



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



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ABSTRACT

In East Africa, lepidopteran stem borers 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 Gershenson, 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

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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 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

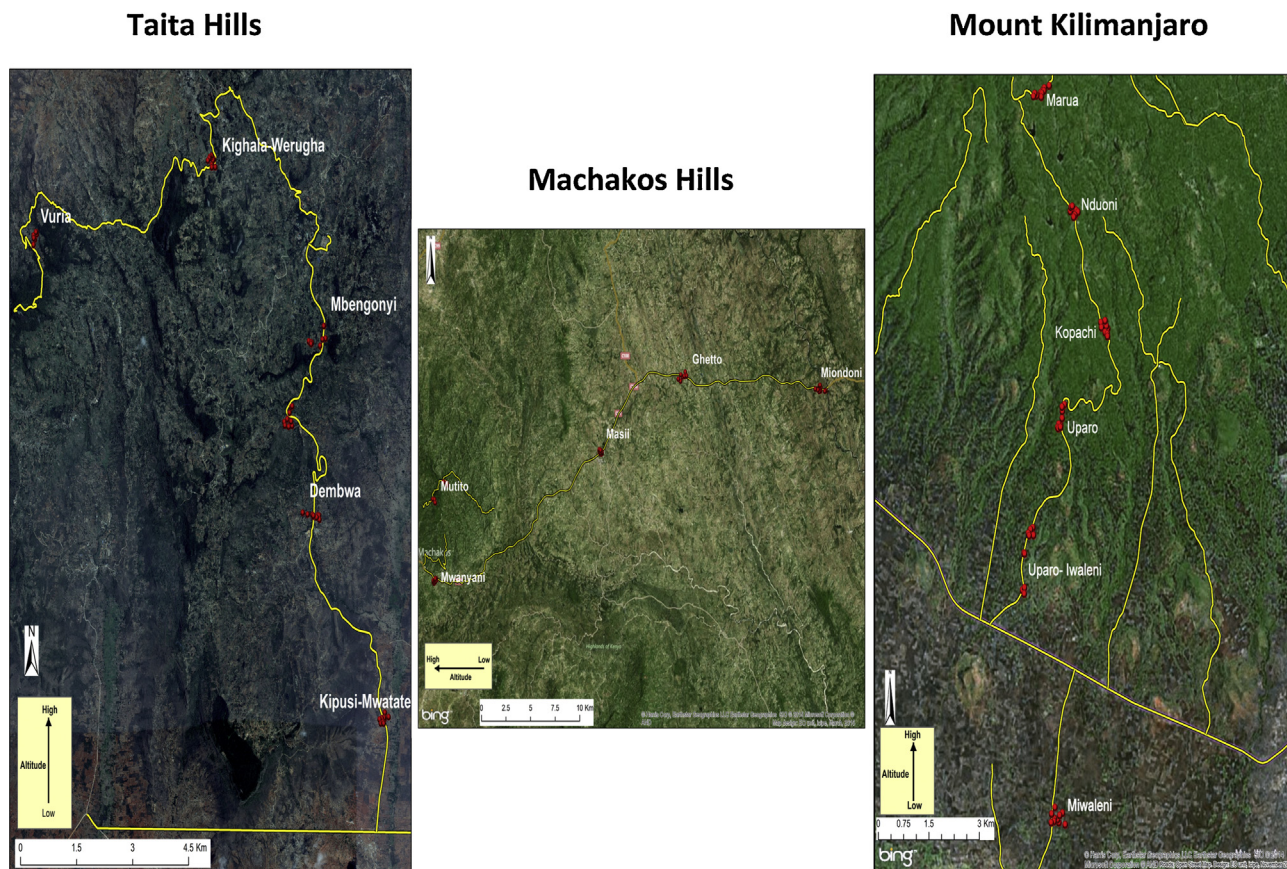


Fig. 1. The study areas: Taita Hills, Machakos Hills and Mount Kilimanjaro transects. The circles in red indicate the 10 maize plots selected at each locality.

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