Capítulo 6

Silicon in Ornamental Crops: Detection, Delivery, and Function

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Introduction

Silicon (Si) is not considered to be an essential plant nutrient because most plant species can complete their life cycle without it (Marschner, 1995). Still, some plant species can accumulate Si at concentrations higher than many essential macronutrients (Epstein, 1999). Until recently, it was not known whether ornamental crops, most of which are dicots, can take up and accumulate appreciable amounts of Si in their tissues. Voogt and Sonnenfeld (2001) reported significant uptake in the ornamentals gerbera, rose, and asters, and Voogt (2005) later reported silicon uptake in African violets. Frantz et al. (2006) reported silicon uptake in New Guinea impatiens, and later Frantz et al. (2008) reported silicon concentrations of leaf tissue of fourteen ornamental crop species, ranging from a low of about 200 mg kg^{-1} in petunia to a high of nearly 1.3% (13,000 mg kg^{-1}) dry weight in zinnia. Mattson and Leatherwood (2010) also evaluated nearly two dozen ornamental crops and found approximately half accumulated Si in leaf tissue to above 1,000 mg kg^{-1}. Given the multitude of ornamentals grown commercially, still relatively few species have been evaluated for their uptake potential.

Delivering silicon to plants in a commercial setting is an additional challenge, and there is debate regarding the most effective mechanism of

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delivery (as a spray or fertilizer supplement). A few commercial Si-containing products have become available in retail (e.g. Pro-TeKt, Dyna-Gro, Richmond, CA) in recent years, but growers are reluctant to try these products due to their expense, the perception that silicon-based materials clog nozzles and drippers, and the unknown benefits of Si on their crop. However, the floriculture industry has begun moving towards "sustainable" production, which means among many things, decreasing utilization of synthetic "agricultural chemicals." In other words, naturally derived compounds or natural sources of materials are becoming increasingly preferred over man-made or synthetic materials.

Many materials contain naturally high levels of Si, most notably rice hulls. Rice hulls have been used as a perlite replacement in the last five years (Evans and Gachukia, 2004), but have not been investigated extensively as a Si source. In some cases, it may be possible to incorporate a Si-containing material into a rooting substrate in order to provide a steady supply of Si to the crop. Kamenidou et al. (2009, 2010) utilized rice husk ash as a Si source, and rice husk ash is also being utilized to supplement Si in field plots (Prakash et al., 2010). Calcium silicate slag has also been used in field applications for Si supply (Trenholm et al., 2004).

In research settings, Si can easily be considered a contaminant. This is an important point to consider when samples are prepared for quantitative or qualitative analysis since trace amounts can alter the concentration of a sample easily. Even in typical plant production, we inadvertently add Si in small amounts through substrate selections, fertilizers, water sources, and pesticides. While material safety data sheets list silica by weight of some compounds, soluble Si is not characterized, and it is difficult to evaluate the potential contribution of Si from these sources in research or commercial production.

Beneficial effects from Si are well documented for many field crops and a few ornamentals. Improved dry mass and yield (Ma et al., 1989) and enhanced pollination (Korndorfer and Lepsch, 2001) have been reported in field crops, while increased disease resistance (Bélanger et al., 1995; Datnoff and Rodrigues, 2005; Gillman et al., 2003; McAvoy and Bible, 1996; Rodrigues et al., 2004) is commonly reported for both field and ornamental crops. Mattson and Leatherwood (2010) documented changes in growth habit in a wide range of ornamental species when fertigated with a supplemental Si source. In preliminary studies, they also documented enhanced salt tolerance of most ornamental crops if supplemental Si was present (Mattson, personal communication). Ranger et al. (2009) observed

decreased fecundity of aphids feeding on Si-supplemented zinnia compared to control plants.

Interestingly, Si supplementation does not always provide a benefit to plants. For example, Kamenidou et al. (2008) reported sunflower deformation, stunting, and other growth abnormalities when plants were supplied 100 to 200 mg L^{-1} supplemental Si as drenches. Hogendorp et al. (2009) saw no effect of supplemental silicon fertilization of a woody ornamental ficus (fiddleleaf fig; *Ficus lyrata*) on citrus mealybug (*Planococcus citri*).

This paper discusses the concentrations of Si found in a variety of ornamental crops, as well as a contaminant in commonly encountered materials and solutions. We also investigated different materials that may be cost-effective for use in Si delivery in container agriculture, and documented some benefits from supplemental Si for the ornamental crop *Zinnia elegans* receiving supplemental Si.

Materials and Methods

Evaluating Species for Si Uptake Potential

Seedlings or cuttings were initially germinated or rooted using foam cubes (15-mm x 15-mm x 30-mm each; LC1-type, Smithers-Oasis North America, Kent, OH). When the seedlings or rooted cuttings had visible roots at the edge of the rooting cube (time varied depending on species), they were transplanted into holes in the lids of opaque plastic 5-L, buckets containing aerated hydroponic solution, at a planting density of up to six plants per tub, and placed on a greenhouse bench. The solution was a modified Hoagland's solution containing 2.5 mM KNO_3, 2.5 mM $Ca(NO_3)_2$, 0.5 mM KH_2PO_4, 1.0 mM $MgSO_4$, 70 µM Fe as Fe-DTPA, 4.5 µM MnC12, 0.75 µM ZnC12i 0.75 µM $CuC1_2$, 22.5 µM H_3BO_3, and 0.05 µM Na_2MoO_4 (verbena contained half this rate for macronutrients because of their salt sensitivity) with or without 1.0 mM K_2SiO_3. K_2SiO_3 was synthesized with fumed silica (SiO_2, 0.007 µm particle size) dissolved in 0.1 M KOH. Ten tubs were used for each species with half the tubs containing Si and the other half without Si. No glassware was used in making the nutrient solution, and 18 mega-ohm purified water was used exclusively during the course of the trial to minimize Si contamination. The pH was adjusted to 5.7 with H_2SO_4 or KOH before nutrient solutions were added to the hydroponic containers.

Sampling and analyses were performed according to the ICP-OES method described in Frantz et al. (2008). Briefly, 0.15 g ground tissue or

substrate material was digested in 7.5 M KOH in a programmable microwave (MARS Express; CEM Corp., Matthews NC). One ml of the digested solution was diluted with 9 ml deionized water (18-mega-ohm purity) and injected into the ICP-OES (Model IRIS Intrepid II; Thermo Electron Corp., Waltham, Mass.). Every 20 samples, a rice standard containing 0.44% Si was run that had been digested in a similar manner as the test species.

Analysis of Si-containing Materials

Water extraction of soils showed good correlations with leaf Si concentrations (Prakash et al., 2010), so for simplicity, extractions were performed using deionized water purified to 18.2 mega-ohm. We obtained five slag materials (by-product in the smelting process during metal processing) from different furnace types from a commercial source (The Levy Company, Portage, IN, US) that contained varying amounts of silicates based on preliminary EDXA. About 1.5 g of each of these, along with par boiled rice hulls (PBH), a commercial sphagnum peat mix, Miscanthus x giganteus milled ~ 0.5 mm particle size, and wollastonite (from R.T. Vanderbilt Co., Norwalk, CT, US) were combined with 40 ml deionized water in a 50 ml plastic vial and shaken daily for 3 weeks. Solution was filtered and analyzed by ICP as described above.

If larger sample sizes were analyzed, a glass extraction column was utilized, which enabled component mixtures to be analyzed either singly or as a series of saturated media extracts (SME) in volumes comparable to containerized production volumes. Prior to extraction of materials, empty glass columns were tested for Si leaching; none was detected. Materials were placed in a series of glass columns each with a false bottom made of perforated Plexiglas. Once the materials were added, deionized water was added as the solvent in a SME, once per day for 10 days to simulate irrigations of a pot in a production system. Leachate was collected, filtered, and amount of Si determined in solution by ICP.

Samples of commonly encountered solutions (Table 1) and pesticides (Table 2) were analyzed for Si concentration. The solutions were measured by first mixing the solution with KOH to make a 3% by volume KOH-solution mixture. The solid pesticides were extracted in 20 ml deionized water for 24-h and expressed as mg Si extracted per g raw pesticide. Liquid pesticide samples were made by mixing 0.1 ml of pesticide solution in 100 ml deionized water. Finally, the pesticide mixtures or extractants were mixed

with KOH to make a 3% by volume KOH-solution mixture that was subsequently analyzed by ICP.

Powdery Mildew Inoculations

Zinnia elegans seeds were prepared as described above. After two weeks of seedling establishment, seedlings were transplanted into opaque plastic hydroponic tubs consisting of either half-strength Hoagland's solution or half-strength Hoagland's plus 2.0 mM Si from potassium silicate. Plants were allowed to grow in these solutions for three weeks under controlled environment conditions of 16-h days, 25°C D, 22°C night, with relative humidity approximately 80%.

Table 1. Amount of Si dissolved in solution from various sources. Samples were prepared by mixing the solution with 3.5% HNO3.

Source	Si in solution (mg L^{-1})
Ground water (Ohio, US)	2.49 to 4.94
Ultra-pure water	0.3 (estimated)*
Treated water ("city" water, Ohio, US)	1.56
fertilizer	0.83 to 5.25
Ocean water	0.42 to 0.80
Recirculating/recycled water	1.76 to 4.18
Beer	17.01 to 24.3
Wine	15.35

*background Si concentrations were estimated based on comparing the raw signal from the ICP, above background "noise" level, to the high standard raw signal.

Table 2. Concentration of silicon in some common pesticides. ND indicates Si was not detected in ICP-OES analysis.

Pesticide	Si (mg Si L^{-1} water per g pesticide)	Si (mg Si L^{-1} concentrate)
Marathon Olympic 1% granular & nursing insecticide	3.29	
Merit 75 WP insecticide	8.69*	
Strike 50 WDG systemic fungicide	6.79	
Olympic Compass 50 WDG	1.79	
Bonide remedy fungicide	ND	
Sevin Garden Tech concentrated bug killer		10.97*
Conserve		1.29*
Floramite		3.08
Physan 20 algicide/microbialcide		ND
Mustard algaecide		ND
Volck Oil Spray (Ortho dormant season insect killer)		ND
Sunspray untrafine year round pesticide oil		ND
Safer Insecticidal Soap		ND
Green Light Neem Concentrate		ND
Dyna-Gro Neem Oil		ND
Safer Bioneem Concentrate		ND
Malathion Spectracide		ND
All Natural Deer Stopper		ND
Spinout Root Control Coating		ND
Subdue Maxx		ND
Ortho-Max Bug-b-gone		ND

*indicates Si not listed in Material Safety Data Sheet.

After three weeks of growth, zinnia leaves from infected plants grown in a greenhouse environment were used as inoculum for the treatment plants. A 14.5 mm leaf disk was cut from a heavily infected leaf of the stock plants with a cork-borer and placed directly on a mature leaf of a plant receiving

supplemental Si or no Si. In this way, a single leaf could be monitored for disease progression for the duration of each experiment. Treatments were replicated three times, with each replicate consisting of an equivalent individual leaf on a separate plant, and each experiment was repeated three times. Quantitative analysis for all three trials was calculated based on a ratio of surface area of infection to total leaf surface area. Digital analysis software (Assess, American Phytopathological Society, St. Paul, MN, US) was utilized to calculate all areas of infection relative to the total surface area of the leaf.

Cu Toxicity

Zinnia was grown as described above with the following exceptions: six different nutrient solution combinations were utilized including control (1.5 µM Cu and 0.10 mM Si), +Si (elevated Si, 1.5 µM Cu and 1.7 mM Si), +Cu-1 (elevated Cu-1, 30 µM Cu and either 0.10 mM Si) and +Cu-2 (elevated Cu-2, 50 µM Cu and 0.1 mM Si), +Cu-1+Si (elevated Cu-1 with Si, 30 µM Cu and 1.7 mM Si), and +Cu-2+Si (elevated Cu with Si, 50 µM Cu and 1.7 mM Si) with four replications (each replicate consisted of one hydroponic container that held 3 plants). The experiment was conducted twice with one set used for tissue analysis and the other set used for enzymatic assays.

After 2 weeks of treatment, leaves, stems (combined for enzymatic assays), and roots were harvested, rinsed with distilled water, blotted dry, and fresh weight was determined. For tissue analysis, tissue was dried in a forced air oven at 55°C for 3 d and used for tissue analysis as described above. For other tests, tissue was immediately frozen in liquid nitrogen and stored at -80 °C for subsequent use. Phenylalanine ammonia lyase (PAL, EC 4.3.1.5) activity was measured by the method described in Liang et al. (2005) with some modifications described in Li et al (2008).

Results and Discussion Species Uptake Potential Utilizing ICP-OES Quantification

Si was detected in all tissue samples harvested from plants supplied with Si, but the value varied greatly among species (Table 3). Nearly 50% of all species evaluated had leaf tissue concentrations above 1,000 mg kg^{-1} (0.1%). This is the approximate nutrient concentration threshold that is used in distinguishing micronutrients from macronutrients. Zinnia (12,000 mg kg^{-1}; 1.2%), cucumber (10,400 mg kg^{-1}; 1.04%), garden mum (10,100 mg kg^{-1};

1.01%) and verbena (8,000 mg kg^{-1}; 0.8%) had the highest concentrations while onion (121 mg kg^{-1}; 0.012%), ornamental tobacco (102 mg kg^{-1}; ;0.01%), and sedum (87 mg kg^{-1}; 0.0087%) had the lowest. Si was not detected in many of the control leaves (data not shown) indicating the concentration of Si was below detectable limits in all replicate samples.

Table 3. Silicon concentration in the leaves of many horticultural crops grown hydroponically with 1.0 mM Si. Plants were exposed for 3 weeks after transplanting and establishment in a nonrecirculating hydroponic system. Values of Si are in newly fully matured leaves initiated after Si exposure. Not shown are the control plants grown without supplemental Si in solution.

Crop	Si Content (mg/kg)	Crop	Si Content (mg/kg)
Zinnia elegans (Zinnia)	12,682 +/- 615	*Begonia semperflorens* (Begonia)	649 +/- 128
Chrysanthemum x morifolium (Garden Mum)	10,430 +/- 253	*Coleus forskohlii* (Coleus)	615
Cucumis sativas (Cucumber)	10,164 +/- 133	*Coreopsis verticillata* (Coreopsis)	891+/- 135
Verbena × hybrida (Verbena)	8,417 +/- 2080	*Cyclamen persicum* (Cyclamen)	613 +/- 256
Citrullus lanatus (Watermelon)	6,340+/- 154	*Capsicum annuum* (Bell pepper)	550 +/- 16
Helianthus annuus (Sunflower)	5,180 +/- 194	*Pelargonium × hortorum* (Zonal Geranium)	539 +/- 57
Cucurbita pepo (Pumpkin)	4,591+/- 605	*Salvia splendens* (Salvia)	529 +/- 98
Torenia *fournieri* (Torenia)	4,341 +/- 937	*Antirrhinum majus* (Snapdragon)	501 +/- 68
Dahlia × hybrida (Dahlia)	3,714 +/- 1,243	*Rosa chinensis* (Mini Rose)	478 +/- 165
Streptocarpella saxorum (Streptocarpella)	3,704 +/- 289	*Euphorbia pulcherrima* (Poinsettia)	465 +/- 213
Echinacea purpurea (Purple Coneflower)	3,589+/- 472	*Celosia argenta* (Celosia)	246 +/- 17
Cucurbita pepo (Summer squash)	3,497+/- 135	*Dianthus chenensis* (Dianthus)	362 +/- 94
Rudbeckia hirta (Rudbeckia)	3,469 +/- 781	Hibiscus *moscheutos* (Hibiscus)	362 +/- 32
Phlox subulata (Phlox)	3,249 +/- 870	*Tagetes erecta* (Marigold)	330 +/- 39

Chrysanthemum × *morifolium* (Florist Mum)	2,641 +/- 342	*Vinca* × *hybrida* (Vinca or periwinkle)	330 +/- 36
Impatiens × *hawkeri* (New Guinea Impatiens)	2,314 +/- 135	*Gerbera jamesonii* (Gerbera daisy)	266
Abelmoschus esculentus (Okra)	2,130+/- 360	*Petunia* × *hybrida* (Petunia)	197 +/- 12
Saintpaulia ionanth (African violet)	2,041+/- 45	*Primula polyantha* (Primula)	182
Cucurbita pepo (Winter squash)	2,031 +/- 839	*Spinacia oleracea* (Spinach)	152+/- 22
Impatiens walleriana (Impatiens)	2,008 +/- 131	*Beta vulgaris* (Swiss chard)	152+/- 28
Arabidopsis thaliana (Arabidopsis)	2,000 +/- 91	*Viola* × *wittrockiana* (Pansy)	126 +/- 32
Calibrachoa × *hybrida* (Calibrachoa)	1,536 +/- 50	*Allium cepa* (Onion)	121+/- 14
Lycopersicum esculentum (tomato)	747 +/- 61	*Nicotiana sylvestris* (Ornamental tobacco)	102+/- 17
Lantana camara (lantana)	8780 +/- 1719	*Nicotiana tabacum* (traditional tobacco)	290 +/- 39

Given the thousands of species and cultivars of ornamental plants on the market today, relatively few have been evaluated for potential uptake of Si. *Rosa hybrida* (Gillman et al., 2003; Datnoff et al., 2006), poinsettia (MeAvoy and Bible, 1996), paper daisies (*Helichrysum adenohorum*; Muir et al., 1999) snapdragons (*Antirrhinum majus*; Muir et al., 1999), and New Guinea impatiens (*Impatiens hawkeri*; Frantz et al., 2005) have been investigated previously. Voogt and Sonneveld (2001) and Voogt et al. (2005) evaluated the floricultural crops gerbera (*Gerbera* spp.), carnation (*Dianthus caryophyllus*), heath aster (*Aster ericoides*), poinsettia (*Euphorbia pulcherrima*), African violets (*Saintpaulia ionantha*), and rose (*Rosa*) with aster, poinsettia, African violets, and rose containing appreciable amounts of Si (more than 25 mmol kg^{-1} dry mass). In the most comprehensive survey of ornamental plants yet, Mattson and Leatherwood (2010) evaluated 21 species or cultivars for Si uptake and morphology differences. They found that roughly half accumulated Si above the 1000 mg kg^{-1} threshold. They evaluated nine similar species that we evaluated and the leaf Si concentrations agreed with one another between the two studies.

Is it important for plants to accumulate significant (above 0.1% dry weight) amounts of Si to derive a biological effect? The widespread

assumption has been that non-accumulating species (species that accumulate concentrations similar to micronutrients) do not respond. Voogt and Sonneveld (2001) reported improved manganese distribution in lettuce thereby reducing manganese toxicity in spite of the fact that little Si was taken up (533 mg kg^{-1}). Mattson and Leatherwood (2010) found horticultural traits (size, stature, appearance, etc.) were altered, both positively and negatively, in some crops that did not accumulate Si in leaves compared to control plants. Are the observed effects biological responses (active changes in metabolism) or physical responses occurring in the rootzone (e.g. pH or changes in solubility)? The biological effect in "non-accumulating" species deserves further study.

Background Sources

Silicon was detected in all materials tested (Table 1). While not an exhaustive survey, these numbers represent a sampling of typical Si concentrations in many commonly encountered solutions. Drinking and irrigation water reached up to 5 mg L^{-1} in our tests and fertilizer could potentially add an additional 5 mg L^{-1} of Si. If one assumes a water use efficiency (WUE) of 300 ml of water per g tissue (a typical WUE for a C3 crop) and Si moved passively with the water, tissue concentrations could be expected to be around 3,000 mg kg^{-1}. Since we often observe less than this concentration in Si amended solutions, it suggests an inhibition of Si uptake (less than passive uptake), accumulation in tissues other than leaves, or a lack of Si availability. It was estimated by comparing raw electrical signal at the Si wavelength on the ICP to high standard electrical signal that about 0.3 ing L^{-1} was still present in deionized water that was purified to 18.2 megaohm resistance. For this table, we added this concentration to all other solutions. Since this Si was found in solution, we assume that the measured Si would be plant available.

The presence of Si in these solutions poses a problem in accurately controlling Si "contamination" in research and production scenarios for control plants. Pesticides are another potential source of Si. A common management approach is to utilize various pesticides for controlling unwanted organisms. One-third of the 21 pesticides evaluated contained measurable Si including three in which Si was not listed in the Material Safety Data Sheet (Table 2). Note that the 0.3 mg L^{-1} trace Si detected in the deionized water noted above was not added to each material in this table leading to many non-detectable Si measurements.

Delivery of Silicon

An appropriate and predictable supply of Si to crops is an important aspect of utilizing this element in crop production. As previously discussed, Si is found in varying amounts in a variety of materials and solutions. Slag is a solid material that contains Si and other elements that is produced during the processing of metal. Some companies have expressed interest in its use as a fertilizer supplement in field production, and slag produced from blast oven furnace smelting has been successfully tested in small-scale studies with sugarcane and maize (John Yzenas, Edward C. Levy Company, personal communication). Its chemical composition and properties depends on the origin as well as the metal processing method.

Based on a single, replicated water extraction, we found variation in the amount of Si in aqueous solution among six slag materials, but little variation was observed based on the particle sizes (Figure 1). Interestingly, Slag type #3 that was successful in field application showed the second lowest amount of Si released into solution. Slag type #1 released the most Si in solution of all slag types at 5 mg L^{-1} per g material.

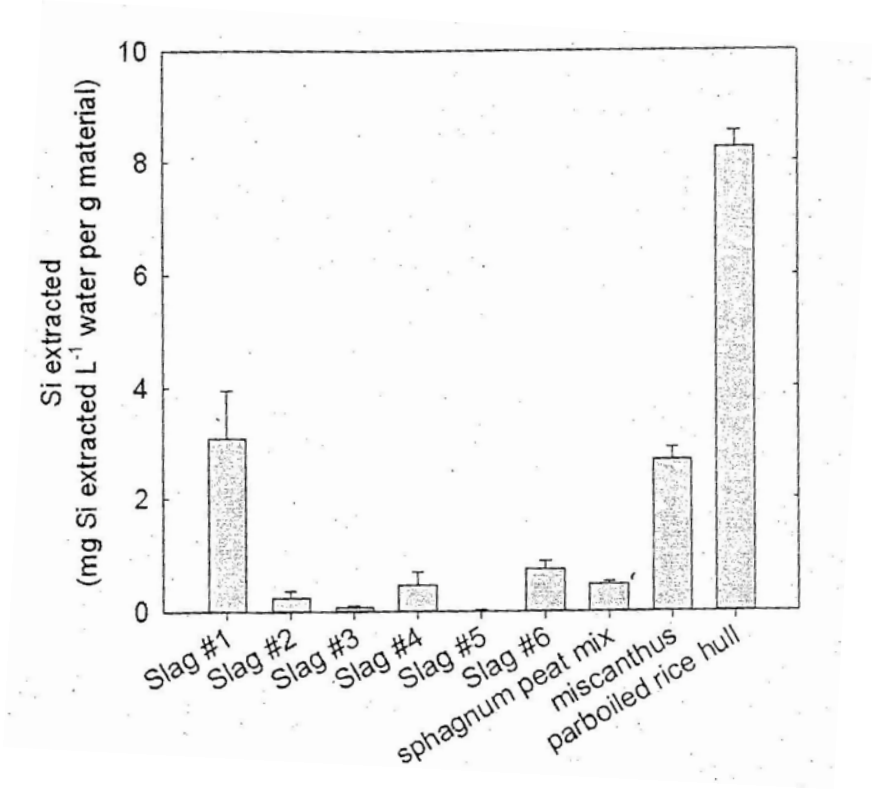

Figure 1. Silicon extracted in 40 ml water from six different slag materials compared to parboiled rice hulls, commercially available peat-based potting mix, and miscanthus biofuel crop. Bars represent average Si in solution of 3 replicate samples. Error bars are one standard deviation of the mean.

Biological materials may also contain significant amounts of Si that is released in solution. A commercial sphagnum-peat based material provides less than 1 mg L^{-1} per g material while par-boiled rice hulls, a material touted to replace perlite in commercial mixes, provides over 8 mg Si extracted L^{-1} solution per g material (Figure 1). Miscanthus is a plant increasingly utilized as a biofuel crop in the US and it too provides appreciable levels of Si.

The approach described here points to a problem inherent in Si research, which is: what is the most appropriate way to evaluate a material's ability to provide Si to a plant? A total Si digestion of a material is useful in some regards, but as Epstein (2001) describes, so much Si is not soluble and

therefore has no role in controlling solution Si. Still, for biological materials, a total Si digestion describes how much is added to a system within a structure that is biodegradable. Therefore, we analyzed total Si as a measure of the maximum amount of Si that may become available in time.

Par-boiled rice hulls contained over 7.5% dry weight of Si, by far the most of any material tested (Table 4). Miscanthus contained well over 1% dry weight and ryegrass straw contained nearly 1% Si. All other materials were well below this threshold, with sphagnum peat moss, the most commonly used substrate in the greenhouse industry, containing only about 500 mg kg^{-1}.

Table 4. Average total Si concentrations in various biological materials potentially useful for substrate amendments and average total Si concentrations (+/- one standard deviation) in leaf tissue of zinnia grown with unamended or amended sphagnum peat mix. N/A indicates not applicable because zinnia were not tested in those materials.

Material	Total Si (mg Si kg^{-1} dry wt)	Total Si in Zinnia leaves* (mg Si kg^{-1} dry wt)
Sphagnum peat mix	498	842 +/- 230
Ryegrass (*Lolium multiflorum*)	9627	N/A
Bamboo (*Phyllostachys aureosulcata*)	2890	3711 +/- 500
Bamboo (*Phyllostachys edulis*)	803	N/A
Par-boiled rice hulls (*Oryza sativa*)	75,468	15,727 +/-1991
Miscanthus (*Miscanthus x giganteus*)	12, 989	14,456 +/- 2281
Switchgrass (*Panicum virgatum*)	3,550	4,394 +/- 685
Willow (*Salix* spp.)	60	680 +/- 91
Pine bark (*Pinus taeda*)	3,544	917 +/- 143
Coconut Coir (*Cocos nucifera*)	3,141	2,168 +/- 284
Wheat straw (*Triticum aestivum*)	13,700	N/A
Cedar chips (*Juniperus virginiana*)	95	N/A
Cypress bark (*Taxodium distichum*)	277	N/A

*zinnia were grown in sphagnum-peat based substrates amended with 10% by volume of the alternative material, except sphagnum peat mix, which served as the control.

The availability and release rates of Si over time of different materials are largely unknown as well. Excellent extraction methods have been developed to identify other nutrients' availability (Mehlich, 1984), but no consensus has been reached regarding predicting how much Si is supplied from various solid materials. In fact, in a survey of different extraction methods, Prakash et al. (2010) found high correlations between final rice tissue Si concentration and solution Si regardless of extracting solution and method. We placed different materials in glass columns and performed a series of saturated media extracts with deionized water or mild salt solutions. There was no difference in the amount of silicon that was in the solution between water or salt extractant (data not shown). Only the water extractant data is shown for simplicity. Materials varied greatly in the amount of Si in solution among materials released through time (Figure 2). On the initial day, 100 % rice hull had the lowest amount of Si in solution (dark line Figure 2). Days 2 through 7, however, resulted in much higher amounts of Si that were extracted reaching a peak of about 18 mg L^{-1} in solution. After day 7, however, the amount in solution decreased. The sphagnum peat-based substrate (sunshine mix) was the lowest on all days except the first and declined slightly over time. Other mixes, which were blends of either Slag # 6 (wollastonite) or rice hull with sunshine mix tended to show increased release of Si over time. The difference between rice hull alone and rice-hull:peat mix is especially interesting and suggests that microbial activity began to play a larger role in the solubility of Si within the hulls, resulting in more Si released over time. In fact, a sphagnum peat: rice hull mix of only 5% rice hull resulted in more release of Si in solution after 10 days than 100% rice hull at the same time. Both slag and rice hulls behaved as "slow release" Si sources for this isolated, unplanted study.

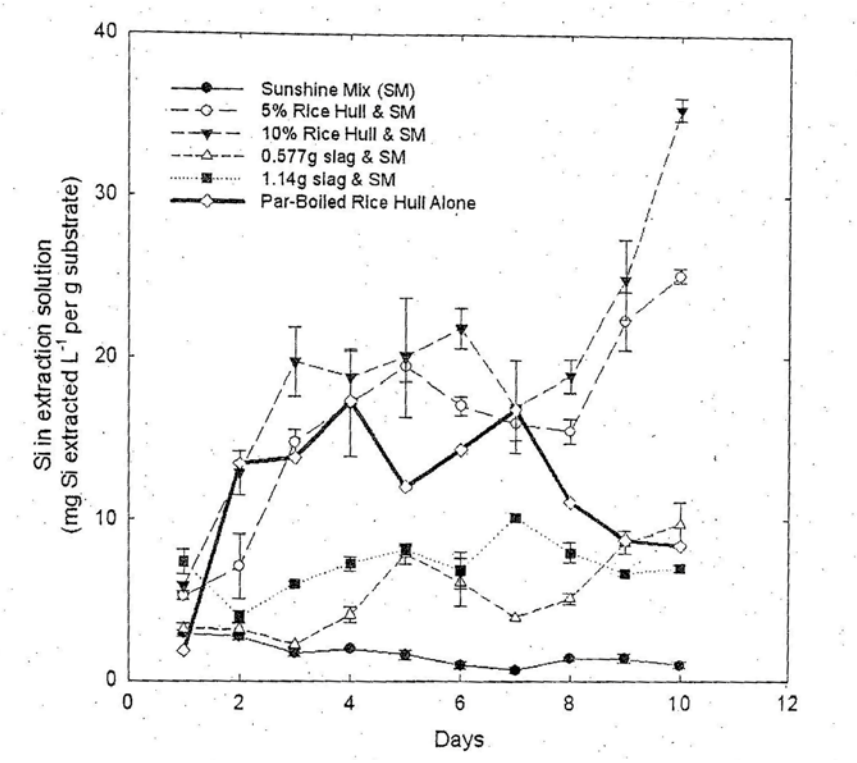

Figure 2. Silicon extracted with water using a series of saturated media extracts. All materials consisted of the same volume (-0.5 L) and were extracted in series over a period of ten days. Error bars represent +/- 1 standard deviation of the mean. Three replicate samples were extracted each day. The "slag" used in this case is the same as Slag # 6 in Figure 1.

Ultimately, the ability for a substance to supply Si to plants must be tested in planted containers and the plant tissue must be tested for efficacy of Si delivery. Zinnia, the highest tested Si accumulator of all dicot plants investigated so far in our systems, was grown in eight substrates for three weeks. Not surprisingly, leaf tissue concentrations were highest in plants grown with sphagnum-peat amended with 10% par boiled rice hulls. Somewhat surprising was that miscanthus-amended peat produced zinnia tissue was not significantly different from rice-hull-grown zinnia in spite of there being nearly 6-fold more total Si in rice hull than miscanthus. This suggests either a saturation of Si uptake, a difference in mineralization rates and forms within the two materials, or differences in immediately available

versus total Si. In these examples, there was general correlation between the total amount of Si a material contained and leaf concentration of zinnia grown in a substrate containing that material. An exception, however, is with pine bark (3,544 mg kg^{-1} total versus 917 mg kg^{-1} in tissue) and coconut coir (3,141 mg kg^{-1} total versus 2,168 mg kg^{-1} in tissue). Due to high rates of total Si and acceptable rates of mineralization or availability, both par-boiled rice hull and miscanthus can supply significant amounts of Si to zinnia even if supplied as only 10% of the total substrate volume.

Function: Powdery Mildew

Silicon addition through fertigation (irrigation with fertilizer amended with Si) helped control powdery mildew on zinnia (Figure 3A). The experiment was repeated three times, but only results of the third experiment are shown for simplicity. This is similar to the finding of Kamenidou et al. (2009). The control of powdery mildew was not complete, however (Figure 3B and 3C). Initial symptoms of powdery mildew were delayed by up to a week, while expansion of colony size and further spread was delayed up to two weeks. Practically speaking, this delay in spread and suppression in severity would be beneficial to commercial producers by giving them more time to manage disease and potentially eliminate one or more pesticide applications in a period of time. Frantz et al. (2008) did not detect a complete physical barrier of Si deposited within the epidermal layer of leaves. Therefore, it is likely that the mechanism for disease suppression is active as is the case with cucumber (Cherif et al., 1994).

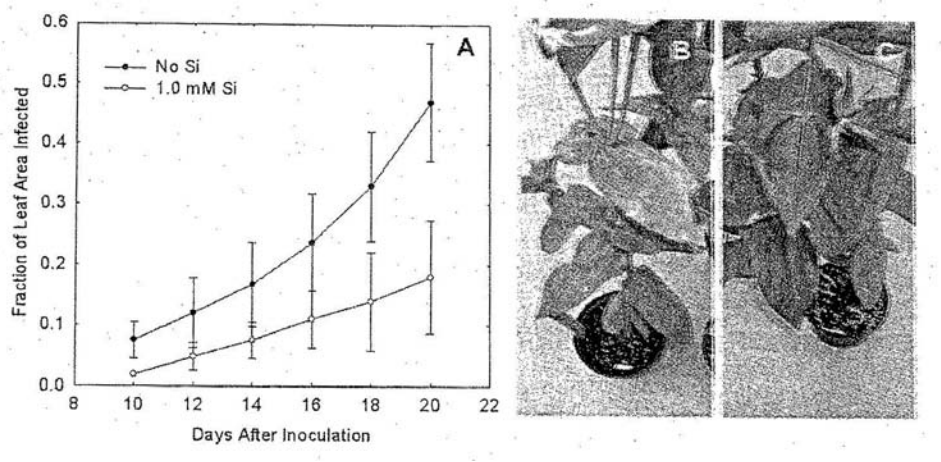

Figure 3. Area of inoculated zinnia leaf covered with powdery mildew with and without supplemental Si addition (A). Error bars represent +/- one standard deviation of the mean. Zinnia grown in soilless media without (B) and with (C) supplemental Si approximately 3 weeks after exposure to powdery mildew showed a reduction in symptomatic leaf surface area.

Function: Cu Toxicity

Si has been reported to combat abiotic stress as well including micronutrient toxicities (Voogt and Sonneveld, 2001; Horst and Marschner, 1978). Li et al (2008) tested the ability for Si to help suppress Cu toxicity stress utilizing the model plant Arabidopsis. It was found that Cu transporters are differentially regulated in the presence of supplemental Si, toxic Cu, and toxic Cu with supplemental Si. This results in decreased PAL activity in the leaves, increased PAL in the roots, and leads to less visible symptoms of stress in the roots and shoots.

In a similar growth study, zinnia were grown with and without supplemental Si and exposed to Cu toxicity. Visible symptoms of stress mirrored those patterns observed in the Arabidopsis study, with supplemental Si significantly lowering stress symptoms from Cu toxicity stress (Figures 4 and 5). PAL activity was lower in tissue from plants supplemented with Si. Plant dry mass, both root and shoot, was larger in supplemented Si treatments at similar Cu supply rates, with supplemental Si completely compensating for growth in very high Cu supply. Shoot and root copper concentrations were lower in plants supplemented with Si suggesting

that Si caused suppression in Cu uptake (Figure 5). This result is different than Cu tissue concentrations found in Arabidopsis (Li et al., 2008), and suggests a difference in Si-induced tolerance to copper stress among species.

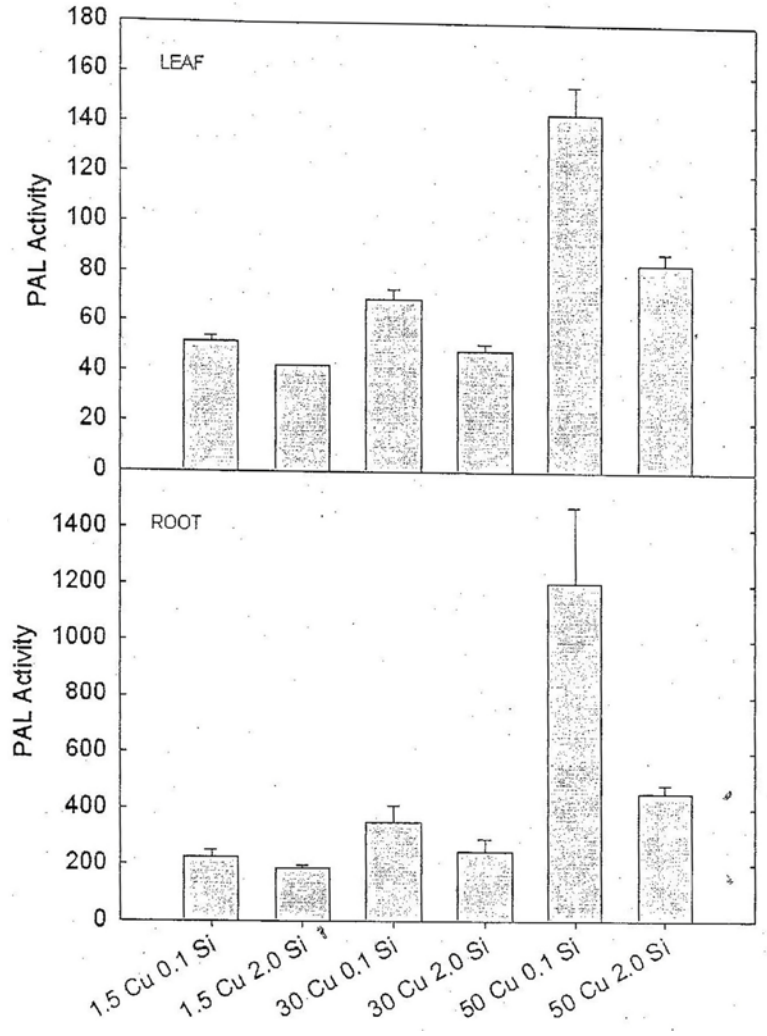

Figure 4. Average PAL activity of zinnia roots and shoots, with one standard error of the mean. Number before Cu is concentration of Cu in µM and number before Si is concentration of Si in mM.

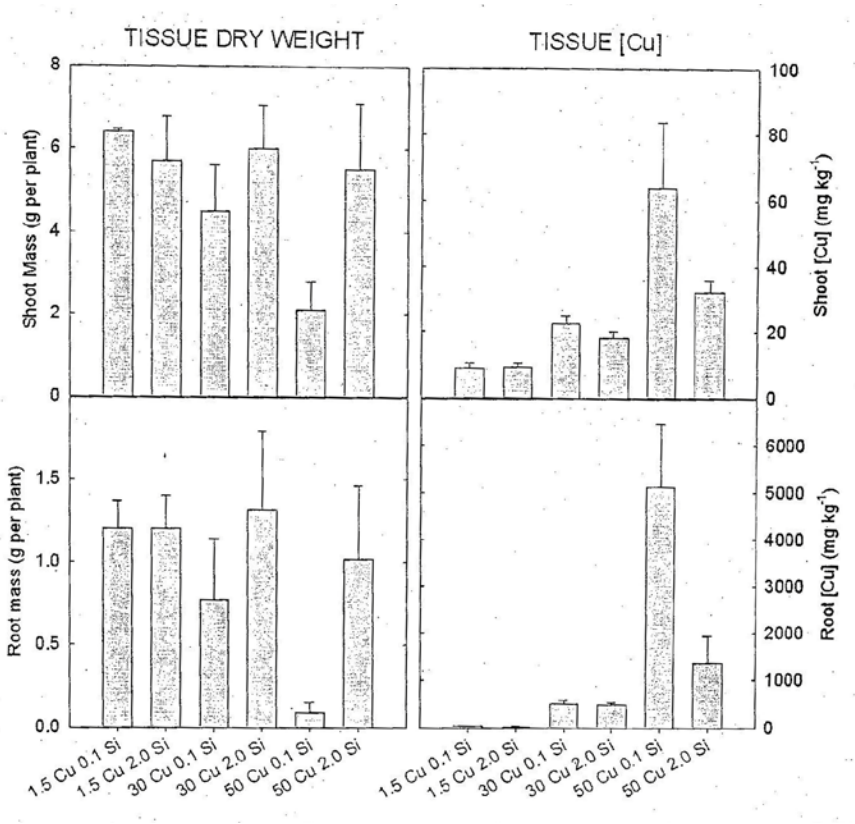

Figure 5. Average zinnia shoot (leaf + stem) and root dry mass and Cu concentrations of the same tissues. Each value is an average of three replicate samples, +/- one standard deviation. Number before Cu is concentration of Cu in µM and number before Si is concentration of Si in mM.

Acknowledgments

The authors would like to thank Craig Ford, Alycia Pittenger, Stephen Ohene-Larbi, Ann Widrig, and James Feasel for laboratory assistance. Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the USDA, and does not imply its approval to the exclusion of other products or vendors that also may be suitable.

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