

REVIEW

A lag in the advancement of biotechnology: reliable control of maize stem borers in Africa

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Abstract

The future of food security in Africa is being severely threatened due to an exponential increase in population, which is almost three times the increase of food production. Maize production is constrained by stem borers which cause significant yield losses. Yield losses can be further compounded by higher temperatures due to climate changes, which are expected to increase the population of maize stem borers. While several methods have been employed in stem borer management, there is still significant damage caused by maize stem borers. This necessitates better control methods including the adoption of recent biotechnological advancement in RNA interference (RNAi) technology. This review highlights evidence of an increase in the stem borer population as well as the foreseen decline in maize production worldwide due to the effects of climatic changes. Furthermore, we have drawn attention to improved methods that have been used to control stem borers in maize production as well as a reluctant acceptance of traditional biotechnology in Africa. Finally, we suggest the application of alternative RNA interference techniques to breed maize for efficient pest control in order to achieve food security, improve nutrition and promote sustainable maize production.

Key words: climatic changes, food security, Integrated Pest Management, maize, stem borer, RNAi technology

Introduction

Maize is an important staple food for Africans and is widely used in livestock feed formulation. There are nearly 800 million people who suffer from hunger worldwide and the vast majority is present in developing countries. Maize is an essential crop towards achieving the second goal (Zero Hunger) of sustainable development goals to transform the planet. At present, the average maize yield in Africa is about $1.5 \text{ t} \cdot \text{ha}^{-1}$, which is significantly lower than the global average yield of $4.9 \text{ t} \cdot \text{ha}^{-1}$. Africa's average maize production is approximately 7.2% of the total world production even though there has been an increase in area under cultivation. The low production rate is further caused by changes in the climate, consequently contributing to the poor quality and aggravating maize insecurity

in Africa. Food security risk is increasing due to such factors as: increased demand, higher input costs, the degradation of soil nutrients and greater competition for land and water from non-food uses. Both abiotic and biotic factors restrain maize yields. Temperature is an important abiotic factor and a major determinant to crop growth and development, affecting planting date, length of growing season, and yield. Additionally, climatic changes affect seasonality of precipitation (Liebmann *et al.* 2012; Wang and Alo 2015; Omoyo *et al.* 2015) and seasonality of rainfall (Owiti and Zhu 2012; Dunning *et al.* 2016) which further poses a great threat to total maize output because farmers depend mainly on rainfall in sub-Saharan Africa. The changing climate has an effect on insect populations especially the

Lepidopteran pests of maize. Five economically important species in Africa are: i) the spotted stem borer which corresponds to *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae); ii) the African stem borer which corresponds to *Busseola fusca* Fuller (Lepidoptera: Noctuidae); iii) coastal stem borer which corresponds to *Chilo orichalcocillielus* Strand (Lepidoptera: Crambidae); iv) pink stem borer which corresponds to *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae); v) sugarcane stem borer, which refers to *Eldana saccharina* Walker (Lepidoptera: Pyralidae) (Bonhof 1997; Polaszek 1998).

Predicted effects of climate changes on maize yield

The Intergovernmental Panel on Climate Change (IPCC) predicts an increase in temperature between 0.3 and 0.7°C over the next two decades and an increase of 0.3–4.8°C by the end of the 21st century as a result of greenhouse gas (GHG) emissions. Global warming factors, such as, an increase in temperature, changes in precipitation patterns and integrity, and increased atmospheric water vapor, have a cumulative effect on crop yields. Various models have predicted a significant decrease in maize yield as a result of expected climatic changes. In the USA which produces more than 53% of the world's maize (Fig. 1) (FAOSTAT 2017), the aggregate maize yields are projected to decrease by an average of 18% by 2030–2050 (Urban *et al.* 2012). A 10–20% decline in maize yield has been suggested even if it received sufficient water (Xu *et al.* 2016). Similar climatic effects on maize yields have been reported in other maize growing regions around the world. Zhang *et al.* (2015) predict a 13% yield reduction by 2021–2050 and a 3–12% yield

decline was projected in China by 2100 (Blanc 2012). However, Africa is envisaged to be the most vulnerable to climatic changes (Cairns *et al.* 2013; Chen *et al.* 2016). Several predictions have indicated that maize yield would be adversely influenced by climate warming in Africa (Schlenker and Lobell 2010; Muller *et al.* 2011; Knox *et al.* 2012; Estes *et al.* 2013; Araya *et al.* 2015; Sultan and Gaetani 2016). An overall reduction of about 10% in maize yields, which is equivalent to losses of \$2 billion per year, has been predicted by 2055 (Jones and Thornton 2003). Historical trials show a nonlinear relationship between warming and maize yields in Africa (Lobell *et al.* 2011). Food insecurity in sub-Saharan Africa by 2050 may worsen due to the negative impact of climatic changes on maize consumption and a reduction in daily calorie intake (Kindie *et al.* 2015).

Effects of climatic changes on stem borer growth and population

Insects are the most diverse species and adaptable form of life since they outnumber any other animal category. Provision of food for people is greatly challenged by the competition from insect pests. Herbivorous insects are believed to be accountable for one-fifth of the world's total crop production damage. Insects are ectotherms. Their body temperature varies with the environmental temperature which therefore has an impact on insects, specifically the lepidopteran (Harrington *et al.* 2001; Kocsis and Hufnagel 2011). Changes in climatic conditions have influenced the abundance, range of distribution and phenology of lepidopterans (Woiwod 1997). Changes in temperature can modify the length of the life cycle (development rate), voltinism, density and population size, the genetic structure of the population, the extent of host plant exploitation, colonization of new areas and geographical distribution of lepidoptera in many ways (Bale *et al.* 2002). The effects of different levels of relative humidity and temperature regimes on the development and fecundity of *Chilo partellus* revealed that developmental time is reduced with an increase in temperature. The mean duration of *C. partellus* life cycle was 70.2 days at 22°C and 80% relative humidity (RH), whereas it took 26.5 days to complete its life cycle at 30°C and 40% RH (Tamiru *et al.* 2012). Also, Khadioli *et al.* (2014) reported that the development time of different stages of stem borers decreased with increased temperature, ranging from 18 to 35°C. Studies conducted in East Africa on the impact of temperature changes on the distribution and abundance of *C. partellus*, *Busseola fusca* and their larva parasitoids indicated a worsening

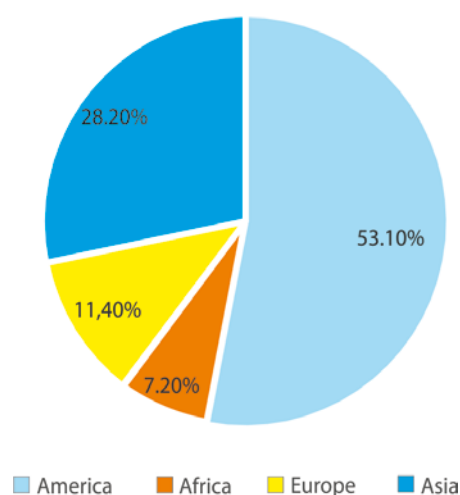


Fig. 1. Average maize production according to region (1994–2014)

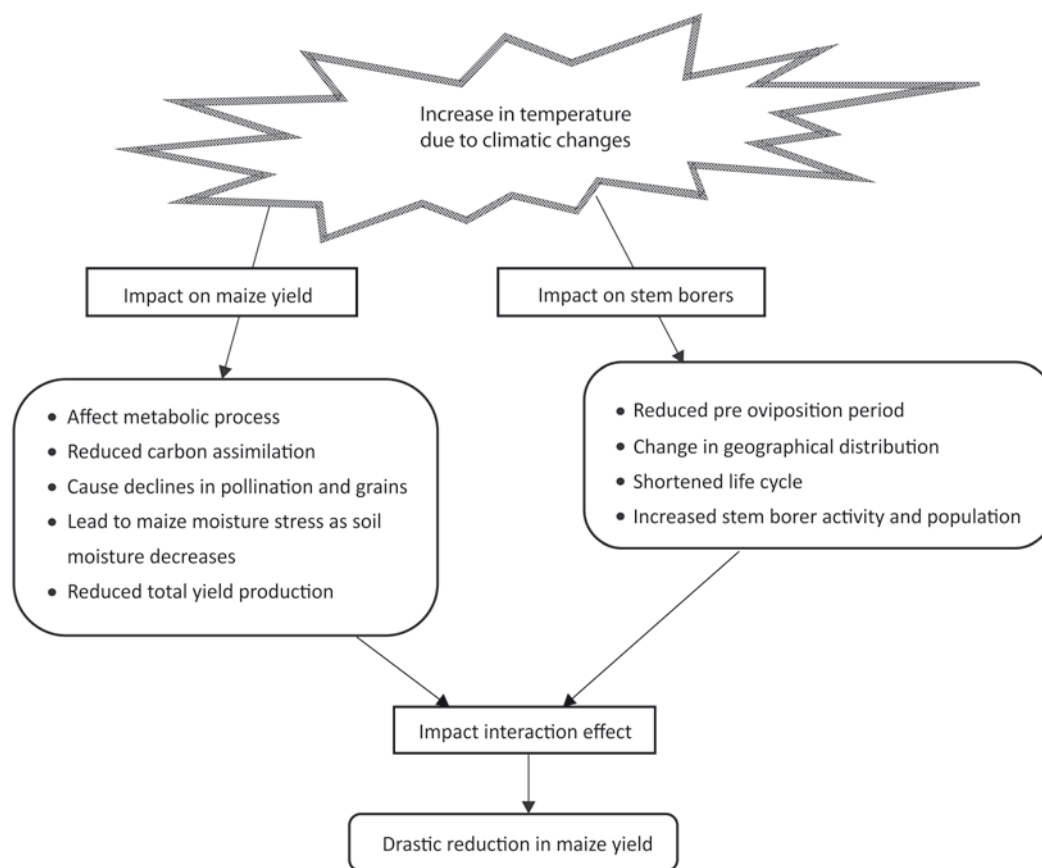


Fig. 2. Illustration on how the interaction between the impact of climate changes on maize and stem borers could result in maize insecurity in Africa

of stem borer impact on maize production. Temperature changes resulted in the expansion of lowland species, increased the number of pest generations and disrupted the geographical distribution of pests and their parasitoids (Mwalusepo *et al.* 2015). Temperature also affected survival and growth rates of the stem borers. For instance, high temperatures favored greater larval survival and faster relative growth rates in *C. partellus* (Ntiri *et al.* 2016). The interaction between climatic impact on maize and stem borer growth can constitute a great limiting factor towards securing maize production (Fig. 2) especially in developing countries.

Dominant stem borers in Africa

Chilo partellus (Swinhoe) and *B. fusca* (Fuller) are the two, major herbivorous maize pests in Africa. Although *C. partellus* originated in Asia it is now prominent in the maize-growing regions of Africa. Nyukuri *et al.* (2014) conducted phytogeography studies and found that *B. fusca* was the most prevalent species in the highlands while *C. partellus* was the most abundant species in the lowlands of Africa. However, *C. partellus* has been reported to widen its distribution from low to high elevations (Emana *et al.* 2001).

The distribution and extent of damage in maize varied between elevations (Dejen *et al.* 2014). Various studies have predicted that *C. partellus* in Africa will likely expand towards higher altitudes, highland tropics and moist transitional regions due to global climate changes (Khadioli *et al.* 2014). Evidence of these changes was given by the first report of *C. partellus* in Israel (Ben-Yakir *et al.* 2013) and in Turkey (Bayram and Tonga 2016). Several reviews have highlighted the biology, distribution, genetics and progress of *B. fusca* (Sezonlin *et al.* 2006; Calatayud *et al.* 2014; Hauptfleisch *et al.* 2014). *Chilo partellus* is an invasive pest because it is currently reported in areas where it was not found before and is rapidly displacing other indigenous stem borers. This occurs because *C. partellus* can terminate diapauses and colonize host plants at an early stage of plant growth and emerge a month before *B. fusca*. Additionally, it has a week shorter life cycle than *B. fusca* (Kfir 1997). These changes can be further compounded by climate warming thus putting Africa at more risk of potential stem borer attack. Recently, armyworm outbreaks which ravage crops, especially maize, have been reported in several countries in Africa. There is an urgent need for the adoption of new and advanced strategies to combat maize yield losses from stem borer damage and to ensure sustainable maize production in Africa.

Stem borer damage on maize

Significant yield losses in maize incurred by stem borers have been reported in various maize producing regions in Africa and the stem borer population was correlated with damages and grain yield losses (Kakule *et al.* 1997). It was speculated that *B. fusca* tends to avoid plants previously infested by *C. partellus* (Kfir *et al.* 2002). However, both species are generally found on the same plant (van den Berg *et al.* 1991) and hence compound the damages. Damages include: reduction in plant stands, decreased photosynthetic capacity, interference of water and nutrient uptake, tassel and stem breakage, ear damage and the loss of a plant's aesthetic value because of damage to the ears (Bosque-Perez and Mareck 1991) (Fig. 3). About 20–40% of potential yield losses have been reported in maize because of stem borers in sub-Saharan Africa (Seshu and Walker 1990). However, stem borers can cause up to 80% loss if not controlled. Songa *et al.* (2001) indicated that tunnel damage length greater than 20 cm caused 40% reduction of potential yield. Yield losses from 7 to 23% were reported in the evaluation of some maize genotypes against stem borers for inclusion in intergraded pest management (Ajala *et al.* 2010). Similarly, about 12.9% yield loss was estimated under natural infestation and incidence of infestation in the major agro-ecological zone in Kenya (DeGroot *et al.* 2002). Okweche *et al.* (2013) indicated that yield loss due to stem borer damage to the early maize crop was 14.0% and there was a higher percentage at later stages of growth. The yield loss varied with region, maize genotype used and the method of extrapolation of percentage loss. All these losses due to stem borers indicated that they are a limiting factor affecting maize productivity in Africa which can be aggravated by the effects of climatic changes.

Current strategies adopted in Africa to overcome maize stem borers

Several cultural practices that have been used to control the severity of stem borers damage include: appropriate residue disposal, planting date manipulation, destruction of volunteer and alternative host plants. The time of planting has a significant effect on levels of infestation and yield loss caused by maize stem borers (Ebenebe *et al.* 1999; Ullah *et al.* 2010). Hence, manipulation of the sowing date ensures that the most susceptible stage in maize growth does not coincide with peak stem borer activity. Similarly, soil tillage practices can significantly reduce insect populations through mechanical damage that includes burying them so deeply that they cannot emerge or by bringing them to the surface where they may be killed by weather factors, birds or other natural enemies. Tillage at off season will destroy volunteer plants, stubble, and weeds that may provide food and breeding sites for stem borers. Oberemok *et al.* (2015) reviewed an evolutionary trend of insect control measures where people capitalized on the negative effects of natural compounds on various insects, with the application of botanicals (Okrikata and Anaso 2008), chemical insecticides and DNA insecticides.

Growing alternative hosts as refugia

Alternative grass species grown as border rows around maize plots have been employed in the management of stem borer densities. Studies have shown that stem borers are more attracted to and lay eggs heavily on some grasses. Forage grasses like *Pennisetum purpureum* (Moench) and *Sorghum sudanensis* (Stapf) grown as



Fig. 3. Different infested parts of the maize plant being damaged by stem borers

border rows significantly reduced attacks by *C. partellus* and *B. fusca*, thus leading to increased maize yields (Khan *et al.* 1997). Evaluation of the effects of common grass species planted as border rows around maize crops on the abundance of pests indicated that elephant grass *P. purpureum* significantly lowered infestations of *B. fusca*, *S. calamistis* and *E. saccharina*. This ultimately led to increased maize yields (Ndemah *et al.* 2002). The misconception that alternative host plants could serve as reservoirs for stem borer pests in Africa during the non-cropping period was due to misidentification of the stem borer species (Le Ru *et al.* 2006). Survey studies conducted to understand the role of wild host plants in the abundance of lepidopteran illustrated that the number of larvae of these species was low in the wild compared to cultivated fields (Ong'amo *et al.* 2006; Otieno *et al.* 2008). A high larval survival rate and production of a sufficient number of high-quality moths are distinct characteristics that differentiate a refugia plant from a wild host plant (van den Berg 2017)

Push-pull strategy

This is an advanced novel approach where alternative grasses are planted to control stem borers. It employs behavioral manipulation of insect pests and their natural enemies through the integration of stimuli. The stimuli make the protected resource unattractive or

unsuitable to the pests (push) while luring them toward an attractive source (pull) from where the pests are subsequently removed. It is a habitat management strategy where natural resources such as wild hosts and non-host plants of stem borers are used against stem borers (Pickett *et al.* 2014; Charles *et al.* 2015). For instance, when maize is intercropped with repellent plants (such as *Desmodium*) and Napier grasses are planted as attractive trap plants along the border, gravid stem borer females are repelled or deterred away from the target crop (push) by stimuli. Simultaneously they are attracted (pull) to the trap crop, leaving the target crop protected (Fig. 4). Volatile chemicals from trap plants were identified as the key physiologically active compounds responsible for the attractiveness of the trap crop to the gravid moths (Khan *et al.* 2000). The push plants produce repellent semiochemicals against the pest while the pull plants produce attractant semiochemicals. The semiochemicals involved in this mechanism, such as hexanal, (E)-2-hexenal, (Z)-3-hexen-1-ol, and (Z)-3-hexen-1-ylacetate, (E)-ocimene, -cedrene, are released in significantly higher amounts in both Napier grass and *Desmodium* than in maize. Therefore maize intercropped with *Melinis minutiflora*, *D. uncinatum* showed a dramatic reduction in stem borer infestation (Khan *et al.* 2000). Preliminary results based on push-pull technology in Kenya indicated a 29% drop in stem borer incidence as compared to control. A good understanding of the

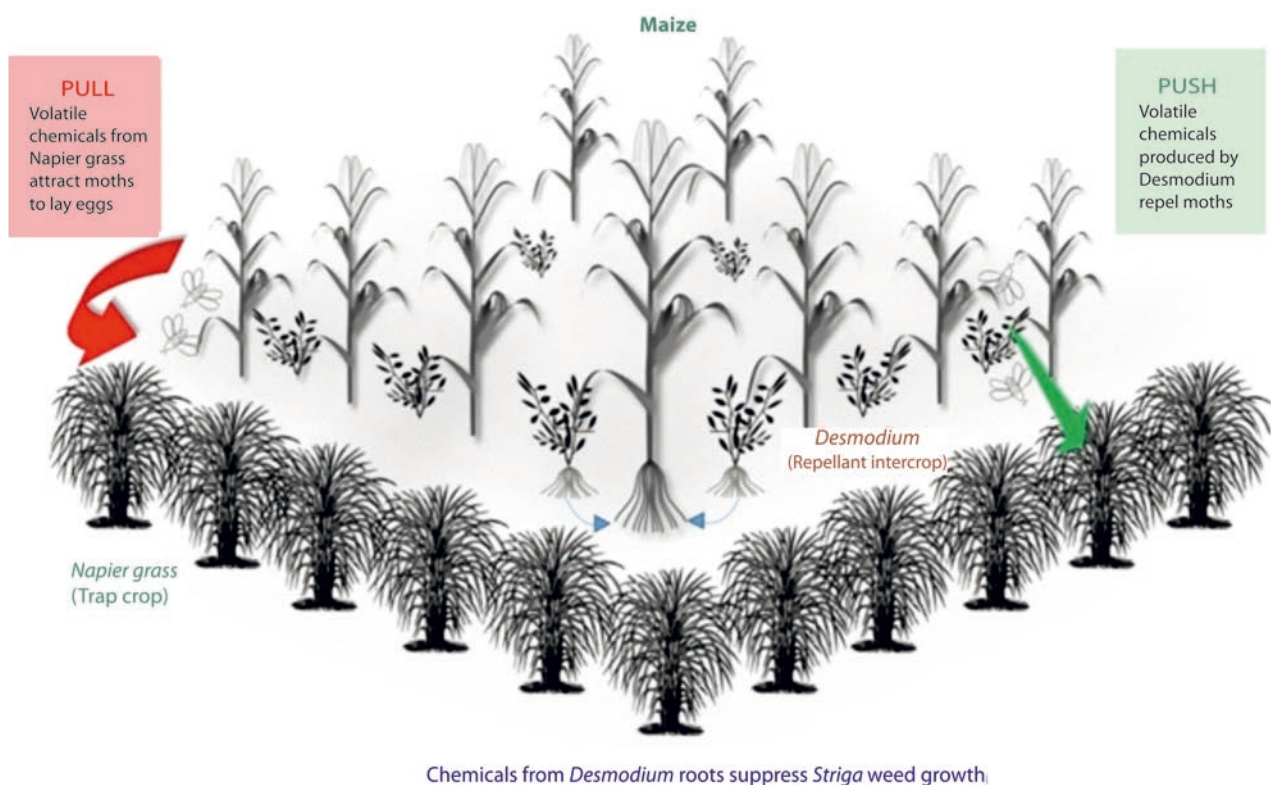


Fig. 4. Stem borer females are repelled away from the target crop (push) by *Desmodium* stimuli while they are simultaneously attracted (pull) to the trap crop (Napier grass), leaving the target maize crop protected

behavioral and chemical ecology of the host-pest interactions is essential for the optimization of this strategy for efficient stem borer management.

Pheromone trap

A pheromone is a chemical messenger which is secreted by a member of an animal species and which elicits a definite behavioral response in other members of the same species. Different sex pheromones that have been employed in lepidopteran mass trapping include: (Z)-11-tetradecane-1-yl acetate (Z11-14: Ac), (E)-11-tetradecen-1-yl acetate (E11-14: Ac), and (Z)-9-tetradecen-1-yl acetate (Z9-14: Ac) and (Z)-11-hexadecen-1-yl acetate. Pheromone trap performance can be affected by several factors: pheromone source, age, and mating status of the female and male, trap attractive range, trap design, height, inter-trap distance, and position. It has been successfully applied in stem borer management for population monitoring, mass trapping, and mating disruption. In mating disruption, the area under treatment is permeated with synthetic sex pheromone so that male moths cannot detect the relatively small amount of pheromone produced by female moths and are attracted to a lethal source (El-Sayed *et al.* 2006) or non-lethal source (Howse 2004). In general, this chemical communication is specific and does not attract other beneficial insects thus preventing mating and subsequent larval infestation (Cork *et al.* 1996; Alfaro *et al.* 2009). There have been improvements in the technology to enhance the efficiency of mass trapping (Félix *et al.* 2009). Pheromone monitoring traps to manage adult stem borer will reduce the release of insecticides into the environment.

Control by parasitoids

Another biological control method to overcome stem borer intensity in Africa is the use of natural enemies. The rate of parasitism varies with the interaction between temperature, rainfall, and altitude that directly influence the presence or absence of parasitoids (Mailafiya *et al.* 2010). Climatic changes are predicted to bring variability in the abundance and distribution of stem borer pests and their natural enemies. Studies have shown that temperature can worsen the impact of stem borers on maize production by increasing the number of pest generations and disrupting the geographical distribution of pests and their larval parasitoids (Mwalusepo *et al.* 2015). It has been reported that the level of parasitism can be enhanced when combined with silicon fertilizer which facilitates soil amendment hence, creating more robust biological control (Nikpay 2016). Several parasitoids have been identified and their impact assessed in various parts of the agro-ecological zone in Africa (Bonhof *et al.* 1997; Zhou

et al. 2003; Moolman *et al.* 2013). Table 1 illustrates the common parasitoids in Africa including various kinds of egg, larval and pupal parasitoids and predators that have been reported for maize and other crops.

Tamiru *et al.* (2011) showed that egg deposition by stem borer moths (*C. partellus*) on maize landrace varieties caused emission of herbivore-induced plant volatiles (HIPVS) that attract both egg parasitoids (*Trichogramma bournieri*) as well as larva parasitoids (*Cotesia sesamiae*). *Procerochasmias nigromaculatus* and *C. sesamiae* have the highest pupa and larva parasitism, respectively, among the 18 parasitoids recorded from *B. fusca* on maize and grain sorghum (Kfir 1995). Mailafiya *et al.* (2011) demonstrated that *C. sesamiae* and *C. flavipes* were the key parasitoids in maize cultivated habitats. Cugala *et al.* (2006) reported that *C. sesamiae*, *C. flavipes* Cameron and *Dentichasmias busseolae* were abundant parasitoids of *C. partellus* (Swinhoe) while *C. sesamiae*, *Sturmiopsis parasitica* and *Procerochasmias nigromaculatus* were abundant parasitoids of *B. fusca* (Lepidoptera: Noctuidae). Conclusively, biological control intervention has contributed to aggregate monetary surplus and underscore the need for increased investment in biological control research to sustain cereal production and improve poor living conditions in Africa (Midingoyi *et al.* 2016).

Chemical control

The usage of chemicals has been the most popular and oldest method to control stem borers. Organophosphates and carbamate chemicals e.g. carbofuran, disulfoton, diazimon and fenthion, ripcord, and tamaron (Mir Khan 2000; Zahid *et al.* 2012) which have acute effects on the parasympathetic, sympathetic, and central nervous systems are greatly used to control maize stem borers among farmers in Africa. Chemicals have been effective in the control of stem borers, but they have not been very efficient because major damage occurs inside the maize stem at the larval stage. Furthermore, due to the extensive use of chemicals by farmers, excess toxic compounds are released which pollute the soil, water and the air. The toxins released in the environment can cause serious health risks like cancer, diseases of the nervous system and reproductive problems in people who are exposed to the pesticides through home and garden exposure. Frequent use of pesticides can result in very frequent evolution of stem borer resistance and abundant field loss of its natural enemies. Pesticides also have proved to be harmful for beneficial insect species, soil microorganisms, and worms which naturally limit the pest populations and maintain soil health (Ubuoh *et al.* 2012). Furthermore, some of the chemicals that are banned in developed countries due to their toxicity are still prevalent among farmers in

Table 1. Common stem borer parasitoids in maize growing habitats in Africa

Parasitoids	Common host species	References
Egg parasitoids	<i>Telenomus isis</i> , <i>Telenomus busseola</i>	<i>Busseola fusca</i> Yaovi <i>et al.</i> 2009
	<i>Trichogramma bournieri</i>	<i>Sesamia calamistis</i> Schulthess <i>et al.</i> 1997 Schulthess <i>et al.</i> 2001
	<i>Trichogrammatoidea bactrae</i>	<i>Chilo partellus</i> Kfir 1990
Larva parasitoids	<i>Cotesia sesamiae</i> <i>Syzeuctus</i> sp. <i>Apanteles sesamiae</i>	<i>Sesamia calamistis</i> Schulthess <i>et al.</i> 1997
	<i>Cotesia sesamiae</i>	<i>Busseola fusca</i> Ndemah <i>et al.</i> 2007
	<i>Sturmiopsis parasitica</i>	<i>Eldana saccharina</i> <i>Busseola fusca</i> <i>Sesamia calamistis</i> Chinwada <i>et al.</i> 2001 Chinwada <i>et al.</i> 2014
	<i>Sturmiopsis parasitica</i>	<i>Sesamia calamistis</i> Ndemah <i>et al.</i> 2002
	<i>Cotesia flavipes</i>	<i>Chilo partellus</i> Zhou <i>et al.</i> 2001 Omwega <i>et al.</i> 2006
	<i>Sturmiopsis parasitica</i>	<i>Sesamia calamistis</i> <i>Eldana saccharina</i> Gounou <i>et al.</i> 2009
Pupa parasitoids	<i>Pediobius furvus</i>	<i>Busseola fusca</i> <i>Sesamia cretica</i> El-Wakeil <i>et al.</i> 2008
	<i>Dentichasmias busseolae</i> <i>Psilochalcis soudanensis</i>	<i>Chilo partellus</i> Songa <i>et al.</i> 2002
	<i>Xanthopimpla stemmator</i>	<i>Busseola fusca</i> <i>Chilo partellus</i> <i>Eldana saccharina</i> Fischer <i>et al.</i> 2004

Africa. Alternative control measures are pertinent to save the local farmer in Africa and other developing countries from exposure to toxic compounds and avoid accumulation of toxic residues in the plants. The development of stem borer resistant maize was anticipated to increase maize yield efficiency by reducing yield losses from stem borer damage and reducing or eliminating the cost of insecticides and other inputs (Mugo *et al.* 2001).

Breeding for stem borer resistant maize varieties

The conventional breeding approach is the major technique employed to breed stem borer resistant maize in Africa. There is a drastic need to optimize maize yield in Africa due to rapid population growth and negative influences of climatic changes. The usage of

biotechnology techniques should be encouraged to facilitate the availability of stem borer resistant maize seed to smallholder farmers in sub-Saharan Africa and improve food security.

Conventional breeding approach

Conventional methods of developing resistant varieties involve the identification and use of resistant germplasm in a breeding program. Germplasm evaluation in the context of genetic resources refers to the description of the material in a collection. It covers the whole range of activities starting with obtaining new samples by the germplasm curator, growing these for seed increase, characterization, preliminary evaluation, and for further or detailed evaluation and documentation. Germplasm enhancement breeding techniques have been carried out to identify potentially useful exotic sources of maize germplasm to develop segregated families with high yield potential

and resistance to stem borers (Ajala *et al.* 2010; John *et al.* 2016). These can be incorporated into commercial and public maize breeding programs by recurrent selection of favorable alleles for stem borer resistance (Rensburg and Klopper 2004) through introgression of one or a few genes into a current elite cultivar via backcrossing. Knowledge about the gene action involved in the inheritance of the stem borer resistant gene and exploitation of heterosis and heterotic patterns in hybrids has been employed to identify potential sources of multiple resistance to stem borers of interest and to generate genetically broad-based reciprocal populations (Derera *et al.* 2016). Likewise, the combining ability has been used in maize to detect good combiners for stem borer resistance because genetic diversity must be balanced by elite performance. Choosing the best parents is a key to maximizing the probability for successful improvement. The combining ability and heterotic orientation of new maize inbred lines under *B. fusca* (Mwimali *et al.* 2016) and *C. partellus* (Mwimali *et al.* 2015) infestation were identified for the development of stem borer resistant maize. Karaya *et al.* (2009) investigated both general and specific combining abilities for insect resistance in maize to produce hybrids or open-pollinated varieties (OPVs) which are resistant to *C. partellus* and *B. fusca* stem borers. Furthermore, knowledge about the best combiner for stem borer resistance and application of molecular markers was further used for fast screening purposes. Molecular markers are currently used in genome scans to select those individuals that contain the greatest proportion of favorable alleles from the recurrent parent genome. Marker-assisted recurrent selection (MARS) significantly associated with target stem borer resistance in maize is used to predict the breeding value, followed by rapid recombination and selfing (Willcox *et al.* 2002; Mwololo *et al.* 2015). Marker technology has made it possible to group germplasm into a larger number of sub-groups

possessing tropical genes. Furthermore, quantitative trait loci (QTL) in marker-assisted selection (MAS) are being employed to select for improved stem borer resistance in elite lines (Samayoa *et al.* 2017). Several national and international research institutes in the past have worked extensively with basic conventional techniques that involved germplasm screening and hybridization for subsequent improvement. They developed stem borer resistant (MBR) maize populations by compositing global maize germplasm reputed to be “resistant” to a number of stem borer species (Smith *et al.* 1989; Mihm 1997). These developments have led to the development of various borer resistant maize populations, such as the BR (borer-resistant) population of IITA developed by screening for *S. calamistis* under natural infestations and the Kenya Agricultural Research Institute (Table 2). These processes can take a decade before the objectives are achieved and undesirable alleles can be introduced. Recently the African Agricultural Technology Foundation (AATF) initiated a public/private sector partnership project (Insect Resistant Maize for Africa; IRMA) to promote technological intervention for the control of insect pests that constrain maize productivity in Africa through the development and deployment of maize that offers resistance to destructive insects. The main goal is to identify conventional and novel sources of stem borer resistance and incorporate them into maize varieties that are well adapted to various agro-ecological zones and well-accepted by farmers and consumers. Biotechnology techniques are needed to complement the progress made in the development of improved varieties that are resistant to stem borers considering the food insecurity of the expected increased population. The amalgamation of advances in biotechnology, genomic research, and molecular marker applications with conventional plant breeding towards breeding borer resistant maize will maximize maize security in Africa and other developing countries.

Table 2. A list of high yielding maize varieties with additional characteristics of resistance towards maize stem borers currently being cultivated in Africa

Maize variety	National code	Institute	Year of release	Characteristics
KEMBU 214	KEMBU 214	KARI	2008	tolerant
KDH4 SBR	KDH4 SBR	KARI	2008	resistant
KDH6 SBR	KDH6 SBR	KARI	2008	resistant
BR9943DMRSR	NGZM-09-67	IITA, Ibadan	2009	highly resistant
Ama TZBR-W	NGZM-09-69	IITA, Ibadan	2009	highly resistant
TZBR Eld C5	NGZM-09-70	IITA, Ibadan	2009	highly resistant
BR9928 DMRSR	NGZM-09-68	IITA, Ibadan	2009	highly resistant
EMB 0702	KH523-1 LGB	KARI-EMBU	2011	resistant
KATEH2007	KH414-4 SBR	KARI-KATUMANI	2011	resistant
MTPEH 0703	KH125-06 SBR	KARI-Mtwapa	2012	resistant

Biotechnological approaches to developing borer-resistant maize

Despite the potential damage that can arise from stem borer populations that is favored by climatic change, little attention has been given to the use of advanced biotechnology techniques to breed for stem borer resistant maize. Breeding for stem borer resistant maize depends greatly on the availability of genetic variability which can be achieved by the application of biotechnology techniques.

Bt protein

The only biotechnology advancement that brings about the control of stem borers is the use of *Bacillus thuringiensis* (Bt) protein. *Bacillus thuringiensis* are gram-positive spore-forming bacteria that have been greatly used for lepidoptera control due to their entomopathogenic properties. At sporulation, Bt produces predominantly parasporal crystal inclusion [crystal (Cry) and cytolytic (Cyt) toxins] referred to as δ -endotoxins or insecticidal crystal proteins. Furthermore, it produces vegetative insecticidal proteins (Vips) during its vegetative growth stages. Osmotic lysis by pore formation (Bravo *et al.* 2004) and signaling cascade that promotes cell death (Zhang *et al.* 2006) are the major explanations for the mode of action of Bt. Briefly, the insect midgut proteases convert protoxins to activate toxins that are incorporated into an insect midgut receptor resulting in pores in the apical microvilli membrane of the cells that cause severe septicemia and insect death (Bravo *et al.* 2002; de Maagd *et al.* 2003). The toxin is activated by proteolytic removal of an N-terminal peptide and amino acid at the carboxyl terminus (Gill *et al.* 1992; Adang *et al.* 2014). The significant development in various Bt proteins; Cry1Ab, Cry1Ac, Cry1Ah, Cry1Ab/2Aj and Cry1Ah/cry1Ie (Wang *et al.* 2012; Yang *et al.* 2012; Lv *et al.* 2013; Wang *et al.* 2014; Wu 2014) have resulted to gradual increase in the world cultivation of Bt maize. However, the toxic effect of Bt protein on insects continues to attract bio-safety critics on the ethical implications for plants, humans and the environment. Government policy in Africa and most developing countries does not promote these biotechnology techniques which are viable means of food security, because large percentages of maize production are directly consumed by people.

There are concerns about human health and the non-target effects of transgenic crops containing transgenes from *B. thuringiensis* (Losley *et al.* 1999). Although it has been demonstrated that Bt protein has no adverse effects on human guts due to the absence of receptors for the endotoxins (Betz *et al.* 2000), the potential risks of Bt protein on human health are still being focused on (antibiotic resistance, allergenicity, nutritional changes and the formation of toxins).

Furthermore, several scientific reports do not report a significant negative impact of Bt-maize on non-target and environmental integrity.

Evaluation by comparing a homogeneous maize field with a conventional and a transgenic maize field indicated that Bt protein does not affect insect biodiversity (Resende *et al.* 2016). Likewise, the impact of Bt maize pollens on monarch butterfly populations has been reported to be negligible (Sears *et al.* 2001). Furthermore, the Bt toxins released from root exudates as well as the biomass of Bt maize have no apparent effects on earthworms, nematodes, protozoa, bacteria, and fungi in soil. Several reports documented that Bt maize is harmless to humans, animals, and a wide array of non-target pests (Saxena and Stotzky 2000; Saxena 2001; Saxena 2002) while several others describe potential effects of Bt proteins on non-target insect populations including beneficial insects (Gatehouse *et al.* 2011). But fear of the unknown, lack of adequate biotechnology know-how and poor awareness sets back the adoption of biotechnology in most African countries.

Despite the increase in the cultivation of Bt maize especially in developed countries, most African nations remain resistant to its acceptance due to widespread negative public opinion. Most Africans are very religious and they believe it is improper to re-modify what the almighty God has created. The media has also compounded the fear of GMO (Bt maize) in the minds of the populace by portraying the genetically modified plant as a poison that could lead to adverse health. Also, government policies in Africa and most developing countries do not promote these biotech techniques which are viable means of food security, because a major proportion of maize production is directly consumed by people. Although farmers are well aware of the likely benefits of planting Bt maize, their fear is how to get returns for their investment because consumers may not buy it due to the misrepresentation of such a product. Apart from all the factors that have a negative influence on the adoption of Bt maize, extra costs may be incurred from refugia maintenance. Commercial cultivation of Bt maize requires refugia (20% refuge of conventional maize, which may be sprayed with insecticides, or a 5% refuge area that may not be sprayed) to optimize the effectiveness of Bt maize. The importance of refugia is to delay development of resistance by producing pest individuals that survive on that particular crop and high-dose/refuge strategy limits the development of insect resistance (Renner 1999; Gould 2000). Additionally, there are reports of field-evolved resistance of *B. fusca* (Fuller) to Cry1Ab in Bt maize (Van Rensburg 2007) and *Helicoverpa zea* resistance to Cry1Ac and Cry2Ab in Bt cotton (Luttrell *et al.* 1999; Ali 2006). The hypothesis of recessive inheritance accounts for most of the success of Bt crops

as a means of sustainable control of pest populations. Studies on the mechanisms involved in the resistance to Bt crops and the inheritance of field-evolved resistance have demonstrated that there is a semi-dominant and dominant inheritance (Nair *et al.* 2010; Campagne *et al.* 2013). However, the understanding of the genetic basis of Cry1F resistance in Asian maize stem borers suggests that pyramiding of Bt protein could be used as a strategy to delay the development of Asian maize borer resistance to Bt proteins (Wang *et al.* 2016). The challenges and the limitations of Bt protein in efficient management of stem borers necessitate alternative methods that would be environmentally friendly, species-specific and attractive to agricultural policy makers in Africa. RNA interference (RNAi) gene silencing technology can be integrated into pest management and can be employed in developing stem borer resistant maize especially in Africa where Bt maize faces adoption challenges.

RNAi approaches as a reliable means of developing stem borer resistant maize for Africa

RNAi technology is growing quickly and its potential has not been fully employed in agrobiotechnology, especially as an alternative for insect control. RNA interference (RNAi) is a conserved and integral aspect of diverse regulatory processes, including regulation of gene expression at the transcriptional and translational levels, protection against viral infection, control of epigenetic modifications, regulation of genome stability, curbing of transposon movement and regulation of heterochromatin formation (Ding 2010). The effectiveness of RNAi to control crop pests depends on the identification of suitable genes leading to aberration in pest growth and metabolism (Yang *et al.* 2011). However, there are still challenges in identification of crucial genes which play a significant function in the life cycles of specific insects (Kola *et al.* 2015). RNAi employs dsRNA-mediated gene silencing which was reported to be conserved in many eukaryotes (Dzitoyeva 2001; Fire 2007; Tomoyasu 2008). Exogenous double-stranded RNA (dsRNA) introduced into the cells of diverse eukaryotic organisms induced speedy and sustained degradation of mRNAs containing sequences complementary to the dsRNA (Mello and Conte 2004). The RNase III enzyme called Dicer, initiates the RNAi pathways and processes dsRNAs into short (21–25 nucleotides), small interfering RNAs (siRNAs) (Elbashir *et al.* 2001). The siRNAs are further incorporated into a protein complex known as the RNA-induced silencing complex (RISC), the RISC and Argonaute cleave the specific mRNA (Hammond *et al.* 2001) that is complementary to one of the strands of the siRNA hence resulting in failure of protein expression (Dykxhoorn *et al.* 2003; Meister and Tuschl 2004; Chen *et al.* 2010;

Liu *et al.* 2010; Zhu *et al.* 2012). Several attempts have been made for dsRNA knockdown in various insects as well as a different method of delivery for efficient uptake of dsRNA in insects (Dykxhoorn *et al.* 2003; Meister and Tuschl 2004; Wang *et al.* 2011; Mao and Zeng 2012). Cell-autonomous and non-cell autonomous are major RNAi responses. Systemic RNAi (non-cell autonomous response) is triggered when a silencing signal spreads to the neighboring cells from the epicenter of the cell (Whangbo and Hunter 2008). Insects exhibit various sensitivities to systemic RNAi and suppression of gene expression is assumed to depend on species, genes and as well as targeted tissues. The midgut of most insects is lined by the peritrophic membrane (PM), or the peri-microvillar membrane (PMM) and it is the only portion of an insect's body that has an active interface with the physical environment. Since insect midgut cells absorb nutrients from the gut lumen, it takes up dsRNA and serves as the path through which RNAi effects would be achieved in insects (Newmark 2003). Therefore, plants fortified with specific dsRNA would prevent insect damage since the dsRNAs target certain genes in insect tissues and result in their mortality (Mao *et al.* 2007). This approach could be effective against stem borers in Africa because significant damage occurs during the larval stage, so the continual uptake of dsRNA transgenic maize could be effective in controlling maize stem borers. Several studies have shown that significant reduction in transcript levels of target vital genes in a specific insect resulted in mortality (Hui *et al.* 2011; Li *et al.* 2015; Malik *et al.* 2016; Kola *et al.* 2016; Vélez *et al.* 2016; Galdeano *et al.* 2017; Lin *et al.* 2017). Recently, SMARTSTAX PRO, jointly developed by Monsanto and Dow AgroSciences and is based on RNAi technology, was reviewed and approved by the three US regulatory agencies (the EPA, FDA and USDA) (EPA 2017), as being safe for human consumption and not harmful to the environment. This transgenic maize contains the expression of the cassette based on the formation of a double-stranded RNA (dsRNA) transcript containing a 240 bp fragment of the Western Corn Rootworm *Snf7* gene (DvSnf7) that confers resistance to corn rootworm by suppressing levels of DvSnf7 mRNA in WCR after root feeding (Bolognesi *et al.* 2012). This breakthrough supported the suggestion that RNAi technology could be a reliable method for developing stem borer resistant maize in Africa if adopted by government policy.

Successful expression of dsRNAs via the chloroplast genome opens the door to study RNA interference/processing within plastids (Shuangxia *et al.* 2015) which confer another advantage over the Bt technology. Long dsRNA has been reported to be stably produced in chloroplast genome rather than the nuclear genome (Zhang *et al.* 2015); mRNA levels of the dsRNAs

targeted against the β -actin gene of the colorado potato beetle were greatly reduced when colorado potato beetles were fed transplastomic potatoes. Hence chloroplast could be a better target because its cellular compartment appears to lack RNAi machinery (Bally *et al.* 2016) that might degrade dsRNA in transgenic plants. Furthermore, awareness of the dsRNA transformed in the chloroplast would lessen the negativity attached to biotechnology and bring about quick adoption by government policy. The schematic diagram (Fig. 5) below illustrates how RNAi technology could be easily adopted in Africa to circumvent the safety challenges associated with Bt maize. Promoting the use of RNAi against stem borers in Africa towards transplastomic maize would eradicate all the fears attributed to modified crops since maize ear contains little or no chloroplast. This technology does not synthesize any foreign or toxic protein in the plant (Dubelman *et al.* 2014). Studies show that dsRNA is unlikely to persist or accumulate in the environment because of its rapid degradation.

Conclusions

Several techniques have been incorporated into Integrated Pest Management (IPM) for food security, in the world and Africa. Classical breeding techniques, as well as cultural practices, have been used to develop maize stem borer resistant varieties and to reduce the population of maize stem borers. Nevertheless, this approach is wearisome and time-consuming. The common approach of stem borer control in Africa and other developing countries is the use of chemical pesticides which have negative health and environmental effects. Since they have been abused in Africa their use is discouraged. Transgene maize fortified with Bt toxins provides toxicity against maize stem borers. However, there is evidence of stem borer resistance to Bt toxins as well as toxicity against some beneficial insects. These effects call for alternative approaches that would easily permeate the agricultural policy in Africa to encourage biotechnology to develop stem borer

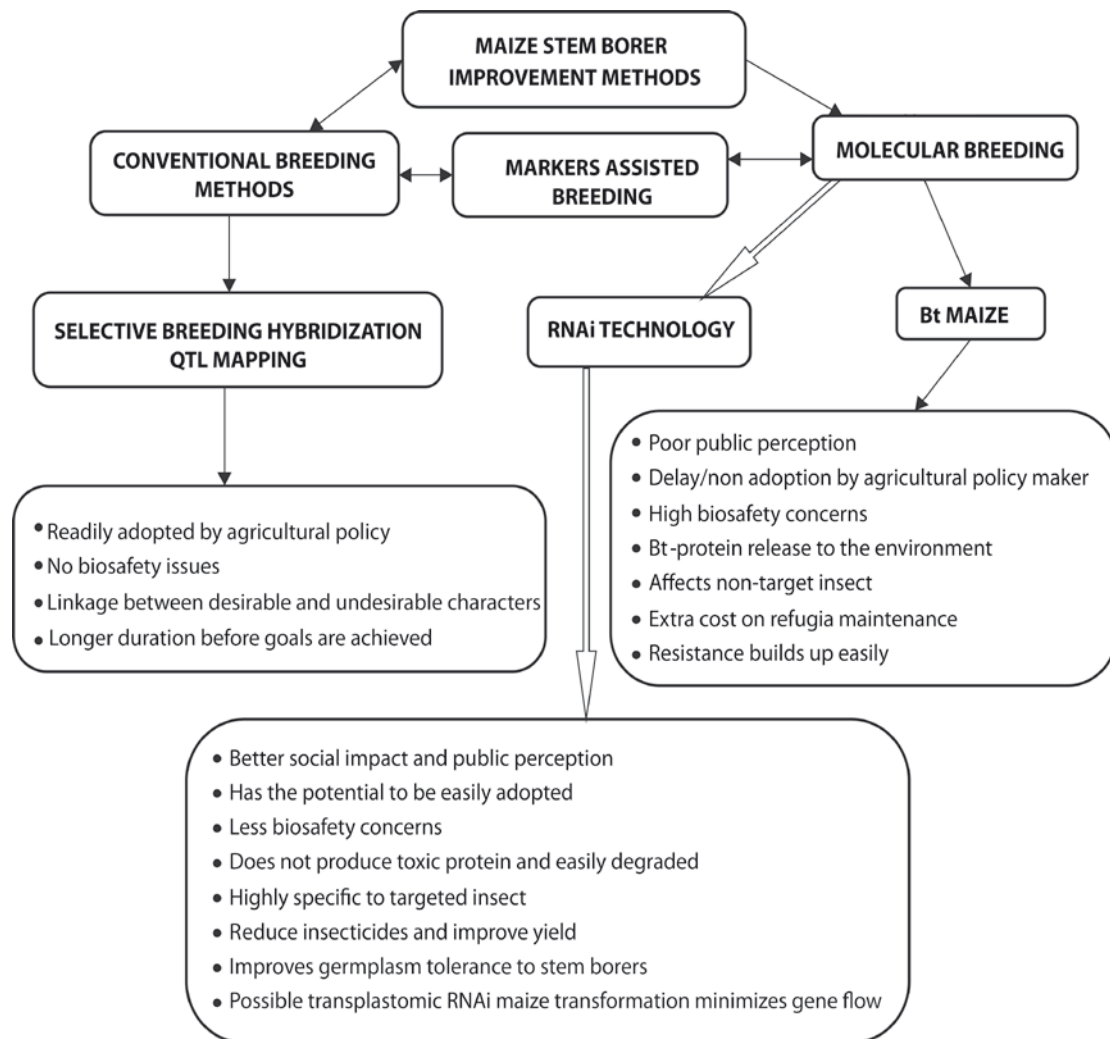


Fig. 5. The potential merit of RNAi over Bt-corn as an alternative if adopted in Africa for breeding stem borer resistant maize

resistant maize. RNAi-technology is an eco-friendly biotech approach for crop improvement by silencing specific crucial genes in insects. A recent report shows that plastids can be engineered to produce the quantities of dsRNA needed to control this major agricultural pest. Optimization of transplastomic mediated-RNAi in maize improvement for Africa would protect the population which is dependent on maize from impending damage, which may result from stem borer infestation and yield losses in maize due to climatic changes. This would further increase the arsenal of stem borer management for African farmers to prevent both native and invasive stem borers devastating maize production especially stem borers that might develop resistance to other pesticides.

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