



Role of Silicon in Providing Defence Against Insect Herbivory in Sugarcane Production

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Abstract

Silicon (Si) is essential to the nutritional status of many monocot and dicot plant species, and it aids them in resisting abiotic and biotic challenges in various ways. This article explained the progress in exploring silicon-mediated resistance to sugarcane insect pests, its role in increasing juice quality attributes and cane production, the silicon status of soil and uptake by sugarcane plant, and the mechanisms involved. The aim is to determine the influence of different sources of Si application on the availability of silicon in soil, silicon uptake by plants, silicon effect in minimizing biotic stresses such as defence against sugarcane insect pest herbivory along with its effect on sugarcane yield in terms of juice and other component traits. There are two basic modes of action: enhanced physical or mechanical barriers and biochemical or molecular mechanisms that activate plant defence responses via bitrophic (plant-herbivore) interactions and tritrophic (plant-herbivore-natural enemy) interactions. By integrating the data reported in this research, a comprehensive understanding of the relationship between various sources of silicon treatments, increased sugarcane plant resistance and decreased sugarcane insect pest damage might be attained.

Keywords Silicon · Herbivory · Borers · Defence

1 Introduction

Silicon is the second most common element in the Earth's crust; however, it is usually found as silica (SiO_2) or silicates because of its strong affinity with oxygen and its tendency to form compounds with other metals [1]. For a long time, nobody paid much attention to the fact that crops lacked silicon, and most people assumed that this element wasn't crucial to plant growth. As mono silicic acid (H_4SiO_4), silicon is taken up by plant roots from the soil, transported via transpiration to all plant tissues, and finally deposited as phytoliths in the epidermal cell walls [2].

Silicon is known to accumulate as silica gel ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) in considerable amounts among the members of grass family that are localized in particular cell types. Samuels and Alexander (1969) [3] reported that sugarcane, during its life span of 12- months accumulates about 380 kg ha^{-1} of silicon, which is higher than the other nutrients uptake by

sugarcane from soil. In some parts of the world, sugarcane (plant growth and development) retorts to silicon fertilization have been observed and usage in commercial fields is common [4].

As the primary source of sugar in human diets, sugarcane has important economic implications. Environmentally, the crop is significant because it can be used to make ethanol, which in turn reduces the need for fossil fuels [5, 6]. Sugarcane being a long-duration crop of 10 to 12 months, it is susceptible to a variety of abiotic and biotic stress [7]. Biotic stress involves the attack of various insect pests such as borers, phloem feeders and root feeders. Conservative calculations suggested that sugarcane growers lose roughly 20% of their production, whereas sugar mills lose about 15% of their sugar production owing to insect pests infestations. Lepidopterous stem borers are a serious pest of graminaceous crops in most countries. About 50 moth species from the genera *Chilo*, *Eldana*, *Sesamia*, *Diatraea*, *Scirpophaga*, *Eoreuma*, *Tetramoera* and *Acigona* attack sugarcane around the world [8, 9]. To assess the monetary loss, many authors measured the connections between stalk borer damage, sugar output and quality and also compared various cultivars of sugarcane. The proportion of bored stalk was reported to

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have a negative association with sugar production, juice purity, stalk weight, cane and sucrose in sugarcane. For example, 19.4% and 10.9% of internodes bored by *Eoreuma loftini* (Dyar) and *Diatraea saccharalis* (F.) were reported to lowered sugar per tonne (95.5 g kg^{-1}) of NCo 310 cultivar and sugar (108 g kg^{-1}) of CP 70-321 cultivar, respectively [10]. However, Goebel and Way (2009) [11] observed a reduction of sucrose by 21.4 to 50% due to heavy infection of *E. saccharina*. Similarly, the reduction of various juice characteristics has been observed due to infection of different borers viz., *Chilo infuscatellus*, *S. excerptalis* and *C. auricilius* [12] *Diatraea tabernella* Dyar [13], *Tetramoera schistaceana* (Snellen) and *C. sacchariphagus* (Bojer) [14]. The agronomic traits of sugarcane have a great impact via infestation of borers i.e., the maximum drop of 26% [11] in cane weight, 34% [15] and 5.92% [14] reduction in cane yield.

Numerous papers have been recording Si's ability to enhance plant tolerance to insect pests in different crops other than sugarcane. Still, relatively few reviews have addressed the importance of silicon in sugarcane cultivation exclusively [4, 16, 17], whereas the most recent review [18] investigates its role in mitigating biotic and abiotic stresses. This review focuses on the availability of silicon in soil, silicon uptake by plants, silicon effect in minimizing biotic stresses such as defence against sugarcane insect pest herbivory (Table 1), increasing juice quality attributes, cane production and silicon's modes of action in the control of insect pests (Fig. 1).

2 Silicon in Soil and Plant

On the periodic table of elements, silicon is represented by the symbol "Si" and has of 28.09 and 14 atomic weight and atomic number respectively [19]. Silicon has melting and boiling temperatures of $1,410^\circ\text{C}$ and $2,355^\circ\text{C}$, respectively [20]. Jöns Jakob Berzelius (1824) was the first to produce amorphous silicon by combining heated potassium with silicon tetrafluoride and then purifying the compound by removing fluorosilicates via repeated rinses [20, 21]. Overall, silicon is comparatively inert element that is vital to animal and plant life [20, 22].

2.1 Silicon in Soil: Soil Silicon Content Response to External Application of Silicon

Si constitutes 28% of the soil components in the earth's crust (w/w basis). Orthoquartzite and basalt rocks contain 23–47% Si, but carbonates and limestones contain traces of this element [23]. In soil, silicon occurs in three forms viz. solid, liquid and absorbed fraction. A solid fraction consists of a crystalline form (poorly and microcrystalline forms

like; opal-CT, allophane, chalcedony, imogolite, secondary quardz.) amorphous form (lithogenic and pedogenic forms, for example, silanes, pedogenic oxides, opal-A sphere, silicon glass and biogenic form like; phytolithes, microorganism residues and plant) and poorly and microcrystalline form includes primary silicates (olivine, feldspar, pyroxene mica,) secondary silicates (clay minerals) and silicate materials (quartz, disordered silica). Liquid fraction involves dissolved form in soil solution & absorbed fraction consists of Fe-Si and Al-Si complex and adsorbed to soil particles (polysilicic acid and mono-silicic, silicon-organic & inorganic compound complexes) [24].

Many factors influence the quantity of mono-silicic acid, H_4SiO_4 (plant-available silicon) in the soil solution, notably temperature, pH, water, organic matter and content and particle size & redox potential influence the solubility of silicon-containing minerals [25]. The concentration of H_4SiO_4 in the soil solution is affected by the adsorption–desorption processes, which are highly dependent on the soil pH which influences silicon solubility and mobility [23]. The highest adsorption of H_4SiO_4 occurs around pH 9–10, while adsorption is decreased at pH values lower or above these values [26]. In saline soils, H_4SiO_4 adsorption, polymerization and coagulation are all quite high. In soils with a lot of allophanes, Fe-enriched crystal minerals, and especially the more reactive multivalent metal hydroxides, the quantity of adsorbed H_4SiO_4 rises. Availability of Si is affected by the Si uptake rate by plants, weathering rate and silicon replenishment [27]. The estimated amounts of Si released into soil solution by granodiorite, amphibolite and feldspar were, 2.18, 5.57 and 1.35 mmol m² d⁻¹ SiO₂, respectively. [28]. Though, it is crucial to understand that a number of factors, such as mineral characteristics, soil solution composition, reactions happening inside and outside of mineral rocks, other existing primary and secondary fractions, and rhizosphere microorganism communities, influence the release of Si into a soil solution in an open soil ecosystem. [29]. The amount of phosphate available soil silicon was investigated by Priya and Kumar 2023; Priya et al. 2023a; Priya et al. 2023b [30–32] and reported the drop of silicon level from 211.50 to 140.02 kg acre⁻¹, 206.17 to 113.88 kg acre⁻¹, 208.49 to 115.02 kg acre⁻¹, 209.82 to 126.94 kg acre⁻¹, 210.81 to 135.55 kg acre⁻¹ in cultivar Co 118, CoPb 95, CoPb 96, CoPb 98 and Co 238 from planting to harvest respectively this shows the soil silicon level depends upon the uptake of different cultivar of silicon.

2.2 Silicon in Sugarcane Plant: Uptake and Response to Silicon

Plants absorb silicon from the soil solution as H_4SiO_4 , which is usually present in quantities ranging from 0.1 to 0.6 mM at most agricultural soil pH values [33]. Plants can be classified

Table 1 Sugarcane plant–insect associations on which the role of silicon in decreasing pest preference and growth rates with different sources of silicon has been observed

Insect pest	Species of insect pest	Source of silicon	References
Borers	African sugarcane borer, <i>Eldana saccharina</i> Walker (Lepidoptera: Pyralidae)	Calcium silicate (CaSiO ₃)	Keeping and Meyer (2002); Kvedaras et al. (2007); Keeping et al. (2009)
	<i>Diatraea saccharalis</i> Fabricius (Lepidoptera: Crambidae)	Calcium silicate (CaSiO ₃)	White and White (2013)
	Stalk borer, <i>Sesamia</i> spp. (Lepidoptera: Noctuidae)	Calcium silicate (Ca ₂ SiO ₄) (soluble SiO ₂ ≥ 20%)	Nikpay et al. (2015b)
	Stalk borer, <i>Eldana saccharina</i> Walker (Lepidoptera: Pyralidae)	Slagment® (13.0% total Si), Calmasil® (9.85% Si)	Keeping et al. (2013)
	Stalk borer, <i>Eldana saccharina</i> Walker (Lepidoptera:Pyralidae) and sugarcane thrip, <i>Fulmekiola serrata</i> Kobus (Thysanoptera:Thripidae)	Agrisil (potassium silicate), potassium silicate formulation and Silamol (silicon-based formulation)	Keeping et al. (2014)
	Stalk borer, <i>Sesamia</i> spp. (Lepidoptera: Noctuidae)	Agrisil (potassium silicate, 28% silicic acid, potassium salt and potassium as silicate, Potassium silicate formulation (17.3% silicon with 13.5% potassium as silicate and Silamol, a silicon-based formulation (17.5% silicon)	Nikpay et al. (2015a)
	Sugarcane borer, <i>Diatraea saccharalis</i> Fabricius (Lepidoptera: Crambidae)	Silicic acid solution (SiO ₂ .XH ₂ O)	Vilela et al. (2014)
	Stalk borer, <i>Diatraea tabernella</i> Dyar (Lepidoptera: Pyralidae)	Granular silicon (Tecnosilix 250 kg/ha) and liquid silicon	Atencio et al. (2019)
	Sugarcane borer, <i>Chilo sacchariphagus</i> Bojer (Crambidae: Lepidoptera)	Silicon fertilizer (SiO ₂ 31.71%, CaO 20.02%, MgO 12.33%)	Lin et al. (2021)
	Stalk borer, <i>Sesamia</i> spp. (Lepidoptera: Noctuidae)	Silicon (Ca ₂ SiO ₄) (powder formulation; soluble SiO ₂ ≥ 20%)	Nickpay (2016)
	Top borer, <i>Scirpophaga nivella intacta</i> Snellen (Lepidoptera: Pyralidae)	Bagasse furnace ash	Saeroji and Sunaryo (2010)
	Sugarcane early shoot borer, <i>Chilo infuscatellus</i> Snellen (Crambidae: Lepidoptera)	Bagasse ash, rice husk ash, sodium metasilicate and calcium silicate	Indhumathi et al. (2019)
	Sugarcane top borer, <i>Scirpophaga excerptalis</i> Walker (Crambidae: Lepidoptera)	Straw compost, Sugarcane leaf compost, corn leaf compost and inorganic Si fertilizer (Silica; SiO ₂)	Rahardjo et al. (2020)
	Early shoot borer, <i>Chilo infuscatellus</i> Snellen (Crambidae: Lepidoptera)	50% Silicon material, Rice husk ash and Bagasse ash	Priya and Kumar (2023)
	Top borer, <i>Scirpophaga excerptalis</i> Walker (Crambidae: Lepidoptera)	50% Silicon material, Rice husk ash and Bagasse ash	Priya et al. (2023a)
	Stalk borer, <i>Chilo auricilius</i> Dudgeon (Crambidae: Lepidoptera)	50% Silicon material, Rice husk ash and Bagasse ash	Priya et al. (2023b)
Phloem feeders	Spittlebug, <i>Mahanarva fimbriolata</i> Stål (Hemiptera: Cercopidae)	Potassium silicate (K ₂ SiO ₃)	Korndörfer et al. (2011)
	Sugarcane yellow mite, <i>Oligonychus sacchari</i> (Acari: Tetranychidae)	Agrisil (potassium silicate), potassium silicate formulation and Silamol (silicon-based formulation)	Nikpay and Nejadian (2014)
	Leafhopper, <i>Pyrilla perpusilla</i> Walker (Hemiptera: Lophopidae)	Calcium silicate	Indhumathi et al. (2018)
	Yellow mite, <i>Oligonychus sacchari</i> (Acari: Tetranychidae)	AB Yellow ® (Silicic acid)	Nikpay and Laane (2020)
Root feeders	Greyback canegrub, <i>Dermolepida albobirtum</i> (Coleoptera: Scarabaeidae)	Soluble silicon in the form of NaSiO ₃ .9H ₂ O	Frew et al. (2017)

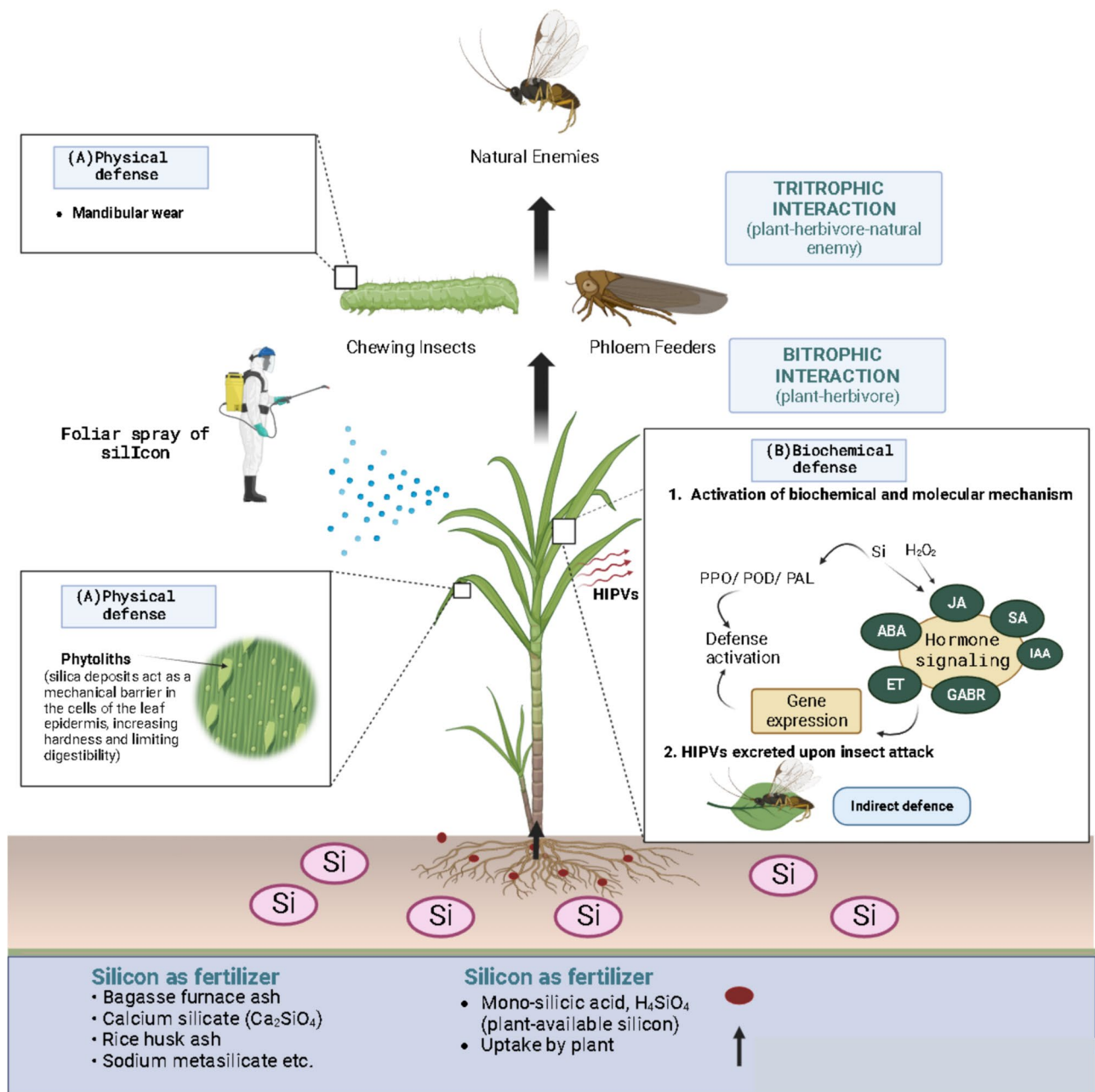


Fig. 1 Summary of mechanisms by which application of different silicon treatments to plants may affect the plant, herbivores and natural enemies

based on their shoot silicon content into accumulators with more than 1.5% silicon like crops in the Poaceae family, such as rice (*Oryza sativa* L.) and sugarcane (*Saccharum officinarum* L.), sugarcane is typical silicon accumulating graminaceous species can actively absorb silicon from the soil, these plants have many silicon transporters, passive (Neutral) plants 0.5–1.5% silicon like wheat and oat, rejective plants less than 0.5% silicon plants like tomato and clover [4]. They cannot absorb silicon in their tissues due to a lack of silicon transporters [34, 35].

However, for most plants, silicon has not proved as a beneficial element [36, 37]. Silicon uptake by the roots, transferred to the shoot via xylem vessels and accumulated as a double epidermal silica coating on the cell walls, at least in rice, strengthening the plant structure. The amount of silicon transporters in the roots and shoots, which facilitate the absorption progression through the membranes of root cells, was related to the fact that the quantity of silicon uptake by the active mechanism was frequently more than that expected based on mass flow. This study characterized

and demonstrated the active, passive, and rejective methods by which plants take up silicon [38].

Less than 1% of plant Si is soluble in ionic form or colloidal or associated with organic molecules; the majority of plant Si is opaline [39]. Additionally, sugarcane is observed as a Si accumulator plant even though the majority of plant species are capable of absorbing Si [40]. The levels of Si that sugarcane absorbs in the field, which vary depending on the soil texture, amount of Si applied and age of plant are still mostly unknown. However, some of the studies demonstrated that in clay soil the amendment of silicate fertilizer @ 1.6 t ha⁻¹ [41], 12 t ha⁻¹ [42] and 14 t ha⁻¹ [43] to 18 (plant cane + 1 ratoon) and 14 months old sugarcane plants able to uptake Si 215, 207 and 408 kg ha⁻¹, respectively. While without application of Si to a variable clay [3, 44–46] and medium [47] texture soil for plant age of 2nd ratoon, variable and 36 (plant cane + 2 ratoons) months reported to have an uptake of Si varied from 86, 200–379 and 406 kg ha⁻¹ respectively.

3 Role of Silicon in Sugarcane Insect Pest Management

In contrast to dicotyledonous plants like soybeans, cotton and some vegetables (such as cucurbits, and tomatoes), monocotyledonous plants like wheat, rice, maize and sugarcane actively absorb and accumulate silicon [48]. Plants absorb silicon by transpiration (passive uptake), which transfers monosilicic acid from the roots to the shoots, where it is deposited as plant silica [49]. However, the focus of this review is on silicon as a crop protection agent in sugarcane ecosystems.

Several researchers investigated whether silicon-based fertilizer applications might alter insect-eating habits, thereby influencing life-history parameters such as development time, fecundity and reproductive success rate. There are different types of silicon sources used to protect against the sugarcane insect pest viz., Calcium silicate (CaSiO₃), bagasse furnace ash, Slagment® (13.0% total Si), Calmasil® (9.85% Si), silicic acid, potassium silicate, etc. Growing data from the published work suggests that nutrients like nitrogen and Si have significant roles in how susceptible and resistant the cultivars of sugarcane crops towards the stalk borer damage. The susceptible varieties showed more benefits from the application of silicon than the resistant varieties as Keeping and Meyer (2002) [50] evaluated a decrease of 19.8% in mass and 24.4% in the length of African sugarcane borer, *Eldana saccharina* Walker and stalk bore respectively with the application of Ca₂SiO₄. Similarly, the borer-resistant (N33) cultivar showed a higher percentage of the weight of total epidermal silicon (both in silicon treated and untreated) compared with the borer-susceptible (N11) cultivar (Keeping

et al. (2009). While Kvedaras et al. (2007) [51] reported that there was an increase in the silicon content in the stalks of all cultivars of sugarcane they studied. The resistant cultivar treated with silicon has a significant reduction in damage to the stalk by borers and reduces borer growth rate, especially at internode sites. Even though the internode had the hardest rind, silicon did not affect hardness at any of the sites. The preferred entry point for *E. saccharina* was the leaf bud on the sugarcane stalk due to the observation that the higher accumulation of silicon was restricted to the epidermis of the root band and internode, and no such evidence was reported in the case of the leaf bud with the help of X-ray mapping. So, silicon provides mechanical resistance for the penetration of the *E. saccharina* into the sugarcane stalk [52]. The response of sugarcane to calcium silicate fertilization in providing defence against stalk borers, *Sesamia* spp as studied by (Nikpay et al. 2015b) [53] suggested a reduction in the percentage of boring internodes, length of borer tunnel (mm), percentage of stalk damaged, number of larvae and pupae per 100 stalks and the number of exit holes in the susceptible variety CP69-1062. Another study of Ca₂SiO₄ amendment in the potting medium reported an influence on the sugarcane borer *Diatraea saccharalis* resistance in sugarcane [54]. The experiment was conducted in a greenhouse condition using sugarcane borer susceptible (HoCP 96–540) and resistant genotypes (L 99–226). They found that when Ca₂SiO₄ was added to the potting media, bored internodes in the susceptible variety HoCP 96–540 and the resistant variety L 99–226 were decreased by 45 and 40%, respectively. The larvae recovered after 14 days of eating on Ca₂SiO₄-supplemented plants and weighed 130% less than those fed on Ca₂SiO₄ deficient plants. Tunnelling within the stalk was also decreased by around 25% after Ca₂SiO₄ was added. This research suggests that feeding sugarcane with Ca₂SiO₄ may likely boost resistance to the sugarcane borer, but more research, particularly field studies is needed to confirm these findings. Slagment® as a silicon source applied @ 8 tons ha⁻¹ can significantly increase soil, stalk and leaf silicon content, but leaf silicon levels were rarely exceeded by 0.5%. In all three crops (planted crop, first ratoon and second ratoon), there was a reduction in % stalks borer and also reduced stalk length borer in the second ratoon crop. Significant decreases in stalk damage and sucrose loss might be achieved in susceptible cultivars in low-silicon soils by utilizing materials that release silicon slowly and have more than 0.8% of silicon [55]. The authors such as Keeping et al. (2014) [56] and Nikpay et al. (2015a) [57] focused on the association of potassium silicate as silicon sources in providing borers resistance against *E. saccharina* and *Sesamia* spp. Nikpay et al. (2015a) [57] tested silicon formulations (potassium silicate) on sugarcane stalk borers, finding foliar spray at 1.5 L ha⁻¹ improved biological control and significant differences in borer damage and quality parameters.

The impact of silicic acid solution treatment on sugarcane resistance to *Diatraea saccharalis* found that silicon deposition increased in susceptible cultivars, but the concentration remained consistent. Also, the silicon treatment thickened the cuticle and formed crystals on leaf stomata [58].

Silicon and nitrogen have been reported to respond to changes in fertilizers and soil constituents for defence against insect pests. The impact of silicon in reducing plant nitrogen content and stalk borer, *E. saccharina* but no impact was found in the case of infestation of sugarcane thrip, *Fulmekiola serrata* Kobus (Thysanoptera: Thripidae) and also reported that silicon has a greater impact on the susceptible cultivars of sugarcane (N27) as compared to the resistant cultivars (N33) of sugarcane. The distinct ways that silicon affects thrips and stalk borer demonstrate that the mechanical and biochemical components of silicon-mediated insect herbivore resistance in sugarcane are well-developed in the stalk tissues that *E. saccharina* targets, but poorly developed in the developing leaf spindles where *F. serrata* was discovered [56]. Similarly, the consequences of silicon and nitrogen on *Diatraea tabernella* Dyar (Lepidoptera: Pyralidae) in sugarcane. They utilised two silicon and nitrogen-based products applied at two rates for borer infestation and found that silicon-based fertilizer lowered internode borer (% IB) by up to 50%, proving silicon's involvement in damage mitigation. The damage level increased from 5.2% IB (untreated control plots with 110 kg N ha⁻¹) to 6.9% IB (treatment with the maximum dosage of 210 kg N ha⁻¹) when high nitrogen doses were used [59]. The use of silicon fertilizer (SiO₂ 31.71%, CaO 20.02%, MgO 12.33%) @ 562.5 kg/hm² may have the best benefits for *Chilo sacchariphagus* Bojer control in terms of reducing the rate of dead heart at sowing, bored internode rate and adult emergence rate at developed stage [60].

In addition to enhancing the soil's organic matter, both inorganic and organic sources have been utilised as Si sources to increase the soil's silicon content for the purpose of boosting insect resistance. Organic sources such as rice husk ash, bagasse furnace ash etc. The number of top borers, *Scirpophaga nivella intacta* larvae successfully boring into the leaf spindle was 20.7% lower and 19.2% fewer larvae pierced into the growth point and internodes with the application of bagasse furnace ash @ 40, 80 and 120 t ha⁻¹. Also, the length of bored tunnels was reported to be reduced as compared to the control with 120 t ha⁻¹ treatment. Therefore, it was proposed that using 120 t ha⁻¹ bagasse furnace ash with 7.97% silicon concentration improved the resistance toward top borer incidence among susceptible sugarcane varieties [61]. The amendment of Ca₂SiO₄ @ 500 and 1000 kg ha⁻¹ led to lower mean damage of 4.87% and 4.63% respectively and was analogous to bagasse ash @ 1000 kg ha⁻¹ + SSB (silicon solubilizing bacteria) @ 2 kg ha⁻¹ and 500 kg ha⁻¹ + SSB @ 2 kg ha⁻¹ with 4.99% and 5.28% subsequently sodium metasilicate @

1000 and 500 kg ha⁻¹ with 7.14 and 7.13% [62]. Comparing organic silica fertilizer (compost) and inorganic silica fertilizer indicated that they have the same effect, and rice straw compost was the most effective in providing resistance against sugarcane top borer (*S. excerptalis*) in sugarcane resistance [63]. While in the most recent studies, the comparison of rice husk ash, bagasse ash and inorganic Si sources suggested that the higher sugarcane borers viz., early shoot borer, *Chilo infuscatellus* [30], top borer, *Scirpophaga excerptalis* [31] and stalk borer, *Chilo auricilius* [32] resistance was provided by silicon material (50% Si) followed by rice husk ash and bagasse ash treated various sugarcane cultivars. Silicon material (50% Si) has been found to reduce the maximum incidence of early shoot borer by 40.86% [30], top borer by 37.62% [31], and stalk borer by 39.56% [32].

There are few studies involving the effect of silicon application on resistance to the phloem feeders in sugarcane as compared to the borers. Sugarcane cultivar 'SP79-1011 have high silicon content in its leaves and has the shortest female longevity and high nymphal mortality of *Mahanarva fimbriolata* with the application of potassium silicate (K₂SiO₃). Although silicon did not affect the egg viability, fecundity and pre-oviposition period of the cultivar used [64]. For the management of sugarcane yellow mites, *Oligonychus sacchari* silicon-based fertilizers and formulations were used which resulted in a reduction of the population of mites in all the varieties of sugarcane (CP57-614, CP48-103, SP70-1143 and CP69-1062,) as compared to the control, where the number of mites in all varieties was ranging between 9.17 and 14.02 after 40 days of application [65]. Likewise, the population of sugarcane leafhopper, *Pyrilla perpusilla* had been reduced by the application of calcium silicate with a minimum of @1000 kg ha⁻¹ followed by @ 500 kg ha⁻¹ and a maximum in control [66]. The foliar application was also found to be effective against *O. sacchari* in sugarcane. The treatment of four sprays @ 0.5, 1, 1 and 1 L ha⁻¹ demonstrated substantial effects on the mite population and leaf dryness [67]. Both roots and shoots have the ability to defend themselves from insect attacks. Interestingly, the comparative growth rate of the greyback canegrub, a sugarcane root-feeding insect, can be significantly reduced by high Si concentrations in the roots due to the application of soluble silicon in the form of NaSiO₃·9H₂O [68]. So, Si might be used with other management measures in sugarcane-integrated pest management (IPM).

4 Influence of Silicon Application on Juice Quality Traits

In addition to enhancing sugarcane's resistance to insect pests, Si acted as an enzyme regulator in sugar formation, storage and retention in the sugarcane plant. Alexander et al.

concluded in 1968 that within the plant, Si seems to play the role of an equilibrium protector, acting as a buffer of enzyme activity to assist the plant in maintaining normal enzyme activity against factors that may act to disrupt it. It has been demonstrated that this role involves preserving green foliar tissue against the action of desiccants, protecting photosynthetic activity, inhibiting phosphatases that may destroy organic phosphates directly involved in sugar synthesis, suppressing amylase activity to prevent starch accumulation and subsequent competition for organic phosphate reserves, and inhibiting invertase activity to stop excessive sucrose inversion in pre-harvest and post-harvest stages [16]. Different authors have identified various cane juice quality characteristics influenced by the application of different types of Si sources in varied forms. Some of the examples are discussed here.

The silicon amendments also show positive interactions with applied N, P and K fertilizers [4, 25, 49]. It was found that in plants under salt stress, adding potassium and silicon boosted their concentrations and lowered Na^+ accumulation considerably, as well as cane yield and juice characteristics (Pol (% sucrose in juice), Brix (% soluble solids in juice), commercial cane sugar (CCS) and recovery of sugar in both the cultivars improved considerably. In both sugarcane genotypes, potassium alone or in combination with silicon was shown to be more efficient than silicon alone in alleviating salt stress for the majority of growth metrics [69]. Different cultivars respond differently towards the Si in altering the juice quality characteristics like study of five commercial varieties of sugarcane to evaluate the efficacy of silicon formulations on quality parameters (% Pol, % Brix, % purity, % refined sugar) of sugarcane juice demonstrated that there were no significant differences between silicon treatments and control for all quality parameters except % refined sugar (which increased significantly) in the case of variety CP48-103, although silicon treatments increased the quantity of assessed characteristics. Except for % brix, the results of all quality parameters for cultivar CP69-1062 showed a significant difference from the control. Compared to the control, the SP70-1143 variety indicated a significant difference in % refined sugar and the rest of the measured quality factors were non-significant. The % pol indicated a significant difference between silicon treatments and the control group in IRC99-01 variety and other quality parameters were non-significant. The CP57-614 variety showed a non-significant difference in % brix and a significant difference in all other measured factors was reported [57]. According to Nikpay et al. (2015b) [53] 800 kg ha⁻¹ of calcium silicate was adequate to enhance the percentage of polarity (Pol;16.4%), Brix (18.9%), refined sugar (0.1%) and purity (86.9%) of cultivar, CP69-1062 stalks. When compared to the control, 800 kg/ha with calcium silicate considerably enhanced purity (87.6%) and % of refined sugar (11.1%) in

the cultivar IRC99-01. Furthermore, plants treatment with orthosilicic acid granules had increased juice purity, sucrose % juice, Brix, juice extraction, CCS % juice, ratio of sucrose to reducing sugar (S/R ratio) and sucrose phosphate synthase (SPS) activity. CCS increased by 15.2–31.8%, with orthosilicic granules @ 80 kg/ha therapy showing the largest rise of 31.8% compared to silicon untreated plants [70]. The combined effect of Si treatments and biocontrol agents also adds positive to cane juice quality i.e., silicon amendment along with 2,500 parasites was sufficient to increase Pol (18.82%), Brix (20.7%), Purity (90.9%) and refined sugar (11.77%) [71]. Similarly, along with reducing the population of *O. sacchari* and enhancing biocontrol by its predatory beetle, *Stethorus gilvifrons*, the foliar application of silicic acid when compared to control reported to had greater pol percentages (18.9 and 18.5%), brix amount (20.4 and 20.6) and purity percentages (89.5 and 90.4%) in variety CP57-614 and CP48-103, respectively [67]. The enhancing effect of biostimulant @ 3 L/ha along with Si application @ 200 kg/ha on juice quality parameters showed a rise in Brix and Pol values of 21.60% and 19.46%, respectively, as well as this treatment, demonstrated the greatest increase in sugar production of 28.53% [72]. Commercial cane sugar (CCS) is a crucial industrial component that shows how to estimate the amount of sucrose that can be recovered from cane sugar output, which affects cane yield and quality. The most recent studies investigated the rise in CCS (%) resulting from the rise in other juice quality parameters viz., brix % juice, sucrose % juice, purity % and pol% cane with application of rice husk ash, bagasse ash and inorganic Si sources in different cultivars of sugarcane. The maximum rise of CCS% was reported with silicon material 50% followed by rice husk ash and bagasse ash [30–32].

5 Influence of Silicon Application on Cane Yield and Component Traits

The silicon has a considerable effect on the various cane yield and component traits. Various authors investigated the role of silicon sources on these parameters.

Elawad et al. (1982) [73] investigated the importance of silicon in sugarcane development. They reported that in both plant and ratoon crops, silicate minerals enhanced number of millable stalks, plant height, stem diameter and cane and sugar yields. The supplement of 15 metric tons/ha of silicate minerals boosted plant crop cane and sugar yields by 68 & 79%, respectively and ratoon crop yields by 125 and 129%. role of silicate source and rate in sugarcane growth and yield. The amendment with bagasse furnace ash @ 120 t ha⁻¹ at the time of sowing increased diameter, height and stalk population which resulted in augmentation of the cane yield by 39.89% [61]. The application of orthosilicic acid

granules @ 40 kg ha⁻¹ showed maximum shoot population, specific leaf weight, and total dry matter accumulation along with enhanced height, girth and yield of the canes. A recent study evaluated that among the inorganic 50% silicon material, bagasse ash and rice husk ash, inorganic silicon improved the % germination, single cane weight, stalk diameter, stalk length, number of millable canes, and ultimate sugarcane yield. The maximum rise of yield had been reported in cultivar CoPb 95 (371.96 q acre⁻¹) [30] followed by CoPb 98 (360.55 q acre⁻¹) [32], CoPb 96 (361.26 q acre⁻¹) [30], Co 238 (350.39 q acre⁻¹) [31] and Co 118 (311.24 q acre⁻¹) [30].

6 Mode of Action of Silicon in Defence Against Insect Herbivory

There is strong evidence that high quantities of silica present in many plants, especially grasses, exert broad antiherbivore impacts on both invertebrates and vertebrates [51, 74–77]. Two important defensive mechanisms owing to silicon treatment for the management insect pest damage have been explained in the literature: physical and biochemical [48, 78, 79]. Physical defence is linked to a buildup of absorbed silicon in the epidermal tissue, which acts as a mechanical barrier in the cells of the leaf epidermis, increasing hardness and limiting digestibility. The increased synthesis of defensive enzymes and phenolic compounds is linked to soluble silicon being implicated in triggering biochemical defence against insect pest assault. Furthermore, silicon can trigger both types of defensive systems by reducing digestibility, increasing roughness of plant tissues and increasing the formation and storage of lignin, peroxidases, phenolics and chitinases [48, 78, 79].

6.1 Physical Defence

The amount of silica deposition in the plant reflected different physical defence mechanisms as reported by Agarwal (1969) [80] that sugarcane clones having maximum silica cells in the wax band of the inter-node were subjected to significantly lower sugarcane scale, *Melanaspis glomerata* (Green) (Homoptera: Coccidae) infestation rates. Similar results have been observed by Barker (1989) [81]. The author found that feeding intensity correlated with oviposition preferences, with the number of feeding marks on these plants accounting for 29–86% of the difference in egg counts per plant. Likewise, the number of eggs deposited on the plants have negative correlation with the density of intercostal silica deposits (including trichomes) on the abaxial surface of the grass sheaths. This study proved a causal association between silicification and oviposition preference via a pot experiment. Increasing silica absorption and deposition

reduced egg-laying on two ryegrass varieties. The quantity and location of intercostal silica deposits and trichomes on the sheath appeared to be linked to the dispersion of eggs in different grasses. Chu and Horng (1991) [82] findings suggested that excessive silica deposition causes leaves to become hard and abrasive and may be related to borer resistance was supported by the application of calcium silicate slag to corn plants, which increased the stem resistance to the Asian corn borer, *O. furnacalis* and decreased pest consumption of the leaves.

Miller et al. (1960) [83] studied the relationship of silicon and the resistance development in the wheat plant against Hessian fly, *Phytophaga destructor* Say and they found that the resistance varieties to Hessian fly possess a significant amount of silica uniformly deposited on the surface of the leaf sheath in the form of rod-shaped arranged in dispersed rows and concluded that this may be one of the factors responsible for the development of resistance among certain cultivars of wheat plants.

Kvedaras et al. (2007) [51] observed the presence of silica bodies dispersed across the pseudostem in resistant sugarcane cultivars provided greater protection against the African sugarcane borer, *E. saccharina* Walker (Lepidoptera: Pyralidae) than those deposited in distinct rows in susceptible cultivars. The authors also found the number of larvae reduced with even slight increases in plant silicon fertilization. Similarly, the scanning electron microscope images of different sugarcane cultivars viz., CoPb 95, CoPb 96, Co 238 and Co 118 depicted enhancement of epidermal silicon deposition as phytoliths in Si-treated plants with the external application of Si in soil at the time of planting of sugarcane provides higher resistance toward early shoot borer *C. infuscatellus* [30], top borer, *S. excerptalis* [31] and stalk borer, *C. auricilius* [32].

6.1.1 Mandibular Wear

The silicon impact is indefinite due to the replacement of mandibles at each moult. Increased mandible wear, on the other hand, caused larvae fed on silicon-rich plants to moult earlier than usual, which might be linked to lower body weight in insect pests. Numerous studies, as mentioned in Table 2, have found increased mandible wear among lepidopteran larvae fed on silicon-rich plant cultivars in different crops including sugarcane [48, 78, 79]. A few studies of mandibular wear in the case of sugarcane borers are available viz., SEM images reveal slight mandibular wear as reported by Kvedaras et al. (2009) [84] in *E. saccharina* larvae. In addition, recent mandibular studies reported the decrease in the length of right as well as left mandibles along with reduction in width at the base of early shoot borer *C. infuscatellus* [30], top borer, *S. excerptalis* [31] and stalk borer, *C. auricilius* mandibles [32] as compared to control.

Table 2 Role of silicon in increased mandibular wear in sugarcane and other crops

Host plant/ Artificial diets	Insect	References
<i>Significant mandible damage</i>		
Rice	Stem-borer, <i>C. suppressalis</i>	Djamin and Pathak (1967)
Rice	Yellow stem borer, <i>Scirpophaga incertulas</i> (Walker) (Lepidoptera: Crambidae)	Jeer et al. (2018)
Artificial diets containing silicon at elevated concentrations	Leaf rice roller, <i>C. medinalis</i> (larvae)	Ramachandran and Khan, (1991)
Corn	Fall armyworm, <i>S. frugiperda</i>	Goussain et al. (2002)
Grass species	<i>S. exempta</i>	Massey and Hartley (2009)
Maize	True armyworm, <i>Pseudeletia unipuncta</i> Haworth (Lepidoptera: Noctuidae)	Moise et al. (2019)
Sugarcane	Early shoot borer, <i>Chilo infuscatellus</i> Snellen (Crambidae: Lepidoptera)	Priya and Kumar (2023)
	Top borer, <i>Scirpophaga excerptalis</i> Walker (Crambidae: Lepidoptera)	Priya et al. (2023a)
	Stalk borer, <i>Chilo auricilius</i> Dudgeon (Crambidae: Lepidoptera)	Priya et al. (2023b)
<i>Slight mandible damage</i>		
Sugarcane	Slight mandible wear in <i>E. saccharina</i> larvae	Kvedaras et al. (2009)
Penncross creeping bentgrass	Black cutworm, <i>Agrotis ipsilon</i> Hufnagel (Lepidoptera: Noctuidae) and the root-feeding masked chafer grubs, <i>Cyclocephala</i> spp.	Redmond and Potter (2006)

6.2 Biochemical Defence

Higher expression of defensive enzymes like, phenylalanine ammonia-lyase and polyphenoloxidase, peroxidase in leaves, as well as increased synthesis of defensive compounds such as phenols, tannins and lignin, may be induced by soluble silicon in plant tissue. The quality of phloem sap may be harmed as a result of biochemical changes caused by silicon absorption and pest insect growth requirements may be affected [48, 78, 79].

One of the sustainable methods to effectively reduce insect pest populations is to utilise plant resistance inducers. Si not only serves as a physical deterrent, but it also helps plants recover from insect attacks by increasing their natural chemical defences. Silicon is an abiotic stressor that triggers the production of defence chemicals through the activation of phytohormone pathways [85]. Defence mechanisms in plants are extremely complex and can change depending on the eating habits of their insect predators [86].

Ethylene, salicylic acid (SA) and jasmonic acid (JA) are all common phytohormones that play important roles in a plant's defence mechanisms and are triggered by the unique signal characteristics of various plant invaders [87]. It has been believed that JA's role in defence regulation is directed at insects that feed on cellular content and tissue [88]. As a defence mechanism against insects that feed on the phloem, plants use the SA and JA signals [89]. There is growing evidence that Si enhances insect resistance through

a mechanism including a substantial interaction between Si and JA against insects. The host plant may also be ready to fight insect pests as a result of Si-induced resistance. The effect of silicon could be on bitrophic (plant-herbivore) interactions or tritrophic (plant-herbivore -natural enemy) interactions. Although the biochemical route of action of silicon in protecting sugarcane against insect pests is not well understood and significance of metabolic defence in mitigating the damage caused by insects requires additional study. The path for future inquiry in sugarcane crop may be outlined by studies conducted on other crops.

6.2.1 Silicon in Bitrophic (plant-herbivore) Interactions

Si-induced resistance could potentially be expressed by preparing the host plant for insect pest invasion [90]. The process of preparing and sensitizing a plant's defences to be quicker and more effective against future herbivorous insect is called as Priming [91].

It is unknown how silicon interacts with the lignin production process in cell walls. So, the recent study conducted by [92] evaluated the interaction of SiO₂ with the peroxidase-catalyzed polymerization of a lignin monomer into the lignin model compound in an in vitro condition by simulating the circumstances of lignin formation's final stage. They showed silicon was attached to the final polymer and the structure of Si-DHP (dehydrogenative polymer) varied from pure DHP, according

to FTIR and fluorescence spectroscopy and microscopy. As reported by fluorescence spectroscopy, silicon limits the development of bigger lignin fragments, as indicated by HPLC–DAD (high-performance liquid chromatography with diode array detection), by binding to dimmers generated during DHP synthesis. This polymer's structural alterations were connected to the altered proportion of distinct MW (molecular weight) fractions. They also found that silicon did not affect the enzyme that catalyzed DHP production. Except for 6 mM silicon, HRP (horseradish peroxidase) activity increased in the presence of silicon. This might imply that the combination produced with silicon and small oligomers stimulates the enzyme while inhibiting the production of big fragments.

Silicon improved wheat defensive mechanisms against the greenbug aphid by increasing the activities of defensive enzymes peroxidase (POX), polyphenoloxidase (PPO), and phenylalanine ammonia lyase (PAL), as reported by [93], who investigated the effect of silicon and previous aphid infection on the induction of resistance to this pest in wheat plants. Biochemical research indicates that plants benefit more from silicon treatment prior to an aphid invasion.

Ranger et al. (2009) [94] reported that on plants of *Zinnia elegans* treated with silicon, there were decreases in total cumulative fecundity and the intrinsic rate of increase of the green peach aphid, *Myzus persicae*. These decreases were linked to higher levels of p-coumaroylquinic acid and 5-caffeoylquinic acid, rutin in silicon-supplied *Z. elegans* plants compared to non-supplied *Z. elegans* plants.

Ye et al. (2013) [95] investigated silicon treated rice plant and feed by *C. medinalis*, the amounts of transcripts for defence marker genes, jasmonate (JA) accumulation, PPO and POX activity along with the level of a trypsin protease inhibitor rose. Silicon was unable to boost resistance to this insect in plants whose genes associated with JA production or sensing were silenced, indicating that JA is vital in providing resistance against leaf borer in rice. JA signaling was disrupted, demonstrating a substantial relationship between JA-mediated insect herbivore responses and silicon accumulation, as well as JA's encouragement of silicon accumulation.

The study conducted by Han et al. (2016) [96] showed that plants receiving silicon were pre-programmed to increase antioxidant metabolism and defensive systems in response to pest invasion. Rice plants infected with the leaf folder, *Cnaphalocrocis medinalis* in a silicon-amended soil had increased catalase (CAT), phenylalanine ammonia-lyase (PAL), peroxidase (POX), polyphenol oxidase (PPO) and superoxide dismutase (SOD) activity and lower malondialdehyde (MDA) levels than plants in a nonamended soil.

6.2.2 Silicon in Tritrophic (plant-herbivore–natural enemy) Interactions

The secondary metabolites produced by plants are crucial in their interactions with natural enemies and other insect pests. Volatile emissions from plants can be either constitutive or produced in response to stressors. Herbivore-triggered defence reactions always involve volatiles, regardless of emission method [97]. In tritrophic systems, plants generate chemical substances in response to insect-caused damage in the form of HIPVs. These chemicals can serve as either direct insect attractants or repellents, and can therefore be exploited as host-finding cues by insect-eating parasitoids and predators [98] (Fig. 1). Enhanced synthesis of plant hormones such as jasmonate and salicylate might be linked to increased plant resilience as a result of silicon treatment. Many plants generate hormones that attract helpful natural enemies into silicon treated plants when they are injured by insect pests [78, 79]. When cucumber plants attacked by *Helicoverpa armigera* larvae were treated with potassium silicate, they attracted more adults of the predator *Dicranolaius bellulus* than cucumber plants not treated with silicon [99]. In sugarcane crop silicon did not affect *C. flavipes* parasitism of the sugarcane borer or the morphometric characteristics of this parasitoid but enhanced the biological control as the length of tunnels bored by *D. saccharalis* was decreased by 43% when silicate was added to IACSP 96–2042 (susceptible variety). With silicon treatment, the tunnel length in the resistant cultivar (IACSP 96–3060) did not alter. The treatments did not affect the sugarcane borer's fresh mass or larval body size [100]. Similarly, an increase in parasitism of *Epiricania melanoleuca* (Fletcher) on sugarcane leafhopper, *Pyrilla perpusilla* Walker with the application of calcium silicate, maximum @ 1000 kg per ha followed by @ 500 kg ha⁻¹ and minimum in control. Furthermore, no effect on the population of predatory beetles, *Stethorus* sp. as biocontrol agent for management of sugarcane yellow mite, *Oligonychus sacchari* has been reported by Nikpay and Nejadian (2014) [65] and Nikpay and Laane (2020) [67].

7 Conclusion

The key objective of current review is to deliver in-depth knowledge concerning the function of Si in providing defence against insect herbivory in sugarcane production. The sugarcane has been classified as a silicon-accumulating plant known to deposited considerable amounts of silicon as silica gel. As detailed in this review, Si plays a crucial role in enhancing plants' direct and indirect defences against several insect pests through two basic modes of action: enhanced physical or mechanical barriers and biochemical or

molecular mechanisms that activate plant defence responses via biotrophic (plant-herbivore) interactions and tritrophic (plant-herbivore-natural enemy) interactions. Relevant research has been done on variety of sugarcane cultivars to demonstrate the effect of different silicon sources, both inorganic and organic, along with their role in enhancing the juice quality characteristics, yield, and component traits. Though, there is a lack of understanding of the detailed mode of action and transporters involved in the uptake of Si in sugarcane, as has been described in other crops like rice. Considering all the points, the conclusion of the current review revealed that plants use both Si-based resistance mechanisms together, not just one at a time. Instead, they use a combination of physical, chemical, and biochemical mechanisms to protect themselves from insect pests. However, extensive research on Si in sugarcane plants is still limited.

Author Contributions P collected the research papers. RK wrote the original draft.

Data Availability No datasets were generated or analysed during the current study.

Declarations

Ethics Approval Both the authors state that all the ethical standards required for the preparation and publication have been complied with.

Consent to Participate The authors have given their consent for participation.

Consent for Publication Both the authors of this paper consent for publishing manuscript, tables and figure in this journal.

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