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Influence of Si in maize plants in Kenyan populations of *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

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Abstract The fall armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera: Noctuidae), native to the Americas, was confirmed in West and Central Africa in 2016 and reported in almost all countries of sub-Saharan Africa in 2017, becoming thereafter one of the major constraints on the production of maize, the main staple food crop in the region. Cereals depend on silicon (Si)-based defences to fight off herbivores. Both FAW strains, namely rice and corn strains, have been found to be present in Kenya. The present study tested the influence of Si on larval survival and

relative growth rate according to the FAW strain, using potted maize plants treated with 10 and 20 g of Si. The results showed that plants treated with Si disturbed the larval growth of FAW larvae only from the corn strain but not from the rice strain. Overall, the corn strain performed better on maize as compared to the rice strain regardless of Si treatment, explaining why it has become the most abundant strain in Africa.

Keywords Silicon · Fall armyworm · Rice strain · Corn strain · Maize · Sub-saharan Africa

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Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), native to the Americas, was first reported in early 2016 in West and Central Africa (Georgen et al., 2016), before being detected and reported in most sub-Saharan African countries in 2017 (Day et al., 2017; FAO, 2018). FAW is highly polyphagous, attacking 353 host plant species belonging to 76 families, including 106 plant species in the Poaceae family (Montezano et al., 2018). In Africa, FAW represents a major threat to food security (Devi, 2018), and since 2018, the pest has infested tens of millions of hectares of maize (FAO, 2018) which is, on the continent, the second main food crop behind cassava in terms of annual production (FAOSTAT, 2020) and the most important cereal crop (FAOSTAT, 2020; IITA, 2020). In the African context, where most

maize producers are small farmers with limited access to knowledge and adequate inputs for conventional controls of FAW (FAO, 2018), the control of this pest by use of resistant varieties of the host, obtained either by conventional plant breeding or by induction, is therefore one of the most effective means of control in Africa, compatible with other integrated management strategies for the pest.

Compared to dicotyledonous plants, monocots have low levels of secondary metabolites, which are generally involved in plant defence against herbivorous insects (Elger et al., 2009). They therefore use silicon (Si) to protect themselves against attack by pests (Massey & Hartley, 2009). Silicon (Si) is the second most abundant chemical element in the earth's crust after oxygen (Richmond & Sussman, 2003). Plants take Si in the form of monosilicic acid through their roots in the soil by transpiration and deposit it in the tissues of other plant organs in the form of phytoliths (Jones & Handreck, 1967). Si is one of the most abundant mineral elements in plant tissues, generally representing a content of 0.1–10% of the dry weight (Hodson et al., 2005), and this concentration of 0.1% is equivalent to that of other, more important elements, such as phosphorus, sulphur, calcium, or magnesium in plant tissues (Epstein, 1994). Several authors have reported the beneficial effects of Si on plant growth and its induction effect on plant resistance against crop pests, particularly chewing insects, by increasing plant tissue toughness and thus disrupting the insects' feeding patterns (Calatayud et al., 2016a, b; Epstein, 1999, 1994; Juma et al., 2015; Ma & Yamaji, 2006; Mir et al., 2019; Reynolds et al., 2009; Sasamoto, 1955). The beneficial effects of Si against FAW larvae have been proven on rice crops, where significant reduction of food preference and foliar feeding plus a sharp fall in the weight and survival of larvae were reported (Nascimento et al., 2014, 2017). In maize, where FAW causes more damage than other crops (Cruz et al., 1999; Sarmiento et al., 2002), these beneficial effects of Si against FAW are less evident. For example, Goussain et al. (2002) found that leaves from Si-treated maize plants increased FAW larval mortality, cannibalism and wear on the larval mandibles, but Alvarenga et al. (2017) and Mondego et al. (2018) observed no significant effect on the larval survival and weight. Nevertheless, Mondego et al. (2018) found that Si negatively affected food preference and foliar

consumption of 1st and 3rd instar FAW larvae under choice conditions.

This variation in results on the beneficial effects of Si against FAW among plant species can be explained by the fact that the rate of Si uptake in soils also varies among plant species (see Calatayud et al. (2016a) for review).

Rice is among the plant species able to take up the highest level of Si via a Si accumulator (Takahashi et al., 1990), whereas maize is less able to take up Si as compared to rice, thus rendering rice richer in Si as compared to maize (Ma & Takahashi, 2002; Tamai & Ma, 2003; Liang et al., 2006). Another factor that can influence these varying results on the beneficial effects of Si against FAW may be due to the subpopulation characteristic of the insects. In the Americas, two subpopulations of FAW, namely the rice-strain and corn-strain, co-exist (Pashley et al., 1987; Nagoshi & Meagher, 2004; Juárez et al., 2014). They are morphologically indistinguishable but differ in their host plant distribution. Rice-strain is associated with millet and grass species associated with pasture habitats, while corn-strain is associated with maize/sorghum (Pashley, 1986, 1988; Pashley et al., 1992). A study that deployed the use of the barcode region of the *mtCOI* gene established the presence of both strains of FAW in Kenya and in Africa (Nagoshi et al., 2018; Rwomushana et al., 2018; Gichuhi et al., 2020). More recently, it has been reported that finally the rice strain is rare or even absent in Africa (Nagoshi et al., 2021).

We hypothesized that increased Si levels in leaf tissue would disturb the development of FAW larvae depending on their strain origin, the corn strain being potentially more sensitive than the rice strain. In this context, the purpose of this study was to assess the influence of Si on larval survival and relative growth rate of both corn and rice strains of FAW using potted maize plants amended with Si.

Materials & methods

Spodoptera frugiperda colonies

Spodoptera frugiperda colonies were initiated from field-collected samples in 2018. Larvae of FAW were either collected at Kitale (34.777E, 1.203 N) and Bungoma (34.557E, 0.655 N) in Western Kenya,

or at Makutano (37.273E, 0.727 S) and Murang'a (37.150E, 0.923 S) in the Central region. Both colonies (i.e. Western and Central colonies) were maintained separately at 25 ± 2 °C, used as the standard reference temperature by Schoolfield et al. (1981); 50–70% RH and a photoperiod of 12:12 (L:D) h., at the Animal Rearing and Containment Unit (ARCU), *icipi*, Nairobi, for at least two generations before being used for the bioassays. Third instar FAW larvae from each colony were randomly collected and, after both DNA extraction and mitochondrial COI gene amplification by PCR, were sent to Macrogen Europe BV (Meibergreef, Amsterdam, the Netherlands) for bi-directional sequencing. Individuals from the Western colony were shown to belong to the rice strain haplotype, whereas individuals from the central colony belonged to the corn strain haplotype.

For each colony, adult moths were then placed in cages (40×40×45 cm) made of Perspex with netting materials fitted at the rear and a sleeve on the front side. They were fed with a 1:9 honey:water solution soaked in cotton wool. Moths were provided with potted maize plants for oviposition, which were removed after one night. The leaves with eggs were then transferred into plastic boxes (15×7×5 cm) lined with a paper towel to absorb excess moisture until the eggs hatched. The hatched larvae were reared on freshly detached maize leaves kept in plastic boxes until pupation. The leaves were changed every two days during the rearing process. Pupae were incubated under similar rearing conditions until adult emergence. For all experiments, 1-day-old neonates were used.

Plants

The maize hybrid 513 (among the most popular hybrids used by farmers in Kenya), provided by the Simlaw, Kenya Seeds Company, Nairobi, was used. Maize was planted in plastic pots (diameter 14 cm, height 15 cm) (one plant per pot) using the same type of soil for all potted plants in a greenhouse at *icipi*, Nairobi, Kenya. The environmental conditions were about 31/17°C (day/night) with a 12:12 h (L:D) photoperiod. The protocol of Juma et al. (2015) and Calatayud et al. (2016b), which used two dose treatments 14 days after planting, 10 and 20 g per pot of calcium

silicate were used as a Si source from Sigma (Ref 742,503). For each Si-treated plant, the calcium silicate was well mixed into the top layers of the soil in each pot. Some pots were left untreated to serve as controls.

Larval development and survival

Similar to Juma et al. (2015) and Calatayud et al. (2016a, b), all treated and untreated two-week-old potted plants were individually infested with twenty neonates (i.e. freshly hatched larvae) of FAW. For each potted plant, the percentage of live larvae remaining and relative growth rate (RGR) were assessed 19 days after infestation (DAI) (i.e., the minimum time required for Si to show a significant effect on larval development (Juma et al., 2015)). RGRs were calculated by subtracting the average weight per larva on each plant at infestation from the average weight per larva on the same plant at 19 DAI, divided by the number of days in between (Ojeda-Avila et al., 2003). This experiment was repeated using either the rice or corn strain of *S. frugiperda*.

In addition, 33 days after germination, the root collar diameter, the number of leaves per plant and the height of each plant were measured on the Si-treated and control potted plants.

Determination of the Si concentration in maize leaves

For all plants (both Si-treated and untreated), leaf Si was analyzed at (14 + 19 days) 33 days after planting. All leaves of each potted plant were harvested, dried, and grounded to a fine, homogenous powder using a Bolmill Grinder (type MM40) prior to Si analyses.

Silicon in maize leaves were extracted using the rapid dilute hydrofluoric acid (HF) extraction method and their concentrations (in mg g⁻¹) determined by the spectrometric molybdenum-yellow method of Saito et al. (2005). Briefly, 100 mg of dried leaf powder were digested first in a hydrofluoric acid (HF) solution, and thereafter the same spectrophotometric protocol as adapted by Juma et al. (2015) was used.

Data analyses

Data on Si content in maize leaves, the % of live larvae remaining and RGR were subjected to the Shapiro-Wilk and Bartlett test at a p value of 0.05 respectively to determine whether their distributions

were normal, and their variances homogenous. Not all data passed the normality test. The Si content of maize leaves was analyzed using the Kruskal-Wallis test. Using the Dunn test (Package `Dunn.test`) (Dinno, 2017), the significant differences ($p \leq 0.05$) between the treatments were statistically assessed. The generalized linear model (GLM) was used to analyze the % of live larvae remaining with a Poisson distribution and the RGR with a Gaussian distribution. Significant differences were compared using the multiple comparisons test with Tukey's contrast test in the `multcomp` package (Hothorn et al., 2021). A significance level of 0.05 was used for all comparison tests. All statistical analyses were performed with R software version 3.5.1 (R Core Team, 2018).

Results

Following Si treatment, the Si level of plant leaves increased significantly (Table 1). Consequently, both the root collar diameter and plant height increased significantly during the highest Si treatment (20 g of calcium silicate per pot). In contrast, the number of leaves was not significantly affected (95%CI=0.42–0.67, $F=2.89$, $p=0.07$).

Although FAW larvae survival tended generally to decrease with increasing Si level regardless of the FAW strain, FAW larvae growth was significantly influenced by Si treatment according to the colony used. For individuals belonging to the rice strain, their RGR remained similar, whereas for individuals belonging to the corn strain their RGR decreased when Si level increased in plants, indicating that the larvae performed less well on plants treated with 10 g of Si than on those of the control treatment (Fig. 1).

Overall, the individuals belonging to the corn strain performed better on maize than individuals

from the rice strain. The highest RGR were obtained on individuals of corn strain regardless of the plant treatment.

Discussion

Not surprisingly the soil amendment carried out in our study induced a significant increase of Si level in plant leaves of potted maize plants, as already obtained by Juma et al. (2015) and Calatayud et al. (2016a, b). These increasing Si levels in maize plants enhanced plant growth through a rise in both plant root collar diameter and plant height. This agrees with what is generally known in the literature, namely that Si enhances the growth and yield of annual and vegetable crops (Epstein & Bloom, 2005).

Looking at the impact of increasing Si levels in leaves on FAW larvae, FAW larval growth of the rice strain was not affected by increasing leaf Si levels. This could be because such population being associated to millet and grass species, namely rice strain, is used to feed on plants richer in Si as compared to the corn strain associated with maize/sorghum.

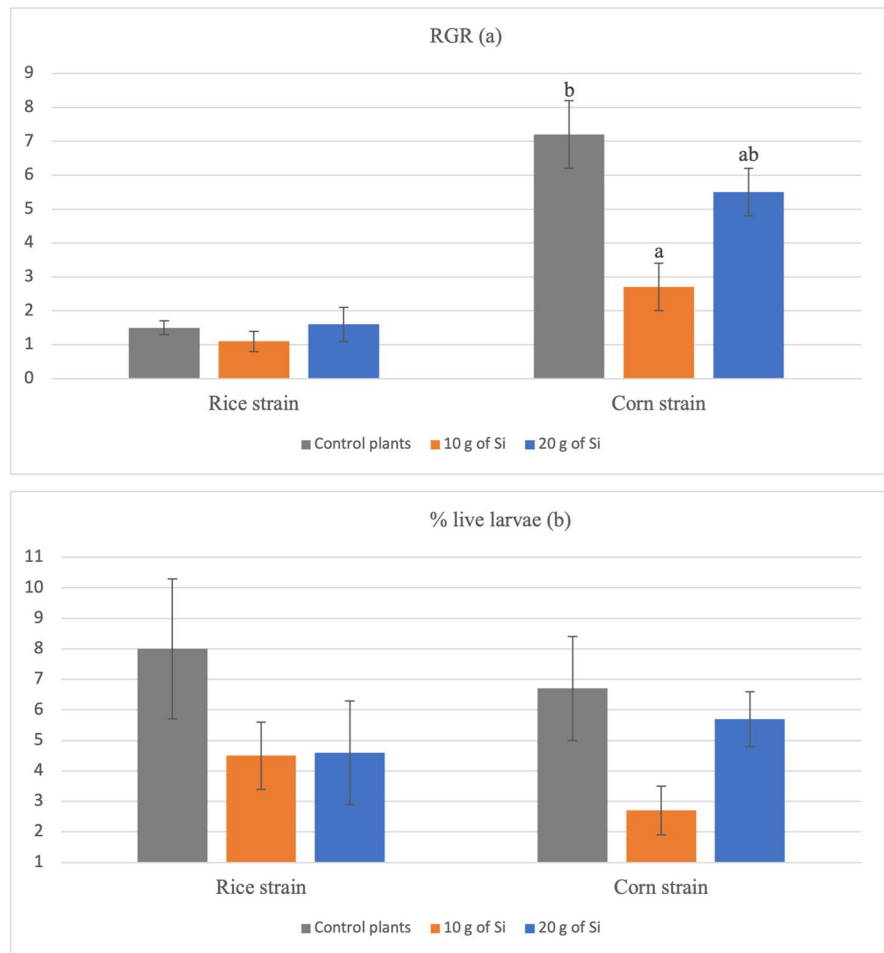
Although increasing Si levels in maize plants have a negative impact on the corn strain larval development by a decrease of about 2.5 times of RGR on Si-treated plants as compared to the control plants, this decrease is however less marked than in another maize pest in the region, such as the maize stemborer, *Busseola fusca* (Lepidoptera: Noctuidae), for which Si-treated plants induced around a fourfold decrease of RGR (Juma et al., 2015; Calatayud et al., 2016b). FAW appears less sensitive to an increasing Si level in plants than *B. fusca*. This explains why FAW can be found in the region at both low and high altitudes and even more abundantly in the lowlands (Sokame et al., 2021), which is not the case for *B. fusca*, since

Table 1 Si levels (in mg g^{-1}), root collar diameter (in cm), number of leaves and plant height (in cm) of control and Si-treated maize plants 33 days after planting (means^a \pm SE, $n=12$)

| Treatment | Si in plant leaves | Root collar diameter | Number of leaves | Plant height |
|----------------|--------------------|----------------------|------------------|--------------------|
| Control plants | 0.682 \pm 0.07a | 1.5 \pm 0.03a | 9.2 \pm 0.3 | 95.7 \pm 2.26a |
| 10 g of Si | 1.051 \pm 0.13b | 1.5 \pm 0.05a | 9.4 \pm 0.2 | 103.2 \pm 3.07ab |
| 20 g of Si | 1.157 \pm 0.08b | 1.8 \pm 0.10b | 10.0 \pm 0.0 | 111.6 \pm 1.91b |

^a The means within column followed by different letters are significantly different at the 5% level (Pairwise comparisons using Dunn test for Si levels and root collar diameters, and Tukey's contrasts test following ANOVA performed after the generalized linear model for the numbers of leaves and plant heights)

Fig. 1 Relative growth rates (RGR, mg d^{-1} , mean \pm SE) (a) and percentage of live larvae (mean \pm SE, $n=10\text{--}14$) (b) *Spodoptera frugiperda* larvae of the rice and corn strain haplotype remaining after 19 days of infestation on control and Si-treated maize plants. Means within strain with different letters are significantly different at the 5% level (Tukey's contrasts test following ANOVA performed after the generalized linear model for RGR and % live larvae comparisons)



the latter prefers to develop in highland areas. This is partly explained by low Si soil levels and maize cultivation in the highlands as compared to the lowlands (Calatayud et al., 2016a, b).

Regarding the FAW strains, corn strain performed better on maize as compared to the rice strain, as shown by the generally highest RGRs obtained with maize-strain larvae in our study. It was already shown that the corn strain performs better on maize than the rice strain (e.g., Nagoshi & Meagher, 2004). Avacedo et al. (2018) attributed these different performances of the two strains on maize plants to the existence of specific elicitors in the saliva of FAW strains that trigger differential levels of plant defense responses, with the rice strain eliciting greater maize plant defenses than the corn strain, affecting larval growth. This may influence host plant associations in field conditions

(Avacedo et al., 2018), with a disadvantage for the rice strain on maize fields, explaining why the rice strain is rare or even absent in African maize fields (Nagoshi et al., 2021).

In conclusion, Si-treated plants disturbed the larval growth of FAW larvae only from the corn strain but not from the rice strain. Overall, the corn strain performed better on maize as compared to the rice strain, regardless of Si treatment, thus justifying the abundance of corn rather than the rice strain attacking maize in different regions where the crop is cultivated, (Nagoshi et al., 2021) and more recently in China (Wang et al., 2020a, b; Zhang et al., 2020).

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

- Acevedo, F. E., Peiffer, M., Ray, S., Meagher, R., Luthe, D. S., & Felton, G. W. (2018). Intraspecific differences in plant defense induction by fall armyworm strains. *New Phytologist*, *218*, 310–321.
- Alvarenga, R., Moraes, J. C., Auad, A. M., Coelho, M., & Nascimento, A. M. (2017). Induction of resistance of corn plants to *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae) by application of silicon and gibberellic acid. *Bulletin of Entomological Research*, *107*, 527–533. <https://doi.org/10.4172/2161-0983.1000e125>
- Calatayud, P.-A., Njuguna, E., & Juma, G. (2016a). Silica in Insect-Plant Interactions. *Entomology, Ornithology & Herpetology*, *5*, 4. <https://doi.org/10.4172/2161-0983.1000e125>
- Calatayud, P. A., Njuguna, E., Mwalusepo, S., Gathara, M., Okuku, G., Kibe, A., Musyoka, B., Williamson, D., Ong'amo, G., Juma, G., Johansson, T., Subramanian, S., Gatebe, E., & Le Ru, B. (2016b). Can climate-driven change influence silicon assimilation by cereals and hence the distribution of lepidopteran stem borers in East Africa? *Agriculture Ecosystems and Environment*, *224*, 95–103.
- Cruz, I., Figueiredo, M., Oliveira, A. C., & Vasconcelos, C. A. (1999). Damage of *Spodoptera frugiperda* (Smith) in different maize genotypes cultivated in soil under three levels of aluminium saturation. *International Journal of Pest Management*, *45*, 293–296.
- Day, R., Abrahams, P., Bateman, M., Beale, T., Clotey, V., Cock, M., Colmenarez, Y., Corniani, N., Early, R., Godwin, J., Gomez, J., Moreno, P. G., Murphy, S. T., Oppong-Mensah, B., Phiri, N., Pratt, C., Silvestri, S., & Witt, A. (2017). Fall armyworm: impacts and implications for Africa. *Outlooks Pest Management*, *28*, 196–201.
- Devi, S. (2018). Fall armyworm threatens food security in southern Africa. *Lancet*, *391*, 727.
- Dinno, A. (2017). Package 'dunn.test'. <https://cran.r-project.org/web/packages/dunn.test/dunn.test.pdf>. Accessed 30 Sept 2020.
- Elger, A., Lemoine, D. G., Fenner, M., & Hanley, M. E. (2009). Plant ontogeny and chemical defence: older seedlings are better defended. *Oikos*, *118*, 767–773.
- Epstein, E. (1994). The anomaly of silicon in plant biology. *Proceedings of the National Academy of Sciences USA*, *91*, 11–17.
- Epstein, E. (1999). Annual review of plant physiology and plant molecular biology. *Silicon*, *50*, 641–664.
- Epstein, E., & Bloom, A. J. (2005). Mineral nutrition of plants: principles and perspectives, 2nd Edn. Sinauer Associates Inc.
- Food and Agriculture Organization (FAO) (2018). Fall Armyworm threatens food security and livelihoods across Africa. Rome. <http://www.fao.org/3/i8503en/i8503en.pdf>. Accessed January 2018.
- Food and Agriculture Organization (FAO) (2020). FAOSTAT crop production compare data. Rome. <http://www.fao.org/faostat/fr/#compare>. Accessed 1 May 2020.
- Gichuhi, J., Subramanian, S., Khamis, F. M., van den Berg, J., du Plessis, H., Ekesi, S., & Herren, J. (2020). Diversity of fall armyworm, *Spodoptera frugiperda* and their gut bacterial community in Kenya. *PeerJ*, *8*, e8701.
- Goergen, G., Kumar, P. L., Sankung, S. B., Togola, A., & Tamò, M. (2016). First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in West and Central Africa. *PLoS One*, *11*, e0165632.
- Goussain, M. M., Moraes, J. C., Carvalho, J. G., Nogueira, N. L., & Rossi, M. L. (2002). Efeito da aplicacao de silicio em plantas de milho no desenvolvimento biológico da lagarta-do-cartucho *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae). *Neotropical Entomology*, *31*, 305–310.
- Hodson, M. J., White, P. J., Maed, A., & Broadley, M. R. (2005). Phylogenetic variation in the Silicon composition of plants. *Annales of Botany*, *96*, 1027–1046.
- Hothorn, T., Bretz, F., Westfall, P., Heiberger, R. M., Schuetzenmeister, A., & Scheibe, S. (2021). Package 'multcomp'. <https://cran.r-project.org/web/packages/multcomp/multcomp.pdf>. Accessed April 26 2022
- International Institute of Tropical Agriculture (IITA) (2020). Maize. Nigeria. <https://www.iita.org/cropsnew/maize/>. Accessed 1 May 2020.
- Juárez, M. L., Groot, A. T., Hänniger, S., Heckel, D. G., Murúa, M. G., Schöfl, G., Vera, M. T., Vilardi, J. C., & Willink, E. (2014). Population structure of *Spodoptera frugiperda* maize and rice host forms in South America: are they host strains? *Entomologia Experimentalis et Applicata*, *152*, 182–199.
- Jones, L. H. P., & Handreck, K. A. (1967). Silica in soils, plants and animals. *Advances in Agronomy*, *19*, 107–149.
- Juma, G., Ahuya, P. O., Ong'amo, G., Le Ru, B., Magoma, G., Silvain, J. F., & Calatayud, P. A. (2015). Influence of plant silicon in *Busseola fusca* (Lepidoptera: Noctuidae) larvae – Poaceae interactions. *Bulletin of Entomological Research*, *105*, 253–258.

- Liang, Y., Hua, H., Zhu, Y. G., Zhang, J., Cheng, C., & Römhöld, V. (2006). Importance of plant species and external silicon concentration to active silicon uptake and transport. *New Phytologist*, *172*, 63–72.
- Ma, J. F., & Takahashi, E. (2002). *Soil, fertilizer, and plant silicon research in Japan*. Elsevier Science.
- Ma, J. F., & Yamaji, N. (2006). Silicon uptake and accumulation in higher plants. *Trends in Plant Science*, *11*, 392–397.
- Massey, F. P., & Hartley, S. E. (2009). Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. *Journal of Animal Ecology*, *78*, 281–291.
- Mondego, J. M., Machado, K. K. G., Oliveira, L. J. M. G., Lemos, R. N. S., Bastista, J. L., Junior, A. S. L. F., Araujo, A. M. S., Melo, P. A. F. R., & Mesquita, M. L. R. (2018). Effect of resistance elicitors on the biology and feeding preference of *Spodoptera frugiperda* (J.E.Smith) (Lepidoptera: Noctuidae) in corn. *Australian Journal of Crop Science*, *12*, 1774–1781.
- Zhang, L., Liu, B., Zheng, W., Liu, C., Zhang, D., Zhao, S., Li, Z., Xu, P., Wilson, K., Withers, A., Jones, C. M., Smith, J. A., Chipabika, G., Kachigamba, D. L., Nam, K., d'Alencón, E., Liu, B., Liang, X., Jin, M., Wu, C., Chakrabarty, S., Yang, X., Jiang, Y., Liu, J., Liu, X., Quan, W., Wang, G., Fan, W., Qian, W., Wu, K., & Xiao, Y. (2020). Genetic structure and insecticide resistance characteristics of fall armyworm populations invading China. *Molecular Ecology Resources*, *20*, 1682–1696.
- Montezano, D. G., Specht, A., Sosa-Gómez, D. R., Roque-Specht, V. F., Sousa-Silva, J. C., Paula-Moraes, S. D., Peterson, J. A., & Hunt, T. E. (2018). Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. *African Entomology*, *26*, 286–300.
- Mir, S. H., Rashid, I., Hussain, B., Reshi, Z. A., Assad, R., & Sofi, I. A. (2019). Silicon supplementation of rescuegrass reduces herbivory by a grasshopper. *Frontiers in Plant Science*, *10*, 671.
- Nagoshi, R. N., & Meagher, R. L. (2004). Behavior and distribution of the two fall armyworm host strains in Florida. *Florida Entomologist*, *87*, 440–449.
- Nagoshi, R. N., Goergen, G., Tounou, K. A., Agboka, K., Koffi, D., & Meagher, R. L. (2018). Analysis of strain distribution, migratory potential, and invasion history of fall armyworm populations in northern Sub-Saharan Africa. *Scientific Reports*, *8*, 3710.
- Nagoshi, R. N., Koffi, D., Agboka, K., Adjevi, A. K. M., Meagher, R. L., & Goergen, G. (2021). The fall armyworm strain associated with most rice, millet, and pasture infestations in the Western Hemisphere is rare or absent in Ghana and Togo. *PLoS One*, *16*(6), e0253528. <https://doi.org/10.1371/journal.pone.0253528>
- Nascimento, A. M., Assis, F. A., Moraes, J. C., & Sakomura, R. (2014). Feeding non preference of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) induced by silicon application in rice crop. *Revista Brasileira de Ciências Agrárias*, *9*, 215–218.
- Nascimento, A. M., Assis, F. A., Moraes, J. C., & Souza, B. H. S. (2017). Silicon application promotes rice growth and negatively affects development of *Spodoptera frugiperda* (J. E. Smith). *Journal of Applied Entomology*, *142*, 241–249.
- Ojeda-Avila, T., Woods, H. A., & Raguso, R. A. (2003). Effects of dietary variation on growth, composition and maturation of *Manduca sexta* (Sphingidae: Lepidoptera). *Journal of Insect Physiology*, *49*, 293–306.
- Pashley, D. P. (1986). Host-associated genetic differentiation in fall armyworm (Lepidoptera, Noctuidae) - a sibling species complex. *Annals of the Entomological Society of America*, *79*, 898–904.
- Pashley, D. P. (1988). Quantitative genetics, development, and physiological adaptation in host strains of fall armyworm. *Evolution*, *42*, 93–102.
- Pashley, D. P., Sparks, T. C., Quisenberry, S. S., Jamjanya, T., & Dowd, P. F. (1987). Two fall armyworm strains feed on corn, rice and bermudagrass. *Louisiana Agriculture Magazine*, *30*, 8–9.
- Pashley, D. P., Hammond, A. M., & Hardy, T. N. (1992). Reproductive isolating mechanisms in fall armyworm host strains (Lepidoptera, Noctuidae). *Annals of the Entomological Society of America*, *85*, 400–405.
- R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved August 17, 2018 Retrieved from <https://www.R-project.org/>
- Richmond, K. E., & Sussman, M. (2003). Got silicon? The non-essential beneficial plant nutrient. *Current Opinion in Plant Biology*, *6*(268), 272.
- Reynolds, O. L., Keeping, M. G., & Meyer, J. H. (2009). Silicon-augmented resistance of plants to herbivorous insects: a review. *Annals of Applied Biology*, *155*, 171–186.
- Rwomushana, I., Bateman, M., Beale, T., Beseh, P., Cameron, K., Chiluba, M., Clotey, V., Davis, T., Day, R., Early, R., Godwin, J., Gonzalez-Moreno, P., Kansime, M., Kenis, M., Makale, F., Mugambi, I., Murphy, S., Nunda, W., Phiri, N., Pratt, C., and Tambo, J. (2018). Fall armyworm: Impacts and implication for Africa. Evidence NoteUpdate. CAB International. Retrieved the 1st of August 2022 <https://www.invasive-species.org/wp-content/uploads/sites/2/2019/02/FAWEvidence-Note-October-2018.pdf>
- Saito, K., Yamamoto, A., Sa, T., & Saigusa, M. (2005). Rapid, micro-methods to estimate plant silicon content by dilute Hydrofluoric acid extraction and spectrometric molybdenum method. *Soil Science and Plant Nutrition*, *51*, 29–36.
- Sarmiento, R. A., Aguiar, R. W. S., Vieira, S. M. J., de Oliveira, H. G., & Holtz, A. M. (2002). Biology review, occurrence and control of *Spodoptera frugiperda* (Lepidoptera, Noctuidae) in corn in Brazil. *Bioscience Journal*, *18*(2), 41–48.
- Sokame, B. M., Musyoka, B., Obonyo, J., Rebaudo, F., Abdel-Rahman, E. M., Subramanian, S., Kilalo, D. C., Juma, G., & Calatayud, P.-A. (2021). Impact of an Exotic Invasive Pest, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), on Resident Communities of Pest and Natural Enemies in Maize Fields in Kenya. *Agronomy*, *11*, 1074.
- Sasamoto, K. (1955). Studies on the relation between insect pests and silica content in rice plant (III). On the relation between some physical properties of silicified rice plant and injuries by rice stem borer, rice plant skipper and rice stem maggot. *Oyo Kontyu*, *11*, 66–69.
- Schoolfield, R. M., Sharpe, P. J. H., & Magnuson, C. E. (1981). Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *Journal of Theoretical Biology*, *88*, 719–731.
- Tamai, K., & Ma, J. F. (2003). Characterization of silicon uptake by rice roots. *New Phytologist*, *158*, 431–436.

- Takahashi, E., Ma, J. F., & Miyake, Y. (1990). The possibility of silicon as an essential element for higher plants. *Comments on Agricultural and Food Chemistry*, 2, 99–122.
- Wang, P., Kong, B. Y., Zhu, J. S., Guo, D., Kong, Z. Y., Hu, L., & Chu, D. (2020a). Rapid differentiation of corn- and rice- strain of *Spodoptera frugiperda* using mtCOI PCR-RFLP technique. *Shandong Agricultural Sciences*, 52, 19–23.
- Wang, P., He, P. C., Zhu, J. S., Guo, D., & Chu, D. (2020b). Molecular identification of invasive *Spodoptera frugiperda* individuals in Shandong Province based on mtCOI Gene. *Shandong Agricultural Sciences*, 52, 97–100.

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