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Impact of nitrogen and importance of silicon on mechanical stem strength in *Schoenoplectus acutus* and *Schoenoplectus californicus*: applications for restoration

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Abstract Nitrogen (N) and Silicon (Si) availability can affect the vigor and resiliency of plant communities. The effects of N on plant growth has been investigated in multiple species and is understood to promote growth. Though it is generally understood that Si aids in plant functions such as stem strength enhancement and herbivory defense, the role Si has not been explored in many wetland plant species. Tidal wetland plants are often subjected to high wind and wave energy, which can cause breakage or collapse of stems. This body of research investigated the combined effects of Si and N regimes to reduce the occurrence of stem collapse through its influence on stem strength. We investigated the effects of Si and N concentration on the growth, morphology, and physiology of *Schoenoplectus acutus* and *Schoenoplectus californicus*, two species of macrophytes that are commonly used in freshwater tidal restoration plantings. Individuals of each species were grown hydroponically in four different nutrient combinations (low Si and low N, low Si and high N, high Si and low N, and high Si and high N). Results indicated that increased N concentrations promoted aboveground biomass production, whereas increased Si concentration enhanced stem strength and decreased the

likelihood of stem collapse and herbivory. Plants receiving a high Si and low N nutrient combination exhibited the most robust stems. Our findings emphasize the importance of Si, as well as N, in *Schoenoplectus* spp. growth and highlight the potential applications for these nutrients in enhancing tidal marsh management.

Keywords Nutrient regime · Nitrogen · Silicon · *Schoenoplectus* · Stem strength · Lodging

Introduction

Plant species' interactions with the abiotic environment can influence their distribution and abundance (Menninger and Palmer 2006; Lambers et al. 2008). Nutrient and resource availability, in particular, can influence plant morphology and physiology (Schubert and Mengel 1989) as well as influence which species can survive and thrive (Grime 1977, 1979). Plants use multiple primary macronutrients (i.e., N, P, K), secondary macronutrients (Ca, Mg, S), essential micronutrients (Fe, B, Cl, Cu, Mn, Mo, Zn), as well as elements classified as non-essential micronutrients (Co, Si, Al, Na, V, Ga) for carbohydrate synthesis, growth, and other physiological functions (Taiz and Zeiger 2010). Nitrogen (N), is typically considered to be the most limiting nutrient in freshwater and terrestrial ecosystems (Tamm 1991; Vitousek and

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Howarth 1991; Kenk and Fischer 1988; Hooper and Johnson 1999; Elser et al. 2007; LeBauer and Treseder 2008) indicating that plant growth and net primary production (NPP) is directly related to the amount of nitrogen that the plant can access. Nitrogen is generally understood to enhance plant growth and biomass production, however excess nitrogen loading can result in plants with lower root to shoot ratios (Turner 2010; Deegan et al. 2012).

The existing body of literature explains silicon (Si) is not generally considered an essential element for most terrestrial higher plants, except for *Equisetaceae* (Epstein 1994), largely because the role of Si in plant biology is not well understood (Ahmed and Asif 2012). Silicon is the second most common element on Earth and is considered ubiquitous in soil in the form of mineral quartz and clay (Ary and Lujan 1992). However, its abundance in a bioavailable form (monosilicic acid) is more variable, ranging between 0.08 and 0.67×10^{-3} mol SiO₂ L⁻¹ (5–40 mg SiO₂ L⁻¹) (Dietzel 2002). The majority of research that addresses the role of Si in plants has been conducted in oceanic environments regarding diatoms and eutrophication (Garnier et al. 2010) and in agricultural crops such as corn, rice, tomato, cucumber, and tobacco (Adata and Besford 1986; Horiguchi 1988; Samuels et al. 1991; Gao et al. 2005). From the existing body of research, Si is known to promote plant growth, enhance photosynthesis, deter herbivory, enhance water loss efficiency, and strengthen the stem by thickening the culm wall and size of the vascular bundles (Shimoyama 1958; Epstein 1994; Ma and Takahashi 2002; Massey and Hartley 2006; Gao et al. 2005; Mitani and Ma 2005; Kamenidou and Cavins 2008). The concentration of Si has even been found to surpass the concentration of N and P in some plant tissues (Epstein 1994, 1999). However, the actual role and influence of this nutrient is complex and the role of Si in plant growth and physiology requires additional research; especially in wetland ecosystems.

Wetlands are understood to be important in the biogeochemical cycling of N and P, but there is little information regarding the role of Si in wetland ecosystems (Struyf and Conley 2009). Tidal marshes have been found to accumulate large quantities of biogenic silica, with some species of vascular plants (*Spartina alterniflora* and *Juncus roemerianus*) containing up to 0.5% biogenic silica by weight (Hackney et al. 2002). Yet, Si is continuously lost from the soil

due to leaching and depletion by the plant community, making its concentration variable (Körndorfer and Lepsch 2001). Agronomists have long understood the beneficial effects of using a Si amendment to improve crop yield and resistance to disease and herbivory (Savant et al. 1997; Alvarez and Datnoff 2001); however, Si is often omitted from nutrient amendments in restoration scenarios (Epstein 1999).

It has been well established that marshes exposed to increased nitrogen supply can exhibit lower root to shoot ratios, lower soil strength, and cause marsh loss (Turner 2010; Deegan et al. 2012). Enhanced nitrogen loading may also contribute to an increase in stem lodging (the complete breakage or collapse of the stem from which it will not recover) (Bertness and Ellison 1987; Neill 1990; Valiela and Rietsma 1995; Wigand et al. 2013). Previous studies by Crook and Ennos (1995) investigated the effects of nitrogen on stem growth and lodging in wheat and found that increased levels of soil nitrogen resulted in increased height of stems, thus weakened the stems. We have witnessed stem lodging of *Schoenoplectus acutus* (Muhl ex Bigelow) Á. Löve and D. Löve and *S. californicus* (C.A.Mey.) Soják (commonly referred to as tules) at Liberty Island (38.308359, – 121.686974), an agriculturally influenced freshwater tidal marsh restoration site located in the Sacramento–San Joaquin Delta, California, USA that has historically received nitrogen fertilizers. Both *Schoenoplectus* species are widely distributed (de Lange et al. 1998; Hoag 1998; Vasey et al. 2012) and are desired to stabilize levees and meet the goals of many freshwater tidal marsh restoration efforts (Kimble and Ensminger 1959; Sloey et al. 2015; Hester et al. 2015).

We used a controlled greenhouse study to investigate the effects of N and Si nutrient regimes on *S. acutus* and *S. californicus* growth, morphology, and physiology. We hypothesized that silicon may function to strengthen the stems of these relatively tall plants, making them more resistant to lodging from the high wind and wave energy—characteristic of tidally-influenced ecosystems. Understanding the role of Si and its interactions with N on marsh species will improve understanding of nutrient dynamics, species morphology and physiology, as well as enhance marsh management in dynamic tidal wetlands.

Materials and methods

Experimental design

A full-factorial experimental design with randomized organization of experimental units was implemented to examine the influence of nutrient regimes on tidal marsh plant growth and morphology. This factorial experiment consisted of two species (*S. acutus* and *S. californicus*), two Si treatments (low and high), two N treatments (low and high), with four replicates of each combination for a total of 32 experimental units. Individuals were organized in a randomized fashion in a greenhouse at the University of Louisiana at Lafayette's Ecology Center (30.3041, – 92.0097).

Schoenoplectus acutus and *S. californicus* rhizomes were purchased from a native plant nursery in California, USA, in January 2014 and allowed to grow in Sta-Green™ potting soil for 6 months. Experimental plants were weighed and selected for similar sized rhizomes. All plants had three stems cut to 0.25 m in height at the initiation of the experiment. Plants were rinsed of soil with deionized water. Each plant was placed in a 3.8 L plastic nursery pot that was perforated at the bottom. The pot was set inside a plastic water reservoir. We used glass spheres as an inert hydroponic growth substrate in order to maintain upright orientation of plants without influencing the manipulated nutrient solutions (Audebert 2012; Giurghi et al. 2014). Glass did not create any additional SiO₂ whereas using sand, soil, or vermiculite would. Each plant received the same baseline Hoagland's nutrient solution with modified concentrations of N

and Si depending on the treatment combination (Table 1). All other nutrients, including P, were kept consistent for the purpose of isolating effects of Si and N only. Silicon was added in the form of soluble sodium silicate pentahydrate (Na₂SiO₃ × 5H₂O). Individuals receiving a low Si treatment received no Si additive whereas plants receiving the high Si treatment received a 1.7 mM SiO₂ solution. Nitrogen was added in the form of ammonium nitrate (NH₄NO₃). During our previous work at the Liberty Island restoration site, we've observed that soil ammonium ranged between 10.3 μg g⁻¹ and 31.0 μg g⁻¹ (0.57–1.71 mM) (Hester et al. 2015). Numerous nutrient studies have tested plant response to low nutrient regimes at 1.0 mM concentration of NH₄NO₃ (Makino et al. 1988; Griffin et al. 1993) to and high N treatments ranging from 7.0 mM NH₄NO₃ (Griffin et al. 1993) to as high as 45 mM NH₄NO₃ (Jackson and Caldwell 1989). For this study, low and high N treatments contained 1 and 10 mM concentrations of NH₄NO₃ respectively. The reservoirs holding the water for each plant were filled to the top with their respective nutrient solution. Plants were watered with deionized water every 2 days throughout the experiment and received a fresh nutrient solution every 3 weeks. The experiment ran for a duration of 12 weeks from June to September 2014. Prior to experiment initiation, the nutrient solutions and deionized water were tested for water chemistry (Si, P, N) to ensure that the nutrient concentrations were held at the correct level. Pore water nitrate-nitrite and ammonium concentrations were determined using EPA-approved spectroscopic methods (Parsons 2013).

Table 1 Hoagland's nutrient solution concentrations for each experimental treatment

Nutrient	Low Si and low N	High Si and low N	Low Si and high N	High Si and high N
MgSO ₄	1.0 mM	1.0 mM	1.0 mM	1.0 mM
KH ₂ PO ₄	2.0 mM	2.0 mM	2.0 mM	2.0 mM
Ca(Cl) ₂	2.5 mM	2.5 mM	2.5 mM	2.5 mM
NH ₄ NO ₃	1.0 mM	1.0 mM	10 mM	10 mM
Fe-EDTA	1.0 ml	1.0 ml	1.0 ml	1.0 ml
Boric acid	23 mM	23 mM	23 mM	23 mM
Molybdic acid (H ₂ MoO ₄ × H ₂ O)	0.05 mM	0.05 mM	0.05 mM	0.05 mM
MnCl ₂ × 4H ₂ O	0.20 mM	0.20 mM	0.20 mM	0.20 mM
ZnSO ₄ × 7H ₂ O	0.38 mM	0.38 mM	0.38 mM	0.38 mM
CuSO ₄ × 5H ₂ O	0.16 mM	0.16 mM	0.16 mM	0.16 mM
Na ₂ SiO ₃ × 5H ₂ O	0 mM	1.7 mM	0 mM	1.7 mM

Plant analyses

Plants were monitored for stem density (number of stems per plant), and stem height. Observed herbivory damage from grasshoppers and cutworms was measured at the conclusion of the experiment by enumerating the stems in each plant that had evidence of herbivore damage. Stems were visually determined to be live or dead based on presence of green photosynthetic material, and dead stems showed no green material. A subset of two undamaged stems was collected from each plant and analyzed for stem strength and cross sectional formation of aerenchyma. Stem strength was determined by hanging a series of increasing weights from a fixed point on the freshly cut stem, which was secured to a platform with the majority of the stem overhanging, and measuring the deflection to obtain the modulus of elasticity, or E (Albert et al. 2013). As E increases, it is assumed that the stem is stronger, more rigid, and less likely to be deformed with the stress of weight. Measurements from the tip, middle, and base sections of the stem were averaged to obtain a representative reading for each stem. To analyze aerenchyma formation, cross-sections were collected from the middle section of two representative stems from each plant and analyzed less than 12 h after collection. Cross-sections were dyed with Tolluidine Blue and photographed using a dissecting microscope. Images were analyzed for percent area of aerenchyma (open conduits) compared to plant tissue using Image JTM (Schneider et al. 2012).

We also looked at the effect of wind on stem lodging using a 1998 Robicheaux airboat (Chevy 350 V8 motor) to control wind exposure. The plants were placed on a 1 m tall table located 5 m behind an airboat which was parked on a trailer. The planted pots were secured upright on the table using cinderblocks. Different wind speeds were generated by adjusting the rpms of the boat engine and the resulting wind speeds were measured using an anemometer (Kestrel 1000 Pocket Anemometer, Neilsen-Kellerman, Pennsylvania) placed adjacent to the plant. Ambient wind was 0 kmph during the testing period and did not register on the anemometer. Each plant was subjected to incremental wind trials of increasing speed (8, 16, 24, 40, 80, and 120 kmph) for 30 s. After each wind trial, the number of lodged stems was enumerated. Data was analyzed using an ANOVA assuming that stems that break at lower wind speeds would have also broken as wind speed became incrementally faster.

Aboveground, belowground, and inflorescence tissues were collected at the conclusion of the experiment and total live weights were obtained. Inflorescences were only produced in *S. acutus*. Inflorescences are distinct structures from the stems which were removed, dried, and weighed separately. Aboveground material was dried in a convection oven at 65 °C to a constant weight for biomass determination. Dried stems were ground in a Wiley mill (Thomas Scientific, #3383L10, New Jersey) and analyzed for total C, N, and fiber (lignin and cellulose) at the Ecosystems Analysis Laboratory at the University of Nebraska at Lincoln. A subset of ten live roots was collected from each plant and analyzed for root morphology (percent root length at different root diameter size classes after Reinhardt and Miller (1990): < 0.1 mm (very fine fibrous), 0.1–0.2 mm (fine fibrous), 0.2–0.5 mm (fibrous), 0.5–1.0 mm (coarse fibrous), 1.0–2.0 mm (fine root), and > 2.0 mm (coarse root) using WIN Rhizo Image Analysis program. Various root diameter size classes were analyzed to understand the effects of nutrient regime on root architecture, as root architecture can mediate the adaptation of plants to soils in which nutrient availability is limited by increasing the total absorptive surface of the root system (López-Bucio et al. 2003). All belowground tissue was then dried in a convection oven at 65 °C to a constant weight for biomass determination.

The effects of species, N concentration, and Si concentration on above- and belowground plant metrics and porewater chemical analyses were compared using a 3-way analysis of variance (ANOVA) in JMP 11.0 (SAS Institute Inc. Cary, NC) with Tukey post hoc comparisons. Since stem production significantly differed between species, species were analyzed separately to determine the effect of N and Si on the percentage of stems with herbivore damage.

Results

Cellulose concentrations were higher in *S. californicus* individuals compared to *S. acutus* and percent lignin was significantly higher in plants receiving a high Si nutrient regime for all species (Fig. 1; Appendix 1). Total percent Si in plant tissue was significantly higher in plants receiving a high Si nutrient concentration, especially in plants receiving a high Si and low N

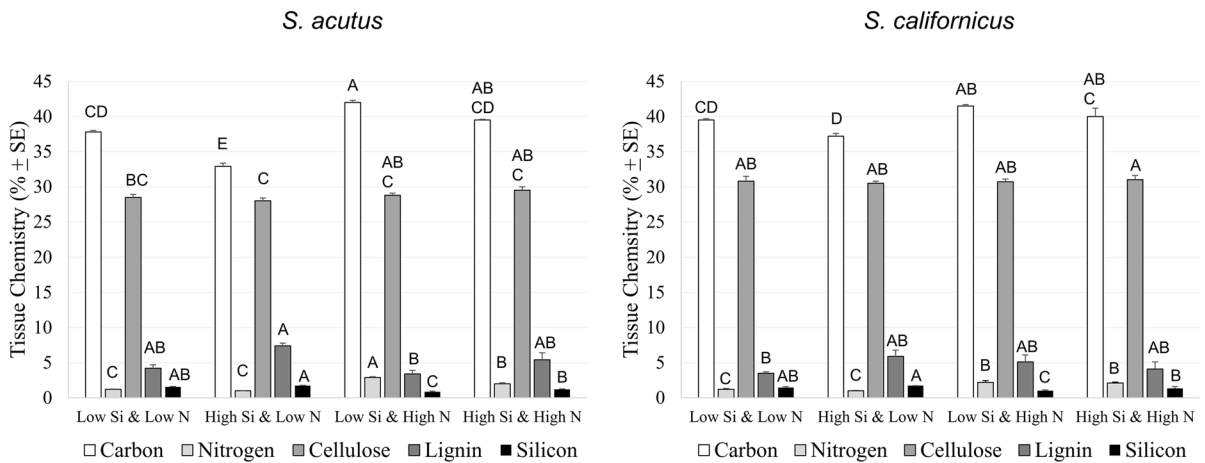


Fig. 1 Percent chemical composition of plant tissue (mean ± SE) of *S. acutus* and *S. californicus* subjected to different nutrient regimes. Means within the same element or

compound (C, N, Cellulose, Lignin, Si) marked by the same letter are not significantly different ($\alpha = 0.05$)

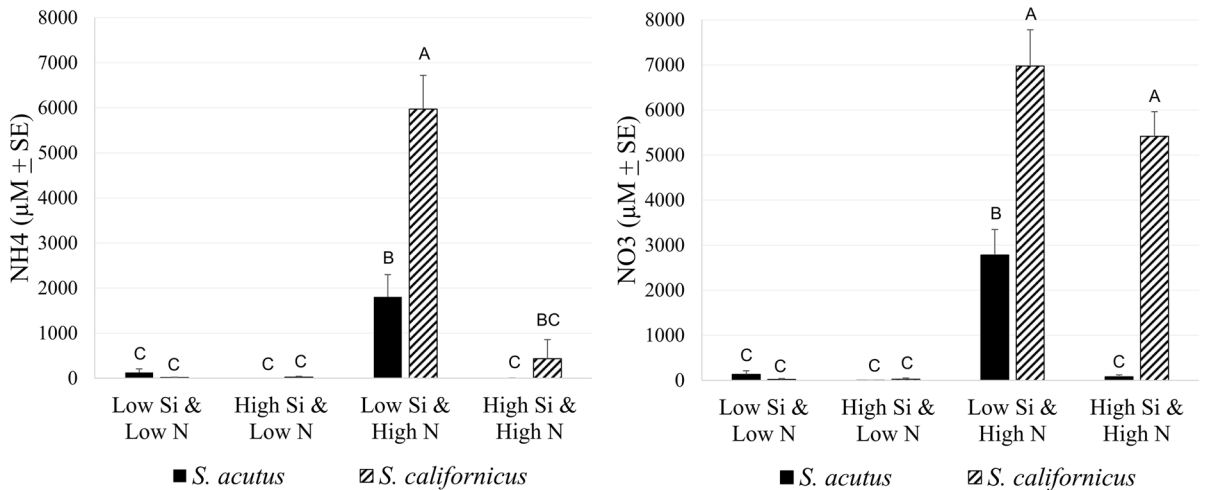


Fig. 2 Concentration (μM) of NH_4 and NO_3 (mean ± SE) in pore water collected from individuals subjected to different nutrient regimes. Means marked by the same letter are not significantly different ($\alpha = 0.05$)

combination (Fig. 1). Percent total carbon in plant tissue tended to be higher in *S. californicus* compared to *S. acutus* and also tended to be higher in plants receiving a high N nutrient regime (Fig. 1). Analysis of total percent nitrogen in plant tissue revealed that total nitrogen was higher in plants receiving a high N concentration. A Tukey-post hoc comparison revealed that in *S. acutus*, %N in tissue was highest in plants receiving a Low Si and High N combination (Fig. 1). Pore water analyses of NH_4 showed concentrations being one to two orders of magnitude higher in pore water extracted from low Si and high N treatment combinations compared to other treatments for both species (Fig. 2). Pore water

concentration of NO_3 revealed significant interactions between N and species and between Si and N (Fig. 2).

Percent live material was lowest in units that received a nutrient combination of low N and low Si (Fig. 3a; Appendix 2;). Stem density was greater in *S. acutus* individuals, producing more stems than *S. californicus*, and high N nutrient treatments resulted in greater stem production in *S. acutus* (Fig. 3b, c). Stem height was significantly higher in *S. californicus* than *S. acutus* and an interaction between N and Si indicated that stem height was greater in *S. californicus* individuals receiving a high Si and high N nutrient solutions (Fig. 3d).

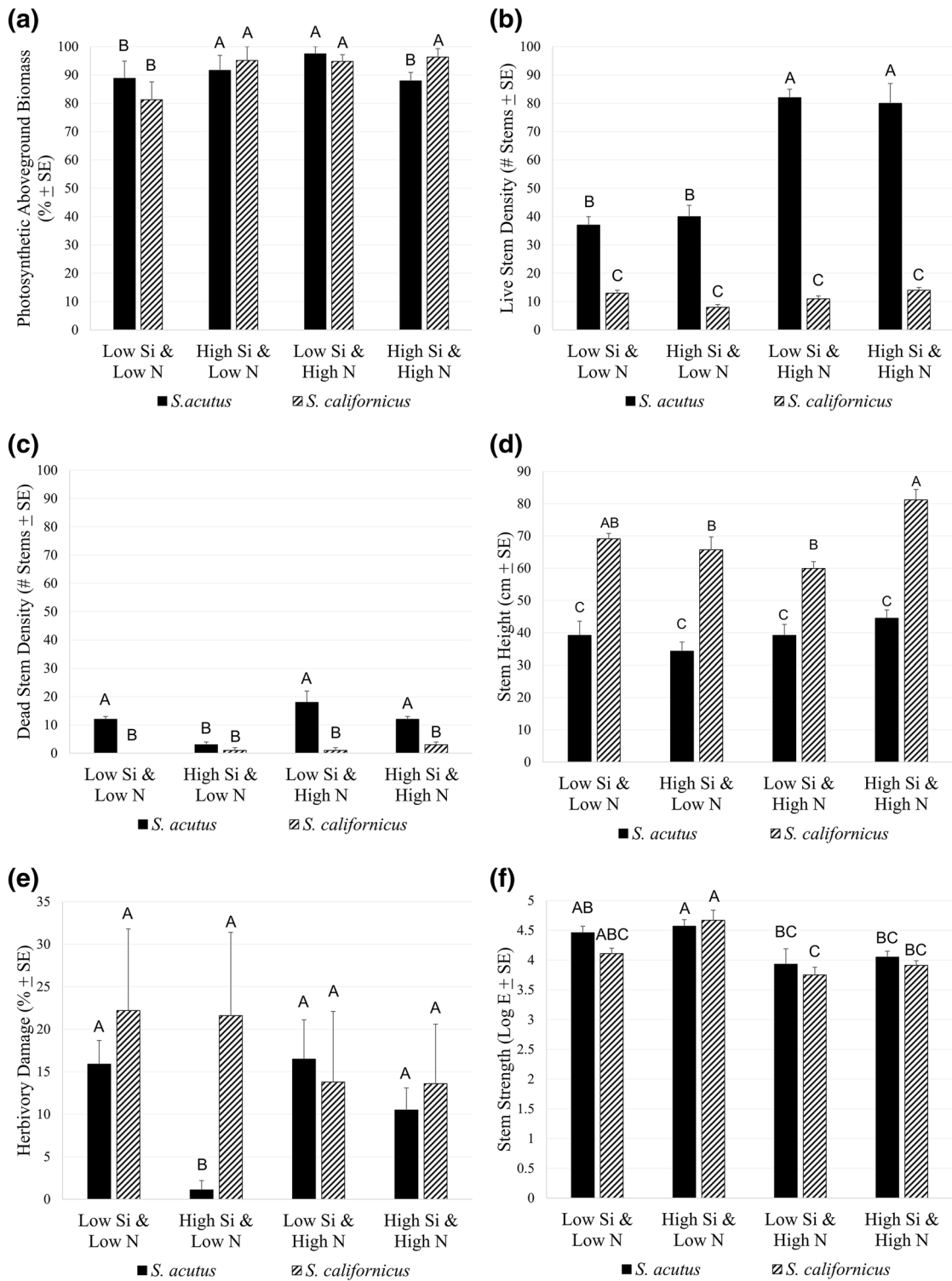


Fig. 3 Plant growth metrics (photosynthetic aboveground biomass, stem density, stem height, herbivory damage, stem strength) of *S. acutus* and *S. californicus* (mean ± SE)

individuals subjected to different nutrient regimes. Means within the same metric marked by the same letter are not significantly different $\alpha = 0.05$

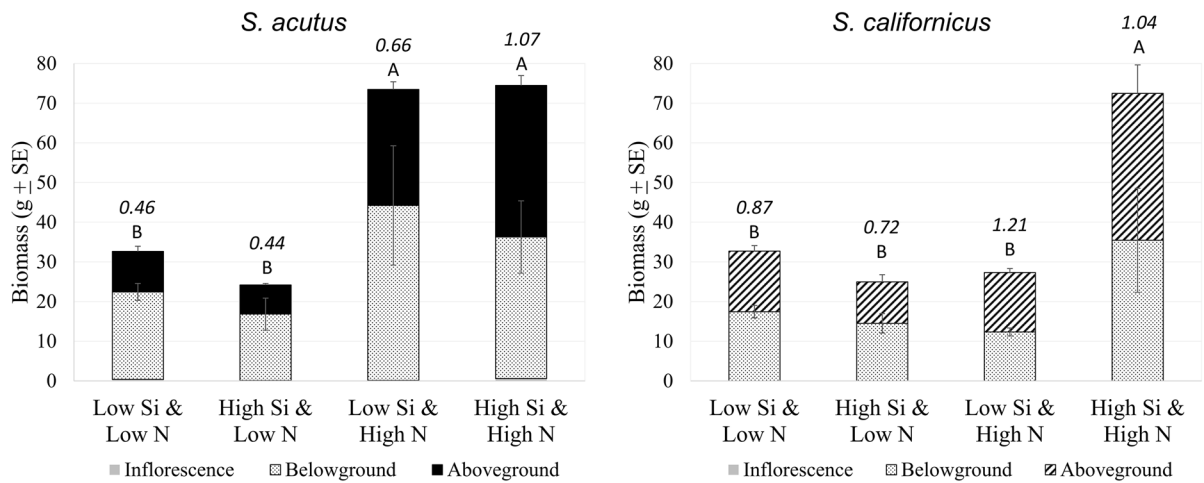


Fig. 4 Total mass (g) of inflorescences, above-, and below-ground biomass (mean ± SE) of *S. acutus* and *S. californicus* individuals subjected to different nutrient regimes. Means

within species marked by the same letter are not significantly different ($\alpha = 0.05$). Numbers above each bar represent average aboveground-to-belowground biomass ratio

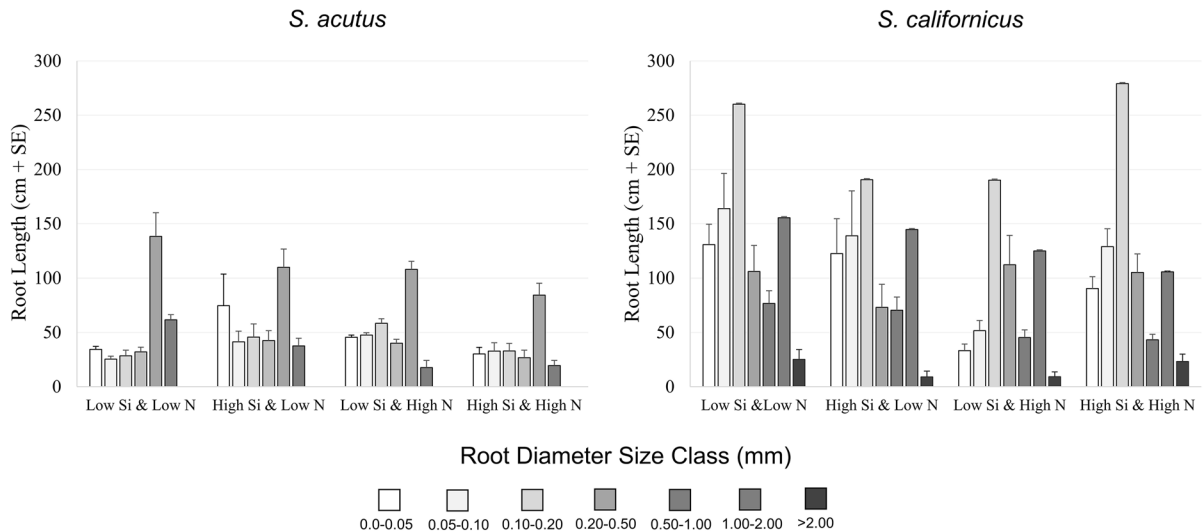


Fig. 5 Root morphology of *S. acutus* and *S. californicus* individuals subjected to various nutrient solutions as indicated by total root length at different root diameter size classes (mean ± SE)

There was no effect of nutrient regime on herbivory in *S. californicus*. However, for *S. acutus*, higher Si concentrations did have a significant effect on reducing herbivory (Appendix 2; Fig. 3e). Total above-ground biomass production was greater in *S. acutus* individuals receiving a high N treatment and in *S. californicus* individuals receiving a combination of high N and high Si (Fig. 4; Appendix 2). Inflorescence biomass was higher in *S. acutus* compared to *S. californicus* ($P < 0.0001$), because the duration of the experiment did not include the *S. californicus*

flowering period. Within *S. acutus*, inflorescence biomass production was 2–6 six times greater in plants receiving a high N & high Si nutrient combination than in other treatments. In general, N had a significant positive effect on total belowground biomass revealed a significant positive effect of N (Fig. 4; Appendix 2).

Image analyses of root morphology showed significantly greater root length in *S. californicus* than *S. acutus* (Fig. 5; Appendix 3). There was a significant interaction between species, N, and Si in root diameter size classes

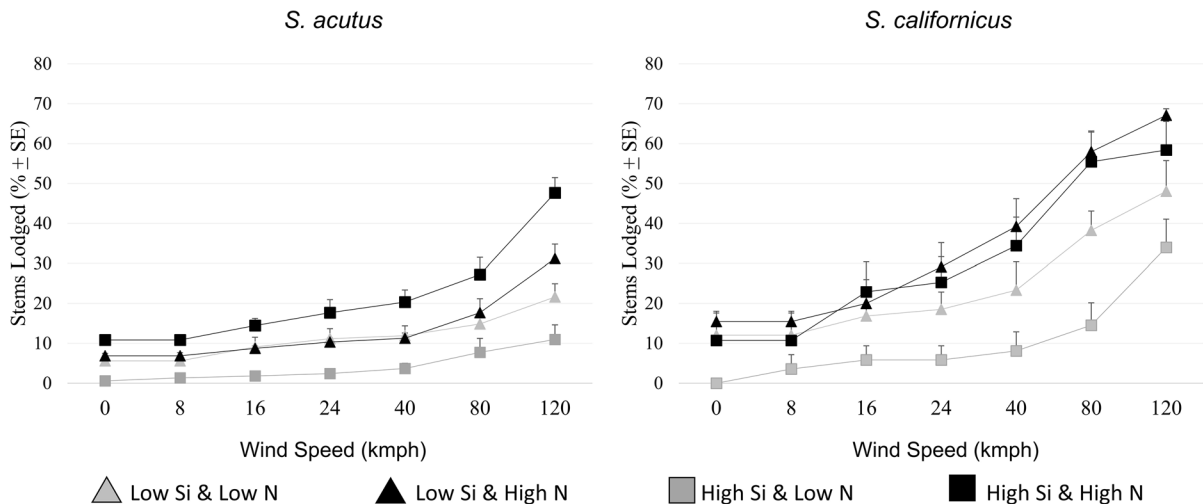


Fig. 6 Percentage of total stems lodged (mean \pm SE) with increasing wind speed

up to 0.2 mm and the > 2.0 mm diameter size class (Appendix 3). Nitrogen had a significant effect on root length in 0–0.5, 0.5–1.0, and 1.0–2.0 mm diameter size classes. In these root diameter size classes, plants receiving low N treatments, generally had longer roots (Fig. 5; Appendix 3). We saw a similar distribution of root diameter sizes between nutrient treatments within each species, however *S. californicus* roots tended to have a greater proportion of fine roots (0–0.5 mm root diameter size classes) whereas *S. acutus* had the largest proportion of roots within the 0.50–1.00 mm root diameter size class (Fig. 5; Appendix 3).

Our tests of stem strength using the modulus of elasticity showed the highest stem strength in plants receiving a high Si and low N nutrient combination (Fig. 3f; Appendix 2). Our analyses of aerenchyma formation revealed no significant trends between species or nutrient treatment. The wind exposure trials revealed important differences between species and nutrient treatments (Appendix 4). N had a significant effect on stem lodging at all wind speeds (Appendix 4) as the greatest wind damage was observed in plants receiving the high N solution (Fig. 6). At wind speeds 16 kmph or higher, species showed a significant effect on stem lodging, as a greater percentage of *S. californicus* stems broke with increasing wind speeds. A significant interaction between Si and N was evident at the majority of wind speeds (16, 24, 80, and 120 kmph) and plants receiving a high Si and low N nutrient combination exhibited the least stem lodging with increasing wind speed.

Discussion

Our research highlights some important considerations for wetland restoration practitioners and further scientific inquiry. First, the role of soil nutrient balances, specifically N and Si, deserve greater consideration in the context of wetland restoration. Many of the world's tidal wetlands are impacted by excess N and nutrient loading due to anthropogenic actions (Boesch et al. 2001; Deegan et al. 2012). Former agricultural systems tend to be characteristically low in bioavailable Si after years of depletion by crops or weathering of the soil (Datnoff et al. 2001). In areas of high nutrient loading, or in post-agricultural reclamation wetland restoration sites, the availability of bioavailable Si in relation to N should be assessed prior to restoration to determine if soil nutrient amelioration could benefit plant growth, performance, and resistance to pests while minimizing the potential for stem lodging. Additionally, strengthened stems are particularly important for wetland vegetation, such as *Schoenoplectus* spp., that may be implemented for the purpose of wave attenuation and stabilization of earthen levees. Houser et al. (2015) found that blade/stem rigidity is relative to the drag and energy dissipation created by submerged and emergent vegetation. Vegetation that easily lodges, or is highly flexible, provides minimal shoreline protection (Houser et al. 2015), therefore Si availability, as well as species morphology, should be important considerations for species selection in shoreline protection

and restoration efforts. When stems from our experimental plants did break in the wind trial experiment, the majority broke at the base, which could create greater negative consequences for shoreline protection as opposed to stems that break at the top of the plant. Sloey et al. (2015) found that *S. acutus* and *S. californicus* survival is significantly reduced when stems are overtopped by water, therefore stems broken at the base of the plant in flooded environments may result in plant mortality. Silica amendments have been used in agricultural settings (Savant et al. 1997; Alvarez and Datnoff 2001), and the results from this greenhouse study suggests that a Si amendment could be beneficial for wetland restoration and shoreline protection field settings as well.

Our findings also illuminate subtle differences between *S. acutus* and *S. californicus* species. *Schoenoplectus acutus* and *S. californicus* fill similar ecological niches, except for their variation in tolerance to flooding regime (Sloey et al. 2015, 2016), and are commonly referred to as a tule association (Billings 1945). The differences in plant response to nutrient regime may further separate the two species ecologically. Increased concentrations of Si possibly provided greater herbivore resistance as the silicification of vascular tissue and epidermal cell walls restricts chewing or rasping herbivores (Reynolds et al. 2009). Higher concentrations of N optimized *S. acutus* growth and biomass production, whereas *S. californicus* growth was only significantly greater in treatments that received both elevated N and Si. Therefore, nutrient availability may partition species by impacting survival and competition dynamics.

Drawing on principles from Keddy's centrifugal organization theory (Keddy 1990; Wisheu and Keddy 1992), which explain changes in species composition and abundance along environmental gradients, we can conclude that *S. acutus* growth and expansion may be favored in high nutrient environments, whereas *S. californicus* would be a dominant competitor in more stressful, nutrient poor environments. In an inclusive fundamental niche, all species within the niche are expected to exhibit optimal performance on the same end of a gradient (Colwell and Fuentes 1975), whereas the realized niche represents differences in species tolerances and performance abilities along a stress or resource gradient. Differences in plant performance under different nutrient regimes partitions the realized niches of *S. acutus* and *S. californicus*.

This research has application for constructed wetland wastewater assimilation scenarios. Shallow rooted emergent macrophytes are ideal in constructed wetlands as they provide attachment surface for microbes and assimilate nutrients into organic plant material (Brix 1987). Brisson and Chazarenc (2009) conducted an overview of macrophyte species used in constructed wetlands and found that *Schoenoplectus* spp. were commonly implemented. Unfortunately, few studies compare the differential efficiencies between species for nutrient assimilation and uptake. However, the existing studies do emphasize the importance of healthy plants in functioning to remove nitrates (Tanner 2001). Because constructed wetlands are constantly exposed to high levels of N, Si additions may help improve plant health, thus facilitating more functional constructed wetlands.

This study also illustrates the importance of Si as a beneficial plant nutrient despite its status as a non-essential nutrient (Ahmed and Asif 2012). Access to Si reduced herbivory in *S. acutus*, and increased stem strength, decreased stem lodging in response to wind force, and increased concentration of lignin in plant tissue in both species. Transport of Si occurs strictly within the xylem in the form of silicic acid (Jones and Handreck 1967) and is deposited in outer epidermal cells (Parry and Smithson 1964; Savant et al. 1997). Silicon has been observed to occur in association with lignin- or phenol-moiety of the lignin-carbohydrate complexes (LCC) in the cell wall of plants (Inanaga et al. 1995). It is believed to play an essential role for lignin synthesis (Epstein 1994) and maintaining the structural integrity of the xylem and cell walls (Mengel et al. 2001; Taiz and Zeiger 2010), which supports our observations that plants grown in conditions with higher concentrations of bioavailable Si exhibited stronger stems and increased lignin concentration.

A nutrient is considered limiting if depletion of that nutrient restricts plant growth or distribution (Smith and Smith 2009). Generally, N is considered a limiting nutrient for net primary production throughout terrestrial ecosystems of the world (LeBauer and Treseder 2008). Our findings support that N plays a crucial role in growth of the species investigated. Higher concentrations of N in the nutrient solution were reflected in plant tissue total % N. In both species, greater aboveground biomass production and stem height corresponded with high N treatments, but was greatest

in plants receiving a high N and high Si combination. Liebig's law of the minimum (Liebig 1855) explains that plant growth is controlled by the amount of the scarcest resource, in this case Si. Plants receiving lower concentrations of N also exhibited greater aboveground-to-belowground biomass ratios and longer average root lengths in the small root diameter size classes. It has been well established that biomass allocation, specifically aboveground-to-belowground biomass ratios are affected by soil nitrogen availability, except in plants that are capable of nitrogen fixation (Markham and Zekveld 2007), and higher concentrations of bioavailable soil nitrogen results in higher aboveground-to-belowground biomass ratios. Due to the inherent patchiness of nutrient availability in soils, plants generally respond to heterogeneity by localized proliferation of roots. Although the number of roots may be greater when encountering a nutrient-rich patch (Hodge 2004), the length of roots may be shorter. A study on 13 species of co-occurring pasture grasses found that when total N influx capacity decreased, an increase in root area was observed (Maire et al. 2009). The relatively longer roots in our experimental plants treated with low concentrations of N may indicate that *Schoenoplectus* spp. 'forage' for nutrients when in low supply.

The benefits of increased Si concentrations were most apparent in plants that received a high Si and low N nutrient combination, which suggests that Si may be limiting in the presence of plentiful N. Interestingly, the pore water analyses showed significantly higher concentrations of NH_4 and NO_3 remaining in the pore water of plants receiving a high N and low Si nutrient combination compared to other treatments. A build-up

of NH_4 and NO_3 in the hydroponic nutrient solution may suggest that the plants in the high N and low Si treatment combinations were not uptaking as much N. However, further research is required to better understand the mechanisms by which the absence of Si resulted in reduced uptake of NH_4 and NO_3 . Although Si has not been proven to be an essential element for higher plants, previous studies have shown it has beneficial effects on the growth of a variety of terrestrial crop species including rice, wheat, barley, cucumber, and corn by strengthening stems and enhancing resistance to herbivory (Wallace 1989; Ma et al. 2001). Our results show that this also holds true for the wetland plant species investigated in this study. Our study, like many before us, demands further research on the role of Si in plants, suggests application for creating robust shorelines, and gives impetus to reconsider historic classification of Si as a non-essential plant nutrient.

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Appendix 1

See Table 2.

Table 2 Results of 3-way ANOVA testing the effects of nitrogen, silicon, and species on pore water and stem plant tissue chemistry

Effects	Pore water NH ₄ (uM)			Pore water NO ₃ (uM)			Plant tissue % total carbon			Plant tissue % total nitrogen		
	df	F	P	df	F	P	df	F	P	df	F	P
Nitrogen	1.24	65.7484	< 0.0001	1.24	178.40	< 0.0001	1.24	105.0650	< 0.0001	1.24	150.18	< 0.0001
Silicon	1.24	56.5223	< 0.0001	1.24	15.11	0.0007	1.24	53.0093	< 0.0001	1.24	13.3458	0.0013
Species	1.24	20.6154	0.0001	1.24	70.00	< 0.0001	1.24	14.7040	0.0008	1.24	2.1857	0.1523
Nitrogen × silicon	1.24	52.9657	< 0.0001	1.24	13.41	0.0012	1.24	4.3659	0.0474	1.24	2.0721	0.1629
Nitrogen × species	1.24	22.2648	< 0.0001	1.24	72.50	< 0.0001	1.24	15.9864	0.0005	1.24	3.7287	0.0654
Silicon × species	1.24	13.2192	0.0013	1.24	1.28	0.2682	1.24	5.3058	0.0302	1.24	3.4584	0.0752
Nitrogen × silicon × species	1.24	15.1663	0.0007	1.24	0.80	0.3787	1.24	1.0280	0.3207	1.24	2.5901	0.1206
Effects	Plant tissue % cellulose			Plant tissue % lignin			Plant tissue % silicon					
	df	F	P	df	F	P	df	F	P			
Nitrogen	1.24	2.4173	0.1331	1.24	1.8365	0.1880	1.24	37.2494	< 0.0001			
Silicon	1.24	0.0562	0.8146	1.24	8.6889	0.0070	1.24	10.7738	0.0031			
Species	1.24	32.8122	< 0.0001	1.24	0.6515	0.4275	1.24	0.4567	0.5056			
Nitrogen × silicon	1.24	1.8052	0.1917	1.24	4.3622	0.0475	1.24	0.3405	0.565			
Nitrogen × species	1.24	1.1534	0.2935	1.24	1.3798	0.2517	1.24	1.436	0.2425			
Silicon × species	1.24	0.0247	0.8763	1.24	2.9477	0.0989	1.24	0.0422	0.839			
Nitrogen × silicon × species	1.24	0.1430	0.7086	1.24	1.0419	0.3176	1.24	0.086	0.7718			

Appendix 2

See Table 3.

Table 3 Results of 3-way ANOVA testing the effects of nitrogen, silicon, and species on a variety of plant parameters

Effects	Photosynthetic AGBM (%)			Stem density			Stem height		
	df	F	P	df	F	P	df	F	P
Nitrogen	1.24	11.40	0.0023	1.24	115.46	< 0.0001	1.24	3.29	0.0821
Silicon	1.24	43.56	< 0.0001	1.24	2.56	0.1226	1.24	4.07	0.0550
Species	1.24	3.98	0.0575	1.24	586.07	< 0.0001	1.24	171.06	< 0.0001
Nitrogen × silicon	1.24	20.74	0.0001	1.24	0.28	0.5986	1.24	14.62	0.0008
Nitrogen × species	1.24	2.52	0.1257	1.24	93.67	< 0.0001	1.24	0.18	0.6750
Silicon × species	1.24	0.04	0.8398	1.24	2.10	0.1606	1.24	3.72	0.0658
Nitrogen × silicon × species	1.24	0.51	0.4807	1.24	1.08	0.3080	1.24	2.57	0.1222

Effects	Herbivory (%) <i>S. acutus</i>			Herbivory (%) <i>S. californicus</i>		
	df	F	P	df	F	P
Nitrogen	1.12	2.55	0.1363	1.12	0.93	0.3701
Silicon	1.12	11.21	0.0058	1.12	0.05	0.9616
Species	–	–	–	–	–	–
Nitrogen × silicon	1.12	1.99	0.1833	1.12	0.02	0.9864
Nitrogen × species	–	–	–	–	–	–
Silicon × species	–	–	–	–	–	–
Nitrogen × silicon × species	–	–	–	–	–	–

Effects	Aboveground biomass			Inflorescence biomass			Belowground biomass			Stem strength		
	df	F	P	df	F	P	df	F	P	df	F	P
Nitrogen	1.24	83.52	< 0.0001	1.24	1.66	0.2099	1.24	6.30	0.0192	1.64	30.52	< 0.0001
Silicon	1.24	7.82	0.0100	1.24	1.09	0.3073	1.24	0.08	0.7780	1.64	5.90	0.0180
Species	1.24	0.76	0.3914	1.24	33.97	< 0.0001	1.24	2.95	0.0988	1.64	2.11	0.1513
Nitrogen × silicon	1.24	21.55	0.0001	1.24	14.94	0.0007	1.24	1.02	0.3225	1.64	0.98	0.3251
Nitrogen × species	1.24	7.99	0.0093	1.24	1.66	0.2099	1.24	1.24	0.2773	1.64	0.03	0.8680
silicon × species	1.24	1.81	0.1912	1.24	1.09	0.3073	1.24	2.25	0.1470	1.64	1.52	0.2224
Nitrogen × silicon × species	1.24	3.24	0.0845	1.24	14.94	0.0007	1.24	1.67	0.2091	1.64	1.12	

Appendix 3

See Table 4.

Table 4 Results of a 3-way ANOVA testing the effects of nitrogen, silicon, and species on root length

Effects	Root size 0.0–0.05 mm			Root size 0.05–0.10 mm			Root size 0.10–0.20 mm			Root size 0.20–0.50 mm		
	df	F	P	df	F	P	df	F	P	df	F	P
Nitrogen	1.24	10.94	0.0030	1.24	3.57	0.0710	1,24	0.18	0.6752	1.24	0.42	0.5244
Silicon	1.24	2.27	0.1447	1.24	0.86	0.3643	1,24	0.02	0.8964	1.24	0.83	0.3719
Species	1.24	15.26	0.0007	1.24	34.27	< 0.0001	1,24	80.17	< 0.0001	1.24	29.38	< 0.0001
Nitrogen × silicon	1.24	0.04	0.8460	1.24	1.55	0.2245	1,24	1.89	0.1823	1.24	0.00	0.9681
Nitrogen × species	1.24	3.81	0.0628	1.24	5.61	0.0262	1,24	0.00	0.9867	1.24	0.96	0.3381
Silicon × species	1.24	0.24	0.6300	1.24	0.79	0.3838	1,24	0.11	0.7448	1.24	0.62	0.4398
Nitrogen × silicon × species	1.24	6.08	0.0212	1.24	5.36	0.0295	1,24	5.72	0.0250	1.24	1.11	0.3036

Effects	Root size 0.50–1.00 mm			Root size 1.00–2.00 mm			Root size > 2.00 mm		
	df	F	P	df	F	P	df	F	P
Nitrogen	1.24	10.04	0.0041	1.24	9.38	0.0053	1.24	0.02	0.8939
Silicon	1.24	2.79	0.1081	1.24	1.48	0.2350	1.24	0.02	0.8887
Species	1.24	32.12	< 0.0001	1.24	84.02	< 0.0001	1.24	24.56	< 0.0001
Nitrogen × silicon	1.24	0.06	0.8042	1.24	0.17	0.6869	1.24	5.03	0.0344
Nitrogen × species	1.24	0.01	0.9313	1.24	0.03	0.8638	1.24	0.02	0.8939
Silicon × species	1.24	1.47	0.2366	1.24	0.04	0.8516	1.24	0.02	0.8887
Nitrogen × silicon × species	1.24	0.00	0.9835	1.24	0.65	0.4294	1.24	5.03	0.0344

Appendix 4

See Table 5.

Table 5 Results of a 3-way ANOVA testing the effects of nitrogen, silicon, and species on stem lodging after exposure to wind at differing speeds

Effects	Original stem broken by own weight			Stems broken by 8 kmph wind			Stems broken by 16 kmph wind			Stems broken by 24 kmph wind		
	df	F	P	df	F	P	df	F	P	df	F	P
Nitrogen	1.24	11.26	0.0026	1.24	6.35	0.0188	1.24	7.41	0.0119	1.24	15.47	0.0006
Silicon	1.24	5.49	0.0278	1.24	2.57	0.1218	1.24	0.65	0.4269	1.24	2.50	0.1269
Species	1.24	3.53	0.0726	1.24	4.12	0.0535	1.24	6.96	0.0144	1.24	10.77	0.0031
Nitrogen × silicon	1.24	4.58	0.0426	1.24	2.02	0.1678	1.24	5.08	0.0336	1.24	4.84	0.0377
Nitrogen × species	1.24	0.12	0.7329	1.24	0.00	0.9831	1.24	0.44	0.5122	1.24	1.90	0.1809
Silicon × species	1.24	4.27	0.0498	1.24	2.35	0.1383	1.24	0.30	0.5861	1.24	1.79	0.1930
Nitrogen × Silicon × species	1.24	0.05	0.8272	1.24	0.28	0.5990	1.24	0.01	0.9380	1.24	0.41	0.5289

Table 5 continued

Effects	Stems broken by 40 kmph wind			Stems broken by 80 kmph wind			Stems broken by 120 kmph wind		
	df	F	P	df	F	P	df	F	P
Nitrogen	1.24	17.78	0.0003	1.24	37.18	< 0.0001	1.24	37.91	< 0.0001
Silicon	1.24	1.94	0.1763	1.24	3.06	0.0931	1.24	1.35	0.2562
Species	1.24	17.54	0.0003	1.24	52.71	< 0.0001	1.24	43.47	< 0.0001
Nitrogen × silicon	1.24	4.01	0.0567	1.24	7.74	0.0104	1.24	4.97	0.0353
Nitrogen × species	1.24	3.60	0.0697	1.24	7.93	0.0096	1.24	0.04	0.8486
Silicon × species	1.24	2.27	0.1448	1.24	4.44	0.0458	1.24	3.85	0.0615
Nitrogen × Silicon × species	1.24	0.25	0.6207	1.24	0.11	0.7414	1.24	2.23	0.1481

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