Water stress augments silicon-mediated resistance of susceptible sugarcane cultivars to the stalk borer *Eldana saccharina* (Lepidoptera: Pyralidae)

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Abstract

Silicon (Si) can improve resistance of plants to insect attack and may also enhance tolerance of water stress. This study tested if Si-mediated host plant resistance to insect attack was augmented by water stress. Four sugarcane cultivars, two resistant (N21, N33) and two susceptible (N26, N11) to *Eldana saccharina* Walker were grown in a pot trial in Si-deficient river sand, with (Si+) and without (Si−) calcium silicate. To induce water stress, irrigation to half the trial was reduced after 8.5 months. The trial was artificially infested with *E. saccharina* eggs after water reduction and harvested 66 days later. Silicon treated, stressed and non-stressed plants of the same cultivar did not differ appreciably in Si content. Decreases in numbers of borers recovered and stalk damage were not associated with comparable increases in rind hardness in Si+ cane, particularly in water-stressed susceptible cultivars. Overall, Si+ plants displayed increased resistance to *E. saccharina* attack compared with Si− plants. Borer recoveries were significantly lower in stressed Si+ cane compared with either stressed Si− or non-stressed Si− and Si+ cane. Generally, fewer borers were recovered from resistant cultivars than susceptible cultivars. Stalk damage was significantly lower in Si+ cane than in Si− cane, for N21, N11 and N26. Stalk damage was significantly less in Si+ combined susceptible cultivars than in Si− combined susceptible cultivars under non-stressed and especially stressed conditions. In general, the reduction in borer numbers and stalk damage in Si+ plants was greater for water-stressed cane than non-stressed cane, particularly for susceptible sugarcane cultivars. The hypothesis that Si affords greater protection against *E. saccharina* borer attack in water-stressed sugarcane than in non-stressed cane and that this benefit is greatly enhanced in susceptible cultivars is supported. A possible active role for soluble Si in defence against *E. saccharina* is proposed.

Keywords: calcium silicate, integrated pest management, induced resistance, *Saccharum*, silicon

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Introduction

Although silicon (Si) is abundant in the Earth's crust, it may be depleted in soils that have been intensively cultivated or are highly weathered tropical or organic soils (Epstein, 1999; Savant *et al*., 1999). Approximately 60% of the soils within the South African sugarcane industry are light textured (<20% clay), moderately to strongly acidic (Meyer *et al*., 1998), and are typically deficient in plant-available Si (J.H. Meyer, personal communication). Sugarcane is known to be an Si accumulator (Ma *et al*., 2001). The beneficial effects of Si are usually obvious in crops that actively accumulate Si in their shoots, especially under various abiotic and biotic stress conditions. Most of these effects are expressed through Si deposited in the leaves and stems. Silicon can contribute to the control of insect herbivores and plant pathogens, and may also alleviate the effects of various abiotic stresses including drought and salt stress, metal toxicity, nutrient imbalance, high temperatures and freezing (Ma *et al*., 2001, 2004). Beneficial responses, which are wide-ranging, have been observed in Si-amended barley, rice, sugarcane, maize and other monocotyledonous crops (see review by Epstein, 1999). In solution-cultured cucumber, melon, strawberry, soybean and tomato, which take up Si passively, the beneficial effects of Si are also observed if the Si concentration in the solution is high (see reviews by Jones & Handreck, 1967; Savant *et al*., 1997; Epstein, 1999; Ma *et al*., 2001, 2004).

Silicate fertilizers have been recommended for use in countries where agricultural soils are Si-deficient, including Australia, Brazil, USA (Florida, Hawaii), and Mauritius, and soils under sugarcane cultivation in South Africa (Savant *et al*., 1999), recognizing that the role of Si in agriculture is increasingly important for sustainable production (Savant *et al*., 1997, 1999). Applications of Si fertilizers have many agronomic benefits including improved plant growth, increased yield and positive interactions with applied N, P and K fertilizers (Savant *et al*., 1997; see also Jones & Handreck, 1967 and references cited therein). Silicon amendments reduce the severity of plant pathogens in many crop species (Rodrigues *et al*., 2001; Bélanger *et al*., 2003; Dannon & Wydra, 2004), and enhance resistance to attack by herbivorous insects including borers (Keeping & Meyer, 2002), leaf miners (Goussain *et al*., 2002) and sap feeders (Moraes *et al*., 2004).

Silicon application decreases lepidopteran borer recovery in sugarcane, as observed in, for example, *Diatraea saccharalis* (Fabricius) in Florida (Anderson & Sosa, 2001), and *Chilo infuscatelus* Snell (Rao, 1967) and *Scirpophaga excerptalis* Walker (Gupta *et al*., 1992) in India. Pan *et al*. (1979) also noted a reduction in percentage nodes damaged by stem borers, in general, following Si application. In both field and pot trials, the application of Si to sugarcane plants significantly reduced damage and numbers of borers recovered from stalks of the African sugarcane borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae) (Keeping & Meyer, 2002; Meyer & Keeping, 2005). However, the beneficial effects of Si are usually more apparent in Si-accumulating plants, such as sugarcane, when under abiotic stress, such as increased salinity or drought, or biotic stresses such as pathogens or insect pests (Epstein, 1994; Ma, 2004). Applied Si can reduce water stress by reducing excessive leaf transpiration in rice (Ma *et al*., 2001) and maize (Gao *et al*., 2004), by reducing water loss via decreased water flow rate in the xylem of maize plants (Gao *et al*., 2004), or by increasing plant water uptake ability in sorghum (Hattori *et al*., 2005). Silicon also acts additively with osmotic stress in enhancing pathogen resistance in barley against barley powdery mildew (Wiese *et al*., 2005). The effect of Si on the growth of rice was greater under low humidity (water-stressed) than high humidity conditions (Ma *et al*., 2001).

Historically, drought stress in plants is considered to be a major factor underlying outbreaks of herbivorous insects (White, 1984; but see also Huberty & Denno, 2004), including *E. saccharina* in both rainfed sugarcane in South Africa (Atkinson & Nuss, 1989) and in maize in the Ivory Coast (Moyal, 1995). Insect herbivore populations frequently achieve higher densities on plants that are intermittently, rather than continuously, water-stressed (Huberty & Denno, 2004). Reduction of moisture stress is one of several recommendations for combating *E. saccharina* in the South African sugar industry (Anon, 2005a).

However, a key question, which remains unanswered, is whether Si provides greater protection against insect herbivores when plants are water-stressed, than it does in the absence of water stress. Sugarcane (*Saccharum* spp. hybrids) is an important crop in South Africa, but since 1970 *E. saccharina* has been a major pest, particularly in coastal rainfed areas prone to drought (Atkinson *et al*., 1981). During periods of water stress, susceptibility of sugarcane to *E. saccharina* is significantly increased, particularly in the presence of excess applied nitrogen (Atkinson & Nuss, 1989). Water stress also increases the available stalk nitrogen content of cane, resulting in increased *E. saccharina* larval survival and biomass, as well as shorter development times (Nuss *et al*., 1986; Atkinson & Nuss, 1989). We tested the primary hypothesis that applied Si affords greater protection against *E. saccharina* in plants subjected to water stress. Our secondary hypothesis was that the benefit of Si application to water-stressed plants is likely to be greater in susceptible cultivars than in resistant ones, given that susceptible cultivars are generally less drought tolerant (Keeping & Rutherford, 2004). If applied Si is more efficacious in drought stressed crops, then its use may provide an enhanced benefit to growers by suppressing borer infestations in areas where soils are deficient in Si.

Materials and methods

A potted sugarcane trial (96 pots) was established in a 'shade house' ($14 \times 25 \times 3.3$ m) with transparent fibreglass roofing and walls of 40% green shade cloth, at the South African Sugarcane Research Institute (SASRI), Mount Edgecombe, KwaZulu-Natal. Sugarcane transplants were produced from single budded setts, cut from mature stalks of four commercial cultivars, resistant (N21, N33) and susceptible (N11, N26) to *E. saccharina* attack. One-month-old transplants of each cultivar were planted into 25 l PVC pots containing 31 kg (dry weight) of clean, sieved and thoroughly leached river sand, which allowed control of the nutrient supply. Pots were randomly arranged (using the random function in Microsoft® Office Excel, 2003) in a split plot design, where whole plot was 'cultivar' and sub-plot was 'silica'. There were six replicates for each cultivar, each pot containing four transplants of one cultivar. Guard pots (N33) were placed at the end of each row to reduce differences in growth between inner and outer pots, which probably derive from prevailing winds. Before planting, half

the pots were treated (Si+) with 124 g (equivalent to 10 t ha^{-1}; 4000 ppm) of wollastonite (i.e. calcium silicate, CaSiO$_3$; 7.9% Si; 60% plant available Si), and the other half left untreated (Si−). The calcium silicate was mixed thoroughly with the sand, dampened and the filled pots left to stand for one week before planting.

All pots were treated monthly with 4:1:1 (44) N:P:K fertilizer or ammonium sulphate (250 g per 25 l water) at 500 ml per pot and Hygrotech® Hydroponic Nutrient Mixture for seedlings (25 g per 25 l water) at 500 ml per pot at planting and every two months thereafter, to provide micronutrients (excluding Si). Fertilizer application ceased to all treatments when the plants were water-stressed. This was done as the rate of crop growth under stress declines dramatically; and, therefore, the demand for nutrients declines accordingly (Marschner, 1986). Continuous application of fertilizer results in a build up of nutrients and unused fertilizer, which in turn may result in increased salinity and further stress, as well as a nutrient imbalance (Marschner, 1986). Plants were drip irrigated using tap water (3 ppm Si), at 0.20 to 2.0 l water per pot per day, depending upon the stage of plant growth and stress treatment. Insecticide spray was applied monthly (chlorpyriphos 2 ml/l^{-1} water or alphacypermethrin 1 ml/l^{-1} water) to prevent feral infestations of *E. saccharina* and other pests. Spraying was halted two months before inoculation with *E. saccharina* to ensure no pesticide residue remained on the plants.

At 8.5 months, plants in 48 pots (half the trial) were water-stressed intermittently through a staged reduction in their water supply, such that at the end of the stress periods the susceptible cultivars, N11 and N26, had a mean of four green leaves and the resistant cultivars had an average of five green leaves. With the onset of stress, leaf senescence and reduced new leaf appearance combine to reduce green leaf number per stalk compared to non-stressed plants, a recognized indicator for measuring plant water stress in sugarcane (Inman-Bamber & De Jager, 1986; Inman-Bamber, 2004). Typically, at the time of larval inoculation non-stressed cultivars held an average of 12 green leaves per stalk. Watering was increased slightly after 11 weeks, after which the plants were again water-stressed for three weeks according to a different schedule. This regime was followed because it emulates the variable water availability prevailing in rain-fed sugarcane in South Africa (K.J. Nuss, personal communication). The watering schedules for the two stress periods were as follows. Stress period one: week one, 1.0 l per pot per day; week two, 0.7 l per pot per day; week three, 0.5 l per pot per day; week four, 0.3 l per pot per day; weeks five to 11, 0.2 l per pot per day. Stress period two: week one, 0.5 l per pot per day; week two, 0.3 l per pot per day; week three, 0.2 l per pot per day. The final irrigation rate was maintained until harvest. Manual control of irrigation was sometimes necessary, especially during very hot periods when the plants could be killed.

At 12 months, the trial was hand inoculated with 150 *E. saccharina* eggs per pot (eggs placed on two stalks per pot at 75 eggs per stalk), following the methods of Keeping (2006). At the time of inoculation, most of the eggs were in the 'black head' stage of development and hatched within 24 h, reducing exposure to egg predation. Larvae were allowed to develop for 66 days (520 degree days; t = 10°C; Tempest® Degree-day Units; Insect Investigations Ltd, Cardiff, UK) before harvesting.

At harvest, stalk length, rind hardness at the mid-point of the central internode (Durometer, Rex Gauge Company, Glenview, Illinois 60025, US), and total length of borings per stalk were measured. Thereafter, all stalks were dissected, and leaves and leaf sheaths inspected. Pupal numbers were low. The number of surviving larvae + pupae recovered and the length of stalk bored were used as measures of borer numbers and stalk damage, respectively. Stalk samples for Si analysis were taken at the time of harvest from the same pots used for the borer assessment. Stalk Si% was determined using the procedures of Fox *et al*. (1967).

All the variables analysed were first submitted to the Anderson Darling test for univariate normality and Bartlett's test for homogeneity of variance. Log transformations were employed to stabilize variances and normalize the data where necessary. However, for the sake of clarity, figure axes and means (±1 SEM) show untransformed data. To test for differences in stalk damage, stalk Si content and rind hardness among treatments, these were analysed using a three-way ANOVA with Si, stress and cultivar as main effects. Borer numbers were analysed using a generalized linear mixed model (GLMM), with a Poisson error distribution and a logarithm link function. In a separate analysis of borer numbers and stalk damage, cultivars were grouped and classified as susceptible (N11, N26) and resistant (N21, N33), to reveal differences between susceptible and resistant cultivars. A three-way ANOVA and GLMM (Poisson error distribution and logarithm link function), with Si, stress and 'combined cultivar' as main effects, were used to analyse stalk damage and borers recovered from stalks, respectively. For all analyses, where applicable, the least significant difference (LSD) method was used to determine where significant differences lay. Rind hardness and percentage stalk length bored were analysed at a 'stalk-within-a-pot' level. The stalks were considered to be subsamples within the experimental unit (pot). This allowed for two sources of error to be identified, i.e. sampling and experimental error, where the differences between the stalks within a pot (observational differences) could be separated from the differences between the experimental units, increasing the precision of the analysis (Steel *et al*., 1997). For logistical reasons, stalk Si% and borer numbers were analysed at the pot level (i.e. the sum of borers within each pot). All statistical analyses were performed using Genstat 8.0 for Windows (Genstat, 2005).

Results

Silicon content

Silicon treatment had a significant effect on stalk Si content ($F_{1,20}$ = 160.83, $P < 0.001$), which was higher in Si+ plants than in Si− plants (fig. 1). Stalk Si differed significantly between cultivars ($F_{3,15}$ = 5.29, $P = 0.011$), being lowest in N11 (fig. 1). There was no significant effect of stress on stalk Si ($F_{1,32}$ = 2.02, $P = 0.165$), nor were there any significant interactions. As the trial was only stressed after 8.5 months of normal watering and plant growth, the plants had ample time for Si uptake prior to stressing, as illustrated by the uptake in all Si+ cultivars (fig. 1).

Borer numbers

There was a significant effect of Si on numbers of borers ($F_{1,78}$ = 6.87, $P = 0.009$) with fewer borers recovered from
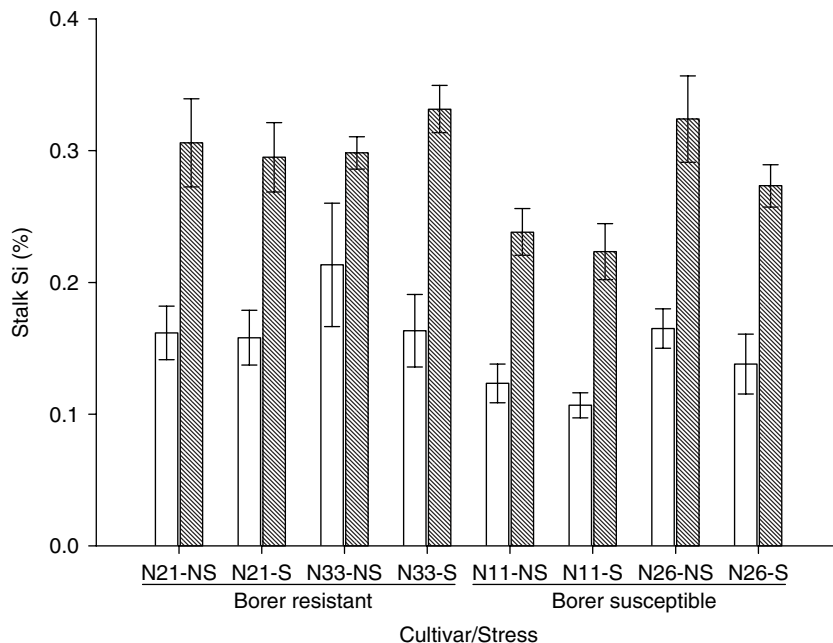
Fig. 1. Percentage of stalk Si at age 14 months in four cultivars (N21 and N33 (resistant), and N11 and N26 (susceptible)) of non-stressed (NS) and water-stressed (S) sugarcane, treated (Si+, ▨) and untreated (Si−, □) with Si. Bars are SE.

Si+ cane than Si− cane (fig. 2). There was also a significant effect of cultivar ($F_{3,78} = 24.84$, $P < 0.001$), with fewer borers found in the resistant cultivars N21 and N33 than in susceptible cultivars N11 and N26 (fig. 2). There was no significant effect of stress on borers recovered from stalks ($F_{1,78} = 3.1$, $P = 0.078$); however, there was a significant

Si × stress interaction ($F_{1,78} = 7.52$, $P = 0.006$), with significantly less borers in stressed Si+ cane compared with either stressed Si− or non-stressed Si− and Si+ cane. There were no other significant interactions. Similarly, when results from the susceptible cultivars (N11 + N26) were combined and compared with combined resistant cultivars
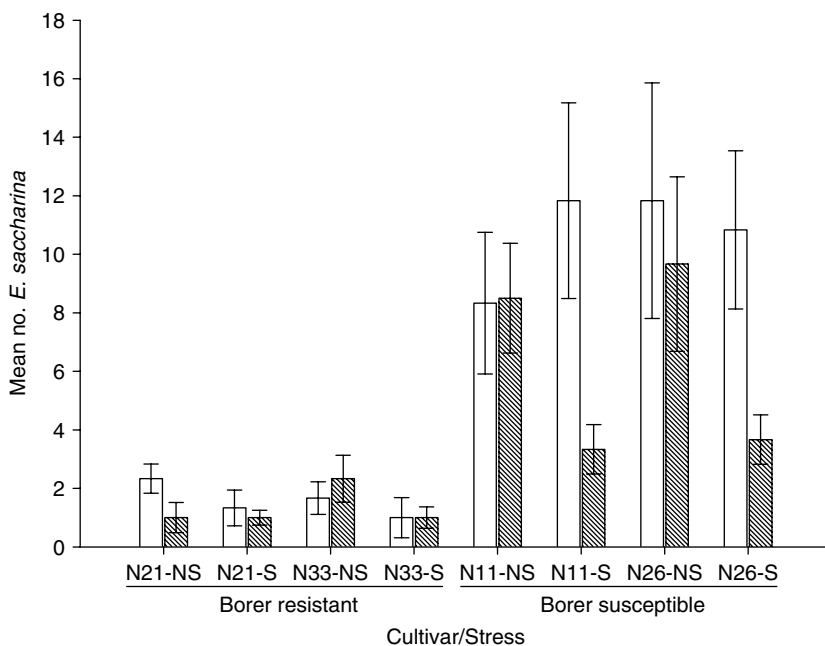

Fig. 2. Mean number of *Eldana saccharina* larvae and pupae recovered from Si-treated (Si+, ▨) and untreated (Si−, □), resistant (N21, N33) and susceptible (N11, N26) sugarcane cultivars under non-stressed (NS) and water-stressed (S) conditions. Bars are SE.
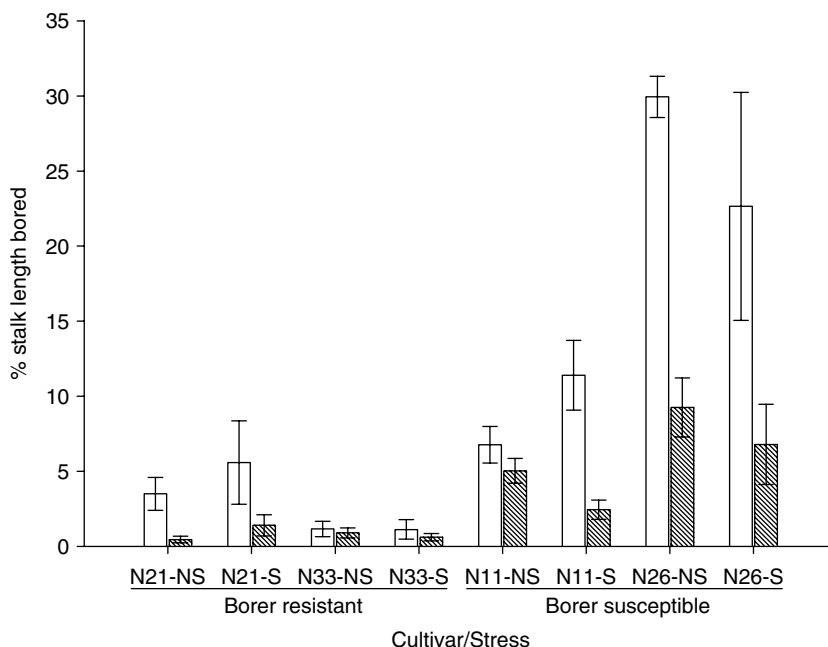
Fig. 3. Percentage stalk length bored by *Eldana saccharina* in Si-treated (Si+, ▨) and untreated (Si−, ▢), resistant (N21, N33) and susceptible (N11, N26) sugarcane cultivars under non-stressed (NS) and water-stressed (S) conditions. Bars are SE.

(N21 + N33), there were significantly lower borer numbers on combined resistant cultivars compared with combined susceptible cultivars ($F_{1,86} = 78.54$, $P < 0.001$) and significantly fewer borers recovered from stalks on Si+ cane compared with Si− cane ($F_{1,86} = 7.02$, $P = 0.008$). There was no significant effect of stress on borer recovery from stalks ($F_{1,86} = 3.07$, $P = 0.08$). However, a significant Si × stress interaction ($F_{1,86} = 7.92$, $P = 0.005$) showed that significantly fewer borers were recovered from stalks in stressed Si+ cane compared with stressed Si− cane, non-stressed Si− and non-stressed Si+ cane (LSD, $P < 0.05$). There was a significant negative correlation between stalk Si% and borer numbers when all cultivars were combined in the analysis (Spearman rank order correlation; r = −0.30; $P < 0.05$; N = 88).

Stalk damage

There was a significant effect of Si on percentage stalk length bored ($F_{1,20} = 34.87$, $P < 0.001$), with the least damage recorded in Si+ cane; and a significant effect of cultivar ($F_{3,15} = 31.82$, $P < 0.001$), with the least stalk damage recorded for N33 (fig. 3). However, there was a significant Si × cultivar interaction for percentage stalk length bored ($F_{3,20} = 5.77$, $P = 0.005$; fig. 3), with N21, N11 and N26 exhibiting significantly less damage on Si+ cane compared with Si− cane (LSD, $P < 0.05$, fig. 3). There was no significant effect of stress ($F_{1,316} = 1.26$, $P = 0.263$), nor were there any other significant interactions. When combined results from the susceptible (N11 + N26) and resistant (N21 + N33) cultivars were compared, there was a significant effect of Si ($F_{1,360} = 27.29$, $P < 0.001$), with less damage recorded on Si+ cane and 'combined cultivar' ($F_{1,360} = 153.54$, $P < 0.001$), with the least damage recorded for combined resistant cultivars.

There was no significant effect of stress ($F_{1,360} = 0.96$, $P = 0.328$), but a significant 'combined cultivar' × Si interaction ($F_{1,360} = 8.28$, $P = 0.004$) and a significant Si × 'combined cultivar' × stress interaction was obtained ($F_{1,360} = 6.08$, $P = 0.014$), with significantly less damage in Si+ combined susceptible cultivars than in Si− combined susceptible cultivars under non-stressed (LSD, $P < 0.05$) and stressed conditions (LSD, $P < 0.001$). There was a significant negative correlation between stalk Si and percentage stalk length bored when data from all cultivars was combined and analysed (Spearman rank order correlation; r = −0.29; $P < 0.05$; N = 88).

Rind hardness

Treatment with Si significantly increased rind hardness ($F_{1,20} = 28.21$, $P < 0.001$; fig. 4). There was also a significant effect of cultivar on rind hardness ($F_{3,15} = 14.09$, $P < 0.001$), being hardest in N33 followed by in order of hardest to softest, N11, N21 and N26. There was no significant effect of stress on rind hardness ($F_{1,256} = 3.75$, $P = 0.054$); however, there was a significant cultivar × stress interaction ($F_{3,256} = 3.7$, $P = 0.012$) and although the trend for all cultivars, except N21, was for a harder rind when non-stressed compared with stressed, this was only significant for N11 (LSD, $P < 0.05$).

Discussion

Silicon application to sugarcane resulted in its increased uptake by four sugarcane cultivars (N21, N33, N11 and N26), regardless of whether the plants were water-stressed at the end of their growth period or not (fig. 1). Treatment with Si
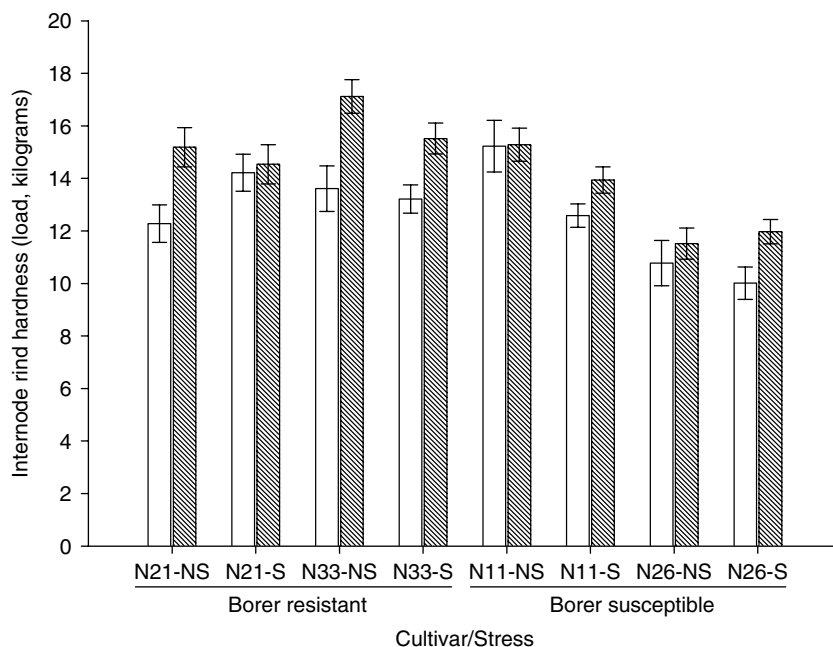
Fig. 4. Internode rind hardness of four sugarcane cultivars, N21, N33, N11 and N26, Si-treated (Si+, ▨) and untreated (Si−, □), under non-stressed (NS) and water-stressed (S) conditions. Bars are SE.

was associated with a reduction in *E. saccharina* borers recovered from stalks and stalk damage, especially in susceptible sugarcane cultivars under water stress. The increase in resistance of Si+ water-stressed susceptible cultivars to *E. saccharina* was such that borer recovery from stalks and damage in these plants approached and, in many instances, was not significantly different from that of resistant cultivars (irrespective of whether the latter were treated with Si and/or water-stressed) (figs 2 and 3). These observations support our primary hypothesis that Si enhances resistance of sugarcane to *E. saccharina* when plants are water-stressed and our secondary hypothesis that the benefit of Si application to water-stressed plants (compared with non-stressed plants) is greater in susceptible cultivars than in resistant ones. The very marked effect of Si in reducing borer numbers and damage in N26 (even when non-stressed for stalk damage), we believe was due to this cultivar's known sensitivity to water stress and poor growth in sandy soils (Anon., 2005b). Inevitably, root binding in pot trials will lead to some degree of stress, even when well watered.

Although the mechanism(s) of Si-mediated resistance has yet to be elucidated, the present results show that its efficacy is enhanced by the simultaneous imposition of water stress and that its action is, therefore, likely to be complex. Silicon application has previously been shown to enhance resistance of sugarcane to *E. saccharina*, especially in susceptible cultivars (Keeping & Meyer, 2002, 2006; Kvedaras *et al.*, 2005; Meyer & Keeping, 2005), but the effect of water stress was not investigated. Comparison of the Si− controls shows that water stress alone neither significantly nor consistently increased borer recovery (fig. 2) or borer damage (with the exception of N11) (fig. 3). Only N11 showed an increase for both variables and N21 for % stalk length bored in response

to stress. This is contrary to Atkinson & Nuss (1989), who reported increased *E. saccharina* performance in drought-stressed cane.

All sugarcane cultivars in the Si+ treatments doubled, or almost doubled, their stalk Si content compared with their respective controls (fig. 1). Keeping & Meyer (2006) demonstrated that cultivars differed in Si assimilation and found that Si− resistant cultivars (N21, N33) had higher stalk Si content (i.e. concentration) than Si− susceptible cultivars (N26, N30). American researchers also reported significant differences in Si accumulation between sugarcane cultivars (Deren *et al.*, 1993; Savant *et al.*, 1999). However, Keeping & Meyer (2002) found that plant Si content of Si+ resistant cultivars was not consistently higher than that of Si+ susceptible cultivars, as was noted in the current study (fig. 1). Furthermore, in the present study Si content did not differ in any consistent way between Si+ cultivars or stress treatments; in particular, a much larger decrease in borer recovery and stalk damage was obtained in Si+ stressed susceptible cultivars (figs 2 and 3) than would be expected based on the corresponding increases in stalk Si content (fig. 1) in these treatments. While there was a significant negative correlation between stalk Si and percentage stalk length bored and between stalk Si and borer numbers when cultivars were combined, this does not provide an adequate explanation for why Si supplementation increased plant resistance to a greater extent in water-stressed susceptible cultivars than in non-stressed susceptible cultivars.

The mechanical barrier hypothesis has traditionally been advanced as an explanation for Si-mediated resistance to disease, wherein polymerized Si is deposited in epidermal cells and forms a barrier to pathogenic penetration (Ishiguro, 2001), in much the same way that it may hinder feeding

by herbivorous insects (Djamin & Pathak, 1967; Moraes *et al.*, 2004). Internode rind hardness among South African sugarcane cultivars is significantly positively correlated with resistance to *E. saccharina*, making it a likely contributor to mechanical resistance against stalk penetration by early instar larvae (Keeping & Rutherford, 2004). However, increased rind hardness due to Si deposition in the stalk epidermis does not provide a complete explanation for our findings, as this increase (fig. 4) was not associated with comparable decreases in borer numbers or stalk damage (figs 2 and 3), especially in the water-stressed susceptible cultivars. Therefore, the mechanism by which Si-mediated resistance to *E. saccharina* acts cannot be explained by the mechanical barrier hypothesis alone. Several studies comparing total Si content of insect resistant and susceptible crop cultivars have also indicated that the arrangement and site of silica deposition in pest-targeted tissues is important (Miller *et al.*, 1960; Hanifa *et al.*, 1974; Moore, 1984). Similarly, the imposition of water stress may change the arrangement, form or concentration of Si in the stalk tissue in ways that increase its effectiveness as a barrier against larval stalk penetration, without necessarily increasing tissue hardness.

To our knowledge, this is the first report of an interaction between Si-mediated resistance to an insect herbivore and an abiotic stress factor. Our results parallel those of other studies, where the beneficial effects of Si were greater under conditions of biotic or abiotic stress (Ma, 2004; Gong *et al.*, 2005). Wiese *et al.* (2005) showed that Si-mediated resistance of barley to barley powdery mildew could be enhanced by the imposition of osmotic stress (which independently can induce resistance to the fungus (Wiese *et al.*, 2004)) and that the effects of Si and osmotic stress were additive. Such an amplification of Si-mediated resistance to a biotic stressor (plant pathogen) by an abiotic stressor (osmotic stress) bears a strong resemblance to the Si × water stress × *E. saccharina* interaction in the present study. In rice the effect of Si on growth is more pronounced under conditions of water stress than non-stressed conditions (Ma *et al.*, 2001). Similar effects may be at work in sugarcane, which also belongs to the Poaceae. Application of Si under conditions of water stress may have an indirect effect (in addition to any direct effects) of reducing borer numbers and stalk damage by enhancing drought tolerance, especially in susceptible drought-intolerant cultivars with low plant Si content.

Silicon has been implicated in metabolic activities in higher plants under drought (Gong *et al.*, 2005) and may also play a role in activating the plant's natural chemical defences against insect herbivores (Gomes *et al.*, 2005). Specifically in sugarcane, analysis of genes involved in secondary metabolism suggests that most of the expressed compounds may be acting as defensive barriers to insect attack (Falco *et al.*, 2001). Plants that have experienced some form of abiotic stress tend to contain higher concentrations of defence compounds (e.g. Isman & Duffey, 1982; Inbar *et al.*, 2001); indeed, the production of these compounds may represent a general response to stress, and herbivory is merely one form (Myers & Bazely, 1991; Nicholson & Hammerschmidt, 1992). Possibly, under various forms of abiotic stress, including water deficiency, Si augments the production of these defensive compounds, making the plant more resistant to insect attack. Evidence of a role for Si as an activator of plant chemical defences against fungal and bacterial pathogens has been reviewed in recent papers by Ghanmi *et al.* (2004),

Rémus-Borel *et al.* (2005), Rodrigues *et al.* (2005), and an editorial by Hammerschmidt (2005). Fauteux *et al.* (2005) considered that the results from monocotyledons and dicotyledons indicate that the role of Si as an activator of plant defences against pathogens could probably be generalized to the plant kingdom as a whole.

Keeping & Meyer (2002) and Correa *et al.* (2005) proposed that Si may act as an elicitor of allelochemicals or enzymes involved in plant defence against insect herbivores. Gomes *et al.* (2005) found that Si, alone or together with aphid pre-infestation, negatively affected greenbugs', *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae), plant preference and population increase rate, and elicited a significant increase in the activities of the defensive enzymes peroxidase, polyphenoloxidase and phenylalanine ammonia-lyase in wheat. We consider that evidence such as the absence of a clear pattern of association between stalk Si content and resistance to *E. saccharina*, and the observation that rind hardness of susceptible cultivars did not increase with Si treatment to an extent greater than that of resistant ones, provides grounds for arguing in favour of an active role for *soluble* Si that compliments any passive, amorphous Si-based mechanical barrier.

In this study, both susceptible cultivars are drought-intolerant while both resistant cultivars have good drought tolerance. It is possible that, when subjected to water stress, the borer-susceptible drought-intolerant cultivars experienced a heightened stress response compared with that of the borer-resistant cultivars, which in turn led to a greater effect of Si (soluble and/or amorphous) in enhancing resistance in the borer-susceptible cultivars. Rutherford and co-workers (Rutherford *et al.*, 1993; Rutherford & Van Staden, 1996; Rutherford, 1998; Heinze *et al.*, 2001) have demonstrated that various defensive compounds (tannins, chlorogenates, flavonoids, epicuticular waxes, protease inhibitors) differ in quantity and/or in composition between sugarcane cultivars, susceptible and resistant to *E. saccharina*. Possibly, in the presence of Si, water-stressed borer-susceptible cultivars may develop a defensive chemistry with a profile similar to that of borer-resistant cultivars.

From an applied point of view, the finding that Si augments the resistance of water-stressed borer-susceptible sugarcane cultivars is particularly relevant for the Si-deficient soils in the cane-growing regions of South Africa. In these regions, Si amendments for susceptible cultivars may provide improved resistance to *E. saccharina*, but field trials are required to confirm these results.

Acknowledgements

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