is a plant beneficial element associated with the mitigation of abiotic and biotic stresses. Most greenhouse-grown ornamentals are considered low Si accumulators based on foliar Si concentration. However, Si accumulates in all tissues, and there is little published data on the distribution of Si in plants. This knowledge may be critical to using Si to mitigate tissue-specific plant stresses, e.g., pathogens. Therefore, we quantified Si accumulation and distribution in petunia (*Petunia ×hybrida* Hort. Vilm.-Andr. 'Dreams Pink'), a low Si accumulator, and sunflower (*Helianthus annuus* L. 'Pacino Gold'), a high Si accumulator. Plants were grown in a sphagnum peat: perlite substrate amended with 0% (−Si) or 20% (+Si) parboiled rice hulls for 53 (petunia) or 72 days (sunflower). Aboveground dry weight was greater in nonamended petunia (13%) and sunflower (18%), compared with rice hull–amended plants, but days to flower was unaffected. Sunflowers grown in the rice hull–amended substrate had the greatest Si concentration in leaves (10,909 mg·kg^{-1}), whereas roots (895 mg·kg^{-1}), stems (303 mg·kg^{-1}), and flowers (252 mg·kg^{-1}) had lower, but similar Si concentrations. In petunia, Si concentration was greatest in leaves (2036 mg·kg^{-1}), then roots (1237 mg·kg^{-1}), followed by stems (301 mg·kg^{-1}), and flowers (247 mg·kg^{-1}). The addition of rice hulls to the substrate increased Si concentration in sunflower 414% in roots, 512% in flowers, 611% in stems, and 766% in leaves. By contrast, Si concentration in petunia increased only 7% in flowers, 105% in stems, and 115% in leaves, but increased 687% in roots. In rice hull–amended sunflowers, the distribution of Si was 91% in leaves, 3% in stems, 3% in roots, and 3% in flowers, and in petunia, it was 72% in leaves, 17% in stems, 6% in roots, and 5% in flowers.

Silicon is a plant beneficial element. It is associated with several positive physiological responses in plants (Ma, 2004), including reduced lodging (Ma and Yamaji, 2006; Savant et al., 1999), increased stem diameter (Kamenidou et al., 2008), higher rates of photosynthesis (Liang et al., 1996; Romero-Aranda et al., 2006), increased dry weight (Liang et al., 1996; Romero-Aranda et al., 2006), increased yield (Savant et al., 1999), increased flower size (Kamenidou et al., 2010), and earlier flowering (Boldt et al., 2015). Silicon has been shown to mitigate the impacts of many biotic and abiotic stresses, including powdery mildews (e.g., *Blumeria graminis* f. sp. *tritici*, *Erysiphe cichoracearum*, and *Sphaerotheca fulginea*) (Chain et al., 2009; Fauteux et al., 2006; Guével et al., 2007; Menzies et al., 1992), rice blast (*Magnaporthe grisea*) (Datnoff et al., 1997; Ishiguro, 2001), herbivory (Massey et al., 2006; Reynolds et al., 2009), drought (Hattori et al., 2005; Zhu and Gong, 2014), salt stress (Liang et al., 1996; Romero-Aranda et al., 2006), heat stress (Agarie et al., 1998), chilling injury (He et al., 2010; Liang et al., 2008), nutrient deficiencies (Ma, 2004), and heavy metal toxicity (Frantz et al., 2011; Liang et al., 2007).

Foliar Si concentration generally ranges from 0.1% to 10% plant dry weight (Liang et al., 2007; Ma and Takahashi, 2002). Plants are typically classified as Si accumulators or nonaccumulators, with a lower threshold of ≥10,000 mg·kg^{-1} foliar Si (i.e., 1% dry weight) considered the baseline for Si accumulators (Epstein, 1999; Ma et al., 2001). Many species within Poaceae are classified as Si accumulators, including important agronomic crops like wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), corn (*Zea mays* L.), barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), and sugarcane (*Saccharum officinarum* L.). In addition, some species of the horticulturally important Cucurbitaceae [cucumber (*Cucumis sativus* L.), squash, and pumpkin (*Cucurbita* spp.)], and Asteraceae [sunflower and zinnia (*Zinnia elegans* L.)] are Si accumulators (Frantz et al., 2010). However, most greenhouse-grown ornamentals are considered low Si accumulators or nonaccumulators. Frantz et al. (2010) grew 48 horticultural crops hydroponically in a modified Hoagland's solution amended with 1 mM Si and quantified foliar Si concentration. It ranged between 102 and 12,682 mg·kg^{-1} Si [ornamental tobacco (*Nicotiana sylvestris* Speg. & Comes.) and zinnia, respectively], and more than half the species accumulated less than 1000 mg·kg^{-1} Si.

For many years, it has been debated as to whether Si supplementation would be beneficial to nonaccumulators, because they do not accumulate high foliar concentrations (Ma et al., 2001; Mitani and Ma, 2005). The role of Si in plants may be both in a structural capacity and as a signaling compound (Fauteux et al., 2006), and therefore, nonaccumulators could still benefit from Si supplementation and increased Si accumulation following imposition of a stress. For example, the addition of Si to the hydroponic nutrient solution delayed *Tobacco ringspot virus* symptom formation and reduced symptomatic leaf area in tobacco (*Nicotiana tabacum* L.) (Zellner et al., 2011), and it ameliorated copper (Cu) toxicity in arabidopsis [*Arabidopsis thaliana* L. (Heynh.)] (Li et al., 2008) and snapdragon (*Antirrhinum majus* L.) (Frantz et al., 2011), all Si nonaccumulators.

Soluble, plant-available Si can be supplied through substrate components, substrate amendments, liquid fertilization, or foliar sprays. Silicon is absorbed by plants primarily via the roots through passive or active uptake (Liang et al., 2006; Mitani and Ma, 2005). Plants accumulate Si in all tissues, although some may accumulate high Si concentrations in roots, and perhaps other tissues, but not in foliage. Recent studies have shown that root Si fractions in nonaccumulators may be as high as, or higher than, in Si accumulators. For example, we detected low foliar Si concentrations (1473 mg·kg^{-1}) but higher root Si concentrations (2000–7000 mg·kg^{-1}) in rose (*Rosa* 'Radrazz') plants grown at low P (2.5–20 mg·L^{-1}; J.E. Altland and J.K. Boldt, unpublished data). Differences in root and shoot Si concentrations may result from differential regulation of Si uptake, the mechanism of xylem loading (active or passive), transporter concentration, or the stress status of a plant (Liang et al., 2006; Mitani and Ma, 2005).

There is little published research on the distribution of Si in plants. For species in which it has been documented, Si is not uniformly distributed throughout the plant. Rice grown in nutrient solution with 150 ppm SiO_2 (70 mg·L^{-1} Si) averaged 9800 mg·kg^{-1} Si in roots, 57,000 mg·kg^{-1} in leaf sheaths, and 63,000 mg·kg^{-1} in leaf blades, on a dry weight basis, as calculated from values reported as %SiO_2 (Yoshida et al., 1962). In oat, Si ranged from 280 mg·kg^{-1} in caryopses

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to 36,000 mg·kg^{-1} in inflorescences, with more than 40% of total aboveground Si localized in inflorescences (Jones and Handreck, 1967). Kamenidou et al. (2008) compared the effects of different sources of Si supplementation on tissue Si concentration of sunflower 'Ring of Fire' grown in a peat-based soilless substrate, and although tissue concentrations were not compared within a treatment, reported that leaf Si concentrations (4900–15,300 mg·kg^{-1}) were greater than those in flowers (3800–5100 mg·kg^{-1}) or stems (2900–4200 mg·kg^{-1}).

Knowledge of Si distribution in plants is critical for using Si to mitigate plant stresses that are tissue specific. For example, the common greenhouse pathogen botrytis (*Botrytis cinerea*) typically attacks flowers and leaves, whereas pythium (*Pythium ultimum*) causes root rot. If, for instance, flowers were found to contain appreciable quantities of Si, follow-up studies could investigate whether the accumulation of Si can provide protection against fungal pathogens like botrytis and offer growers a nonpesticide alternative to include in their pest management rotation.

The objective of this study was to document Si distribution in greenhouse crops to better understand how it might (or might not) be useful for mitigating stress in these species. Specifically, the experiment was designed to evaluate Si accumulation and distribution in roots, leaves, stems, and flowers of plants, using parboiled rice hulls as the source of supplemental Si. Two species were selected: petunia, classified as a non-accumulator of Si, and sunflower, classified as a Si accumulator.

Materials and Methods

Sunflower 'Pacino Gold' and petunia 'Dreams Pink' (Ball Seed Co., West Chicago, IL) were sown in 288-count plug trays filled with soilless substrate (LB-2; Sun Gro Horticulture, Bellevue, WA) and germinated in a growth chamber (PGR-16; Conviron, Vancouver, BC) maintained at 22 °C d/18 °C night, 200 µmol·m^{-2}·s^{-1} photosynthetic photon flux (*PPF*) from cool-white fluorescent lamps, and an 8 h photoperiod. Plants were irrigated as needed with reverse osmosis (18 MΩ) water until the first true leaves unfolded, then fertigated with 20N–4.4P–16.6K (Jacks 20–10–20; JR Peters, Inc., Allentown, PA) at a concentration of 50 mg·L^{-1} N. Reverse osmosis water was used to mix the fertilizer to minimize the addition of Si.

Seedlings of sunflower and petunia were transplanted on 10 Nov. and 16 Nov. 2015, respectively, into 11.5-cm diameter plastic pots, one plant per pot. The soilless substrate was an 85: 15 blend of sphagnum peat (Sun Gro Horticulture, Seba Beach, AB, Canada) and medium grade coarse perlite (Sun Gro Horticulture) amended with 1.55 kg·m^{-3} laboratory-grade $CaCO_3$ and 0.52 kg·m^{-3} $MgCO_3$ (Fisher Scientific, Fair Lawn, NJ) and 0.196 L·m^{-3} of a wetting agent (SOAX; Smithers-Oasis, Kent, OH). Parboiled rice hulls (Riceland Foods, Inc., Stuttgart, AK) were incorporated at 0% or 20% (by volume). Total Si concentrations for the substrate, rice hulls, fertilizer, and irrigation water are listed in Table 1. Plants were grown in a glass-glazed greenhouse (Toledo, OH), with day/night air temperature set points of 22/18 °C, a 14 h photoperiod, and supplemental lighting from 1000-W high-pressure sodium lamps when ambient irradiance inside the greenhouse was less than 300 µmol·m^{-2}·s^{-1} *PPF*. Mean day and night temperatures were 21.4 ± 0.3 °C and 18.0 ± 0.3 °C, respectively, and mean daily light integral was 5.8 ± 0.8 mol·m^{-2}·d^{-1}.

Forty individual pots of each species, 20 per treatment, were arranged on a bench in a completely randomized design. Plants were fertigated as needed with 20N–4.4P–16.6K at a concentration of 150 mg·L^{-1} N. Date of first flower was recorded and days to flower were calculated. Petunia and sunflower were harvested on 8 Jan. and 21 Jan. 2016, respectively, once all plants had flowered. At harvest, the pour-through method (LeBude and Bilderback, 2009) was conducted and a 50 mL leachate sample was collected from each pot. Samples were stored at 4 °C until the following day, when pH and electrical conductivity (EC) were measured (HANNA HI9814 GroPro; Hanna Instruments, Woonsocket, RI). They were then frozen until they could be analyzed for nutrient concentration. After thawing, the leachates were filtered (Whatman #2 filter paper; Whatman Ltd., Kent, UK). To determine Si concentration, 9.5 mL of 2.1% potassium hydroxide (KOH) was added to a 0.5 mL aliquot of leachate, and the solution was analyzed using inductively coupled plasma optical emission spectroscopy (ICP-OES, iCAP 6300 Duo; Thermo Electron Corp., Waltham, MA). To determine leachate macro- and micronutrient concentrations, 9 mL of 3.89% nitric acid was added to a 1 mL aliquot of leachate, and the solution was analyzed using ICP-OES.

Flower number was recorded for petunia and included open and senesced flowers. Petunia and sunflower plants were harvested at the soil surface and divided into flowers, leaves, and stems. For petunia, flowers were defined as all floral organs except sepals, and included buds with petal coloration, open flowers, and senesced flowers. For sunflower, the primary inflorescence as well as any axillary inflorescences or buds with petal coloration were considered flowers. Leaves were detached at the base of the petiole. The stem component included stems, petioles, sepals (petunia only), and immature flower buds or inflorescences. Roots were gently washed in reverse osmosis (18 MΩ) water to remove the substrate. Each tissue was individually dipped in 0.1 M HCl, rinsed in 18 MΩ water, and placed in a paper bag. Samples were placed in a forced air drying oven at 60 °C for 3 d, and then weighed for dry weight. Each sample was ground individually for tissue elemental analysis using a mortar and pestle (flowers, leaves, and roots) or coffee grinder (stems).

Table 1. Total silicon (Si) concentration in the irrigation water, fertilizer, soilless substrate, and rice hulls used in this study.

Source	Total Si concn
Reverse osmosis water (18 MΩ)	ND[z]
Fertilizer (20N–4.4P–16.6K)	ND
85 sphagnum peat: 15 perlite substrate[y]	23,109 mg·kg^{-1}
Parboiled rice hulls	76,010 mg·kg^{-1}

[z]<0.01 mg·L^{-1}.
[y]Formulated on a volume basis.
ND = not detected.

Foliar nitrogen (N) was determined by measuring ≈2.5 mg of dry tissue into tin capsules (Costech Analytical, Valencia, CA) and analyzing with a CHN analyzer (vario MICRO cube; Elementar, Hanau, Germany). Remaining elements were determined using ICP-OES. For all macronutrients and micronutrients except N and Si, ≈0.25 g of dry tissue was placed in a Teflon vessel and 5 mL of nitric acid was added. Samples were heated in a programmable microwave (MARS 6; CEM Corp., Matthews, NC) by ramping the temperature up to 200 °C over 15 min, maintaining 200 °C for 15 min, and then cooling to room temperature. Next, 1.5 mL of hydrogen peroxide was added, solutions were reheated to 200 °C and maintained for an additional 5 min. After cooling, 12 mL of 18 MΩ water was added and the solutions were filtered (Whatman #2). A 1.3 mL aliquot of solution was diluted with 8.7 mL 18 MΩ water and analyzed using ICP-OES.

Analysis of tissue for Si concentration followed a similar procedure to that described previously. Approximately 0.15 g of dry tissue was weighed and placed in a Teflon vessel. Three milliliter of 7.5 M KOH was added, and the solutions were heated in a programmable microwave as described. After cooling, 2 mL of hydrogen peroxide was added and the solutions were reheated. After the second heating event, 10 mL of 18 MΩ water was added and then the solutions were filtered. Finally, a 1 mL aliquot of solution was diluted with 9 mL of 18 MΩ water and analyzed using ICP-OES.

The experimental design was completely randomized, and each species was analyzed separately. Data were subjected to analysis of variance using SAS 9.3 (SAS Institute, Inc., Cary, NC). Means were separated with Tukey's honest significant difference test.

Results and Discussion

The incorporation of rice hulls to the soilless substrate did not affect flowering for sunflower or petunia. No significant differences in flower number (petunia) or days to flower occurred when 20% rice hulls were added to the substrate (Tables 2 and 3). Previously, we found that Si supplementation, provided as continuous 2 mM potassium silicate fertilization, hastened flowering in sunflower 'Pacino Gold' and increased flower number in petunia 'Dreams

Table 2. Plant growth and tissue silicon (Si) of petunia (*Petunia ×hybrida* 'Dreams Pink') grown in an 85 sphagnum peat: 15 perlite soilless substrate amended with 0% or 20% rice hulls (by volume).

	% rice hulls			
	0	20	HSD[z]	*P* value
Days to flower	42.7	41.6	—	0.0748
Flower number	19.2	17.6	—	0.1113
Leaf dry weight (g)	2.68	2.10	0.21	<0.0001
Stem dry weight (g)	3.85	3.30	0.32	0.0012
Flower dry weight (g)	1.16	1.10	—	0.3756
Root dry weight (g)	0.25	0.30	—	0.0537
Aboveground dry weight (g)	7.69	6.50	0.54	<0.0001
Total dry weight (g)	7.94	6.80	0.57	0.0002
Leaf Si (mg·kg^{-1})	946.3	2,036.2	315.7	<0.0001
Stem Si (mg·kg^{-1})	146.4	300.6	55.5	<0.0001
Flower Si (mg·kg^{-1})	232.0	247.1	—	0.7918
Root Si (mg·kg^{-1})	157.2	1,237.0	637.1	0.0015
Leaf Si (mg/plant)	2.50	4.16	0.66	<0.0001
Stem Si (mg/plant)	0.57	0.98	0.21	0.0003
Flower Si (mg/plant)	0.27	0.28	—	0.2537
Root Si (mg/plant)	0.04	0.36	0.17	0.0006
Aboveground Si (mg/plant)	3.34	5.42	0.64	<0.0001
Total Si (mg/plant)	3.38	5.78	0.69	<0.0001

[z]Tukey's HSD value ($\alpha = 0.05$).
HSD = honestly significant difference.

Table 3. Plant growth and tissue silicon (Si) of sunflower (*Helianthus annuus* 'Pacino Gold') grown in an 85 sphagnum peat: 15 perlite soilless substrate amended with 0% or 20% rice hulls (by volume).

	% rice hulls			
	0	20	HSD[z]	*P* value
Days to flower	63.7	65.1	—	0.2553
Leaf dry weight (g)	2.42	2.20	0.14	0.0022
Stem dry weight (g)	2.89	2.65	—	0.1452
Flower dry weight (g)	3.57	2.99	0.46	0.0144
Root dry weight (g)	1.15	1.03	—	0.0930
Aboveground dry weight (g)	8.87	7.83	0.41	<0.0001
Total dry weight (g)	10.02	8.86	0.44	<0.0001
Leaf Si (mg·kg^{-1})	1,260.1	10,909.9	1,129.1	<0.0001
Stem Si (mg·kg^{-1})	42.7	303.5	20.5	<0.0001
Flower Si (mg·kg^{-1})	41.2	252.3	37.5	<0.0001
Root Si (mg·kg^{-1})	174.1	895.1	19.9	<0.0001
Leaf Si (mg/plant)	3.05	23.76	2.22	<0.0001
Stem Si (mg/plant)	0.13	0.82	0.24	<0.0001
Flower Si (mg/plant)	0.14	0.77	0.08	<0.0001
Root Si (mg/plant)	0.21	0.95	0.25	<0.0001
Aboveground Si (mg/plant)	3.32	25.35	2.47	<0.0001
Total Si (mg/plant)	3.53	26.30	2.60	<0.0001

[z]Tukey's HSD value ($\alpha = 0.05$).
HSD = honestly significant difference.

Pink' across a range of P concentrations (Boldt et al., 2015), but that did not occur in the present study. Kamenidou et al. (2010) observed earlier flowering in gerbera (*Gerbera* hybrid L. 'Acapella') when supplemental Si was provided as rice husk ash substrate incorporation, hydrous potassium silicate substrate incorporation, or weekly sodium silicate foliar sprays, but not weekly potassium silicate drenches. However, although Kamenidou et al. (2008) noted no impact on days to flower for sunflower 'Ring of Fire' when rice husk ash or hydrous potassium silicate was incorporated into the soilless substrate or sodium silicate was supplied as a weekly foliar spray, the application of weekly potassium silicate drenches delayed anthesis by 3–5 d as the concentration of Si supplied increased from 50 to 200 mg·L^{-1}, respectively. These differing results across studies may be because of the Si source, Si concentration supplied, or concentration of plant-available Si, as well as species, cultivar, and environmental conditions.

Petunia flower and root dry weights were similar for plants grown in rice hull–amended and nonamended substrates, whereas leaf and stem dry weights were greater in plants grown in the nonamended substrate (Table 2). Likewise, sunflower root dry weights were similar for both treatments and sunflower leaf dry weight was greater for plants grown in the nonamended substrate (Table 3). However, sunflower stem dry weight was similar for both treatments and inflorescence dry weight was greater in the nonamended treatment. Total aboveground dry weight of petunia and sunflower was 1.04 g (13%) and 1.19 g (18%) greater, respectively, in plants grown in the nonamended substrate. This differs from a previous study in which petunia and sunflower shoot dry weight was unaffected by the addition of 2 mM potassium silicate to the fertilizer solution (Boldt et al., 2015). However, observed differences in aboveground dry weight in the present study may be due to changes to the chemical and physical properties of the soilless substrate due to the incorporation of 20% rice hulls rather than from Si supplementation, factors which are confounded. For example, Evans and Gachukia (2004) observed lower shoot dry weights in tomato (*Lycopersicon esculentum* Mill. 'Better Boy') and pansy (*Viola ×wittrockiana* 'Bingo Azure') when parboiled rice hulls were substituted for perlite in a peat substrate. In spite of the statistically significant differences in tissue dry weights in our study, they were not large enough to affect plant quality, and all plants were commercially acceptable.

In almost every instance, tissue from plants grown in the rice hull–amended substrate had a higher Si concentration compared with those grown in a nonamended substrate. The exception was petunia flowers, which had similar Si concentrations (232 and 247 mg·kg^{-1} in nonamended and amended substrates, respectively; Table 2). Silicon concentration was greatest in leaf tissue for both species. Sunflower, classified as a Si accumulator, had higher leaf Si concentrations than petunia, a low Si accumulator (10,909 and 2036 mg·kg^{-1}, respectively). In sunflower, a comparison of Si concentration revealed leaves had the greatest Si concentration, and roots, stems, and flowers had similar Si concentrations, regardless of Si treatment (statistics not shown). A similar pattern was observed in petunia in nonamended plants. In rice hull–amended petunia, however, Si concentration was greatest in leaves, then roots, followed by stems and flowers.

Differences in Si concentration between nonamended and rice hull–amended plants highlights differential Si accumulation and distribution between sunflower and petunia. The addition of rice hulls to the substrate increased Si concentration considerably in all sunflower tissues: 414% in roots, 512% in flowers, 611% in stems, and 766% in leaves. In petunia, however, aboveground Si concentration did not increase to the same degree; it only increased 7% in flowers, 105% in stems, and 115% in leaves. This is characteristic of nonaccumulators, which do not accumulate high concentrations of Si in foliar tissue, even when Si is amply available. Although nonaccumulators often exhibit an increase in foliar Si concentration in response to biotic or abiotic stress, foliar uptake is still typically much less than in Si accumulator species. However, the addition of rice hulls to the substrate resulted in a 687% increase in root Si concentration of petunia, from 157 to 1237 mg·kg^{-1} (Table 2). Lewin and Reimann (1969) observed a similar phenomenon and reported that plants with a high Si content most often accumulate it in the aerial portion, whereas plants with low Si accumulation may have root Si content equal to or greater than shoot Si content.

Silicon tends to move in the transpiration stream and accumulate at the terminus in

plants, i.e., in leaves, panicles, and grains (Yoshida et al., 1962). Although evapotranspirational water loss via flowers is less than that via leaves, it is a source of water loss. Galen et al. (1999) reported that flower buds and corollas are a source of water loss in *Polemonium viscosum*, averaging 0.036 and 0.024 g of water per flower per hour at the bud phase and at maturity, respectively. Whiley et al. (1988) observed that evapotranspiration in avocado (*Persea americana* cv. Fuerte) flowers was 60% of that of leaves, and ≈13% of total canopy water loss resulted from floral organs. Therefore, flowers could potentially accumulate high concentrations of Si. Sunflower inflorescences did indeed exhibit increased Si accumulation when plants were grown in the rice hull–amended substrate, compared with the nonamended substrate (252 vs. 41 mg·kg^{-1}, respectively; Table 3). Petunia, however, did not show this response (247 vs. 232 mg·kg^{-1}, respectively; Table 2). One plausible explanation may be the fact that sunflowers have a primary inflorescence that remains on the plant for a couple of weeks before senescence, whereas petunia flowers are short-lived in comparison, often lasting only a day or two. This may not be sufficient time to accumulate Si in the flowers.

We were interested in Si accumulation in various plant tissues and the potential implications for biotic and abiotic stress tolerance. Plants often accumulate elevated foliar Si concentrations in response to stress (Frantz et al., 2011; Zellner et al., 2011). Although Si is not very mobile in the plant once deposited in leaves or other aerial portions of the plant (Yoshida et al., 1962), it is currently not clear if plants need to take up additional Si from the soil, substrate, or nutrient solution at the onset of a stress or if they can export some or all of the accumulated Si contained in the roots. It was somewhat surprising that roots of petunia, a nonaccumulator, had a greater Si concentration than roots of sunflower, a Si accumulator, because most of the focus on defining plants as Si accumulators or nonaccumulators is based on foliar Si concentration.

It has previously been shown that Si can mitigate botrytis infection in greenhouse-grown crops. Supplying 0.67 mM Si in a hydroponic nutrient solution reduced the leaf area infected by botrytis 3 d postinoculation in lettuce (*Lactuca sativa* L.), tomato, and pepper (*Capsicum annuum* L.) (Pozo et al., 2015). Flowers are susceptible to botrytis infection, especially during transport from the greenhouse to the final retail destination. Therefore, if flowers accumulated Si (with or without disease pressure), it could be evaluated as a potentially useful disease management strategy. Based on our results, however, petunia flowers did not exhibit increased Si concentrations when grown in a Si-amended substrate in the absence of disease pressure from botrytis. Sunflower did exhibit increased inflorescence Si accumulation, but it was very low compared with foliar Si concentration. Follow-up studies would be needed to determine what concentration of floral Si is necessary to deter botrytis infection, if Si in roots can be mobilized to flowers following infection, and whether the presence of botrytis can result in increased Si uptake.

In addition to observing Si accumulation in plants grown in a Si-amended substrate, the internal distribution of Si was also of interest. Silicon content (g/plant) varied with treatment. Nonamended and rice hull–amended petunias accumulated, on average, 3.38 and 5.78 g Si per plant, respectively, whereas sunflowers accumulated 3.53 and 26.30 g Si per plant, respectively. Silicon was distributed predominantly in leaf tissue, although it varied with species. In rice hull–amended petunia, the distribution was 72% in leaves, 17% in stems, 6% in roots, and 5% in flowers. In rice hull–amended sunflower, Si content was distributed 91% in leaves, 3% in stems, 3% in roots, and 3% in flowers (calculated from Tables 2 and 3). This differs from the aboveground distribution reported by Jones and Handreck (1967) for oat, a monocot and Si accumulator, which accumulated almost 41% of total SiO_2 in inflorescences, 28% in leaf blades, 17% in leaf sheaths, 11% in culms, and less than 1% in caryopses.

Leachate Si concentration was 3.28 and 15.69 mg·L^{-1} for petunias grown in nonamended and rice hull–amended substrates, respectively, and 0.42 and 2.06 mg·L^{-1}, respectively, for sunflowers. The lower leachate Si concentration for sunflower, relative to petunia, was likely the result of increased plant Si uptake (26.30 g for sunflower and 5.78 g for petunia) and depletion of the Si pool in the substrate solution. Silicon supplementation was supplied by the addition of rice hulls. Sphagnum peat also supplies low concentrations of plant-available Si to the substrate solution, as evidenced by Si present in the leachates of the nonamended treatments (Table 4). Frantz et al. (2010) reported less than 1 mg Si extracted per liter of water per gram of sphagnum peat mix, whereas parboiled rice hulls released more than 8 mg of Si per liter of water per gram of rice hulls. In an analysis of total Si following complete digestion, they reported 498 mg·kg^{-1} Si in sphagnum peat mix and 75,468 mg·kg^{-1} in parboiled rice hulls (Frantz et al., 2010). Their Si concentration reported for rice hulls corresponds closely to the total Si concentration we measured for the batch of rice hulls used in our study (76,010 mg·kg^{-1}; Table 1). This calculates to the addition of 956 mg Si per container, although not all of the Si is immediately soluble and plant available.

Leachate pH was similar between rice hull–amended and nonamended treatments for petunia and sunflower (Table 4). Electrical conductivity of sunflower leachates was higher in the nonamended treatment compared with the rice hull–amended treatment (3.58 and 3.07 mS·cm^{-1}, respectively), whereas EC was similar in petunia across both treatments (0.93 and 0.94 mS·cm^{-1}, respectively). These EC values were less than (petunia) or within (sunflower) the optimal range of 2.0–3.5 mS·cm^{-1} (Cavins et al., 2000). Although leachate EC values were low for petunia, both treatments had similar foliar N concentrations and were within the recommended range (Table 5), indicating adequate fertilizer rates. There were some sporadic and inconsequential differences in other foliar nutrient concentrations, as well as some foliar nutrient concentrations falling less than published recommended ranges (Gibson et al., 2007). Petunia foliar S and Zn concentrations were lower than recommended in both treatments, and foliar K and Cu concentrations were lower than recommended in the non-amended treatment only. Sunflower foliar N, K, and Cu were lower than recommended in both treatments. Despite differences and some nutrients being less than recommended ranges, there were no visual symptoms of nutrient deficiency in either species.

In addition to Si, leachates differed in concentration for many macro- and micronutrients (Table 4). For example, leachates

Table 4. Leachate[z] pH, electrical conductivity (EC), silicon (Si), macronutrient, and micronutrient concentrations of petunia (*Petunia ×hybrida* 'Dreams Pink') and sunflower (*Helianthus annuus* 'Pacino Gold') grown in an 85 sphagnum peat: 15 perlite soilless substrate amended with 0% or 20% rice hulls (by volume).

Plant	Rice hull (%)	pH	EC (mS·cm^{-1})	Si	P	K	Ca	Mg	S	B	Cu	Fe	Mn	Zn
				mg·L^{-1}										
Petunia	0	5.66	0.93	3.28	47.4	138.9	429.9	125.6	5.56	0.14	0.08	13.61	0.61	1.13
	20	5.59	0.94	15.69	45.1	184.0	331.5	101.3	4.03	0.14	0.10	9.71	1.21	1.24
	HSD[y]	—	—	1.86	—	40.2	66.5	20.6	0.85	—	—	2.23	0.21	—
Sunflower	0	4.87	3.58	0.42	44.3	31.9	105.3	35.3	3.36	0.20	0.08	4.40	0.16	0.84
	20	4.79	3.07	2.06	49.6	31.0	98.7	36.5	1.93	0.24	0.06	2.73	0.39	0.64
	HSD	—	0.46	0.47	—	—	—	—	0.40	0.03	0.01	0.60	0.08	0.08

[z]Leachates were collected at the end of the experiment, 6 weeks after transplant.
[y]Tukey's HSD value ($\alpha = 0.05$). If the value is not provided, ANOVA P-value >0.05.
HSD = honestly significant difference; ANOVA = analysis of variance.

Table 5. Foliar macronutrient (% dry weight) and micronutrient (mg·L^{-1}) concentration of petunia (*Petunia ×hybrida* 'Dreams Pink') and sunflower (*Helianthus annuus* 'Pacino Gold') grown in an 85 sphagnum peat: 15 perlite soilless substrate amended with 0% or 20% rice hulls (by volume).

		N	P	K	Ca	Mg	S	B	Cu	Fe	Mn	Mo	Zn
Plant	Rice hull (%)	% dry wt						mg·L^{-1}					
Petunia	0	5.78	0.85	2.81	3.04	1.22	0.24	30.9	1.9	112.9	86.6	4.0	26.5
	20	5.76	0.91	3.83	3.31	1.21	0.20	23.9	10.5	111.4	145.7	7.1	31.3
	HSD[z]	—	—	0.28	0.19	—	—	2.7	—	—	8.5	1.2	2.6
Sunflower	0	4.92	1.13	3.08	4.58	1.18	0.25	116.0	1.9	136.0	122.4	2.8	98.6
	20	4.88	1.22	2.89	5.19	1.21	0.22	141.5	2.5	106.4	259.9	6.0	100.6
	HSD	—	0.06	—	0.32	—	0.01	7.8	0.6	16.4	16.1	0.8	—

[z]Tukey's HSD value ($\alpha = 0.05$). If the value is not provided, ANOVA P-value >0.05.
HSD = honest significant difference; ANOVA = analysis of variance.

from rice hull–amended substrates in which petunias were grown had higher concentrations of K and Mn and lower concentrations of Ca, Mg, S, and Fe. Leachates from rice hull–amended substrates in which sunflowers were grown had higher concentrations of B and Mn, and lower concentrations of S, Cu, Fe, and Zn. As stated previously, this may be attributable to the nutrient composition of the rice hulls or to the influence of Si on the uptake of other macro- and micronutrients. In a previous study, the addition of 10% parboiled rice hulls to a sphagnum peat: perlite substrate resulted in increased concentrations of P, K, B, and Mn and a lower concentration of S in leachate samples compared with the nonamended control, all of which were also observed in either petunia or sunflower leachate samples in our present study (J.E. Altland and J.C. Locke, unpublished data).

Conclusions

This study quantified Si accumulation and distribution in roots, stems, leaves, and flowers of two ornamental plant species. It revealed that Si concentration, as well as Si content, varied considerably with species and tissue. Silicon accumulator and nonaccumulator species, although having very different foliar concentrations, can have similar root Si concentrations, as was observed for sunflower and petunia in this study. Therefore, classifying species as Si accumulators or nonaccumulators solely on the basis of foliar Si concentration does not necessarily provide a complete picture of total plant Si accumulation and uptake capacity. The localization of Si within a plant could potentially influence its ability to effectively mitigate stress events (e.g., floral Si accumulation may provide control of botrytis whereas root accumulation may provide control of pythium), but follow-up studies will be needed to test this hypothesis.

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