

Silica in Insect-Plant Interactions

Calatayud PA^{1,2*}, Njuguna E^{1,3} and Juma G⁴

¹International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya

²University of Paris-Sud, 91405 Orsay, France

³Jomo Kenyatta University of Agriculture and Technology (JKUAT), Nairobi, Kenya

⁴University of Nairobi, Nairobi, Kenya

Silicon (Si) is a relatively inert element that rarely occurs freely in nature. Silicon, the second most abundant element on earth. It frequently occurs in plants in its oxidised form, silicon dioxide (SiO₂), commonly known as 'silica'. In soils, Si is mainly present as quartz, alkaline earth or aluminium silicates [1]. Although these forms of silicon are both chemically and biologically inert, they are reported to significantly influence the physical properties of soils including soil texture, water holding capacity and fertility [2]. Silicon content in soils ranges between 20-35% for clay or silt to 40-44% for sandy soils [3]. Although the element is abundant in most soils worldwide, it is rather sparse in weathered tropical soils. In Africa, for example, about 70% of the soils are reported to be either deficient or highly deficient in accessible Si [4].

The rate of uptake of silicon from soils by plants has been reported to vary among species. Whereas most of the higher plants are able to actively uptake Si from soils (e.g., Si accumulator in rice) and/or passively (via evapotranspiration, e.g., sunflower) others have limited capacity to uptake Si (non-accumulator plants, e.g., tomato) [5]. In general, silica can constitute between 0.1-10% of the dry matter in most plant species and it is higher in Poaceae and Cyperaceae families, i.e., in monocotyledons [6], than dicotyledons. It is hypothesized that monocotyledons contain much lower concentrations of secondary metabolites, which are involved in plant defenses against herbivorous insects, than the dicotyledons [7]. Hence monocots depend on other mechanisms such as silicon (Si)-based defences for their protection against pest attack [8,9].

Silicon is absorbed from soil as monosilicic acid [(Si(OH)₄] by plant roots, transported throughout the plant tissue via transpiration and deposited in plant epidermal cell walls as phytoliths [6,10]. Deposition of Si in the plant tissue enhances the strength and rigidity of cell walls and thus increases the resistance of plants to various stresses. The silicified cells also provide useful paleoecological and archaeological information known as plant opal or phytoliths [11]. In addition, silicon in plants has been reported to enhance tolerance to both biotic and abiotic stresses in several crop plants [12].

The protective effect of silica to plants against insect herbivores is related to the level of its accumulation and polymerization in plant tissues with highest levels positively being correlated with increased resistance [4,13-15]. In addition, the level of Si in plants significantly influences insect herbivores distribution, with predominance of insect species being more susceptible to areas where most host plants are less silicified [16]. However, exact mechanisms of action of silica on herbivorous insects are still unclear, though most studies point to use of both physical and/or chemical resistance mechanisms [17,18].

Mechanically, deposition of silica in plant epidermal cells provides a physical barrier against insect's probing and feeding or insect's penetration into plant tissues. For example, silica mediated stem borer resistance to *Eldana saccharina* (Walker) (Lepidoptera: Crambidae) on sugarcane or *Chilo suppressalis* Walker (Lepidoptera: Crambidae) on rice has been partly associated with delayed stalk penetration by larvae as a result of leaf and stalk silification [19-24]. Silica may also

alter the relative palatability of leaves by increasing leaf abrasion, which increases wearing of insects' mandibles and therefore physically deter larval feeding [25,26].

On the other hand, silica in plants has been shown to modulate the production and accumulation of herbivore defensive allelochemicals including phytoalexins, lignin and phenolics in plant tissues [13,27-30]. Similarly, silica is also reported to elicit the production of plant defensive enzymes including peroxidase, polyphenoloxidase and phenylalanine ammonia lyase which are induced in response to plant damage by herbivorous insects [21,31,32]. These enzymes have been implicated in a number of plant defenses processes such as lignification and/or production of antiherbivore plant metabolites [33].

Nevertheless, the effects of plant tissue silification as a defense mechanism against insect herbivores seem not universal. For example, high silica levels in turf grass had no influence on feeding and development of *Herpetogramma phaeopteralis* Guenée (Lepidoptera: Pyralidae), nor on growth, survival, feeding preference or mandibular wear of *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) [34]. Similarly high silica levels in maize crops had no influence on larval growth of *Chilo partellus* (Swinhoe) (Crambidae) [16].

In conclusion, even though monocotyledonous plants (Poaceae, Cyperaceae, Typhaceae...) are highly resistant to most of insect herbivores due to the high level of plant tissue silification, it is suggested that insects with the ability to feed on these plants, have co-evolved with these plants rendering them less susceptible or have become well adapted to high silica levels in these plants.

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*Corresponding author: Calatayud PA, Institute for Research for Development (IRD), UMR 247, c/o ICIPE (African Insect Science for Food and Health), P.O. Box 30772, Nairobi, Kenya, Tel: 254 (20) 8632161; E-mail: pcalatayud@icipe.org

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