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# Can climate-driven change influence silicon assimilation by cereals and hence the distribution of lepidopteran stem borers in East Africa?

P.-A. Calatayud[a,b,*], E. Njuguna[a,c], S. Mwalusepo[a,d], M. Gathara[e], G. Okuku[a], A. Kibe[a], B. Musyoka[a], D. Williamson[f,g], G. Ong'amo[a,h], G. Juma[h], T. Johansson[a], S. Subramanian[a], E. Gatebe[c], B. Le Ru[a,b]

[a] International Centre of Insect Physiology and Ecology (icipe), P.O. Box 30772-00100, Nairobi, Kenya
[b] UMR Laboratoire Evolution, Génomes, Comportement et Ecologie, groupe IRD, Diversité, Ecologie et Evolution des Insectes Tropicaux, UPR 9034, 22 CNRS, 91198 Gif-sur-Yvette, France and Université de Paris-Sud, 91405 Orsay, France
[c] Jomo Kenyatta University of Agriculture and Technology (JKUAT), P.O. Box 62000, Nairobi, Kenya
[d] Department of General Studies, Dar es Salaam Institute of Technology (DIT), P.O. Box 2958, Dar es Salaam, Tanzania
[e] Kenya Forestry Research Institute (KEFRI) P.O. Box 20412-00200, Nairobi, Kenya
[f] World Agroforestry Centre (ICRAF), Gigiri, P.O. Box 30, 677-00100, Nairobi, Kenya
[g] Institut de Recherche pour le Développement (IRD), UMR-7153 LOCEAN, Université Pierre et Marie Curie, Centre IRD France Nord, 32 av. Henri-Varagnat, F-93143, Bondy cedex, France
[h] University of Nairobi, P.O. Box 35062, Nairobi, Kenya

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ABSTRACT

In East Africa, lepidopteran stemborers such as *Chilo partellus* and *Busseola fusca* are major constraints to production of maize, which is the main staple food crop in the region. Cereals depend on silicon (Si)-based defences to fight off herbivores. Using altitudinal ranges in the East African highlands as ecological surrogates for inferring climate change, it was shown that Si concentrations in soil and maize decreased with altitude. This was attributed, in part, to low temperatures at high altitudes, which negatively affected Si assimilation by maize. Experiments showed that *B. fusca* was more susceptible to Si than *C. partellus*. Hence the predominance of *B. fusca* in the highlands and of *C. partellus* in the lowlands could be partly explained by altitudinal differences in Si concentrations in maize plants. Therefore, a rise in temperature due to climate change should enhance the plants' Si assimilation and as a result *C. partellus* might move into the higher altitudes and increasingly displace *B. fusca*.

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## 1. Introduction

Global warming is forecasted to drastically change plant-insect interactions in the near future and thus influence insect herbivore community compositions (see Rasmann et al. (2014) for review). Thus, understanding climate change-driven herbivore responses towards plant defence mechanisms is key to forecasting insect-plant interactions in the near future. Plants employ different defence mechanisms that can partly explain the distribution of insect herbivores (see Rasmann et al. (2014) for review). In plants, most of the chemical defence systems are conferred by secondary metabolites such as phenolic compounds, alkaloids and terpenoids (Wittstock and Gershenzon, 2002; Schoonhoven et al., 2005). However, monocotyledons usually contain much lower concentrations of secondary metabolites than dicotyledons (Elger et al., 2009). Monocotyledons may depend on other mechanisms such as silicon (Si)-based defences (e.g. Massey and Hartley, 2006; Reynolds et al., 2009). Silicon accumulated in grasses mediates plant resistance to insect herbivores, particularly to chewing insects, through enhancement of plant phytoliths, which provide a mechanical resistance barrier to insect feeding (Vicari and Bazely, 1993). In Lepidoptera stem borers, Si was shown to be harmful to *Sesamia calamistis* Hampson (Lepidoptera, Noctuidae) (Sétamou et al., 1993), *Eldana saccharina* Walker (Lepidoptera, Pyralidae) (Keeping and Meyer, 2006; Kvedaras and Keeping, 2007; Kvedaras et al., 2009) and *Busseola fusca* (Fuller) (Noctuidae) (Juma et al., 2015), which are key pests of cultivated grasses (maize and

* Corresponding author at: International Centre of Insect Physiology and Ecology (icipe), P.O. Box 30772-00100, Nairobi, Kenya.
*E-mail address:* pcalatayud@icipe.org (P. -A. Calatayud).

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sugarcane) in Sub-Saharan Africa. It has been suggested that Si increases leaf abrasion, which may increase wear of insect mandibles, and physically deters stem borer larvae from feeding (Massey and Hartley, 2009; Keeping et al., 2009; Kvedaras et al., 2009). However, variations of Si effect on Lepidoptera larval development have been well reported in the literature (Schoonhoven et al., 2005; Redmond and Potter, 2007), and even no effect was reported for *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) living on the creeping bent grass (Redmond and Potter, 2007).

In eastern Africa, the stem borers *Chilo partellus* (Swinhoe) (Crambidae) and *B. fusca* are the most notorious insect pests of maize. These species are oligophagous feeding only on Poaceae (Le Ru et al., 2006). Their distribution in the region varies with altitude. Whereas, *C. partellus* dominates the lowlands, *B. fusca* is the predominant species at high altitudes (Kfir et al., 2002; Ong'amo et al., 2006). Temperature differences between low and high altitudes can partly explain the differences in the distribution of these two species. In ectotherms, such as insects, temperature plays an important role in their development and thus geographic distribution (Stange and Ayres, 2010; Rasmann et al., 2014) by directly affecting their metabolism (Hochachka and Somero, 2002) and lifespan (Munch and Salinas, 2009). Khadioli et al. (2014a,b) showed that *C. partellus* was more susceptible to low temperatures than *B. fusca*. In addition to the temperature, the differences in the distribution of *C. partellus* and *B. fusca* between lowlands and high altitudes can also be attributed to their different in sensitivity towards Si accumulation in maize plants related to differences in Si accumulation in maize between altitudes. Higher plants are able to uptake Si from soil actively (e.g. Si accumulator in rice) and/or passively (via evapotranspiration, e.g. sunflower) (Takahashi et al., 1990). Recently Si transporter genes have been identified in maize indicating an active Si transfer from the soil to root cells (Mitani et al., 2009a). Temperature has generally a pronounced effect on the element uptake from the soil and their use by plants (Pregitzer and King, 2005; Hussain et al., 2010; Hussain and Maqsood, 2011). Root enzymes and cell membrane activities linked to nutrient and soil element uptake are directly related to soil temperatures (Taiz and Zeiger, 1991; Larcher, 1995) and thus variations in temperatures between lowlands and high altitudes can have a significant influence on the active Si accumulation process in maize. However, Mitani et al. (2009b) showed that maize has a Si uptake system different from that in rice indicating that we cannot exclude a passive process behind Si accumulation. Plant species having an active Si accumulation process can also take up Si passively (Takahashi et al., 1990). The passive process is controlled by transpiration, which is controlled by plant traits such as leaf size and pubescence, and environmental factors such as temperature, relative humidity and wind (e.g. Schuepp, 1993). Therefore, warmer air at low altitudes creates a larger driving force for water movement out of the plant thereby increasing transpiration rates (e.g. Dey et al., 2015) and thus Si uptake from soil. It is hence hypothesized that the differences in the pest distribution between lowlands and high altitudes could also be linked to differences in Si concentrations in maize plants due to differences in environmental factors between low and high altitude regions.

Altitudinal ranges, which characterize numerous tropical and subtropical regions, are optimal ecological surrogates for inferring global change-driven dynamics (see Rasmann et al. (2014) for review). Hence altitudinal ranges can act as 'natural experiments' that provide variations in environmental factors such as temperature, rainfall pattern and soil elements, which affect biotic interactions. The aim of this study was to evaluate Si

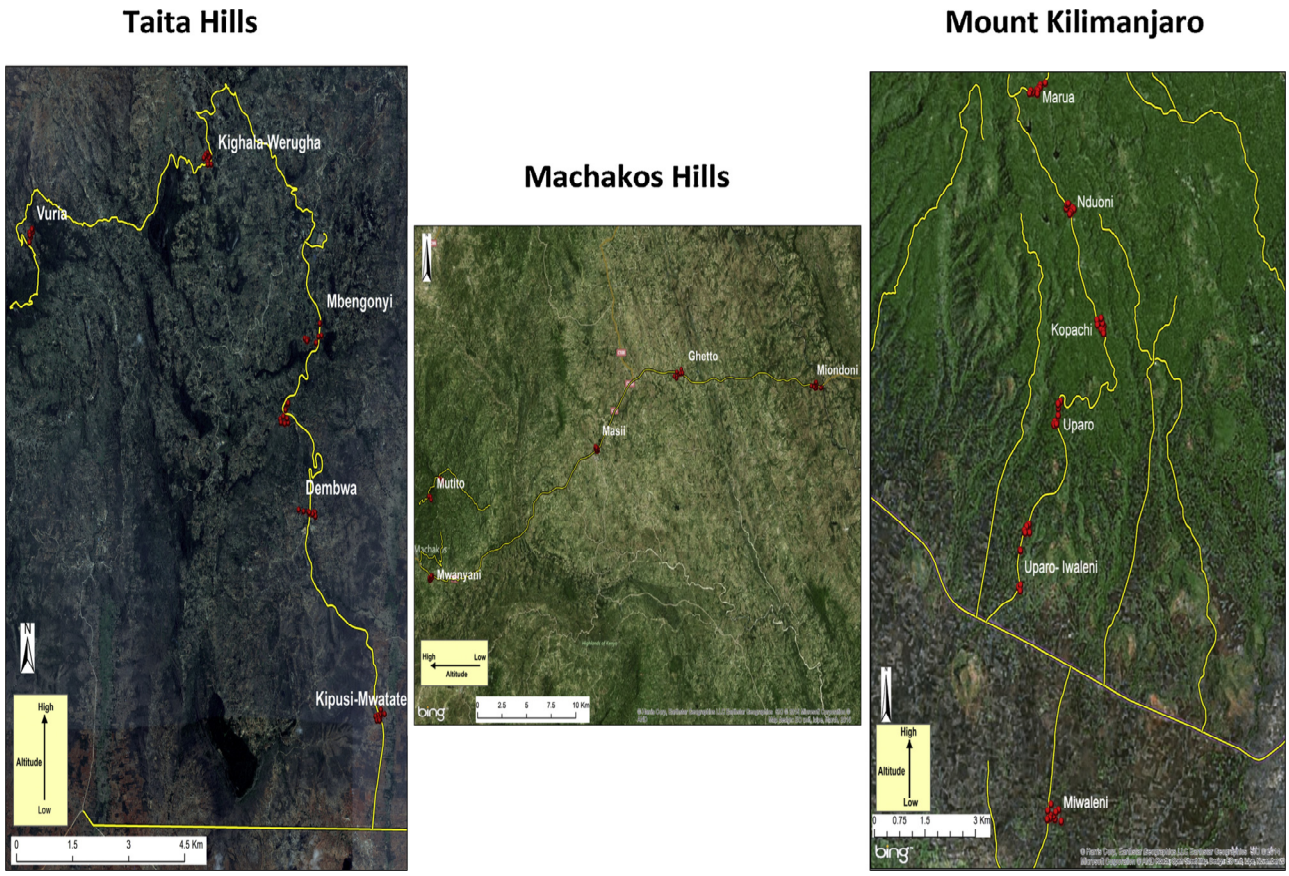



**Fig. 1.** The study areas: Taita Hills, Machakos Hills and Mount Kilimanjaro transects. The circles in red indicate the 10 maize plots selected at each locality.

concentrations in both soil and maize plants grown along three altitudinal (i.e., climatic) ranges in the East African highlands (namely Machakos Hills, Taita Hills and Mount Kilimanjaro), in order to evaluate and predict how increasing temperatures as a result of global warming will affect the availability of Si to the plant and how this will potentially influence the distribution of *C. partellus* and *B. fusca* in the region.

## 2. Material and methods

### 2.1. Study sites

Three altitudinal transects were set up in the Eastern Afromontane Biodiversity Hotspot in Kenya and Tanzania. In Kenya, one target area was situated along the slopes of the granitic gneisses Taita Hills in the Taita Taveta County at an elevation ranging from 700 to 2228 m.a.s.l., between latitude 3°25′ and longitude 38°20′ (Fig. 1). Mean annual rainfall ranges from 500 mm to over 1500 mm and mean annual temperature from 16.5 to 23.5 °C in, respectively, the high and low altitudes. The second target area in Kenya is situated along the slopes of the Machakos dome, a strongly weathered paleozoic inselberg of (acidic) metamorphic rocks at an elevation ranging from 1083 to 2048 m.a.s.l., between latitude 1°24′ and longitude 37°63′ (Fig. 1). Mean annual rainfall ranges from 700 mm to over 1100 mm and mean annual temperature from 18.5 to 23.0 °C in, respectively, the high and low altitudes. These two areas are characterized by a bimodal rainfall distribution with a long rainy season occurring from March to May/June and a short one from September/October to December. In Tanzania, the target area was situated along the slopes of the Kilimanjaro volcano and Pangani river basin from 700 to 1800 m.a.s.l., between latitude 3°4′ and longitude 37°4′ (Fig. 1). Mean annual temperature ranges from 18 to 23.6 °C and mean annual rainfall between 1000 mm to 1300 mm in, respectively, the low and high altitudes. It experiences two distinct rainy seasons: a long season from March to May and a short one between October and December (Mwalusepo et al., 2015).

Field surveys were carried out in maize fields along these three-altitudinal gradients. Permission to visit and sample the fields was obtained from the owners of the maize plots. The field studies did not involve endangered or protected species.

For each altitude, 6 study sites for Taita Hills and mount Kilimanjaro, and 5 study sites for the Machakos Hills, where the farmers were used to cultivate annually maize, were selected (Mwalusepo et al., 2015). Each study site represented a specific altitude; and for each study site of each transect, 10 maize plots were surveyed (Fig. 1). GPS coordinates were taken from the middle of each plot. The average plot size was about 50 m × 100 m or 5000 $m^2$.

### 2.2. Determination of the Si concentration in soils

Soil samples were taken from each maize plot. Therefore for each altitude of each transect the number of replicate for soil analysis was 10. Prior to sampling, the upper 1–2 cm layer was removed to avoid contamination by Si from crop residues. Three to four sub-samples were randomly taken from each plot and pooled. Soil samples were collected at a depth of 0–25 cm and 25–50 cm using a soil auger. The soil sub-samples were bulked and homogenized according to sampling depth to obtain two samples per plot. Sampling was done in October 2012 in the Taita Hills and Mount Kilimanjaro transects, and in February 2013 in the Machakos Hills transect, during a period that coincided with either the off-season or beginning of the planting season, depending on the altitude. For all transects, the maize-cropping season began during the long rainy season in March-May at low altitudes whereas at high altitudes it began in or after August.

For each sample, the determination of soil Si was done by a private laboratory (Crop Nutrition—Laboratory Services, P.O. Box 66437-00800, Nairobi, Kenya www.cropnuts.com). Soil Si was extracted using the Mehlich 3 extraction method (Mehlich 1984) that uses diluted ammonium fluoride ($NH_4F$) and ammonium nitrate ($NH_4NO_3$) reagents. Silicon concentrations (in mg $g^{-1}$) were determined within 24 h of extraction by inductively coupled plasma atomic emission spectrometry (ICP-OES).

### 2.3. Determination of the Si concentration in maize leaves

Maize leaves were sampled from plants in the above plots. For each plot, seven borer-infested (less if the number of plants infested was low) and seven uninfested plants were sampled randomly across the entire plot. The third leaf from the apex (i.e. mature leaf) of each plant collected was used for Si analyses. The leaves from each plot were pooled, shredded and dried at 60 °C for 7 days constituting one replicate per type of sample (infested or not) and per plot. Thereafter, they were grounded to a fine, homogenous powder using a Bolmill Grinder (type MM40) prior to Si analyses. Since 10 plots of each study site of each transect were targeted, the number of replicate per study site was 10 for each type of sample.

In a preliminary experiment (see results under Supporting information), it was shown that mature leaves had the highest Si concentration irrespective of the developmental stage of the plant and it is thus a good indicator for the Si status of the entire plant (Tables S1 and S2). Due to differences in the maize cultivation seasons, sampling was carried out at all altitudes in June 2013 in the Machakos Hills, and several times (in November and December of 2012 and February, May and June of 2013) in the Taita Hills and Mount Kilimanjaro transects.

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 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.

### 2.4. Composition of maize stem borer species in the different transect sites

Field surveys for stem borer data were carried out in the maize plots along the three-altitudinal gradients for the same periods of the aforementioned plant sampling process according to the protocol of Mwalusepo et al. (2015). For each maize plot at each studied site of each transect, 12 infested plants were sampled every 5–6 weeks in each plot and dissected. All stem borers recovered were sorted according to their developmental stage and species name if possible, counted and placed individually in a glass vial containing artificial diets developed for *B. fusca* (Onyango and Ochieng'-Odero, 1994) or *C. partellus* (Ochieng et al., 1985) until pupa formation. Pupae were kept until adult emergence for confirmation of species identity. For each plot, the relative proportion of a species was expressed as the percentage of the total number of the two species collected from the 12 plants. The number of replicates ranged from 80 to 102.

### 2.5. Influence of altitude on Si absorption by maize plants

The purpose of this experiment was to determine the influence of altitude on Si absorption by maize plants. The experiment was carried out during mid-October to mid-November 2013 in the six

study sites of the Taita Hills transect. At each study site (or altitude), temperature was recorded hourly using automatic onset TMHOBO data loggers while rainfall was recorded daily using GENERAL$^R$ wireless rain gauges placed permanently in one plot per study site during this field experiment.

The maize hybrid 513 provided by Simlaw, Kenya Seeds Company, Nairobi, was used in all sites. Maize was planted in plastic pots (diameter 14 cm, height 15 cm) using the same type of soil from a field that had been in a long-term fallow previously. The soil originated from Mbengonyi situated in the mid-altitudes of the Taita Hills transect to minimize the logistics of transporting the soil to the low or high altitudinal study sites. The soil was well homogenised before being used. Potted plants were kept on one farm at each study site and watered when necessary by the farmer. In this experiment, the altitude (study site) was considered as a treatment. Two weeks after planting, each potted plant was treated with 10.0 g of calcium silicate from Sigma (Ref 742503), a material frequently used as a Si source, by mixing it into the top layers of the soil of each pot while some pots were left untreated to serve as controls. The number of treated and untreated pots was five (n = 5) and the positions of the pots randomized at each study site. The pots were kept in trays to prevent loss of silicate through leaching during watering or natural rainfall. During this experiment, the natural rainfall was similar between altitudes (see Table 1), with most days without any rainfall in all altitudes. Silicon concentrations in leaves were evaluated after two weeks following silica amendments using the aforementioned dilute hydrofluoric acid and the spectrometric molybdenum yellow method of Saito et al. (2005).

### 2.6. Larval development on potted plants treated with soluble Si

To evaluate the effect of increased Si concentrations in maize plants on growth of *C. partellus* and *B. fusca*, potted plants kept in a greenhouse at the *African Insect Science for Food and Health (icipe)*, Nairobi, Kenya, were treated with two dosage treatments, 10 and 20 g calcium silicate per pot two weeks after planting. Since for the Si-treated plants calcium was also present, the control plants were also amended with two dosage treatments of 10 and 20 g calcium carbonate. For each case, the material was mixed first into the top layers of the soil of each pot. The number of Si-treated and control pots for each dosage treatment was twenty (n = 20) and the positions of the pots randomized in the greenhouse. Two weeks later, for each stem borer species (*B. fusca* and *C. partellus*) the plants were individually infested with thirty neonates (i.e. freshly hatched larvae). For each stem borer species the number of infested plants was 10. For each potted plant, the percentage of live larvae remaining and relative growth rate (RGR) were assessed at 15 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 15 DAI divided by the number of days in between (Ojeda-Avila et al., 2003). For all plants, leaf Si was analysed at 15 DAI as above.

**Table 1**
Daily rainfall (mean ± SE[a], n = 61) and temperature registered at noon of each day (mean ± SE[a], n = 61) along the different altitudes of the Taita Hills during the pot experiment.

| Altitude (m) | Rainfall (mm) | Temperature (°C) |
|---|---|---|
| 818–871 | 1.8 ± 0.8a | 31.7 ± 0.2e |
| 1063–1102 | 0.6 ± 0.3a | 29.3 ± 0.3d |
| 1340–1358 | 4.4 ± 1.9a | 27.3 ± 0.3c |
| 1467–1490 | 1.1 ± 0.4a | 24.6 ± 0.3b |
| 1678–1709 | 4.9 ± 1.3a | 23.7 ± 0.4b |
| 1797–1814 | 6.8 ± 3.4a | 12.6 ± 0.1a |

[a]Means within a column followed by different letters are significantly different at 5% level (Tukey's contrasts test following ANOVA).

### 2.7. Data analyses

Silicon concentrations (in mg g$^{-1}$) were log-transformed whereas data on the relative proportion of a stemborer species (in%) were arcsin-transformed to fit a normal distribution as well as to fulfil the requirements of homoscedasticity of the variance. However, untransformed values are presented in the figures. Our measurements of temperature, rainfall, RGRs and proportion of surviving larvae (Tables 1 and 2) fulfilled the requirements for normality and homoscedasticity of the variance. Two-way analyses of variance (2-way ANOVAs) were used to assess the effect of different factors (depth and altitude in Fig. 2; plant sample [infested or not] and altitude in Fig. 3; stem borer species and altitude in Fig. 4; Si-treatment and altitude in Fig. 5) or interactions between factors. In case of significant F-values, treatment means were compared via post hoc Tukey's contrast tests. All statistics were done using R 2.15.3 (R Development Core Team, 2013).

## 3. Results

### 3.1. Silicon in soils

In all transects, soil Si concentrations at both depths decreased significantly with altitude (Fig. 2; results of 2-way ANOVA for altitude [A] factor: F = 28.2333, P < 0.0001 for Machakos Hill; F = 87.4644, P < 0.0001 for Taita Hills; F = 78.302, P < 0.0001 for Mount Kilimanjaro). Except for the Machakos Hills, where Si concentrations were significantly lower in the deeper than the upper soil layers (result of 2-way ANOVA for depth [B] factor: F = 4.5401, P = 0.03673), Si concentrations did not vary significantly between the two soil depths (results of 2-way ANOVA for depth [B] factor: F = 0.0067, P = 0.9351 for Taita Hills; F = 0.558, P = 0.4567 for Mount Kilimanjaro). There was no significant interaction between altitude and soil depth in all transect (results of 2-way ANOVA for A × B: F = 0.7215, P = 58021 for Machakos Hill; F = 0.6127, P = 0.6904 for Taita Hills; F = 0.341, P = 0.8870 for Mount Kilimanjaro).

### 3.2. Silicon in maize leaves

Silicon concentrations decreased significantly with altitude in both infested and uninfested plants (Fig. 3; results of 2-way ANOVA for altitude [A] factor: F = 7.4745, P < 0.0001 for Machakos Hill; F = 27.2954, P < 0.0001 for Taita Hill; F = 24.2989, P < 0.0001 for Mount Kilimanjaro). Leaves of infested plants exhibited lower Si concentrations than uninfested ones in most study sites (altitudes) of all transects (results of 2-way ANOVA for plant status [B] factor: F = 3.1607, P = 0.07959 for Machakos Hill; F = 13.4892, P = 0.0002607 for Taita Hill; F = 7.1538, P = 0.007801 for Mount Kilimanjaro). A significant interaction between altitude and infestation status was obtained only for Taita Hills (results of 2-way ANOVA for A × B: F = 0.3170, P = 0.86572 for Machakos Hill; F = 2.8381, P = 0.0152079 for Taita Hill; F = 0.1919, P = 0.965572 for Mount Kilimanjaro).

### 3.3. Influence of altitude on the composition of stem borer species

In all transects, there was a significant effect of the altitude on species proportions (Fig. 4; results of 2-way ANOVA for altitude [A] factor: F 6.0870, P = 0.0001913 for Machakos Hill; F = 6.3076, P < 0.0001 for Taita Hill; F = 14.3615, P < 0.0001 for Mount Kilimanjaro). The insect species factor (i.e. composition of insect

**Table 2**
Relative growth rates (RGR, mg $d^{-1}$, mean[a] ± SE) and percentage of live *Busseola fusca* and *Chilo partellus* larvae (mean[a] ± SE, n = 10) remaining after 15 days of infestation on control and Si-treated maize plants.

| | | *Busseola fusca* | | *Chilo partellus* | |
|---|---|---|---|---|---|
| | Si in plant leaves (mg $g^{-1}$) | % live larvae | RGR | % live larvae | RGR |
| Control plants | | | | | |
| 10 g of Ca | 0.540 ± 0.04a | 16.3 ± 2.1bc | 0.22 ± 0.03b | 52.2 ± 8.0b | 0.10 ± 0.001a |
| 20 g of Ca | 0.546 ± 0.03a | 18.0 ± 1.9c | 0.24 ± 0.05b | 48.9 ± 4.0b | 0.11 ± 0.003a |
| Si-treated plants | | | | | |
| 10 g of Si | 0.800 ± 0.05b | 10.7 ± 1.9ab | 0.09 ± 0.005a | 27.0 ± 3.4a | 0.10 ± 0.009a |
| 20 g of Si | 0.923 ± 0.04b | 6.7 ± 1.3a | 0.06 ± 0.01a | 25.6 ± 3.0a | 0.12 ± 0.02a |

[a] Means within a column followed by different letters are significantly different at 5% level (Tukey's contrasts test following ANOVA).

species) was not influencing significantly borer species compositions in the Machakos Hills and Mount Kilimanjaro (results of 2-way ANOVA for species [B] factor: F = 2.9951, P = 0.0864552 for Machakos Hill; F = 1.5600, P = 0.2135 for Mount Kilimanjaro) whereas a significant effect was obtained in the Taita Hill (results of 2-way ANOVA for species [B] factor: F = 20.1790, P < 0.0001). There was no significant interaction between altitude and insect species in the Taita Hills (results of 2-way ANOVA for A × B: F = 5.3594, P = 0.0005750 for Machakos Hill; F = 0.3771, P = 0.8644 for Taita Hill; F = 7.7523, P < 0.0001 for Mount Kilimanjaro). In all transects, the relative proportion of *C. partellus* in infested plants decreased whereas that of *B. fusca* increased with altitude.

### 3.4. Influence of Si treatment and altitude on Si absorption by maize plants in the Taita Hills

During the experiment rainfall did not vary significantly between altitudes whereas the temperatures decreased significantly with altitude (Table 1; results of ANOVA for rainfall: F = 1.965, P = 0.0832 for rainfall; F = 543, P < 0.0001 for temperature). In the pot experiment, leaf Si concentrations decreased significantly with altitude (Fig. 5; results of 2-way ANOVA for altitude [A] factor: F = 7.7014, P < 0.0001). The Si treatment had a significant influence on leaf Si concentration (results of 2-way ANOVA for Si treatment [B] factor: F = 14.5778, P = 0.0003855) but

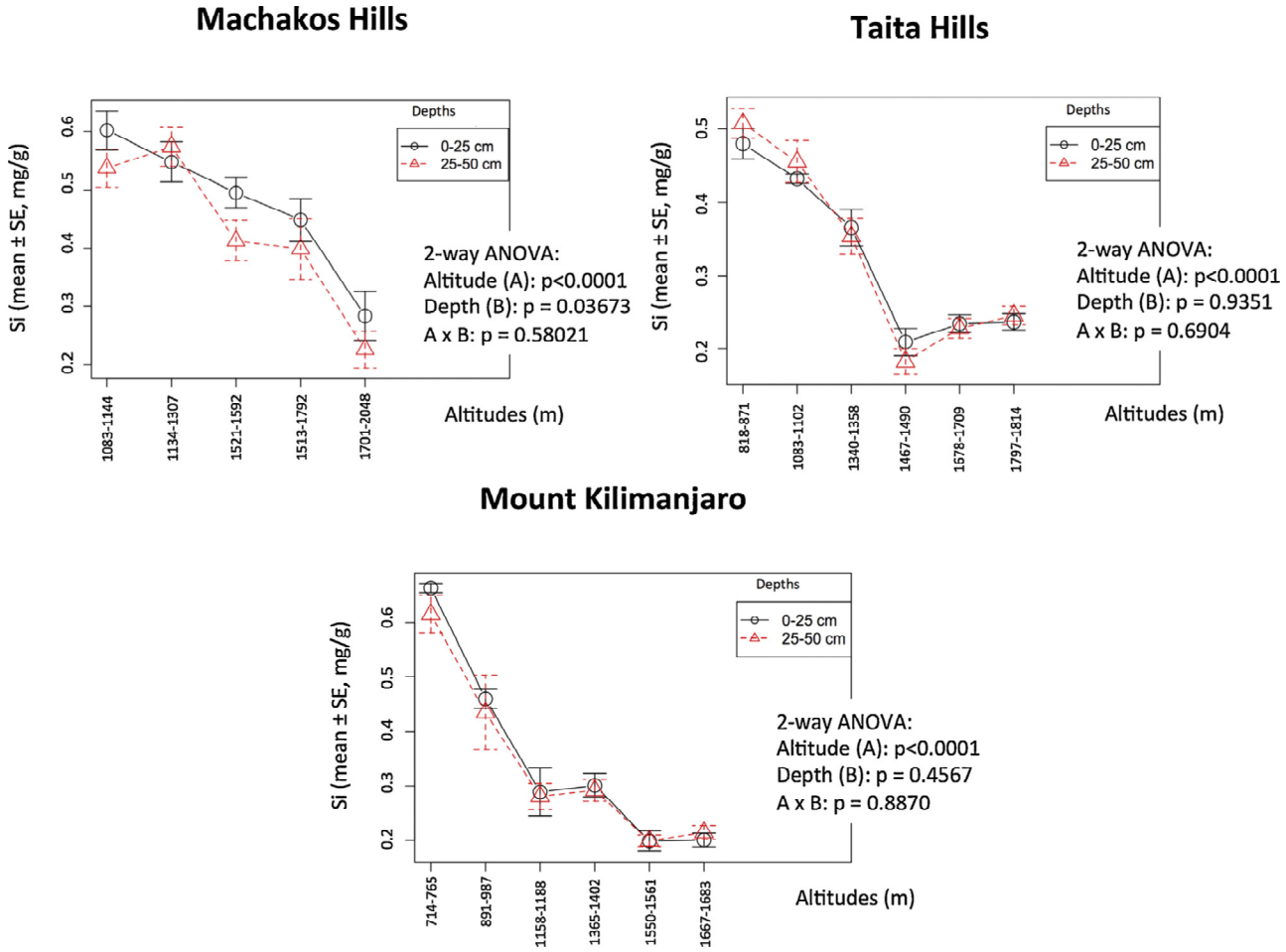



**Fig. 2.** Concentration of soil Si (in mg $g^{-1}$) according to depth and altitude in the three transects (Machakos Hills, Taita Hills and Mount Kilimanjaro) (mean ± SE, n = 10).

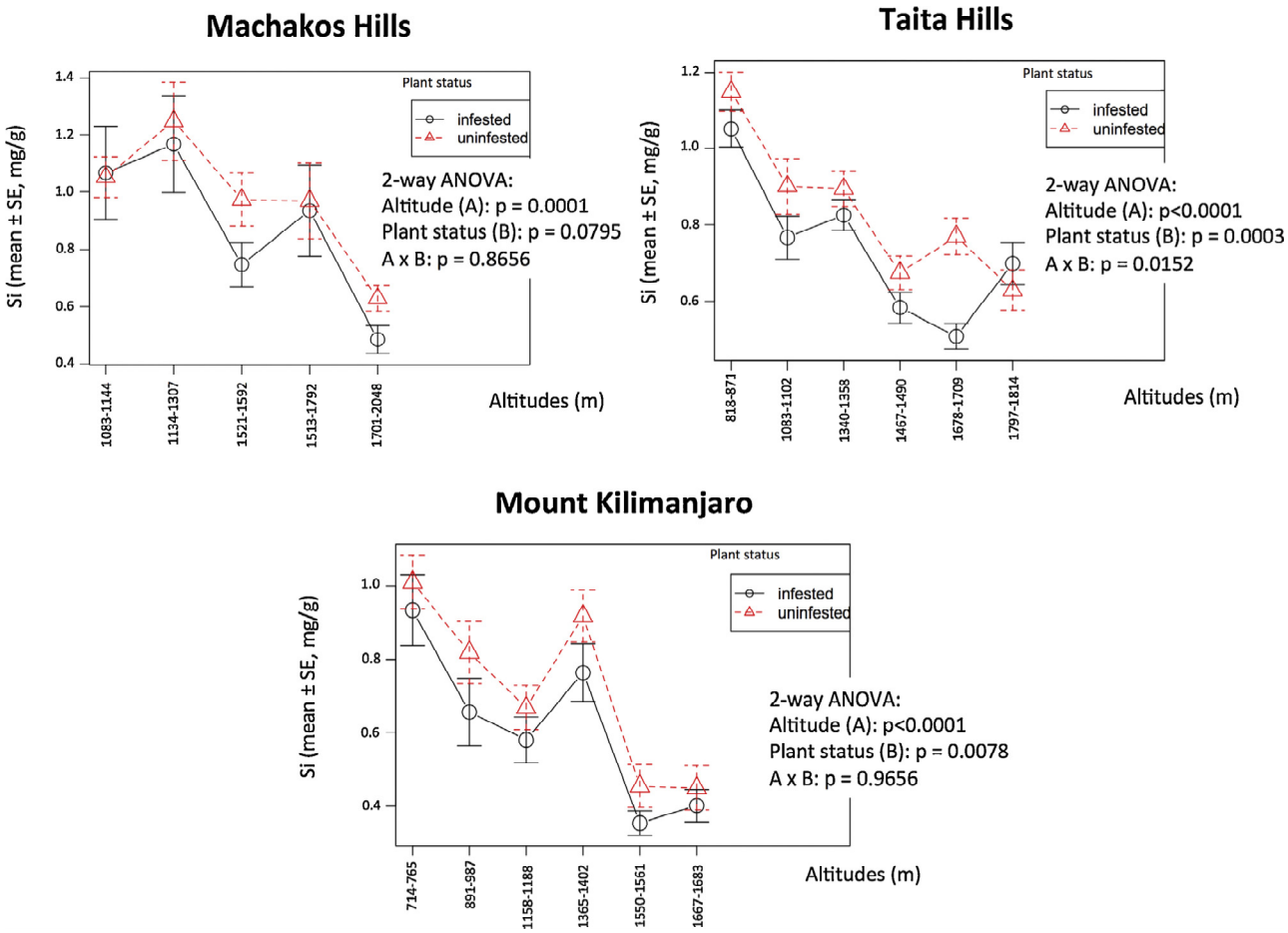



**Fig. 3.** Concentration of Si (in mg $g^{-1}$) in maize leaves of infested or non-infested plants according to altitude in the three transects (Machakos Hills, Taita Hills and Mount Kilimanjaro) (mean ± SE, n = 10).

only in the lower three and not in the upper three altitudes (ANOVA for the lower 3 altitudes F = 14.01, P = 0.000832; ANOVA for the upper 3 altitudes: F = 1.701, P = 0.203).

### 3.5. Larval development on potted plants treated with soluble Si

Soil Si-amendments to potted plants induced a significant increase in the concentration of Si in maize leaves (Table 2; result of ANOVA: F = 22.43, P < 0.0001). Concomitantly, the percentage of larvae recovered for each stem borer species decreased significantly (results of ANOVA: F = 9.491, P < 0.0001 for *B. fusca*; F = 8.514, P = 0.000682 for *C. partellus*). RGR of *B. fusca* also decreased significantly (result of ANOVA: F = 7.868, P = 0.000452) but not for *C. partellus* larvae (result of ANOVA: F = 0.264, P = 0.85), indicating that *C. partellus* was less susceptible to increasing Si in maize than *B. fusca*.

## 4. Discussion

The level of Si generally depends on the soil type (Alexandre et al., 1997). At Machakos and Taita Hills the soils mainly developed from Si rich basement parent material such as granites, while at mount Kilimanjaro the soils developed from volcanic materials, which tend to be relatively poor in Si. However, the Si for plant growth is generally not available from soil in more granitic areas where the soils are sandy. The sand in the sandy soils is mainly composed of quartz ($SiO_2$), which Si is not available for plant growth. In our study, the levels of Si in soils tended to be slightly higher only for Machakos Hills as compared to Taita Hills and Mount Kilimanjaro.

However, all transect showed the same trend, both Si in soils and in maize plants decreased with altitude. Silicon concentrations in plant tissues depend largely on plant-available Si in soils (Epstein, 1999; Savant et al., 1999; Guntzer et al., 2012). Silicon availability in soils is influenced by several factors, such as pH, soil texture, organic matter and soil weathering processes favourable to Si weathering and to the existing pool of plant biogenic Si (Alexandre et al., 1997). For example, acidic soils, typically found in the highest altitudes of all transects (see data on soil characteristics published by Njuguna et al. (2015)), are known to be highly weathered soils with low nutrient/element-holding capacity (Alexandre et al., 1997). In our study, high rainfall at higher altitudes probably induced significant mineral weathering processes and thus a significant loss of Si by leaching. In addition, organic carbon is involved in the synthesis of primary silicates resulting in the formation of silicic acid ($H_4SiO_4$), the main soluble component in soil solutions (see Alexandre et al. (1997) for review). In fact, higher plant biomass at high than low altitudes (Mwalusepo et al., 2015), can explain why soils in the high altitudes are rich in organic carbon compared to the lowest altitudes (see data on soil characteristics of these transects published by Njuguna et al. (2015)). We would therefore expect to get highest levels of soluble Si at the highest elevation. However, the results revealed the opposite. This can be explained by a strong leaching of soluble Si from the top to the bottom part of the hill as the result of high precipitation, low pH and low nutrient/element-holding capacity, superimposed on a probable poor turnover of Si by plants.

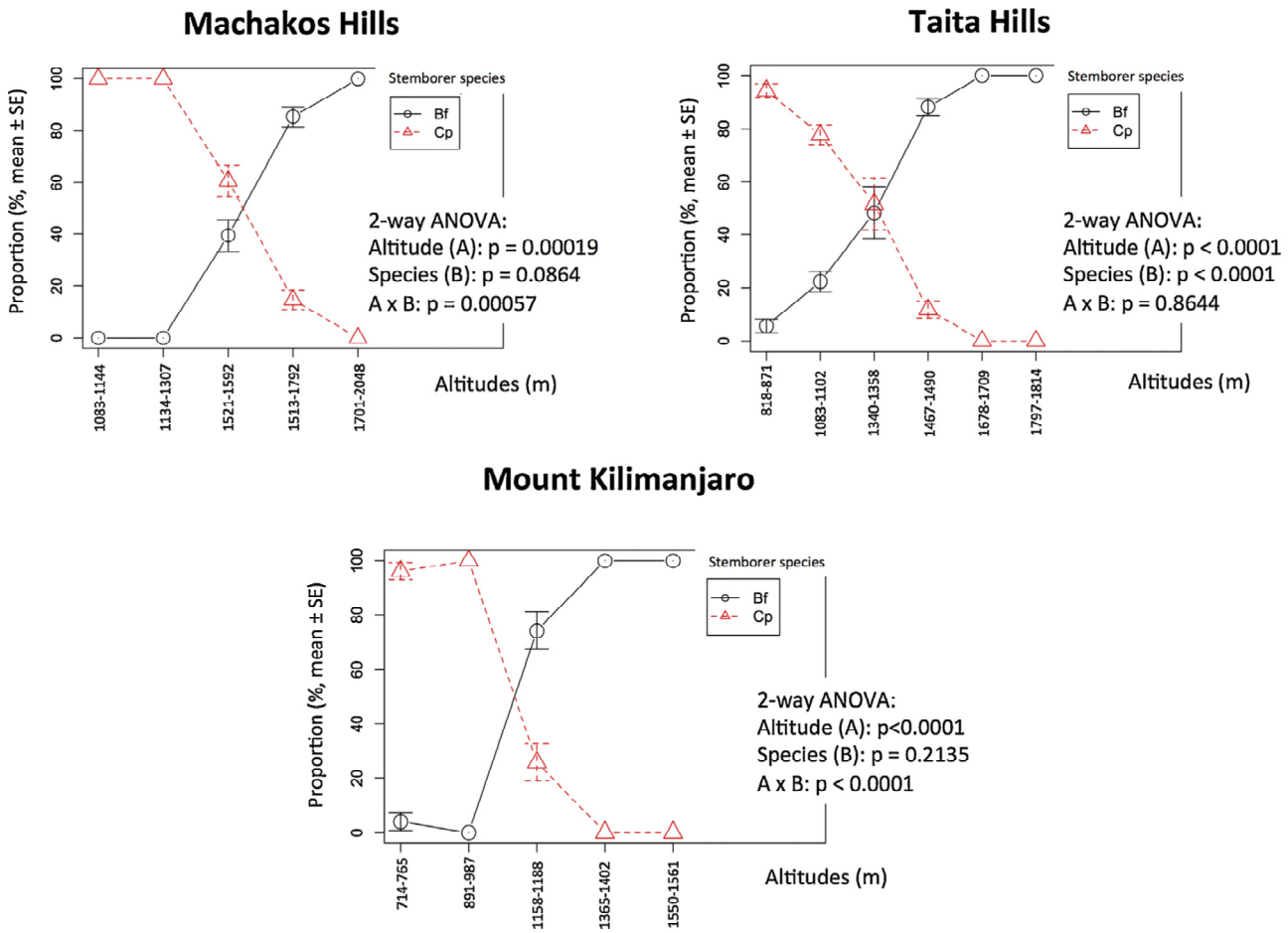



**Fig. 4.** Proportion (%) of *Busseola fusca* (Bf) and *Chilo partellus* (Cp) on infested plants along the altitudinal ranges of the three transects (Machakos Hills, Taita Hills and Mount Kilimanjaro) (mean ± SE, n ranged between 80 to 102).

However, soil Si alone does not explain the decrease of Si in maize leaves with altitude. In the pot experiment, where the same soil was used in all altitudes, Si amendments increased Si in leaves at the lower but not higher elevations. The same trend was observed in the control plants without Si amendments. This indicates that other environmental factors such as temperature, which decreased drastically with altitude (Table 1), thereby affecting soil Si absorption by the plants. In the field experiment, the temperature was significantly lower at high altitudes than low altitudes, while the rainfall pattern was similar between altitudes. Therefore most likely temperature was an important parameter responsible for the differences of Si absorption in potted plants between altitudes. As mentioned in the introduction, root-zone temperature has a pronounced effect on nutrient uptake from soil and their use by plants and hence on plant growth (Pregitzer and King, 2005; Hussain et al., 2010; Hussain and Maqsood, 2011). In addition, it also influences root physiology since the enzymes and cell membrane activities linked to nutrients and soil elements

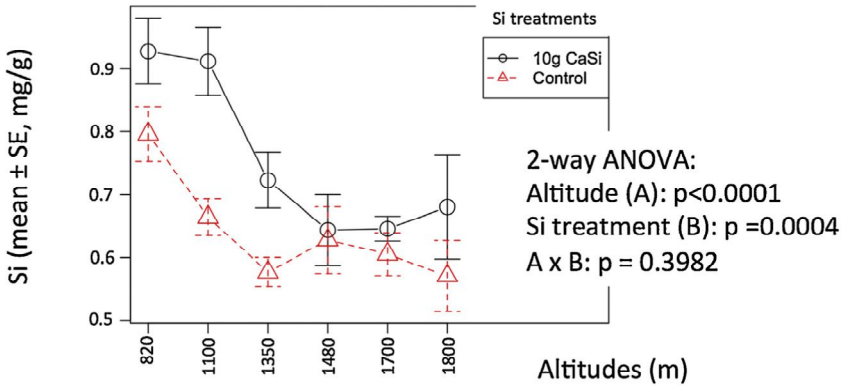



**Fig. 5.** Concentration of Si (in mg $g^{-1}$) in maize leaves according to treatment (control or addition of 10 g of CaSi per plant) in the Taita Hills transect (mean ± SE, n = 5).

uptake are directly related to soil temperatures (Taiz and Zeiger, 1991; Larcher, 1995). In addition, solubility of Si in soil increases with an increase in temperature (McKeague and Cline, 1963). Moreover, taking into account the possible passive Si uptake process in maize the warmer air at low altitude as compared to the high altitudes should trigger higher evapotranspiration and thus should facilitate Si uptake from the soil in maize plants. In conclusion, the environmental conditions in our study sites should favour Si absorption by maize at lower altitudes.

In addition, the present finding confirmed that an increase in maize Si significantly affects survival of both *B. fusca* and *C. partellus*. This was already showed for *B. fusca* by Juma et al. (2015). Moreover, this was corroborated by field observations that infested plants had generally lower Si concentrations than uninfested ones. However, whether this was the result of a higher attraction to ovipositing female moths of plants low in Si, higher survival of larvae, or reduced soil absorption of Si by infested plants cannot be determined with the experimental set-up used.

In all transects, *B. fusca* was the main species in the higher altitudes whereas *C. partellus* was predominant in the lowlands as also reported by Ong'amo et al. (2006). Temperature differences can partly explain the differences in the distribution of the two species. As shown by Khadioli et al. (2014a,b),*C. partellus* was more susceptible to low temperatures than *B. fusca*. In addition, the present findings showed that an increase in maize Si significantly affected development of *B. fusca* but not that of *C. partellus*, indicating that *C. partellus* is less sensitive to Si than *B. fusca*. Therefore besides temperature, Si appears to be an important driving factor determining the geographic distribution of *C. partellus* and *B. fusca*.

In conclusion, our results indicate that the projected rise in temperature due to climate change will enhance the maize plants' Si assimilation thereby significantly influencing the composition of lepidopteran stem borer pest species at higher altitudes of the East African highlands. As temperatures increase, *C. partellus* will likely spread to the higher altitudes where it will encounter maize plants low in Si, which will promote growth and expansion of populations of this pest. On the other hand, *B. fusca* will likely not benefit from the projected higher temperatures and may in South Africa (Kfir, 1997) partly be displaced by *C. partellus*. However, climate change may also affect carbon dioxide levels and precipitation patterns, which can also affect plant-insect interactions (e.g. Hamilton et al., 2005; Zavala et al., 2008; Cornelissen, 2011) and therefore may contribute to changes in stem borer species abundance and composition. In addition, Si has effects on plant defenses that go beyond simple changes in tissue toughness. For example, it modulates the accumulation of herbivore defensive allelochemicals in plant tissues including phytoalexins, lignin and phenolics (Chérif et al., 1994; Rodrigues et al., 2004; Rémus-Borel et al., 2005). Therefore, changes in Si levels may also interfere with stem borer development *via* changes in herbivore defensive allelochemicals in maize.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.03.040.

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