Silicon (Si) improves plant resistance to insect attack and may also enhance tolerance of water stress. The objective of this study was to evaluate whether Si-mediated resistance of sugarcane to the borer *Eldana saccharina* Walker (Lepidoptera: Pyralidae) is enhanced by water stress. Sugarcane cultivars, two resistant to *E. saccharina* (N21, N33) and two susceptible (N26, N11) 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 of the trial was reduced prior to inoculation with *E. saccharina* eggs, and harvested 66 days later. Stressed and non-stressed plants of the same cultivar did not differ significantly in Si content. However, Si+ plants exhibited increased resistance to *E. saccharina* attack. In Si+ cane, *E. saccharina* larval survival and biomass was lower than in Si- cane, significantly so for stressed, susceptible cultivars N26 and N11, and for larval mass in non-stressed N26. Stalk damage was reduced in Si+ cane, significantly so for the stressed, susceptible cultivars N26 and N11, and non-stressed N26. This study showed that Si provides greater protection against *E. saccharina* attack in susceptible, water-stressed sugarcane than in non-stressed cane and/or resistant cultivars.

**Keywords:** calcium silicate, silicon, sugarcane, induced resistance, *Eldana saccharina*, water stress

**Introduction**

Silicon (Si) is abundant in the Earth’s crust. However, in soils that have been intensely cultivated, or in weathered tropical or organic soils, Si may be depleted. Approximately 60% of the soils within the South African sugarcane region are sandy, acidic soils and are typically deficient in plant-available Si (Meyer et al., 1998). It is now established that Si can enhance the resistance of plants to attack by insect pests, including leaf miners (Hanifa et al., 1974; Goussain et al., 2002), sap feeders (Salim and Saxena, 1992; Moraes et al., 2004) and borers (Djamin and Pathak, 1967; Wang, 2005), including *Eldana saccharina* Walker (Lepidoptera: Pyralidae) on sugarcane (Keeping and Meyer, 2002; Kvedaras et al., 2005).

Historically, drought stress in plants is believed to be a major factor underlying outbreaks of herbivoruous insects (White, 1984, but see also Huberty and Denno, 2004), including the African stem borer *E. saccharina* in sugarcane in the rainfed areas of South Africa (Atkinson...
et al, 1981; Atkinson and Nuss, 1989), and in maize under water stressed conditions in the Ivory Coast (Moyal, 1995). Reduction of moisture stress is one of the current recommendations for combating E. saccharina in the South African sugar industry (Anon, 2005). However, more recent studies have shown that the application of Si can reduce water stress by reducing transpiration (Ma et al, 2001; Gao et al, 2004), by reducing water loss via decreased water flow rate in the xylem (Gao et al., 2004), or by increasing plant water uptake ability (Hattori et al, 2005).

However, it remains unanswered 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, and since 1970, E. saccharina has become a major pest, particularly in coastal rainfed areas, where drought stress frequently increases the risk of economically damaging infestations. In the sugarcane-E. saccharina borer system, tests were carried out to determine whether applied Si afforded greater protection against E. saccharina in plants subjected to water stress. A second objective was to determine whether Si application to water stressed plants is likely to be greater in susceptible than in resistant cultivars, given that susceptible cultivars are generally also less tolerant of drought (Keeping and Rutherford, 2004). If applied Si is more efficacious in drought stressed crops than in non-stressed crops, then its use may provide an enhanced benefit to growers for 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 at the South African Sugarcane Research Institute (SASRI), Mount Edgecombe, KwaZulu-Natal. Before planting, half the pots were treated (Si+) with 124 g (equivalent to 10 t/ha) of calcium silicate, CaSiO₃ (7.9% Si), and the other half left untreated (Si-).

At 8.5 months, plants in 48 pots (half the trial) were water stressed intermittently through a staggered reduction in their water supply such that at the end of the stress periods plants had approximately (and no less than) four or five green leaves each, while non-stressed plants typically had 11 green leaves each. Stress was imposed over two stress periods. The watering schedules for the two stress periods were:

*Stress period 1*

- week one: 1.0 L/pot/day; week two: 0.7 L/pot/day; week three: 0.5 L/pot/day;
- week four: 0.3 L/pot/day; week five - 11: 0.2 L/pot/day.

*Stress period 2*

- week one: 0.5 L/pot/day; week two: 0.3 L/pot/day; week three: 0.2 L/pot/day.

The final irrigation rate was maintained until trial harvest.

At 12 months, the trial was inoculated with 150 E. saccharina eggs per pot (eggs placed on two stalks per pot at 75 eggs/stalk), following the methods of Keeping (2006). 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, total number of internodes, rind hardness at the mid-point of the central internode (Durometer, Rex Gauge Company, Glenview, IL 60025), number of internodes bored, and total length of borings per stalk were measured. Number and mass of
recovered *E. saccharina* larvae and pupae are referred to as ‘borer performance’, while number of internodes bored and length of stalk bored are referred to as ‘borer damage’. Stalk Si% was determined using the procedures of Fox *et al.* (1967).

**Results and Discussion**

Silicon application doubled, or almost doubled, stalk Si content in all four sugarcane cultivars (N21, N33, N11 and N26), regardless of whether or not the plants were water stressed. Treatment with Si was associated with a significant reduction in *E. saccharina* borer performance (survival and mass) and borer damage (percentage stalk length and percentage internodes damaged), especially in susceptible sugarcane cultivars under water stress (Figure 1). The increase in resistance of Si+ water stressed susceptible cultivars to *E. saccharina* was such that borer performance and damage in these plants approached that of resistant cultivars (irrespective of whether the latter were treated with Si and/or water stressed) (Figure 1).

There was no significant association between stalk Si content and resistance to *E. saccharina*, nor did rind hardness of susceptible cultivars increase with Si+ to an extent greater than that of resistant cultivars. This provides grounds for arguing in favour of an active role for soluble Si in improving the plant’s defenses against *E. saccharina*, which may complement any Si-based mechanical barrier. 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 and Pathak, 1967; Salim and Saxena, 1992; Moraes *et al.*, 2004). More recently, Si 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 defenses against insect herbivores (Correa *et al.*, 2005; Gomes *et al.*, 2005). Possibly, 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. Another possibility is the enhanced expression of the plant’s natural chemical or physiological defences in the presence of both Si and water stress. Further detailed study will be required to elucidate the mechanism(s) involved.

While it has been demonstrated that Si can increase the resistance of plants to various insect pests, including *E. saccharina* (Keeping and Meyer 2002 and references therein) and can also enhance drought tolerance in several crop plants (Hattori *et al.*, 2005 and references therein), this is the first demonstration that under conditions of water stress, the presence of Si enhances resistance of a host plant to an insect pest above that of Si+ plants not subjected to water stress. Wiese *et al.* (2005) found a similar interaction in barley, where Si and osmotic stress were additive in enhancing pathogen resistance against barley powdery mildew.

The finding that Si enhances the resistance of water stressed borer-susceptible sugarcane cultivars is particularly relevant from an applied point of view, and field trials are now required to confirm these results. Silicon amendments would provide an added advantage for growers in regions with Si-deficient soils, as it means that, where susceptible cultivars become stressed and particularly vulnerable to borer attack, application of Si may provide better than expected resistance to *E. saccharina*. 

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Figure 1. Mean number of *Eldana saccharina* larvae and pupae (a), mean mass (b), percentage stalk length bored (c), and percentage internodes bored (d), when 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.

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