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Fall armyworm in Africa: which 'race' is in the race, and why does it matter?

Fall armyworm (*Spodoptera frugiperda*) has already invaded almost half of Africa since its first observation in the continent in January 2016 (refs 1, 2). At its current rate of invasion, the pest may conquer Africa before the end of 2017. Although this polyphagous pest feeds on more than 80 plant species, it is considered to be a 'pest of grasses'[3], because of its overwhelming preference for Poaceae (or Gramineae). In Africa, maize is the primary host plant of fall armyworm. However, based on feeding preferences, two different races or strains of *S. frugiperda* – a maize strain and a rice strain – have been reported in its native range of the tropical Americas[4]. These two strains occur in Africa as well. For instance, fall armyworm in Nigeria was found to be the rice strain, whereas the population in Sao Tome and Principe was found to be the maize strain[2], despite the fact that both populations severely damaged the maize crop. Understanding the genetic and physiological differences or similarities between these strains is important for the use of pheromone-based monitoring, which has been suggested as a tool for fall armyworm surveillance programmes[1]. Such knowledge also would be useful for the selection of appropriate biocontrol agents and chemical pesticides.

Although *S. frugiperda* has spread to at least 21 countries in Africa[1], the strain that occurs in these countries is unknown, except for Nigeria, and Sao Tome and Principe. As no specific strains from East Africa have been reported, we obtained a *S. frugiperda* population from Arusha, Tanzania (lat. 3°22.646′S, long. 36°48.401′E and altitude 1232 m amsl) feeding on maize, and confirmed it as the rice strain based on a partial *cytochrome c oxidase I* (*coxI*) gene sequence at the World Vegetable Center headquarters in Taiwan. The *S. frugiperda* population in Tanzania GenBank accession numbers: MF278657 to MF278659) is genetically identical to the population in Nigeria. The phylogenetic analysis clearly differentiated the maize (Sao Tome and Principe population) and rice (Nigeria and Tanzania populations) strains into two distinct clades (Figure 1). Based on a pair-wise population comparison, the genetic distance (F_{ST}) between the rice and maize strains was 1 (maximum genetic diversity between the two populations), although the level of significance was found only at $P < 0.10$. However, the use of nuclear regions or genes for population comparison can shed additional light on how far these strains are genetically dissimilar, because the above results and an earlier study in Africa[2] are based on the maternally inherited mitochondrial *coxI* gene that is sometimes disputed in DNA barcoding.

The female moths of *S. frugiperda* were reported to produce Z9–14 : Ac and Z11–16 : Ac as the major pheromone compounds, as well as a number of other compounds such as Z9–12 : Ac and Z7–12 : Ac in low amounts[5–7]. However, two independent studies have shown that the pheromone composition of the two strains differed significantly[8,9]. Maize strain females originating from Florida, USA produced significantly more Z11–16 : Ac than rice strain females[8]. However, maize strain females collected from Louisiana, USA had a higher proportion of Z9–14 : Ac and lower proportions of Z7–12 : Ac and Z11–16 : Ac than their rice strain counterparts[9]. Thus, the same strain produces different proportions of pheromone components in different geographical locations. These variations could contribute to variations in male responses under field conditions. Sex pheromone lures containing three components (Z9–14 : Ac, Z11–16 : Ac and Z7–12 : Ac) attracted almost 60% of maize strain males[10]; hence this commercial lure was biased to attract maize strain males, leading to an underestimation of rice strain populations. A subsequent study that used two different four-component blends resembling the maize- and rice-strain female blend found that both strains showed geographic variations rather than strain-specific differences in their response to pheromone lures[11].

Are these strains reproductively isolated? This is partly answered by the fact that the two strains differ in the timing of their mating activity – the maize strain mates soon after the onset of scotophase, while the rice strain mates at the end of the scotophase[12,13]. Although some evidence is available for naturally occurring hybridization in the field[14], a recent study tracked the basis of allochronic differentiation in mating time, which acts as a premating isolation barrier between the strains of *S. frugiperda*[15]. The study identified a major quantitative trait chromosome underlying differentiation in circadian timing of mating activity and showed strain-specific polymorphisms as well as differential expression of the clock gene *vrille* between the strains. Thus, it

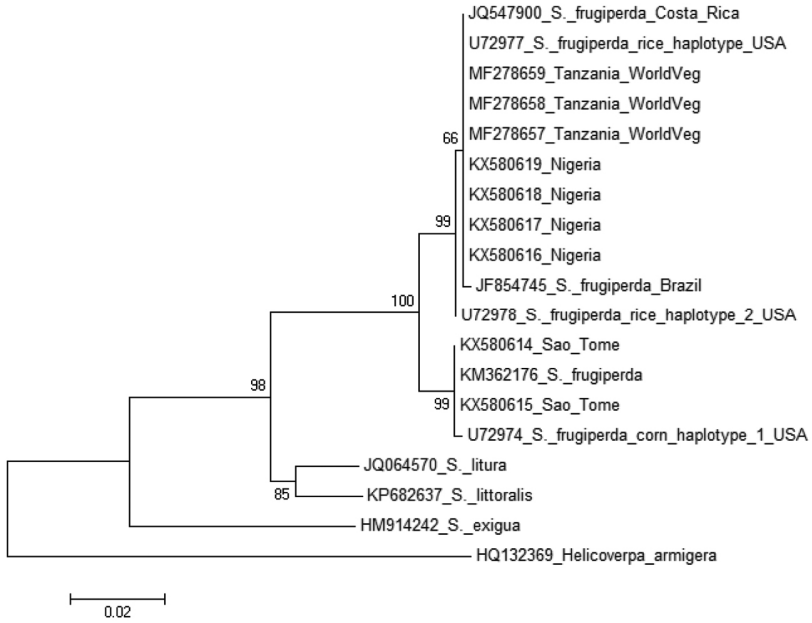

Figure 1. Phylogenetic relationship among *Spodoptera frugiperda* populations and other *Spodoptera* spp. based on a 588 bp mitochondrial *coxI* gene fragments using maximum likelihood analysis. *Helicoverpa armigera* was used as outgroup.

is possible that a premating isolation barrier exists between these sympatrically occurring strains.

Our result and those of Goergen *et al.*[2] confirm that *S. frugiperda* devastating maize in selected locations of Nigeria and Tanzania is the 'rice' strain. If the strains have been designated based on their feeding preferences[4], the most important question to be answered is – why/how has the 'rice' strain adapted to maize in these countries? What would be the pheromone composition of these 'rice' strains feeding on maize? The current studies in Africa used only a few populations. For more robust results, one should also look at whether *S. frugiperda* strains can co-occur in the same location or region using additional populations from distant sites. A third question to be answered is whether the 'rice' strain on maize and the 'maize' strain on maize will maintain reproductive isolation, or mate with each other when they are found in the same location. Pheromones can be used to predict an invasion, so that integrated pest management strategies can be deployed to curtail the further spread of *S. frugiperda.* However, if the commercial lure is biased towards maize strain males[10], can we effectively predict the fall armyworm population in Africa? Hence, for the most effective use of pheromones, it is necessary to confirm the exact identity of the strains, their pheromone composition, and the male fall armyworm moth responses to pheromone blends resembling the maize- and rice-strain females in major maize-producing locations of Africa where the pest is already present.

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