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Plant silicon effects on insect feeding dynamics are influenced by plant nitrogen availability

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Abstract

Although there is growing evidence that silicon (Si)-based plant defenses effectively reduce both the palatability and digestibility of leaves, and thus impact nutrient assimilation by insect herbivores, much less is known about how this is affected by extrinsic and intrinsic factors. For example, do herbivores exhibit compensatory feeding on poor-quality diets with Si or are Si defenses less effective in agroecosystems where high N availability increases plant quality? To investigate the interactive effects of N and Si on insect feeding, we conducted insect performance and compensatory feeding bioassays using maize, *Zea mays* L. (Poaceae), and the true armyworm, *Pseudeletia unipuncta* Haworth (Lepidoptera: Noctuidae). In the performance assay, the addition of Si alone resulted in increased larval mortality compared with the controls, likely because early instars with poorly developed mandibles could not feed effectively. However, larvae fed on plants treated with both Si and N survived better than on plants treated with Si only, although pupal mass did not differ between treatments. In our compensatory assay, Si addition reduced maize consumption, but increased both armyworm approximate digestibility and N assimilation efficiency, suggesting that enhanced post-ingestion feeding physiology, rather than compensatory food intake, could have accounted for the lack of Si effects on pupal weight. Overall, our results demonstrate that, similar to other chemical and mechanical defenses, the effectiveness of plant Si defense is influenced by plant nutrient status and consumer compensatory ability.

Introduction

Plants take up silicon (Si) in the form of monosilicic acid, which is then deposited as solid opaline phytoliths in the epidermis (Cooke & Leishman, 2011; Hartley et al., 2015), and this silicification can increase leaf abrasiveness (Massey et al., 2006) leading to reduced consumption rates and lower levels of insect herbivory (Salim & Saxena, 1992; Kvedaras & Keeping, 2007). Furthermore, once ingested, Si may affect the efficiency of digestion and nitrogen (N) assimilation. This results in increased mortality and lower mass of those that survive (Kvederas et al., 2007; Massey & Hartley, 2009) and may lead to an overall reduction in insect population size (Nikpay & Nejadian, 2014).

The importance of Si-based defenses may be species dependent because monocots accumulate much higher foliar Si than dicots (Hodson et al., 2005) and the importance of Si defenses could be less in low accumulating taxa (Hogendorp, 2008; but see Katz, 2014; Teixeira et al., 2017). Furthermore, the efficacy of Si-based defense may be counteracted to some extent by increased N availability, either through exogenous application or Si-induced root nodulation (Cahenzli & Erhardt, 2012; Nabity et al., 2012; Johnson et al., 2017). Herbivores generally express preference for N-rich plant material (Slansky & Scriber, 1985; White, 1993), although deleterious effects may arise from excessive or imbalanced N (Behmer, 2009; Lebigre et al., 2018). Feeding on plants with high N content can increase dry matter digestibility (Bultman & Conard, 1998; Hwang et al., 2008) and N assimilation (Slansky & Feeny, 1977), leading to increased survival, fecundity, and abundance (White, 1984; Kytö et al., 1996; Awmack & Leather, 2002; Keeping et al., 2014). These benefits can be partially

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attributed to the amelioration of carbon-based plant defenses in response to N amendment (Coley et al., 1985; Stamp, 2003). In contrast, N effects on silicon-based defense, and the resultant consequences for insect feeding and performance, remain poorly understood.

Insect herbivores express compensatory feeding mechanisms in response to plant quality (Simpson & Simpson, 1990), and this could influence the impact of opposing N and Si effects because increased leaf consumption is observed in response to either increases or decreases in food quality (Slansky, 1993; Berner et al., 2005; Behmer, 2009). Also, despite evidence for reduced consumption rates in response to greater leaf abrasiveness following Si addition (Massey et al., 2006, 2007; Frew et al., 2017), the effects vary depending on the species of consumer (Nabity et al., 2012). In addition to altering feeding patterns, an insect's compensatory response may have a physiological basis because some lepidopteran larvae can digest plant N and other cell contents even when leaf mastication is minimal (Barbehenn, 1992). Because Si's major mode of action on insect herbivores is reported to be excessive mandible wear (Djamin & Pathak, 1967; Ebeid et al., 2013), the effects would be most evident with early-instar larvae, and although the impact may be mitigated with each successive molt, sub-lethal Si effects may accumulate across instars (Massey & Hartley, 2009).

Maize (*Zea mays* L.) (Poaceae) accumulates high concentrations of foliar Si (Rojanaridpiched et al., 1984; Goussain et al., 2002). In agroecosystems, it is simultaneously treated with fertilizers to maximize productivity, so we used this model system to study possible interactions between N and Si availability on the performance of herbivores. We conducted a performance assay to determine the response of the true armyworm, *Pseudeletia unipuncta* Haworth (Lepidoptera: Noctuidae), an important pest of maize (Metcalf & Flint, 1962), to host plants subject to different levels of Si and N amendment. We conducted a second, mechanistic assay to explore whether the treatments could influence armyworm leaf consumption, approximate digestibility, or N assimilation efficiency, and how these compensatory responses might account for trends observed in the performance assay. We predicted that (1) the addition of N or Si alone would increase and decrease insect performance, respectively, and (2) when applied simultaneously, the positive effect of the N would at least partially mitigate the negative effects of Si treatments.

Materials and methods

Maize silicon and nitrogen treatments

All maize plants used in the feeding assays were grown for 4 weeks, which reflects a suitable host age for both young and old armyworm larvae (Schaafsma et al., 2007). Maize was grown in pots (10 cm diameter, 20 cm deep) with standard Pro-Mix potting soil (Premier Tech, Rivière-du-Loup, Quebec, Canada) under a L16(25 °C):D8(10 °C) photo- and thermoperiodic cycle at 70% r.h. Plants were randomly assigned to one of four treatment groups consisting of a two-way factorial combination of N (de-ionized water control or 400 mg l^{-1} ammonium nitrate, NH_4NO_3) and Si (de-ionized water control or 150 mg l^{-1} sodium silicate, $NaSiO_3{\bullet}9H_20$), with each plant receiving 100 ml of their respective treatment solution weekly. The N treatment was equivalent to 20 g m^{-2} N, the application rate employed in previous studies (Fernández et al., 1996; Liu & Wiatrak, 2011), whereas the Si treatment followed the protocol used for other Poaceae species (Massey & Hartley, 2006, 2009). Each week plants also received 100 ml of Hoagland's solution (0.02% potassium as K_2SO_4, 0.03% calcium as $CaCl_2$, 0.01% phosphorus as KH_2PO_4, 0.02% magnesium as $MgSO_4$, 0.03% nitrogen as NH_4NO_3, and trace amounts of iron, boron, manganese, zinc, copper, and sodium molybdate). This solution was provided to both avoid premature tissue chlorosis or necrosis of control plants (and applied to all plants to maintain consistency) over the course of the experiment, as well as to provide plants with essential growth micronutrients absent from the potting mix.

Insect performance assays

Assays were conducted at 20 °C, 70% r.h., and L16:D8 photoperiod. Ten plants from each treatment were placed into plastic sleeves with a mesh top to promote air and moisture exchange but leaving the base of the pot exposed for bottom watering. Each plant was infested with 10 neonate *P. unipuncta* larvae, and after 2 weeks, larval survival was assessed. Because late instars are cannibalistic, all survivors were subsequently reared in individual containers and provided daily with maize leaves from their corresponding treatment ad libitum until pupation. The duration of larval development as well as pupal mass were recorded.

Compensatory feeding assay

No-choice feeding assays were carried out under the same controlled conditions, using newly molted fourth instars from the laboratory colony. Leaf disk samples were taken along the mid rib of the two most recently expanded leaves with a cork borer (1 cm radius) and their wet weights were recorded. To develop allometric equations for the conversion of wet to dry weight (DW), 10 leaf disks from plants in each of the four treatments were measured for leaf area, and then dried for 72 h at 70 °C to obtain dry mass. For each of the treatments, 20 larvae that had been starved for 24 h were weighed and then placed individually in Petri dishes each containing five fresh leaf disks of known mass. The assay was terminated after 8 h to ensure that there was still food remaining. The caterpillars and leaf disks were reweighed (wet and dry weights, respectively) so that the amount consumed could be calculated. The larvae were held for an additional 24 h without food and the frass produced was collected, dried, and weighed to calculate approximate digestibility and nitrogen assimilation efficiency, two common nutritional indices used to determine the effectiveness of consumer resource use (Scriber & Slansky, 1981; Manuwoto & Scriber, 1985; Karowe & Martin, 1989). Approximate digestibility was calculated using the equation: [(DW leaf consumed – DW feces)/DW leaf consumed] × 100%.

Leaf and fecal N content were quantified by Kjeldahl digestion followed by colorimetric analysis for ammonium (EPA method 353.2) using a SmartChem 140 discrete auto-analyzer (Westco Scientific Instruments, Brookfield, CT, USA). This was used to calculate N assimilation efficiency using the equation: [(N consumed – N in frass)/N consumed] × 100%.

Because we did not quantify urea, which represents a small fraction of N egestion, N assimilation efficiency results do not account for total N waste nor do our results reflect the total N budget. Leaf silicon content was determined by a portable X-ray fluorescence device (P-XRF), calibrated using Si-spiked synthetic methyl cellulose and validated using certified reference materials of NCS DC73349 'Bush branches and leaves' obtained from China National Analysis Center for Iron and Steel (see Reidinger et al., 2012). Prior to analysis, leaf material was balled and pressed into 13-mm-diameter pellets with a manual hydraulic press using a 13-mm die (Specac, Orpington, UK).

Statistical analysis

We used a series of two-way fixed-effects ANOVAs to test for the effects of N and Si addition, and their interaction (all as between-subjects factors) on maize leaf %N, armyworm survival (early instar), developmental time, pupal mass, leaf consumption, approximate digestibility, and N assimilation efficiency. Because leaf %Si data were not normally distributed, they were analyzed using generalized linear regression models with a gamma distribution link function. When significant main or interactive effects were present ($\alpha = 0.05$), we used a Tukey's test to compare means among all pair-wise treatment combinations. To specifically test our prediction that N fertilization alleviates the negative effects of Si on insect feeding performance, least squares means (LSM) contrasts were used for planned comparisons restricted to the Si and N+Si treatment groups only. All statistical analyses were conducted in R (v. 3.1.1, 'Sock it to Me'), implementing the 'MASS package' (v.7.3-35) to construct GLMs and the 'lsmeans' package (v.2.10) to conduct pair-wise contrasts.

Results

Leaf chemistry

Maize leaf %N content increased significantly in response to N addition (Figure 1; P-values are presented in Table 1), but was unaffected by the addition of Si alone or by Si in combination with N (N+Si). Similarly, leaf %Si content increased significantly with the addition of Si (Figure 1), but was not altered by the addition of N alone or by N+Si (Table 1).

Insect performance assays

Despite the lack of main or interactive effects of N or Si on armyworm survival (Figure 2A), when assessed as an LSM contrast, the N+Si-treated plants significantly increased the survival of armyworms compared with those feeding on Si-treated plants (Table 1). The interaction between N and Si had a significant effect on armyworm development time (Table 1), with armyworms fed N- and Si-treated plant material pupating ca. 1.5 days sooner than those fed control leaves (Figure 2B). However, there were no effects of N or Si addition on final pupal weight (Figure 2C).

Compensatory feeding assays

The Si treatment resulted in a significant decline in leaf consumption, but there were no such decreases with N alone, or in combination with Si (Table 1, Figure 3A). There was a significant interaction between N and Si

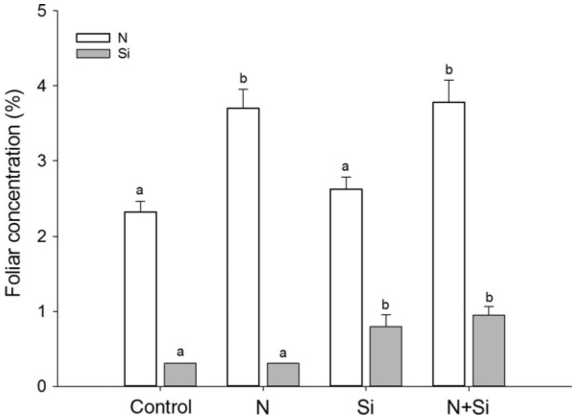

Figure 1 Effect of nitrogen (N) and silicon (Si) addition on the mean (+ SE) foliar concentration of N (n = 8) and Si (n = 10) in maize leaves. Bars within an element capped with different letters are significantly different (Tukey's HSD tests: $P<0.05$).

Table 1 Summary of P-values for the effects of nitrogen (N) and silicon (Si) addition, as well as their interaction (N×SI), on maize foliar chemistry and armyworm feeding and fitness parameters

	N	Si	N×Si	Least squares means contrast (Si vs. N+Si)
Foliar chemistry				
Leaf N	<0.0001	0.43	0.65	0.001
Leaf Si	0.99	0.0005	0.44	0.29
Fitness parameters				
Survival	0.15	0.27	0.27	0.047
Development time	0.18	0.20	0.038	0.55
Pupal weight	0.36	0.76	0.71	0.70
Feeding parameters				
Leaf consumption	0.62	0.03	0.54	0.45
Approximate digestibility	0.99	0.73	0.005	0.045
Nitrogen assimilation	0.007	0.41	0.001	0.66

addition on approximate digestibility, with the digestion of N- and Si-treated maize leaves much higher than control or N+Si-treated leaves (Figure 3B). Furthermore, the N+Si treatment resulted in significantly lower digestibility than Si treatment (Table 1). There was a significant effect of N alone as well as an interaction with Si on leaf N assimilation efficiency, with increased assimilation of the N-, Si-, and N+Si-treated plants relative to control leaves (Table 1, Figure 3C).

Discussion

The results of this study provide some support for our original prediction that the addition of Si would have a negative effect on the true armyworm, and that the simultaneous addition of N would have a mitigating effect. However, the impact observed varied considerably depending on the parameter measured. The addition of Si did result in increased mortality of early instars as reported for other invertebrate taxa (Kvedaras & Keeping, 2007). Neonate armyworm larvae feed collectively, a behavior observed in many lepidopterans that is believed to help overcome plant physical defenses (Fitzgerald, 1993). Consequently, changes in leaf abrasiveness following the addition of Si could increase mandibular wear (Massey & Hartley, 2009; Ebeid et al., 2013) and/or reduce the ability of young larvae to handle and masticate plant matter (Hunt et al., 2008), resulting in higher mortality. However, the deleterious effect of Si was at least partially mitigated when there was a concurrent application of N. This may be explained in part by the increased leaf %N because adding N with Si can improve dry matter assimilation efficiency (Nabity et al., 2012), and thus starvation may have been partially offset by an increased retention of plant material consumed.

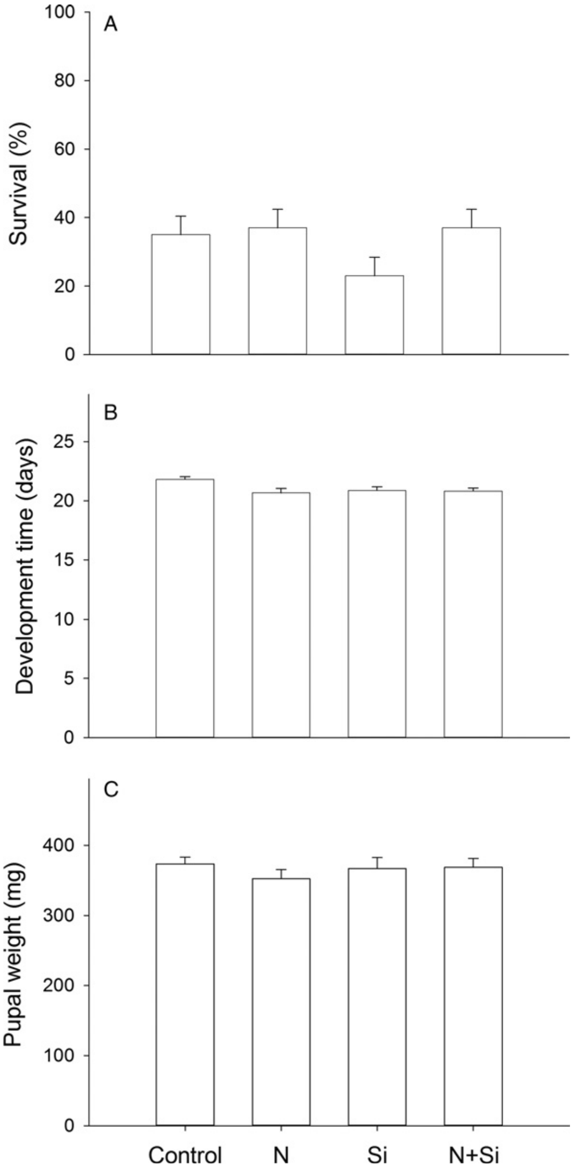

Figure 2 Effect of nitrogen (N) and silicon (Si) addition on mean (+ SE; n = 10) (A) larval survival, (B) development time, and (C) pupal mass of true armyworm larvae reared on maize.

Surprisingly, the larvae that survived on Si-treated plants had the shortest development time (albeit only by an average of ca. 1 day) and had the same pupal mass as individuals from all other treatments, suggesting they exhibited a compensatory response to this suboptimal

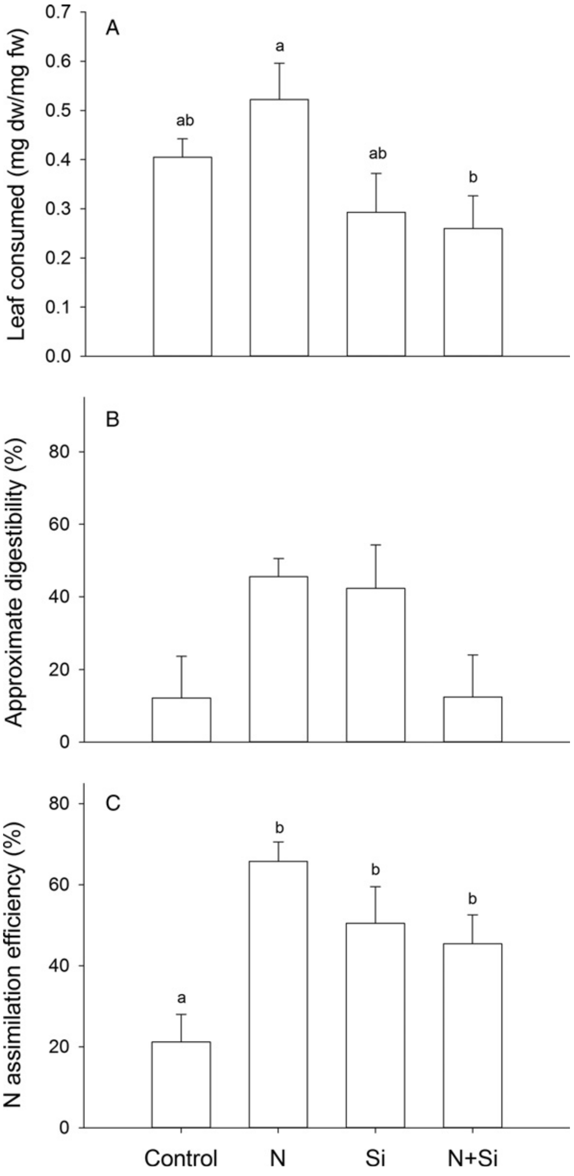

Figure 3 Effect of nitrogen (N) and silicon (Si) addition on mean (+ SE; n = 20) (A) leaf consumption, (B) approximate digestibility, and (C) N assimilation efficiency by true armyworm larvae reared on maize. Bars within a panel capped with different letters are significantly different (Tukey's HSD tests: $P<0.05$).

diet. Although increased food consumption is a common compensatory mechanism when insect herbivores are reared on plants with suboptimal nutrient content (Mattson, 1980; Berner et al., 2005; Stiling & Cornelissen, 2007) or increased leaf abrasiveness (Raupp, 1985; Massey et al., 2006; Han et al., 2015), maize consumption by fourth instars in the compensatory assay significantly decreased in response to Si addition. Instead, compensation can likely be attributed, at least in part, to the increased digestibility and N assimilation efficiency on the Si-treated plants. The observed increase in N assimilation efficiency with Si amendment is consistent with reports for other Lepidoptera, including the fall armyworm (Nabity et al., 2012), and may be associated with enhanced enzyme activity (Hocking & Depner, 1961). Furthermore, the peritrophic membrane in the larval mid-gut offers protection from abrasive food particles (Hegedus et al., 2009), and because the structure can change in response to food quality (Plymale et al., 2008), a Si-induced response may have benefited overall digestion. Interestingly, the growth parameters of larvae fed on plants treated with both Si and N did not differ from those fed plants receiving one or other treatment alone, even though digestibility was reduced.

Silicon has a substantial influence on herbivore fitness at both the individual (Reynolds et al., 2009) and population levels (Massey et al., 2008; Reynolds et al., 2012). However, our findings show that the overall efficacy of Si-based defenses against the true armyworm is contingent on additional factors. Nitrogen availability not only influenced the response of armyworm feeding physiology to Si-treated maize but also significantly reduced overall mortality. Therefore, plant Si defenses can be strongly diluted under conditions of high soil fertility, a response that is largely consistent with the effects of N amendment on carbon-based chemical defenses (Coley et al., 1985; Stamp, 2003). Although negative effects of N addition have been reported for other species (Behmer, 2009; Lebigre et al., 2018), none was observed in any performance or compensatory metrics we carried out on the true armyworm. Also, despite the potential for associational changes in defense metabolites such as Dimboa, previous work has shown its foliar concentration was insensitive to N fertilization (Manuwoto & Scriber, 1985). In addition to plant nutrient status, intrinsic herbivore feeding mechanics and digestive capacity could also dictate the extent of Si effects. Where differential responses between herbivore taxa and larval stages to Si treatment have already been observed (Massey et al., 2006; Massey & Hartley, 2009; Nabity et al., 2012), our results suggest that this relationship further extends to an individual's compensatory ability. The fact that deleterious Si effects were most pronounced for younger instars is of particular significance because early-instar survival is a key component of population dynamics in Lepidoptera (Zalucki et al., 2001, 2002). Overall, our findings further support the role of Si in driving plant–insect interactions, but much like with other forms of foliar defense, both intrinsic and extrinsic factors contribute substantially to dictate the ultimate consequences on herbivore feeding and performance.

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References

Awmack CS & Leather SR (2002) Host plant quality and fecundity in herbivorous insects. Annual Review of Entomology 47: 817–844.

Barbehenn RV (1992) Digestion of uncrushed leaf tissues by leaf-snipping larval Lepidoptera. Oecologia 89: 229–235.

Behmer ST (2009) Insect herbivore nutrient regulation. Annual Review of Entomology 54: 165–187.

Berner D, Blanckenhorn WU & Körner C (2005) Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. Oikos 111: 525–533.

Bultman TL & Conard NJ (1998) Effects of endophytic fungus, nutrient level, and plant damage on performance of fall armyworm (Lepidoptera: Noctuidae). Environmental Entomology 27: 631–635.

Cahenzli F & Erhardt A (2012) Host plant defence in the larval stage affects feeding behaviour in adult butterflies. Animal Behaviour 84: 995–1000.

Coley PD, Bryant JP & Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230: 895–899.

Cooke J & Leishman MR (2011) Is plant ecology more siliceous than we realise? Trends in Plant Science 16: 61–68.

Djamin A & Pathak MD (1967) Role of silica in resistance to Asiatic rice borer, *Chilo suppressalis* (Walker), in rice varieties. Journal of Economic Entomology 60: 347–351.

Ebeid AR, Rahman AAA & Gesraha MA (2013) Impact of diatomaceous earth (silica nano-particles) on alfalfa grasshopper, *Heteracris littoralis* (Rambur) (Orthopetra: Acrididae) under laboratory conditions. Egyptian Journal of Biological Pest Control 23: 325–330.

Fernández JE, Moreno F, Murillo JM, Cayuela JA, Fernández-Boy E & Cabrera F (1996) Water use and yield of maize with two levels of nitrogen fertilization in SW Spain. Agricultural Water Management 29: 215–233.

Fitzgerald TD (1993) Sociality in caterpillars. Caterpillars: Ecological and Evolutionary Constraints on Foraging (ed. by NE Stamp & TM Casey), pp. 327–402. Chapman & Hall, New York, NY, USA.

Frew A, Allsopp PG, Gherlenda AN & Johnson SN (2017) Increased root herbivory under elevated atmospheric carbon dioxide concentrations is reversed by silicon-based plant defences. Journal of Applied Ecology 54: 1310–1319.

Goussain MM, Moraes JC, Carvalho JG, Nogueira NL & Rossi ML (2002) Effect of silicon application on corn plants upon the biological development of the fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae). Neotropical Entomology 31: 305–310.

Han Y, Lei W, Wen L & Hou M (2015) Silicon-mediated resistance in a susceptible rice variety to the rice leaf folder, *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). PLoS ONE 10: 1–13.

Hartley SE, Fitt RN, McLarnon EL & Wade RN (2015) Defending the leaf surface: intra- and inter-specific differences in silicon deposition in grasses in response to damage and silicon supply. Frontiers in Plant Science 6(35): 1–8.

Hegedus D, Erlandson M, Gillott C & Toprak U (2009) New insights into peritrophic matrix synthesis, architecture, and function. Annual Review of Entomology 54: 285–302.

Hocking B & Depner KR (1961) Larval nutrition in *Agrotis orthogonia* (Lepidoptera: Phalaenidae): digestive enzymes. Annals of the Entomological Society of America 54: 86–89.

Hodson MJ, White PJ, Mead A & Broadley MR (2005) Phylogenetic variation in the silicon composition of plants. Annals of Botany 96: 1027–1046.

Hogendorp BK (2008) Effects of Silicon-based Fertilizer Applications on the Development and Reproduction of Insect Pests Associated with Greenhouse-grown Crops. PhD Dissertation, University of Illinois, Urbana-Champaign, IL, USA.

Hunt JW, Dean AP, Webster RE, Johnson GN & Ennos AR (2008) A novel mechanism by which silica defends grasses against herbivory. Annals of Botany 102: 653–656.

Hwang S-Y, Liu C-H & Shen T-C (2008) Effects of plant nutrient availability and host plant species on the performance of two *Pieris* butterflies (Lepidoptera: Pieridae). Biochemical Systematics and Ecology 36: 505–513.

Johnson SN, Hartley SE, Ryalls JMW, Frew A, DeGabriel JL et al. (2017) Silicon-induced root nodulation and synthesis of essential amino acids in a legume is associated with higher herbivore abundance. Functional Ecology 31: 1903–1909.

Karowe DN & Martin MM (1989) The effects of quantity and quality of diet nitrogen on the growth, efficiency of food utilization, nitrogen budget, and metabolic rate of fifth-instar *Spodoptera eridania* larvae (Lepidoptera: Noctuidae). Journal of Insect Physiology 35: 699–708.

Katz O (2014) Beyond grasses: the potential benefits of studying silicon accumulation in non-grass species. Frontiers in Plant Science 5(376): 1–3.

Keeping MG, Miles N & Sewpersad C (2014) Silicon reduces impact of plant nitrogen in promoting stalk borer (*Eldana saccharina*) but not sugarcane thrips (*Fulmekiola serrata*) infestations in sugarcane. Frontiers in Plant Science 5(289): 1–12.

Kvedaras OL & Keeping MG (2007) Silicon impedes stalk penetration by the borer *Eldana saccharina* in sugarcane. Entomologia Experimentalis et Applicata 125: 103–110.

Kvederas OL, Keeping MG, Goebel FR & Byrne MJ (2007) Larval performance of the pyralid borer *Eldana saccharina* Walker and stalk damage in sugarcane: influence of plant silicon, cultivar and feeding site. International Journal of Pest Management 53: 183–194.

Kytö M, Niemelä P & Larsson S (1996) Insects on trees: population and individual response to fertilization. Oikos 75: 148–159.

Lebigre C, Vanderbeken C, Turlure C & Schtickzelle N (2018) Host plant nitrogen enrichment has both positive and negative effects on the larval growth of a specialist butterfly. Ecological Entomology 43: 494–505.

Liu K & Wiatrak P (2011) Corn (*Zea mays* L.) plant characteristics and grain yield response to N fertilization programs in no-tillage system. American Journal of Agricultural and Biological Science 6: 172–179.

Manuwoto S & Scriber JM (1985) Differential effects of nitrogen fertilization of three corn genotypes on biomass and nitrogen utilization by the southern armyworm, *Spodoptera eridania*. Agriculture, Ecosystems and Environment 14: 25–40.

Massey FP & Hartley SE (2006) Experimental demonstration of the antiherbivore effects of silica in grasses: impacts on foliage digestibility and vole growth rates. Proceedings of the Royal Society B 273: 2299–2304.

Massey FP & Hartley SE (2009) Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. Journal of Animal Ecology 78: 281–291.

Massey FP, Ennos AR & Hartley SE (2006) Silica in grasses as a defence against insect herbivores: contrasting effects on folivores and a phloem feeder. Journal of Animal Ecology 75: 595–603.

Massey FP, Ennos AR & Hartley SE (2007) Herbivore specific induction of silica-based plant defences. Oecologia 152: 677–683.

Massey FP, Smith MJ, Lambin X & Hartley SE (2008) Are silica defences in grasses driving vole population cycles? Biology Letters 4: 419–422.

Mattson WJ (1980) Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11: 119–161.

Metcalf CL & Flint WP (1962) Destructive and Useful Insects: Their Habits and Control. McGraw-Hill Book Company, New York, NY, USA.

Nabity PD, Orpet R, Miresmailli S, Berenbaum MR & DeLucia EH (2012) Silica and nitrogen modulate physical defense against chewing insect herbivores in bioenergy crops *Miscanthus × giganteus* and *Panicum virgatum* (Poaceae). Journal of Economic Entomology 105: 878–883.

Nikpay A & Nejadian ES (2014) Field applications of silicon-based fertilizers against sugarcane yellow mite *Oligonychus sacchari*. Sugar Tech 16: 319–324.

Plymale R, Grove MJ, Cox-Foster D, Ostiguy N & Hoover K (2008) Plant-mediated alteration of the peritrophic matrix and baculovirus infection in lepidopteran larvae. Journal of Insect Physiology 54: 737–749.

Raupp MJ (1985) Effects of leaf toughness on mandibular wear of the leaf beetle, *Plagiodera versicolora*. Ecological Entomology 10: 73–79.

Reidinger S, Ramsey MH & Hartley SE (2012) Rapid and accurate analyses of silicon and phosphorus in plants using a portable X-ray fluorescence spectrometer. New Phytologist 195: 699–706.

Reynolds OL, Keeping MG & Meyer JH (2009) Silicon-augmented resistance of plants to herbivorous insects: a review. Annals of Applied Biology 155: 171–186.

Reynolds JJH, Lambin X, Massey FP, Reidinger S, Sherratt JA et al. (2012) Delayed induced silica defences in grasses and their potential for destabilising herbivore population dynamics. Oecologia 170: 445–456.

Rojanaridpiched C, Gracen VE, Everett HL, Coors JF, Pugh BF & Bouthyette P (1984) Multiple factor resistance in maize to European corn borer. Maydica 29: 305–315.

Salim M & Saxena RC (1992) Iron, silica, and aluminum stresses and varietal resistance in rice: effects on whitebacked planthopper. Crop Science 32: 212–219.

Schaafsma AW, Holmes ML, Whistlecraft J & Dudley SA (2007) Effectiveness of three Bt corn events against feeding damage by the true armyworm (*Pseudaletia unipuncta* Haworth). Canadian Journal of Plant Science 87: 599–603.

Scriber JM & Slansky F (1981) The nutritional ecology of immature insects. Annual Review of Entomology 26: 183–211.

Simpson SJ & Simpson CL (1990) The mechanisms of nutritional compensation by phytophagous insects. Insect-Plant Interactions 2: 111–160.

Slansky F (1993) Nutritional ecology: the fundamental quest for nutrients. Caterpillars: Ecological and Evolutionary Constraints on Foraging (ed. by NE Stamp & TM Casey), pp. 29–91. Chapman and Hall, New York, NY, USA.

Slansky F & Feeny P (1977) Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. Ecological Monographs 47: 209–228.

Slansky F & Scriber JM (1985) Food consumption and utilization. Comprehensive Insect Physiology, Biochemistry and Pharmacology (ed. by GA Kerkut & LI Gilbert), pp. 87–163. Pergamon Press, Oxford, UK.

Stamp N (2003) Out of the quagmire of plant defense hypotheses. Quarterly Review of Biology 78: 23–55.

Stiling P & Cornelissen T (2007) How does elevated carbon dioxide (CO_2) affect plant-herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. Global Change Biology 13: 1823–1842.

Teixeira NC, Valim JOS & Campos WG (2017) Silicon-mediated resistance against specialist insects in sap-sucking and leaf-chewing guilds in the Si non-accumulator collard. Entomologia Experimentalis et Applicata 165: 94–108.

White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63: 90–105.

White TCR (1993) The Inadequate Environment: Nitrogen and the Abundance of Animals. Springer, Berlin, Germany.

Zalucki MP, Malcolm SB, Paine TD, Hanlon CC, Brower LP & Clarke AR (2001) It's the first bites that count: survival of first-instar monarchs on milkweeds. Austral Ecology 26: 547–555.

Zalucki MP, Clarke AR & Malcolm SB (2002) Ecology and behavior of first instar larval Lepidoptera. Annual Review of Entomology 47: 361–393.