

Defining biotechnological solutions for insect control in sub-Saharan Africa

Anna-Maria Botha¹  | Karl J. Kunert²  | Joyce Maling'a³ | Christine H. Foyer⁴

¹Department of Genetics, Stellenbosch University, Stellenbosch, South Africa

²Department of Plant Sciences, FABI, University of Pretoria, Pretoria, South Africa

³Kenya Agriculture and Livestock Organization (KALRO), Food Crops Research Institute, Kitale, Kenya

⁴School of Biosciences, College of Life and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, UK

Correspondence

Anna-Maria Botha, Department of Genetics, Stellenbosch University, Private Bag X1, Matieland, Stellenbosch 7601, South Africa.
 Email: ambo@sun.ac.za

Abstract

Africa is burdened by food insecurity with nearly a billion people suffering from starvation, undernutrition, and malnutrition. Climate change prediction models forecast changes in rainfall patterns and rising temperature regimes, with impacts particularly on Southern and East Africa. These predictions are especially concerning for the production of major food crops, such as maize, sorghum, millet, and groundnut, because median temperature increases are associated with increased pest pressure and changes in migratory patterns. These factors will result in significantly more pest invasions and an increased need for innovative insect management practices. This review focuses on pest control strategies, highlighting important examples, their economic impact, and new alternative pest control strategies. African policymakers remain hesitant to move forward with establishing biosafety laws and commercializing GM crops, and it is often difficult to implement regulatory measures in smallholder agriculture to increase efficacy.

KEYWORDS

biotechnology, climate change, CRISPR/Cas, *Diuraphis noxia*, fall armyworm, integrated pest management, invasive pests, iRNA, resistance breeding, Russian wheat aphid, *Spodoptera frugiperda*

1 | INTRODUCTION

Pests and pathogens can severely reduce food security by affecting crop yield and the quality of agricultural produce (Savary et al., 2019). The food-deficit regions in Africa with their fast-growing populations, in combination with emerging or re-emerging pests and diseases, suffer the highest yield losses. Africa is also in a highly vulnerable position with regard to the negative impacts of climate change (IPCC, 2014; Niang et al., 2014). The Food and Agriculture Organization of the United Nations (FAO) has forecast that the current situation of food security is likely to deteriorate further over the next 50 years in Africa unless immediate action is taken (FAO, 2018). The number of people suffering from hunger

as estimated by FAO in 2010 was 239 million in sub-Saharan Africa. This figure is predicted to increase in the near future, and many climate change forecast scenarios are bleak (Sasson, 2012; Serdeczny et al., 2016).

Climate change models forecast future global warming trends with associated changes in rainfall patterns and increases in average temperature and more frequent heatwaves (Davies-Reddy & Vincent, 2017). Such models also predict declines in the rainfall experienced in Southern Africa, while increased precipitation is predicted for East Africa (Figure 1). These predictions are especially worrisome for the production of the major cereal and legume food crops, such as maize, wheat, sorghum, millet, beans, and groundnut, where losses of between 27% and 32% are predicted with a

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Food and Energy Security* published by John Wiley & Sons Ltd. and the Association of Applied Biologists.

warming of about 2°C above pre-industrial levels by mid-century (Schlenker & Lobell, 2010). Thornton, Jones, Ericksen, and Challinor (2011) estimated even higher mean yield losses (71%) particularly for beans under warming exceeding 4°C. In contrast, cassava is the only crop with a better production forecast under these conditions as it appears to be more tolerant to higher temperature regimes and variable rainfall patterns (Niang et al., 2014). Data from different models predict future crop losses for both maize and soybean (Fodor et al., 2017). However, when carbon dioxide (CO₂) fertilization effects are taken into account, significant yield gains are predicted for soybean, together with a shift in global production from the southern to the northern hemisphere (Foyer et al., 2019).

Relatively little information is available in the literature on plant responses to different combinations of biotic and abiotic stress responses (Foyer, Rasool, Davey, & Hancock, 2016). Atmospheric carbon dioxide (CO₂) levels are for example already well over 400 ppm and are increasing annually. Growth under high atmospheric CO₂ had little impact on aphid performance on oilseed rape (Himanen et al., 2008). However, the performance of the pea aphid (*Acyrtosiphon pisum*) was decreased in free-air enrichment (FACE) studies of performance on *Vicia faba* (Mondor, Tremblay, Awmack,

& Lindroth, 2005). Plants grown under elevated CO₂ were more suitable hosts for *A. pisum* than those grown at ambient CO₂. However, when plants were grown at elevated temperature (30°C), the effect of CO₂ fertilization on amino acid content was lost as was the enhanced susceptibility of plants to aphid infestation (Ryalls, Moore, Riegler, Gherlenda, & Johnson, 2015). These findings may be explained by recent reports of the differential effects of high atmospheric CO₂ and elevated temperatures on phytohormone signaling. Plants grown with elevated atmospheric CO₂ levels show activation of salicylic acid (SA)-mediated defense pathways (Mhamdi & Noctor, 2016; Noctor & Mhamdi, 2017). In contrast, increasing evidence suggests that elevated temperatures selectively dampen the SA response, while jasmonic acid (JA) and abscisic acid signaling pathways are favored. Other observed changes in the plant foliage grown under elevated CO₂ levels (550 and 700 ppm) include altered the quality of peanut foliage (i.e., significantly lower leaf nitrogen, higher carbon, higher relative proportion of carbon to nitrogen, and higher polyphenols content expressed in terms of tannic acid equivalents). Similar effects have been reported previously in other plant species and their interaction with pests (Bezemer & Jones, 1998; Hunter, 2001). These measured changes directly affected the tobacco caterpillar (*Spodoptera litura*) resulting

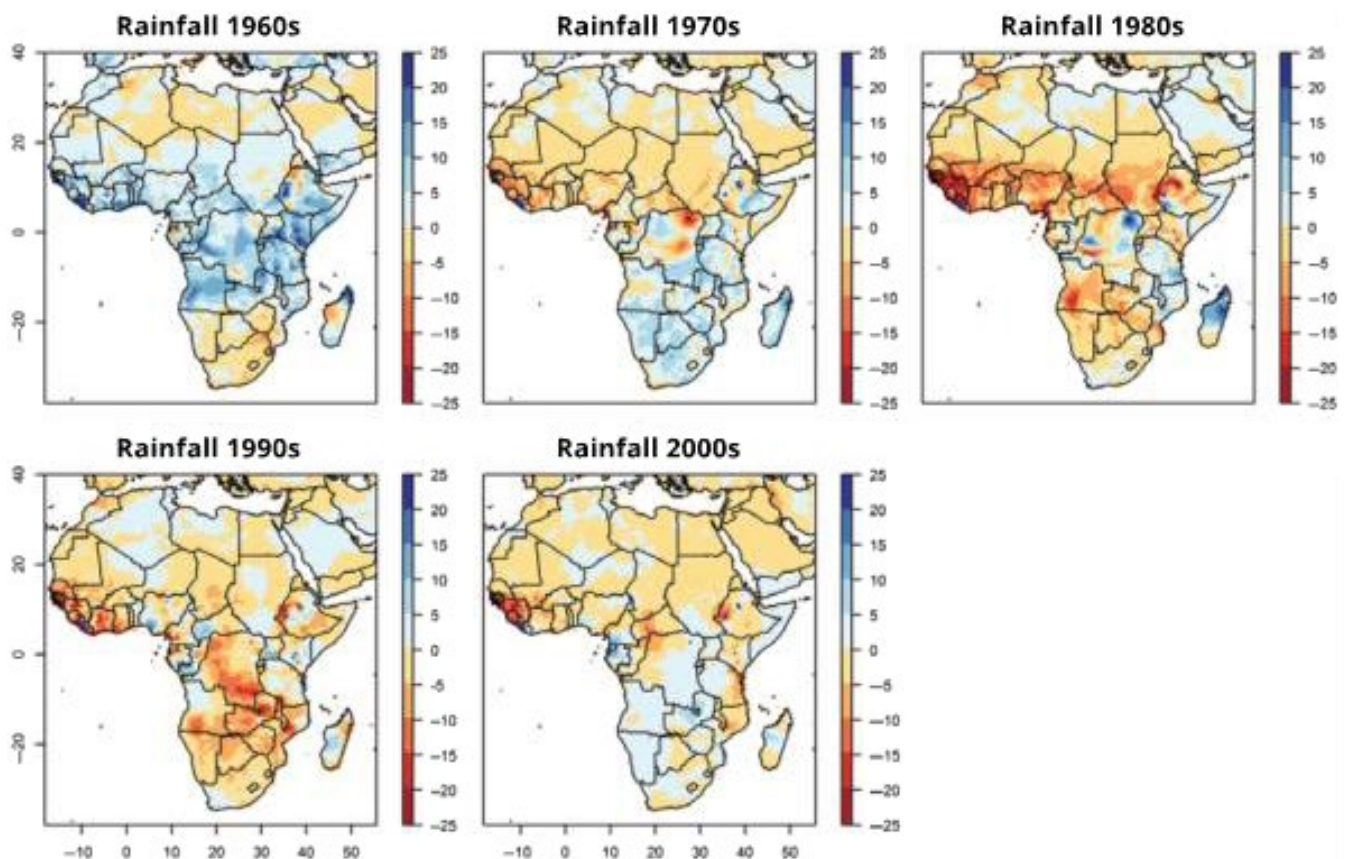


FIGURE 1 Progressively lower average rainfall has been recorded over the past five decades. Changes in measured rainfall (1960–2000) (Taken from Davies-Reddy & Vincent, 2017)

TABLE 1 Estimated annual production losses because of the invasion of new pests (modified from Pratt et al., 2017)

Invasive insect pest	Crop	Eastern African country where IAS currently recorded as present	Estimated current annual production losses to smallholders (million US\$)*		Estimated future annual production losses to smallholders (million US\$) (5–10 year scale)(per country and in total)	
			Lower estimate	Upper estimate	Lower estimate	Upper estimate
<i>Chilo partellus</i> (spotted stem borer)	Maize	Ethiopia	61.3	73.2	47.9	56.6
		Kenya	42.8	51.0	34.4	40.6
		Malawi	104.3	139.1	82.5	106.1
		Tanzania	30.0	42.4	26.5	37.1
		Uganda	118.6	144.3	92.1	108.8
<i>Liriomyza</i> spp. (leaf-mining flies)	Bean and pea (dry/ green)	Kenya	54.0	64.5	61.5	71.7
		Tanzania	49.8	59.3	57.1	66.6
		Uganda	21.3	25.3	25.1	29.3
<i>Tuta absoluta</i> (tomato leafminer)	Tomato	Ethiopia	2.6	2.9	3.4	3.8
		Kenya	45.9	52.4	59.8	66.5
		Tanzania	20.4	23.2	26.5	29.5
		Uganda	0.7	0.8	1.2	1.3
Cumulative losses			551.7	678.4	518	617.9
Cumulative losses (5 year scale)					2,590	3,089.5

*Adjusted to gross production pre-losses.

in higher consumption, lower digestive efficiency, slower growth, and longer time to pupation (Rao, Manimanjari, et al., 2012a; Rao, Rama Rao, et al., 2012b). Similarly, elevated CO₂ on maize resulted in a decrease in fitness of the Asian corn borer (Xie et al., 2015). Rising CO₂ levels also include both indirect (i.e., changes in host plants) and direct (i.e., change in natural enemies) effects on insects (Guerenstein & Hildebrand, 2008). Climate change effects like moderate water deficit stress in combination with high temperatures also negatively affected aphid survival even where night temperatures were lower, and potentially could aid in the recovery from direct heat stress (Beetge & Krüger, 2019).

While the relative importance of abiotic and biotic soil components can differ between plants and their herbivores, a study of the interactions between the aphid *Schizaphis rufula* and its host dune grass *Ammophila arenaria* revealed that aphid population characteristics were dependent on the abiotic properties of the soils in different growing regions, irrespective of whether soil biota were present (Vandegehuchte, de la Peña, & Bonte, 2010). Moreover, herbivore-induced resistance is likely to be constrained in plants growing on degraded soils because of JA-linked responses to prevailing abiotic and biotic stresses (Held & Baldwin, 2005). Of the abiotic properties of the soils, the availability of water and essential nutrients such as nitrogen and phosphate, is the most important in determining plant growth and productivity (Comadira et al., 2015).

Increasing global temperatures will not only have negative impacts on food production by directly influencing plant productivity, but they can also promote more frequent outbreaks of pests and diseases due to enhanced insect growth and development, as well as increased ease of colonizing stressed plants (Mattson & Haack, 1987). Current crop losses due to insect pests in African countries are estimated to average about 49% of the total crop yield each year (Centre for Agriculture and Biosciences International, CABI, <https://www.cabi.org/projects/food-security/tackling-pests-diseases/>). These losses are expected to be even higher in some crops in the future as a result of climate change. Therefore, in the face of such predicted losses, novel strategies are urgently required to control insects by either applying classical breeding approaches with improved markers for selection or by the discovery and implementation of new approaches that are designed to limit these losses. Furthermore, a recent study has specifically modeled the losses in the production of major cereal crops (i.e., maize, wheat and rice) and the associated increased pest incidence in response to global warming (Deutsch et al., 2018). In this model, global yield estimates are projected to decrease by up to 25% per degree increase in global mean surface warming (Dillon, Wang, & Huey, 2010). These authors suggest that predicted losses are the consequence of warming temperatures on increased insect reproductive and metabolic rates, and hence greater food requirements. The median increase in yield losses owing to

pest pressure is expected to be in the ranges of 46%, 19%, and 31% for wheat, rice, and maize, respectively for an increase of 2°C in average global surface temperatures. This would result in total estimated losses to 59, 92, and 62 metric megatons per year (Dillon et al., 2010). In addition to the increased metabolic requirements of insect pests, changes in migratory patterns and dispersion ranges will be exacerbated with median temperature increases, possibly resulting in significantly more pest invasions and introductions. For example, in a recent analysis relating 1,300 invasive species with the main crops in different countries and international trade routes, sub-Saharan African countries were identified as the most vulnerable to invasive species (Paini et al., 2016). In addition, these countries generally have little or no diversification of economic industries, and they are hence highly dependent on agriculture (Organisation for Economic Co-operation and Development/United Nations, 2011). Climate change-associated changes in invasive species will therefore greatly affect them.

The introduction or spread of relatively few invasive species can have a devastating impact on important staple crops such as maize, and other high-value cash crops including tomatoes, peas, and green beans (Pratt, Constantine, & Murphy, 2017). This was highlighted in a recent study (Pratt et al., 2017) on the economic impact that new invasive pests would have on the mixed maize farming of smallholder farmers in six eastern African countries (i.e., Ethiopia, Kenya, Malawi, Rwanda, Tanzania, and Uganda) (Table 1). These countries have large rural communities that are dependent on smallholder farming for their livelihoods. The costs associated with invasive species equated to 1.8%–2.2% of total agricultural GDP per annum for the eastern African region, yet whose GDP is significantly dependent on agriculture contributing between 24.5% and 43% (FAO, 2017). These losses could be even higher in the long term, growing to \$1.0–1.2 billion per year over the coming decade. Such findings clearly highlight the urgent need for strategies for control and coordinated responses to the imminent threat at the regional, national, and international levels.

However predictive these models may be, the establishment, spread, and biological success of invasive species will definitely be altered by climatic change (Ziska, Blumenthal, Runion, Hunt, & Diaz-Soltero, 2011). In fact, diseases have completely blinded the International research community on the emerging importance of insect pests in view of climate change. To date, only limited investigations have been conducted in Africa. Also, little information is available concerning the precautionary measures that should be taken in the event that future climate change causes an increased incidence of insect invasion. Current literature largely focuses on how climate change will affect weather patterns—mostly rainfall and temperature, with little emphasis on how such changes could influence or promote insect invasion, or the

resultant losses in crop productivity. Our aim in this review is therefore to summarize current knowledge on insect pests based largely on the historical record of insect species that are already invasive in Africa, and that greatly affect crop production in Africa, and unfortunately, entering Europe and Asia in the future. The invasiveness of existing insect pests might increase further due to climatic changes that provide a better habitat and environmental conditions for growth and reproduction. In addition to classical insect control strategies, we discuss possible new strategies of insect control, highlighting biotechnological approaches that might limit or prevent climate change-induced insect invasions.

2 | INVASIVE INSECT PESTS IN AFRICA

Invasive insect pests moving to new habitats in Africa will pose a major threat to crop production and food security (<https://theconversation.com/africas-most-notorious-insects-the-bugs-that-hit-agriculture-the-hardest-83107>). Since insect pests are sensitive to climate change (Chakraborty & Newton, 2011), invasive insects are likely to thrive in the more suitable climatic niches of the future causing greater harm, particularly in the absence of natural enemies or any pre-emptive protective measures in these new habitats (Ziska et al., 2011).

Insects are “ectotherm” organisms that rely on heat sources in the environment to control metabolic rate (Heinrich, 1993). Climate change-induced increases in the air or host plant temperatures in Africa will result in faster insect development. In general, future temperature regimes will be more optimal for insect growth even without effects on food supply and will exacerbate proliferation and decrease the time to reproductive maturity. Moreover, insect mortality rates are likely to decrease and more offspring will be produced per unit of food intake (Mattson & Haack, 1987). Taken together, these factors will result in dramatic increases in insect growth and pest population size (Maffei, Mithofer, & Boland, 2007). Insect pests will be more prevalent earlier in the crop growing season due to higher temperatures or new habitats.

The ability to predict insect invasions into new habitats is extremely challenging, particularly in the absence of records concerning the invasion history of selected regions. Also, predicting the impact of an individual insect species on a new habitat is difficult because of spatial and temporal uncertainties. Insects can have a major impact in one location but only a minor impact in another location. Such uncertainties ultimately influence the assessment and predictions of the economic impact that might result from invasion. A further challenge is to acquire precise data on how higher temperatures or changes in rainfall patterns contribute to insect invasion. The extent of insect invasion may also depend on the extent of cultivation of host crops in new locations.

Currently, several insect pests such as the legume pod borer are mainly endemic to Western Africa where it infects cowpeas (Agunbiade et al., 2012). The pod borer is, however, able to attack common beans and soybeans and beans, and hence, it has the potential to become invasive in new areas because of increased legume cultivation as well as climate change. Predicted increases in land area dedicated to the production of legumes particularly soybeans, in wider more favorable regions of sub-Saharan Africa, are needed to satisfy the demands of a rapidly growing population with sufficient cheap protein (Foyer et al., 2019).

2.1 | Russian wheat aphid (*Diuraphis noxia*)

One of the best-documented and studied examples of an invasive pest species in Southern Africa is the Russian wheat aphid (RWA, *Diuraphis noxia* Kurdjumov) (Hemiptera: Aphididae). This phloem-feeding aphid is able to survive in a variety of habitats due to the ability to withstand a wide range of temperatures. The insect lives inside the rolled leaves of cereal crops and grasses all year-round (https://animaldiversity.org/accounts/Diuraphis_noxia/). RWA was first reported as an invasive species and a local insect pest in Southern Africa as early as 1978. This insect was predominant in the summer rainfall area of the eastern Free State province of South Africa, devastating wheat yields with reported losses up to 90% (Fouche et al., 1984; Walters, 1984; Walters et al., 1980). Interestingly, this invasion coincided with prolonged periods of low rainfall and increased temperatures. These conditions are similar to those predicted to occur as a result of future climate change in Africa and they might therefore contribute to further invasiveness of the aphid (Figure 1). It was initially suggested that RWA serves as a virus vector because of the symptoms and responses observed after feeding. This typically includes leaf rolling, with white or yellow chlorotic longitudinal streaks on infested leaves. However, this could not be confirmed (Burger & Botha, 2018). Aphid-induced yield losses are mainly due to chlorosis and decreases in the content of photosynthetic pigments (Botha et al., 2006), leading to a lower photosynthetic capacity (Botha et al., 2011; Fouche et al., 1984) as well as a decrease in effective leaf area (Walters et al., 1980).

Concerted breeding efforts, to limit the spread of the aphid in South Africa, resulted in the development of RWA-resistant germplasm containing different sources of resistance (i.e., *Dn1*, *Dn2*, *Dn5*, Du Toit, 1989). All these resources originated from the Fertile Crescent region of Middle East where RWA is endemic to. In 1992, the first resistant cultivar, TugelaDN, was released (Van Niekerk, 2001), and by 2006, another 27 cultivars conferring resistance to RWA had been identified and released (Tolmay, Prinsloo, & Hatting, 2000). Biological control initiatives

were also launched, but rendered little success, as introduced predator numbers were either too low or failed to adapt to their new habitats (Hatting, Humber, Poprawski, & Miller, 1999; Hatting, Poprawski, & Miller, 2000; Hatting, Wraight, & Miller, 2004; Prinsloo, 1998, 2000; Prinsloo & du Plessis, 2000).

Despite the successful implementation of integrated pest management (IPM) strategies, which includes the planting of resistant varieties, biocontrol agents and insecticide spraying, this IPM only lasted for about 14 years. By 2006, breakdown in resistance to RWA was reported in the Free State province of South Africa (i.e., SA2, Tolmay, Lindeque, & Prinsloo, 2007), with reports of two additional *D. noxia* biotypes (i.e., SA3 and SA4) soon to follow (Jankielsohn, 2011, 2016). Biotypes are morphological similar aphid populations that differ in their virulence to their host. By 2006, the original SA1 biotype invaded the winter rainfall areas in the Western Cape province, previously RWA free, by crossing a natural ecological barrier (i.e., Great Karoo biome, arid region with limited vegetation) causing significant damage to wheat and barley yields in this region (Botha, 2013). This migration coincided with prolonged periods of lowered rainfall and increased temperature trends as forecasted by climatic models for Southern Africa (Figure 1).

In May 2016, this aphid was reported for the first time in Australia (Plant Health Australia, 2017; Yazdani et al., 2017). This invasion was already predicted in 1990, when Hughes and Maywald (1990) using the CLIMEX model, identified regions with climates highly suitable for settlement by the species. Following the early reports, widespread sampling confirmed the migration of the species throughout the south-eastern regions, as well as into northern Tasmania (Plant Health Australia, 2017; Yazdani et al., 2017) confirming the validity of the early predictions. More recently, a modified Hughes and Maywald (1990) CLIMEX model (Table S1) that include irrigation areas as favorable habitat was applied which expanded the previously identified favorable climatic regions in temperate and Mediterranean areas in Australia and Europe; and in more semi-arid areas in north-western China and Middle Eastern countries, but also revealed new areas, not previously reported climatically suitable for the establishment of *D. noxia*, such as parts of France, the UK and New Zealand. (Figure S1).

The RWA was also introduced to Kenya in 1995, with two RWA biotypes (i.e., Njoro and Timau) present in the country (Ngenya, Malinga, Tabu, & Masinde, 2016). These RWA biotypes differ from the biotypes in South Africa and were found to be phylogenetically closest to the Middle East-African RWA group, alongside biotypes RWA1 and RWA2 occurring in the United States and Mexico (Liu et al., 2010). Comparable climatic conditions to those in the Southern

African wheat-producing regions promoted the settlement and proliferation of this aphid, with some regions being more suitable than others. In a study wherein Malinga et al. (2007) compared the RWA biotypes in Kenya, the biotypes from Njoro were shown to be fitter (i.e., experienced higher survival, progeny and estimates of intrinsic rate of natural increase) than the Timau biotypes. RWA severely hampers wheat production (442,000 MT) in Kenya, to the extent that production does not meet annual domestic demand (1,750,000 MT) (Njuguna, Macharia Mwangi, Kamundia, Koros, & Ngotho, 2016). RWA thus causes yield losses of up to 95% when not controlled (Macharia, Gethi, Ngari, & Njuguna, 2012). As in many other wheat production areas, RWA is mainly controlled by insecticide spraying (Macharia et al., 2012), which not only poses a hazard to the environment, but is also costly, especially to rural smallholder farmers. Hence, there is a need for alternative effective methods of control, particularly in the face of climate change, which is likely to spread this aphid into new habitats.

A key question concerns the cause of this breakdown in aphid resistance. The answer is a combination of factors, such as changing climatic conditions that favored the settlement of RWA in new areas that were previously RWA free and farmers relying on limited resistance varieties with a narrow genetic base that were planted on a wide scale, with no or limited refuge. Such practices were associated with heavy insecticide dependence. Moreover, new RWA introductions coincided with wheat grain imports. This practice led to accidental introductions of new insect pests, which rapidly became invasive. This is a common phenomenon (Paini et al., 2016). Wheat import data from 1988 to 2012 have been analyzed (Burger, 2015). This study involved un-milled wheat, either as seed or fresh material, as well as countries with a record of RWA infection. Countries included in this investigation were Argentina, Chile, Canada, Mexico, South Africa, and the United States. In these countries, RWA was either confirmed as an insect pest, or was believed to have acted as a corridor for introduction. Also included in this investigation were major trading partners to South Africa for wheat imports including the United States, Argentina, Canada, and Germany (Figure 2). By making use of online world trade databases, Burger (2015) thereby made the interesting observation that the reports of new RWA biotypes (i.e., SA2, SA3, and SA4) in South Africa followed major wheat imports from the United States (Figure 2). By also studying the genome of the RWA endosymbiont (*B. aphidicola*), Burger (2015) also reported sequence similarities with that of *B. aphidicola* from RWA biotypes US2, US5, and US8, providing evidence in support of the conclusion that the United States was the origin of South African RWA biotypes, SA3 and SA4.

The breakdown in resistance also led to a new wave of breeding efforts to identify alternative sources of RWA resistance. Currently, RWA is controlled through integrated

management practices, consisting of cultural practices, planting of resistance varieties, and frequent insecticide spraying. The latter strategy incurs the additional cost to South African wheat farmers on average by US\$12 per hectare, increasing the annual financial burden of production costs to approximately US\$4 million to wheat farmers that already suffer from low profit margins (De Lange, 2017). In general, all these aspects have to be considered in future strategies to limit damage by this aphid in relation to climate change scenarios, when this aphid will possibly invade new climatically more favorable habitats. Therefore, future controls for the aphid must seek to prevent further extensive spread to new habitats and require much more effective strategies than are presently available.

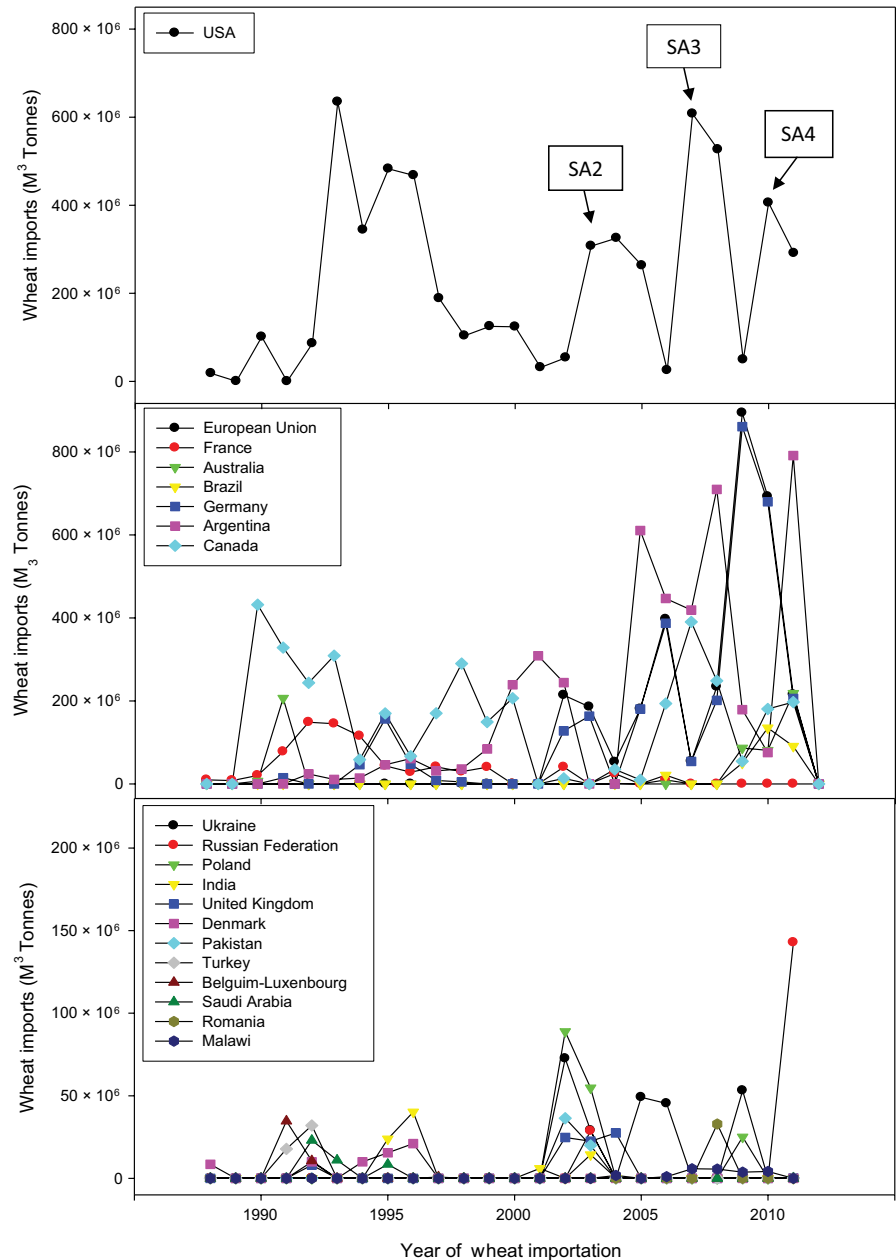
2.2 | Fall armyworm (*Spodoptera frugiperda*)

The armyworm *Spodoptera exempta* is native to Africa (Haggis, 1986). A different armyworm species that is closely related to the native African armyworm is the fall armyworm (*Spodoptera frugiperda*). This species is endemic to North and South America and is a prime noctuid pest of maize. This maize herbivore was introduced into Africa in 2016. It is thought to be a haplotype from South Florida. The presence of this insect has been reported in over 30 African countries including Kenya (Sisay et al., 2018) and South Africa (Erasmus, 2017) (Figure 3). As the fall armyworm has a wide host range with almost 100 recorded plant species in 27 families (Pogue, 2002), this accidental introduction in the African continent will constitute a lasting threat to several important crops. This is especially problematic within the African context, because its preferred hosts are graminaceous plants, including economically important staples such as maize, sorghum, rice, wheat, sugar cane, and napier grass. Female moths normally lay up to 200 eggs at the base of the plant stalk, or protected in a leaf joint, and eggs hatch after 3 days making the dispersal capacity and the potential incurred damage to crops due to feeding colossal as the worm eats the plant's reproductive parts and even eats through the maize cob itself (Prasanna, Huesing, Eddy, & Peschke, 2018).

Damage incurred by the fall armyworm on maize is estimated to be in the range of USD\$3 billion annually, based on data from Centre for Agriculture and Bioscience International (CABI) (April, 2017). This accounts for more than 20 percent of the total production for the region. Feeding damage, however, is not limited to these crops, but is also observed on other major cash crops such as cowpea, groundnut, potato, soybean, and cotton.

Control of the fall armyworm is not easy because of its broad distribution (Figure 3). Additionally, the insect only to emerge at night necessitates the use of systemic insecticides. Even though maize cultivars expressing the *CryIF*

FIGURE 2 Wheat imports to the Republic of South Africa from 1988 to 2012. Reports of *D. noxia* biotypes that coincided with significant wheat imports indicated by arrows (Burger, 2015)



toxin against insect defoliators are widely commercialized in the western hemisphere of South Africa, this is not the case for tropical Africa. The deployment of transgenic Bt maize and application of regular insecticide sprays is hampered by economic, logistic, and socio-cultural and religious considerations. Bt maize has been genetically modified (GM) to produce Bt protein, an insecticide that kills certain insect pests. The gene has originally been isolated from a soil bacterium, *Bacillus thuringiensis* (Bt), which has long been known to possess an insecticide effect.

In general, most of sub-Saharan Africa lack the legal framework to commercialize GM crops. Moreover, where they have been approved as in Kenya, there exists a moratorium against environmental release and trade of GM foods particularly maize. Notwithstanding, reports of fall

armyworm resistance to Cry1F (Storer et al., 2010) increase the need to develop alternative control options such as endophytic entomopathogenic fungi and insect biological control agents. Reports from studies in Ethiopia on *Cotesia icipe*, a dominant larval parasitoid, suggest that parasitism ranges from 33.8% to 45.3%. The tachinid fly, *Palexorista zonata*, resulted in 12.5% parasitism of plants in Kenya. However, the most common parasitoids in Kenya and Tanzania are *Charops ater* and *Coccygidium luteum*, with parasitism ranging from 6% to 12%, and 4% to 8.3%, respectively (based on data from CABI, April 2017).

Various countries have reported crop damage by the fall armyworm that varies from minimal to substantial (Table 2). For example, Mozambique reported crop losses of up to 65% in some regions (African Centre for Biodiversity, 2018). In

Spread of the Fall Armyworm (February 2018)

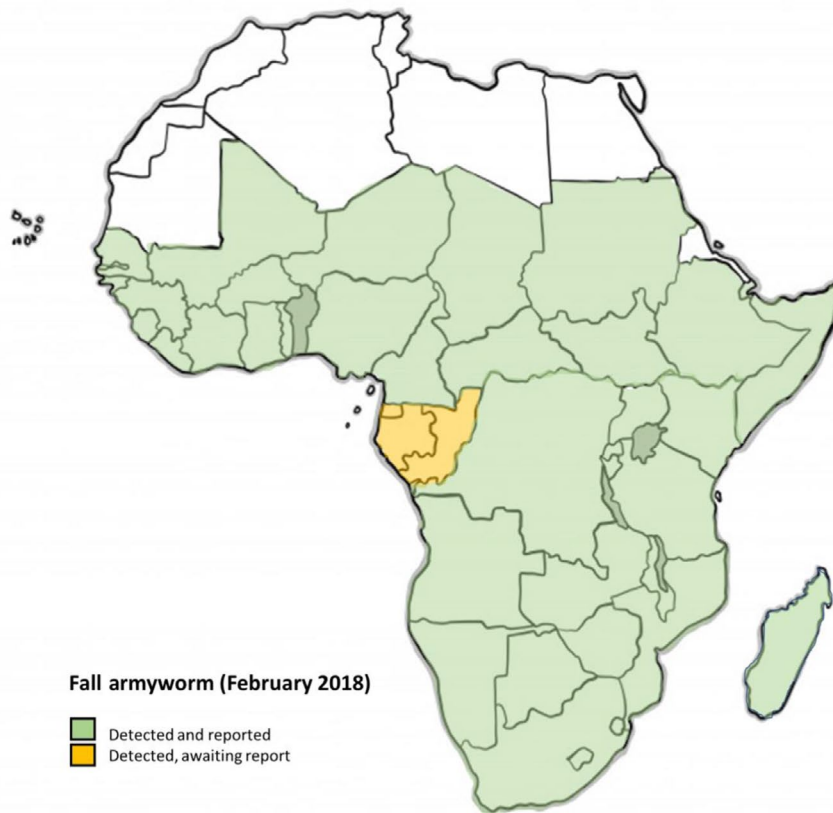
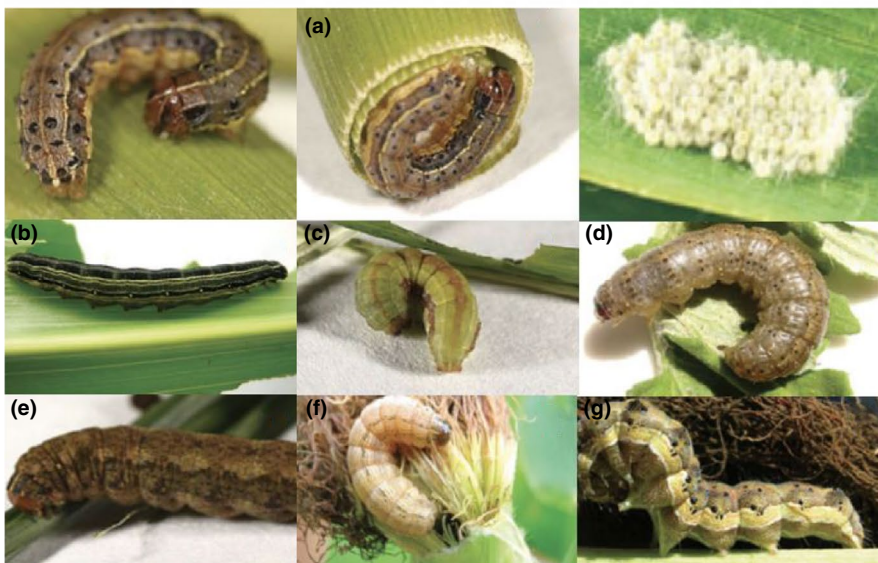


FIGURE 3 (a) Fall armyworm larvae, and eggs (*Spodoptera frugiperda*), and its distribution across the Africa continent (a); (b) The African armyworm (*S. exempta*); (c) The lesser armyworm (adapted from FAO, 2018; Carzoli et al., 2018 <https://doi.org/10.1016/j.gfs.2018.10.004>); (d) The cotton leaf worm (*S. littoralis*); (e) The False armyworm (*Leucania loreyi*); (f) The African boll worm (*Helicoverpa armigera*); and (g) The common cutworm (*Agrotis segetum*) (Photographs: Courtesy of Dr. Annemie Erasmus, ARC Summer Grain Crops, Potchefstroom, SA)



addition, Uganda had an armyworm invasion in half of the country. Other African countries reported low, or even insignificant, infestation (African Centre for Biodiversity, 2018). Without any control measures, the worm has the potential to cause yield losses in a range from 8.3 to 20.6 m tonnes per annum in 12 of Africa's maize-producing countries. This represents a range of 21%–53% of the annual maize production, averaged over a three-year period in these countries (Day et al., 2017; Wild, 2017).

The recent application of control measures, together with increased farmer awareness, and also improved rainfall has served to limit the damage caused by the armyworm. The preferred habitat for the fall armyworm is in regions with little forest cover, an average (500–700 mm) rainfall, with a minimum annual temperature of 18–26°C (Nagoshi, Meagher, & Hay-Roe, 2012). The worm cannot tolerate freezing temperatures. Species distribution modeling indicates that much of sub-Saharan Africa including Kenya which has

TABLE 2 Estimated yield and economic losses for maize and sorghum in Ghana and Kenya due to the fall armyworm (from Abrahams et al., 2017)

Crop	Country	Total Production without fall armyworm (tons M)	Yield loss with fall armyworm (tons M)	Estimated yield loss with fall armyworm (USD \$M)
Maize	Ghana	1.8	0.500	136.1
	Kenya	3.5	0.900	328.1
Sorghum	Ghana	0.3	0.004	17.7
	Kenya	0.2	0.030	14.4

the pest all year-round (Sisay et al., 2018) and South Africa (Erasmus, 2017), is highly suitable for this invasive insect pest. Modeling predicts the possible extinction of the armyworm due to future wetter climatic conditions in areas near to the Equator (Ramirez-Cabarel, Kumar, & Shabani, 2017). However, a further spread of the worm to other regions may occur due to drier climatic conditions that creating a more suitable habitat for the pest (Figure 1) (Davies-Reddy & Vincent, 2017; Wild, 2017).

An important question concerns how future global warming may potentiate future invasions or depress the spread of the fall armyworm in Africa. In this regard, more research is required to increase the predicted periods of drought more accurately, and also the periods of high sporadic rainfall that may favor the spread of the insect. For example, the drought linked to the El Niño weather system of 2014–16, followed by the current high rainfall associated with the La Niña system, created the “perfect conditions” for fall armyworm outbreaks in Africa (Wild, 2017).

The fall armyworm, however, is not the only pest of maize that is likely to become more invasive in Africa. The spotted stem borer, *Chilo partellus*, and the maize stem borer, *Busseola fusca*, which both feed inside the growing maize plants in lowland and highland regions of East Africa, respectively, cause severe damage to crops. These two pests cause as much as \$450 million in grain losses to smallholder farmers each year (CABI, April 2017). These two pests also have a wide distribution (Figure S2) attacking other important crops such as sorghum. However, the distribution of the two insect pests varies with altitude (Glatz, Plessis, & Van den Berg, J., 2017; Khadioli et al., 2014); whereas *B. fusca* prefers mountain sides, *C. partellus* prefer a low altitude. In the future, this spatial distribution may be altered due to climate change, with increasing temperatures and more frequent periods of drought and heavy rainfall. For example, an increase in atmospheric temperatures at high altitude could improve the assimilation of silicon by maize, which fends off *B. fusca* and benefits *C. partellus*. This could lead to an extension of the distribution area of *C. partellus*, which could expand its range into higher altitude areas, highland tropics, and moist transitional regions, which have the highest maize agricultural potential and where the species has yet not been recorded. The spread of these and other insect pests has serious implication in terms

of food security because these areas produce approximately 80% of the total maize in East Africa (Calatayud et al., 2016).

2.3 | Leafminer (*Tuta absoluta*)

Climate change is likely to cause an increase in the range of the damaging leafminer species, particularly for *Tuta absoluta*. Modeling of CLIMEX data to predict future *T. absoluta* distribution patterns of Africa revealed that the pest could invade and become established in most areas of the African continent (Figure 4; Tonnang, Mohamed, Khamis, & Ekesi, 2015).

Introducing irrigation scenarios to optimize the CLIMEX model (Sutherts, Maywald, & Kriticos, 2007), Tonnang et al. (2015) were able to predict that *T. absoluta* not only presents an important threat to West Africa, but most tropical regions in Africa, as well as Asia, Australia, Northern Europe, New Zealand, Russian Federation, and the United States (USA). The model further suggests that the pest may upsurge moderately in areas of Africa where the pest currently exists, or it may expand its range into other regions of tropical Africa with reasonable upsurge of damage potential. These possible outcomes could be explained by the fact that the continent is already warm, with the average temperature in the majority of localities near the threshold temperatures for optimal development and survival of *T. absoluta*. (Tonnang et al., 2015).

The rapid successful invasion is due to the intensive cultivation and cross border trade of tomato fruits, the primary host of *T. absoluta*, but also the prevailing similar ecological and climatic conditions to those of South American countries, the native region of the pest (Tonnang et al., 2015). The insect has so far invaded Tunisia (Desneux et al., 2010), north of the Sahel (Desneux et al., 2010), western Africa, Sudan, and Ethiopia as well as Kenya (Pfeiffer et al., 2013). Collectively, this has already caused significant economic impact, with total annual losses up to \$149.1 million for *Liriomyza* leaf-mining flies and estimated losses of up to \$79.4 million for *T. absoluta*. However, these figures are likely to grow substantially with the rapid spread of the latter pest (CABI, April 2017). The reasons for this rapid spread are that horticultural crops are often grown along with staples, such as maize, where they are valuable nutritionally, and they also serve as cash crops for smallholder growers. In northern Africa, this pest causes

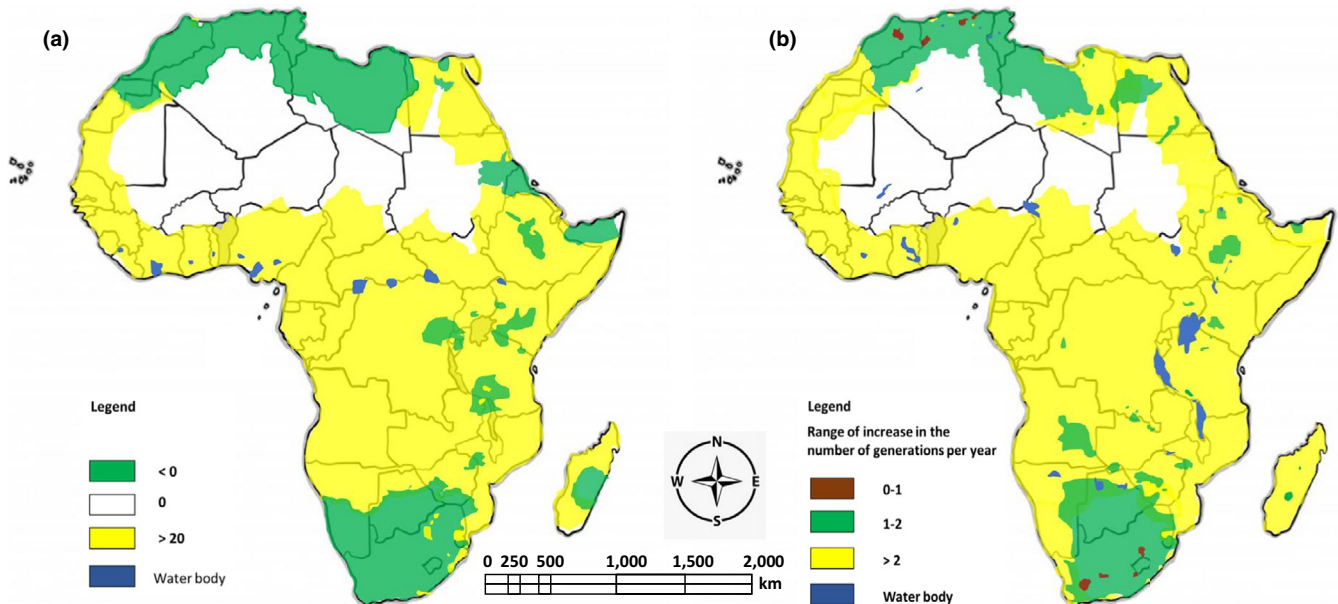


FIGURE 4 (a) Potential range shifts in the distribution of *Tuta absoluta* in Africa using the eco-climatic indices EI under climate change scenario (a rise of 1.5°C Africa wide temperature and 10% increase of rainfall from March 2—September 30 and 10% decrease in the rest of the year). The map was produced from the difference between the values of EI of the predicted future *T. absoluta* distribution (obtained when applying climate change criteria) and the distribution of the pest originated from current climate (year 2000) in Africa. EI = 0 demonstrates no range shift; EI < 0 signifies a reduction of climatic suitability; and EI > 0 represents an increase in the likelihood of survival and permanent establishment of the species. (b) Potential range of increase in number of generations per year of *T. absoluta* under the selected climate change scenario (from Tonnang et al., 2015)

80%–100% crop loss when proper management strategies are not implemented (Giulianotti & Certis, 2010).

3 | DETERMINANTS OF INVASIVENESS

Invertebrates are especially sensitive to changing climatic conditions, and their response to temperature, rainfall, relative humidity, and soil moisture is important predictors of successful colonization (Chen, Xia, Fu, Wu, & Xue, 2014; Klapwijk, Ayres, Battisti, & Larsson, 2012; Macfadyen, McDonnald, & Hill, 2018). As more information becomes available, climate models are becoming increasingly more valuable to assist in the prediction of habitat suitability for invasive species. Although these models prove valuable, the establishment of a suitable model is not a straightforward process (Newbery, Qi, & Fitt, 2016; Macfadyen & Kriticos, 2012; Tonnang et al., 2017; Ward & Masters, 2007) as several factors come into play during the development, selection/choice, and application of these models. Also, the ability of the developed model to accurately predict future invasions is highly reliant on accurate historical data and a good understanding of the factors that determine settlement of the targeted species. Many of these can be species specific, while other factors relate to the resource/niche availability (Ward & Masters, 2007; Wan and Yan, 2016). Hence, the strong notion toward making use

of a whole system approach during the development of such a model as was recently reviewed (Tonnang et al., 2017).

Key factors determining the suitability of a new habitat for insects relate to traits like host range, phenological plasticity, and lifecycle strategies (Ward & Masters, 2007). While some insects have narrow host ranges and therefore are specialist feeders, others have a broad host range including many plant genera, hence generalists, making them likely more successful during their invasions of new habitats. An example of the latter, that are known for their successful colonization of new habitats, are whiteflies (*Bemisia tabaci*) with a host range of more than 600 species (Wan and Yan, 2016 and references within). Whiteflies are pests to crop plants on several continents, including Africa.

Climate change like increased temperature will result in accelerated development and increased voltinism for many pest species (Ziter, Robinson, & Newman, 2012) and may mean species become active earlier in the season (Harrington, Fleming, & Woiwod, 2001; Macfadyen et al., 2018). Close synchrony of insects with their host plants to successfully complete their lifecycles is hampering invasion to new areas. Thus, phenotypically plastic invasive species that are not dependent on close phenological coupling with host plants (e.g., the highly variable egg load of the weevil, *Rhinocyllus conicus* on *Cirsium canescens* plants) increase their successful settlement in a new habitat (Ward & Masters, 2007 and references within).

Another important factor determining the ability to invade new habitats relates to reproduction. The top ten invasive alien species, such as whiteflies (*B. tabaci*) (Goa, Cong, & Wan, 2013) and vegetable leafminer (*Liriomyza sativae*) (Zhang, Yu, & Zhou, 2000), share the following traits; they all have high fecundity, short generation times, and produce multiple generations per year, ensuring long-term persistence at low population density after initial introduction. The ability to reproduce through parthenogenesis provides an advantage as they can exploit new resources without the hindrance of finding a mate and unpredicted Allee effects (Liebhold et al., 2016). A good example of the latter include Russian wheat aphid (*Diuraphis noxia*), known for its invasiveness worldwide (Burger & Botha, 2018; Yazdani et al., 2017). Other traits of importance determining successful invasion include adaptability to changing climates (thermal tolerance—adaptation to low/high temperatures), insecticide resistance, and immune priming (i.e., immune memory to previous pathogen exposure; Wan and Yan, 2016 and references within).

4 | ECOSYSTEM INVASIBILITY AND INTEGRATED PEST MANAGEMENT

Several theories about ecosystem invisibility exist, including crop system complexity, land use patterns, and geographic and climate barriers (Wan & Yang, 2016 and references within). Reduction of habitat heterogeneity and increased in mono-agricultural ecosystems due to farming (maize, wheat, and rice) provides suitable habitats for most invasive crop pests (Knops et al., 1999).

Commercial monoculture farming systems are highly dependent on external inputs (synthesized fertilizers, chemical pesticides, and growth regulators) with simplified ecosystems (Kremen, Iles, & Bacon, 2012; Malézieux, 2012). In contrast, agricultural systems that promote functional biodiversity and support ecological processes allow for benefits from many ecosystem services, such as nutrient cycling, soil structuration, and pest control (Afrin et al., 2017; Altieri & Rosset, 1996; Zhang, Werf, Zhang, Li, & Spiertz, 2007).

Disrupting monoculture agriculture systems through intercropping, using at least two crops species at the same time on the same land (Kahn, 2010; Konar, Singh, & Paul, 2010), enhances pest control (Baidoo, Mochiah, & Apusiga, 2012; Baliddawa, 1985; Rao, Manimanjari, et al., 2012a; Rao, Rama Rao, et al., 2012b; Sharaby, Abdel-Rahman, & Sabry, 2015; Sulvai, Chaúque, & Macuvele, 2016). Intercropping with several crop species assists in pest management because it is unlikely that different crops will be infested by the same pest species (Baidoo et al., 2012).

Field studies have demonstrated that intercropping protects the target crop through several mechanisms, including the release of organic chemicals by non-host crops grown in intercropping which adversely affect the pest insects (Sulvai et al., 2016). The released organic chemicals may act as repellents to insect pests, but also attracts biocontrol agents (natural enemies) of insect pests (Dassou & Tixier, 2016; Letourneau et al., 2011; Song et al., 2013). Mixed crop agriculture has also been shown to sometimes act as barriers that hinder movements of insect pests, providing some protection to susceptible plants (Parker, Rodriguez-Saona, Hamilton, & Snyder, 2013).

Intercropping is commonly used in small-scale farming systems for pest control as it diversifies crops in a given agro-ecosystem to reduce the population of insects and consequently their attack (Degri, Mailafiya, & Mshelia, 2014; Pimental, Hepperly, Hanson, Douds, & Seidel, 2005; Vaiyapuri, Amanullah, Rajendran, & Sathyamoorthi, 2010). Studies in Kenya (Kinama, Habineza, & Jean Pierre, 2018 and references therein) and Egypt (Abdel-Wahab, Abdel-Wahab, & Abdel-Wahab, 2019) demonstrated that cereal–legume intercropping has benefits beyond just pest and disease control, as they also measured increased yield, better biological nitrogen fixation, and better weed control. Consequently, they reported significant economic benefits for these farmers.

5 | BIOTECHNOLOGY, A TOOL TO LIMIT INVASIVE INSECT PEST DAMAGE

The initial commercialization of *Bacillus thuringiensis* (Bt) maize in 1996 was hailed as the ultimate solution for pest control and it was widely adopted. Since then, studies showed that the adoption of Bt maize and cotton has reduced the use of insecticides by 85%. The use of Bt crops also protected neighboring crops such as peppers and beans (Gitig, 2018).

Management of the fall armyworm, for example, already includes the application of GM plants expressing one or more insecticidal proteins derived from *Bacillus thuringiensis* (Bt) (Ingber, Mason, & Flexner, 2018) (Table 2). In sub-Saharan Africa, the Bt technology has also been recommended to limit invasion of the fall armyworm (ISAAA, 2018). Although maize cultivars expressing the Bt *CryIF* toxin are already worldwide applied for control of the fall armyworm, including South Africa, it is not widely used in other African countries with recent invasions. These countries are currently engaged in research and testing of GM crops to limit further spread of this pest (ISAAA, 2017).

Even though planting Bt maize would be useful in these countries and limit the spread of the fall armyworm, this technology is not a lasting solution because of the breakdown of resistance to Bt proteins, as has been observed in *CryIF* and

Vip3AA20 (Haung et al., 2014). Resistance may also develop against Vip3AA20, the latest *Bt* toxin that is effective in the field. Such findings suggest that Vip3AA20 will not be effective for much longer. Therefore, more research is needed to determine which fall armyworm strains are already present in Africa, and whether these strains already carry the *Bt* resistance alleles. This knowledge is essential if future *Bt* varieties are to remain effective in dealing with the insect pest.

Maize plants expressing the *Bt* toxin are also widely applied for control of the insect pests *B. fusca* and *C. partellus* (Mugo et al., 2011; Tefera et al., 2016). However, similar resistance problems as found for the fall armyworm have been found when applying the *Bt* technology for the control of *B. fusca*. A shift in levels of susceptibility of *B. fusca* to *Bt* maize was specifically found with a very low larval survival on *Bt*-maize leaf tissue before the release of *Bt* maize many years ago to current much higher larval survival (Strydom, Erasmus, Plessis, & Berg, 2019). Such reports of *Bt* resistance have already led to also consider alternative control options such as application of endophytic entomopathogenic fungi and application of exotic parasitoids like *Cotesia flavipes*, already released in 1993 in Kenya, for biological control of the introduced stemborer *Chilo partellus* (Overholt et al., 1994).

In addition to protecting maize, the *Bt* technology has also been applied to the control of the tomato leafminer (*Tuta absoluta*). When the *cryIAc* gene was introduced into tomato plants, *Bt*-expressing tomato lines were better protected against the leafminer (Selale, Dağlı, Mutlu, Doğanlar, & Frary, 2017). The recently introduced South American tomato leafminer (also known as the South American pinworm), *Tuta absoluta*, and three species of *Liriomyza* leaf-mining flies are the most important and most widely distributed pests on horticultural crops in Africa. Current control measures rely mostly on chemical spraying, although implementation and pest management practices such as surveillance and the introduction of appropriate phytosanitary activities to manage the spread of *T. absoluta* in Africa have also been widely implemented (Tonnang et al., 2015).

Although the *Bt* technology offers advantages as a measure to limit future invasion by insect pests, the deployment of transgenic *Bt* maize and application of regular insecticide is hampered in Africa by the GMO resistance problem and by economic, logistic, and socio-cultural and religious considerations. Not only is the cost of *Bt*-maize seed an additional burden, as smallholder farmers rarely have the financial means to annually purchase expensive seed (Fischer, Van den, Berg, & Mutengwa, 2015), but most of sub-Saharan Africa still lacks the legal framework to commercialize GMO crops. Where GMO crops have been approved, as in Kenya, a moratorium against the environmental release and trade of GMO foods, particularly maize, still exists. These problems have impeded the utilization of GM crops in Africa, for example during the

2002 food crisis when Malawi, Mozambique, Zambia, and Zimbabwe initially refused US food aid shipments despite widespread food shortages (Zerbe, 2004). The concerns of these countries are based on the perceived potential health impact of GM foods on recipients, the impact of GM food on domestic agricultural biodiversity and impact of GM food on their ability to export agricultural commodities in the future (Zerbe, 2004).

Additional factors contributing to the poor implementation of GMO varieties into smallholder agriculture include (a) a lack of education and technology transfer, (b) conflicts of interest (commercial investment) (Fischer et al., 2015), and (c) the lack of political will and good governance (Zerbe, 2004). It is important to note that most African countries are aligned to their former colonial “masters.” These are mainly European, whose philosophy still plays a leading role in matters of education, science, technology, and trade. It is therefore not surprising that most African countries have adopted the precautionary approach to GMOs that is similar to that of the European Union (Elliot & Madan, 2016). GM crops face strong opposition in most countries of the European Union and Japan (Smyth, 2017). Heated debates still continue in Africa, regarding whether GM crops will help alleviate food insecurity or whether the adoption of this technology could result in negative impacts (Falck-Zepeda, Gruere, & Sithole-Niag, 2012). Consequently, African policymakers are hesitant to move forward with establishing biosafety laws and commercializing GM crops, largely due to risk perceptions and fears spread by anti-biotech lobbying groups (Paarlberg, 2010).

Poor transfer of information on *Bt* maize (genetically modified, GM) underpins the lack of the successful adoption of the GM maize by smallholders in many Southern African countries. One should have in mind that, although risks associated with GM crops are very likely low or non-existent, adoption of a GM technology will not succeed if simply imposed on a farmer (Carzoli et al., 2018). Education on the benefits (such as it provides resistance to stem borers) and prevention of resistance breakdown (i.e., refuge practice—need to plant a refuge crop of non-*Bt* maize next to *Bt* crop) is required to successfully adopt *Bt* maize. Smallholder farmers must also be better informed that the crop protection only lasts while hybrid seed is being planted. In this regard, as seed is mostly distributed by commercial seed companies, governmental regulations for the distribution of *Bt* maize obstruct smallholders from fully benefitting. Education and training on proper insect resistance management following approval of GM maize crops; especially training on proper implementation of refuge is a further a problem for better adoption of the *Bt* technology (FAO, 2018; Fatoretto, Michel, Silva Filho, & Silva, 2017). The reality of a refuge crop means that fall armyworm will destroy the maize in this portion of the field, equaling little or no harvestable yield. However,

TABLE 3 Major insect pests, reported insecticide resistance, methods of control, and new applications (such as iRNA, CRISPR/Cas9) with the objective of insect management

Species	Methods of control	New applications: Genes, delivery, and function	Affected food crops	Distribution in Africa ^a	Reference to technology
<i>Diuraphis noxia</i> (Russian wheat aphid)	Cultural control; chemical control; biocontrol; host plant resistance; mRNA delivery/knockouts	RNA delivery knockouts Gene target: <i>cpRR1</i> (developmental function, cuticle)	Wheat, barley, oats, triticale, rye	South Africa, Zimbabwe, Kenya, Ethiopia, Morocco, Algeria, Egypt, Libya	Botha et al. (2018)
<i>Spodoptera litura</i> (taro caterpillar)	Cultural control; chemical control; biocontrol; host plant resistance; mRNA delivery/knockouts	RNA delivery knockouts Gene targets: <i>Slabd-A</i> ; <i>SlitPPP3</i> (female sex pheromones)	Over 40 families, containing at least 87 species of economic importance (including groundnut, a wide selection of vegetables and beans)	Ghana and Reunion	Bi, Xu, Tan, and Huang (2016) Zhu et al. (2016)
<i>Spodoptera littoralis</i> (cotton leafworm)	Cultural control; chemical control; biocontrol; host plant resistance; mRNA delivery/knockouts	RNA delivery knockouts Gene target: <i>SlitOrco</i>	Over 40 families, containing at least 87 species of economic importance (including groundnut, a wide selection of vegetables and beans)	Widespread across the African continent	Koutroumpa et al. (2016)
<i>Helicoverpa armigera</i> (cotton bollworm)	Cultural control; chemical control; biocontrol; GM technology—Bt varieties; host plant resistance; mRNA delivery/knockouts	RNA delivery knockouts Gene target: <i>HaCad</i> (demonstrated that the <i>HaCad</i> gene is related to Bt toxin Cry1Ac resistance) <i>OR16</i> (control of mating)	Cotton, pigeonpea, chickpea, tomato, sorghum and cowpea; other hosts include groundnut, okra, peas, field beans (<i>Lablab</i> spp.), soybeans, lucerne, Phaseolus spp., other Leguminosae, tobacco, potatoes, maize, flax, a number of fruits (Prunus, Citrus), forest trees, and a range of vegetable crops.	Widespread across the African continent	Wang et al. (2016) Chang et al. (2017)
<i>Plutella xylostella</i> (diamondback moth)	Cultural control; chemical control; biocontrol; host plant resistance; mRNA delivery/knockouts; knockout plasmid, CRISPR/Cas9	CRISPR/Cas9 Gene targets: <i>Pxabd-A</i> , <i>PxCHS1</i>	Pea; horseradish, most Brassica spp.; watercress; radish; lettuce, rocket; cabbage;	Widespread across the African continent	Huang et al. (2016) Douris et al. (2016)

^a<https://www.cabi.org/jisc/datasheet/>.

implementing and monitoring non-*Bt* refuges will likely be a challenge in the smallholder farm context as already found in India and China (Tabashnik et al., 2013). Mixing non-*Bt* seeds into *Bt* seed bags (“refuge in a bag”) may be therefore a more suitable option, at least when seeds are purchased in the formal seed market.

As *Bt* insecticides and *Bt* transgenic crops have been widely used internationally for pest control (Bravo, Likitvivanavong, Gill, & Soberón, 2011), more reports on the development of resistance to *Bt* toxins are surfacing (Elliot & Madan, 2016). Hence, the need to seek alternatives is becoming more urgent. If the transfer of *BT* transgenic crops is not accompanied by effective regulatory requirements, then efficacy may be decreased. For example, in the United States, *BT* crops were introduced with surrounding non-GMO Crop refugia as a regulatory requirement to trap insects. Even with this measure in place, *Bt* breakdown leading to crop susceptibility has occurred. While such regulatory requirements are good practice, they will need to be modified for implementation by small-scale holders in Africa, who mostly lack the land to practice such measures on a large scale. Unfortunately, they are often supported by weak, poorly motivated extension services.

Furthermore, any predicted consequences of climate change in these countries, such as more intense drought conditions, might possibly severely affect the efficacy of the *Bt* toxin for insect control (Martins et al., 2008). The problems *Bt* technology currently faces in Africa raises the question whether new gene silencing technologies, such as RNA interference (RNAi) and CRISPR/Cas9, should be developed as alternatives or additions to limit a possible future spread of invasive insect pests. Also, will these technologies be feasible and acceptable technologies to strengthen particularly food security for poor African farming communities?

Without doubt, RNAi technology with small interfering or silencing RNA (siRNA), when expressed in a plant to target an insect gene, could be useful to specifically protect a crop against invasive insect pests. Usually an instantaneous process, unless the dsRNA is supplied continuously, application of the CRISPR/Cas9 technology generates changes at the genomic level that are stable and heritable, and the mutant gene can be transmitted to the next generation (Perkins et al., 2016). This would clearly have benefits in providing more sustainable pest resistance as targets are specific and, in most, examples either developmental or structural in nature (Sun, Guo, Liu, & Zhang, 2017 and references therein; Botha, Swiegers, & Burger, 2018). Despite the promise this technology offers, only a limited number of pests that damage food crops have so far been targeted. Examples include *H. armigera* (Chang et al., 2017; Sun et al., 2017; Wang et al., 2016 and references therein), *Diuraphis noxia* in our group (Botha et al., 2018), *Spodoptera litura*, *Spodoptera littoralis*,

and *Plutella xylostella*, however all of these are still in the experimental phase (Table 3).

Using CRISPR/Cas9, Wang et al. (2016) provided direct evidence that *HaCad* is a key receptor for Cry1Ac and is related to Cry1Ac resistance, opening up new avenues to prolong the use of *Bt* toxins. CRISPR/Cas9 was also used in a new pest control strategy with *H. armigera* to destroy pest mating through antagonist-mediated optimization of mating time that ensures maximum fecundity (Chang et al., 2017). In *D. noxia*, a significant reduction ($\pm 50\%$) in intrinsic reproduction rate (as measured in nymph production) has been measured targeting *Dncpr1-8*, a gene containing a conserved R&R region (Rebers and Riddiford Consensus) (Rebers & Willis, 2001) and an important cuticular protein (Botha et al., 2018). The same gene is now tested for its potential use to protect leafy crops against other phloem-feeding hemipterans.

Studies have demonstrated that climate change will greatly influence the interactions between plants, phloem-feeding pests like aphids and whiteflies (the latter already a significant problem in Africa), and their natural enemies. Since whiteflies also differ in their adaptability, better adapted species will likely experience increased distribution and abundance provided their tolerance limits are not exceeded, while species with lower tolerance and adaptation limits will suffer reduced fitness, which will have overall effects on their distribution and abundance in space and time. Changes in climatic suitability modifying the distribution and abundance of whiteflies, and environmental suitability for plant viruses, will likely also affect epidemics of viral diseases (Aregbesola, Legg, Sigsgaard, Lund, & Rapisarda, 2019). However, when RNAi technology will be regarded as a technology to limit whitefly spread, it would be essential to express such siRNA/dsRNA in the phloem under a tissue-specific promoter to target these phloem-feeding insects. RNA interference (RNAi)-mediated gene silencing has been indeed explored with some success for the control of the sap-sucking whitefly, a major pest in Africa. In addition to cereals, the whitefly causes damage to root and tuber crops, including cassava and sweet potato, and transmits hundreds of plant viruses including the Cassava Mosaic and Cassava Brown Streak viruses (Mugerwa et al., 2018). Knockdown of whitefly genes involved in neuronal transmission and transcriptional activation of developmental genes reduced the whitefly population size and also decreased any virus spread (Malik et al., 2016).

6 | IMPORTANCE OF COMMUNICATION

By 2017, about 17 million farmers across 24 countries planted biotechnology-derived crops across 189.8 million hectares (ISAAA, 2017), signifying the importance and

impact that biotechnology has had on global agriculture. However, planting these crops also sparked debate on diverse issues that range from scientific, political, economic, ethical, and cultural viewpoints. Also, to ensure an enabling environment where farmers gain the full benefit these crops offer, a scientific-balanced (i.e., evidence based information on advantages/disadvantages/possible risks) view should be communicated effectively to increase public understanding (Traynor, Adonis, & Gil, 2007). Navarro and Hautea (2011) provided additional reasons for proper communication to the public, which include the benefits of having an informed public, improved policy, and better regulatory decisions, as well as increased public confidence.

Communication, however, is not only important for public acceptance of biotechnology crops, but also for maintaining effective networks wherein new pest invasions can be reported, as well as to convey the benefits of planting refuges for the sustainability of the resistance in these crops. The Southern African Development Community (SADC) Multi-Country Agricultural Productivity Programme (MAPP) is an example of such network in Africa (<https://www.sadc.int/themes/agriculture-food-security/>). SADC is a collective of 16 African countries, with the objective to increase agricultural productivity by at least 6% per year. The SADC-MAPP focuses on agricultural research and seeks to strengthen technology development, technology dissemination, and linkages among agricultural institutions in the SADC region, including communication of new pests and diseases that pose risks to food security in the region.

Minimizing the risk of invasions is an important aspect of integrated pest management and ensuring food security. The risk of new pest invasions can be minimized through policies (i.e., National and Regional Guidelines), monitoring technology (i.e., DNA bar coding, etc.), databases, and early-warning systems (e.g., CABI's *Horizon Scanning Tool*, CABI, 2018, <https://www.scidev.net/sub-saharan-africa/agriculture/opinion/insect-pests-invasions-in-africa.html>), as well as a collective eradication and spread blocking (Wan & Yang, 2016).

7 | CONCLUSION

The continent of Africa has been identified to be extremely vulnerable to the negative impacts of climate change. Climate change models forecast global warming, with associated changes in rainfall patterns and increases in heatwaves. These factors alone are predicted to have a negative impact on the yields of most major crops, such as wheat, rice, and maize (Deutsch et al., 2018). This effect may in many cases be exacerbated by insect pests that already consume between 5% and 20% of major grain crops. Studies concerning the effects of temperature on the population growth and metabolic rates of insects suggest that future yield losses caused by insects

will increase by 10%–25% per degree increase in temperature (Deutsch et al., 2018). Such predictions provide a benchmark for future regional and Africa-specific studies on the effect of climate change on crop/insect interactions.

New invasive pests and changes in pest migratory patterns are but a few of the upcoming challenges to African agriculture that collectively add additional burdens to resource-poor farming communities. Key questions concern how further invasions of insect pests can be prevented or contained, particularly when caused by a changing climate. Controlling pests, such as the fall armyworm will certainly be challenging because of the significant ability of the insect to adapt to a broad range of habitats. For example, addressing the feeding habit of the caterpillar within the leaf whorl during the day and emergence only at night requires the application of systemic insecticides. Smallholder farmers would have to spray insecticides like pyrethrins and organophosphates. Since the armyworm has already developed resistance to these insecticides, it is particularly difficult to control the insect at an advanced larval developmental stage. Thus, alternative control methods are essential which may include physically picking the caterpillars off the plants, intercropping with plants not in favor to the insect, application of bio-pesticides, planting early in the season before any insect pest populations can build up or applying genetically modified plants such as plants engineered with the Bt toxin (Niassy & Subramanian, 2018; Yu, 1991). It is thus imperative that key pests and the crops that are susceptible to attack are identified, in order to support prioritized decision-making and support tools, for example policies and sanitary measures, to control the introduction and spread of new pests. It may also assist researchers, governments, and developmental agencies to prioritize their focus areas for research investment and action which may assist in enhanced food security for Africans.

CONFLICT OF INTEREST

None declared.

ORCID

Anna-Maria Botha  <https://orcid.org/0000-0002-9868-1566>

<https://orcid.org/0000-0002-9868-1566>

Karl J. Kunert  <https://orcid.org/0000-0002-7740-3508>

REFERENCES

- Abdel-Wahab, T. I., Abdel-Wahab, S. I., & Abdel-Wahab, E. I. (2019). Benefits of intercropping legumes with cereals. *International Journal of Conference Proceedings*, 1(2), ICP.000510.2019.
- Abrahams, P., Bateman, M., Beale, T., Clotney, V., Cock, M., Colmenarez, Y., &... Gomez, J. L. (2017). *Fall Armyworm: Impacts and Implications for Africa. Evidence Note (2)*. Oxfordshire, UK: CABI.
- African Centre for Biodiversity (2018). *Bt maize and the fall armyworm in Africa: Debunking industry claims, June 2018*, p. 23. Retrieved from <https://acbio.org.za/sites/default/files/documents/BT%20Maize%20Fall%20Army%20Worm%20report.pdf>

- Afrin, S., Latif, A., Banu, N. M. A., Kabir, M. M. M., Haque, S. S., Emam Ahmed, M. M., ... Ali, M. P. (2017). Intercropping empower reduces insect pests and increases biodiversity in agro-ecosystem. *Agricultural Sciences*, *8*, 1120–1134. <https://doi.org/10.4236/as.2017.810082>
- Agunbiade, T. A., Coates, B. S., Kim, K. S., Forgacs, D., Margam, V. M., Murdock, L. L., ... Pittendrigh, B. R. (2012). The spatial genetic differentiation of the legume pod borer, *Maruca vitrata* F. (Lepidoptera: Crambidae) populations in West Africa. *Bulletin for Entomological Research*, *102*, 589–599. <https://doi.org/10.1017/S0007485312000156>
- Altieri, M. A., & Rosset, P. (1996). Agroecology and the conversion of large-scale conventional systems to sustainable management. *International Journal of Environmental Studies*, *50*, 165–185. <https://doi.org/10.1080/00207239608711055>
- Aregbesola, O. Z., Legg, J. P., Sigsgaard, L., Lund, O. S., & Rapisarda, C. (2019). Potential impact of climate change on whiteflies and implications for the spread of vectored viruses. *Journal for Pest Science*, *92*, 381–392. <https://doi.org/10.1007/s10340-018-1059-9>
- Baidoo, P. K., Mochiah, M. B., & Apusiga, K. (2012). Onion as a pest control intercrop in organic cabbage (*Brassica oleracea*) production system in Ghana. *Sustainable Agriculture Research*, *1*, 8–19. <https://doi.org/10.5539/sar.v1n1p36>
- Baliddawa, C. W. (1985). Plant species diversity and crop pest control. An analytical review. *International Journal of Tropical Insect Science*, *6*, 479–487. <https://doi.org/10.1017/S1742758400004306>
- Beetge, L., & Krüger, K. (2019). Drought and heat waves associated with climate change affect performance of the potato aphid *Macrosiphum euphorbiae*. *Scientific Reports*, *9*, 3645. <https://doi.org/10.1038/s41598-018-37493-8>
- Bezemer, T. M., & Jones, T. H. (1998). Plant-insect herbivore interactions in elevated atmospheric CO₂: Quantitative analyses and guild effects. *Oikos*, *82*, 212–222. <https://doi.org/10.2307/3546961>
- Bi, H. L., Xu, J., Tan, A. J., & Huang, Y. P. (2016). CRISPR/Cas9-mediated targeted gene mutagenesis in *Spodoptera litura*. *Insect Science*, *23*, 469–477. <https://doi.org/10.1111/1744-7917.12341>
- Botha, A.-M. (2013). A coevolutionary conundrum: The arms race between *Diuraphis noxia* (Kurdjumov) a specialist pest and its host *Triticum aestivum* (L.). *Arthropod Plant Interactions*, *7*, 359–372. <https://doi.org/10.1007/s11829-013-9262-3>
- Botha, A.-M., Lacock, L., Van Niekerk, C., Matsioloko, M. T., Du Preez, F. B., Kunert, K. J., & Cullis, C. A. (2006). Is photosynthetic transcriptional regulation in *Triticum aestivum* L. cv. “TugelaDN” a contributing factor for tolerance to *Diuraphis noxia* (Homoptera: Aphididae)? *Plant Cell Reports*, *25*, 41–54.
- Botha, A.-M., Swiegers, H. W., & Burger, N. F. V. (2018). Using siRNA as means of broadspectrum aphid control in food crops. PROVISIONAL FILING SA patent application # Draft provisional patent application: siRNA; Our ref: P3482ZA.
- Botha, A.-M., Van Eck, L., Jackson, C. S., Burger, N. F. V., & Schultz, T. (2011). Biotic stress and photosynthetic gene expression. In M. Najafpour (Ed.), *Applied photosynthesis/book 2*. Copenhagen, Denmark: INTECH Inc Open Access Publishers.
- Bravo, A., Likitvivanavong, S., Gill, S. S., & Soberón, M. (2011). *Bacillus thuringiensis*: A story of a successful bioinsecticide. *Insect Biochemistry and Molecular Biology*, *41*, 423–431. <https://doi.org/10.1016/j.ibmb.2011.02.006>
- Burger, N. F. V. (2015). *Characterization of Diuraphis noxia diversity and host responses*, p. 135. M.Sc. Dissertation, University of Pretoria, South Africa.
- Burger, N. F. V., & Botha, A.-M. (2018). Genome of Russian wheat aphid an economically important cereal aphid. *Standards in Genomic Sciences*, *12*, 90. <https://doi.org/10.1186/s40793-017-0307-6>
- Calatayud, P.-A., Njuguna, E., Mwalusepo, S., Gathara, M., Okuku, G., Kibe, A., ... Ru, B. L. (2016). Can climate-driven change influence silicon assimilation by cereals and hence the distribution of lepidopteran stem borers in East Africa? *Agriculture, Ecosystems & Environment*, *224*, 95–103. <https://doi.org/10.1016/j.agee.2016.03.040>
- Carzoli, A. K., Siddique, I., Aboobucker, L. L., Sandall, T. T., Lübberstedt, W., & Suza, P. (2018). Risks and opportunities of GM crops: Bt-maize example. *Global Food Security*, *19*, 84–91. <https://doi.org/10.1016/j.gfs.2018.10.004>
- Centre for Agriculture and Biosciences International (CABI) (2018). Invasive species compendium. *Myzus persicae* (green peach aphid). <https://www.cabi.org/products-and-services/about-cabi-books/ebooks/>
- Chakraborty, S., & Newton, A. C. (2011). Climate change, plant diseases and food security: an overview. *Plant Pathology*, *60*, 2–14.
- Chang, H., Liu, Y., Ai, D., Jiang, X., Dong, S., & Wang, G. (2017). A pheromone antagonist regulates optimal mating time in the moth *Helicoverpa armigera*. *Current Biology*, *27*, 1610–1615. <https://doi.org/10.1016/j.cub.2017.04.035>
- Chen, C., Xia, Q. W., Fu, S., Wu, X. F., & Xue, F. S. (2014). Effect of photoperiod and temperature on the intensity of pupal diapause in the cotton bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae). *Bulletin of Entomological Research*, *104*, 12–18.
- Comadira, G., Rasool, B., Kaprinska, B., García, B. M., Morris, J., Verrall, S. R., &... Foyer, C. H. (2015). WHIRLY1 functions in the control of responses to nitrogen deficiency but not aphid infestation in barley. *Plant Physiology*, *168*, 1140–1151. <https://doi.org/10.1104/pp.15.00580>
- Dassou, A. G., & Tixier, P. (2016). Response of pest control by generalist predators to local-scale plant diversity: A meta-analysis. *Ecology Evolution*, *6*, 1143–1153. <https://doi.org/10.1002/ece3.1917>
- Davis-Reddy, C. L., & Vincent, K. (2017). *Climate risk and vulnerability: A handbook for Southern Africa* (2nd ed.). Pretoria, South Africa: CSIR.
- Day, R., Abrahams, P., Bateman, M., Beale, T., Clotey, V., Cock, M., ... Witt, A. (2017). Fall armyworm: Impacts and implications for Africa. *Outlooks on Pest Management*, *28*, 196–201. https://doi.org/10.1564/v28_oct_02
- Degri, M. M., Mailafiya, D. M., & Mshelia, J. S. (2014). Effect of Intercropping Pattern on Stem Borer Infestation in Pearl Millet (*Pennisetum glaucum* L.) Grown in the Nigerian Sudan Savannah. *Advances in Entomology*, *2*, 81–86. <https://doi.org/10.4236/ae.2014.22014>
- De Lange, W. (2017). *Monetary valuation of the impact of aphids on selected commercial small grains in the Western Cape*. CSIR Report No. CSIR/NRE/GES/ER/2017/0022/A.
- Desneux, N., Wajnberg, E., Wyckhuys, K. A. G., Burgio, G., Arpaia, S., Narváez-Vasquez, C. A., ... Urbaneja, A. (2010). Biological invasion of European tomato crops by *Tuta absoluta*: Ecology, geographic expansion and prospects for biological control. *Journal of Pest Science*, *83*, 197–215. <https://doi.org/10.1007/s10340-010-0321-6>
- Deutsch, C. A., Tewksbury, J. J., Tigchelaar, M., Battisti, D. S., Merrill, S. C., Huey, R. B., & Naylor, R. L. (2018). Increase in crop losses to insect pests in a warming climate. *Science*, *361*, 916–919. <https://doi.org/10.1126/science.aat3466>

- Dillon, M. E., Wang, G., & Huey, R. B. (2010). Global metabolic impacts of recent climate warming. *Nature*, *467*, 704–706. <https://doi.org/10.1038/nature09407>
- Douris, V., Steinbach, D., Panteleri, R., Livadaras, I., Pickett, J. A., Van Leeuwen, T., ... Vontas, J. (2016). Resistance mutation conserved between insects and mites unravels the benzoylurea insecticide mode of action on chitin biosynthesis. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 14692–14697. <https://doi.org/10.1073/pnas.1618258113>
- Du Toit, F. (1989). Components of resistance in three bread wheat lines to *Diuraphis noxia* (Mordvilko). *Journal of Economic Entomology*, *82*, 1779–1781. <https://doi.org/10.1093/jee/82.6.1779>
- Elliot, K., & Madan, J. (2016). @Can GMO Crops deliver for Africa? CGD policy paper No 080. Retrieved from <http://www.cgdev.org/publication/can-gmos-deliver-africa>
- Erasmus, A. (2017). *The invasion of the fall armyworm in South Africa*. GrainSA. Retrieved from <https://www.grainsa.co.za/the-invasion-of-the-fall-armyworm-in-south-africa>
- Falck-Zepeda, Gruere G., & Sithole-Niag, I. (2012). *Genetically modified crops in Africa. Economic and policy lessons from countries south of the Sahara*. Washington DC: International Food Policy Research Institute.
- Fatoreto, J. C., Michel, A. P., Silva Filho, M. C., & Silva, N. (2017). Adaptive Potential of Fall Armyworm (Lepidoptera: Noctuidae) Limits Bt Trait Durability in Brazil. *Journal of Integrated Pest Management*, *8*, 17. <https://doi.org/10.1093/jipm/pmx011>
- Fischer, K., Van den Berg, J., & Mutengwa, C. (2015). Is Bt maize effective in improving South African smallholder agriculture? *South African Journal of Science*, *111*, 1–2. <https://doi.org/10.17159/sajs.2015/a0092>
- Fodor, N., Challinor, A., Droutsas, I., Ramirez-Villegas, J., Zabel, F., Koehler, A.-K., & Foyer, C. H. (2017). Integrating plant science and crop modelling: Assessment of the impact of climate change on soybean and maize production. *Plant and Cell Physiology*, *58*, 1833–1847.
- Food and Agriculture Organization of the United Nations. (2017). Building stronger partnerships for resilience. Food and Agriculture Organisation of the United Nations Statistics Division [WWW Document]. <http://www.fao.org/statistics/en/>.
- Food and Agriculture Organization of the United Nations. (2018). Save food for a better climate: Converting the food loss and waste challenge into climate action. <http://www.fao.org/publications/en/> accessed and downloaded August 2019.
- Fouche, A., Verhoeven, R. L., Hewitt, P. H., Walters, M. C., Kriel, C. F., & De Jager, J. (1984). Russian wheat aphid (*Diuraphis noxia*) feeding damage on wheat, related cereals and a Bromus grass species. In M. C. Walters (Ed.), *Progress in Russian Wheat Aphid (Diuraphis noxia Mordvilko) Research in the Republic of South Africa* (pp. 22–33). Pretoria, South Africa: South African Department of Agriculture, Technical Communication 191.
- Foyer, C. H., Kadambot, H. M., Siddique, H. M., Amos, H. M., Tai, P. K., Anders, S., ... Lam, H.-M. (2019). Modelling predicts that soybean is poised to dominate crop production across Africa. *Plant Cell and Environment*, *42*, 373–385. <https://doi.org/10.1111/pce.13466>
- Foyer, C. H., Rasool, B., Davey, J., & Hancock, R. D. (2016). Cross tolerance to biotic and abiotic stresses in plants: A focus on resistance to aphid infestation. *Journal of Experimental Botany*, *67*, 2025–2037. <https://doi.org/10.1093/jxb/erw079>
- Gitig, D. (2018). Planting GMOs kills so many bugs that it helps non-GMO crops Bt corn protects neighbouring peppers and green beans, cuts pesticide use. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 3320–3325. <https://doi.org/10.1073/pnas.1720692115>
- Giulianotti, L. G., & Certis, G. (2010). IPM programme for the control of *Tuta absoluta*. *Integrated Pest Control*, *52*, 162–165.
- Glatz, J., du Plessis, H., & Van den Berg, J. (2017). The effect of temperature on the development and reproduction of *Busseola fusca* (Lepidoptera: Noctuidae). *Bulletin of Entomological Research*, *107*, 39–48. <https://doi.org/10.1017/S0007485316000572>
- Guerenstein, G. P., & Hildebrand, J. G. (2008). Roles and effects of environmental carbon dioxide in insect life. *Annual Review of Entomology*, *53*, 161–178. <https://doi.org/10.1146/annurev.ento.53.103106.093402>
- Guo, J. Y., Cong, L., & Wan, F. H. (2013). Multiple generation effects of high temperature on the development and fecundity of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) biotype B. *Insect Science*, *20*, 541–549. <https://doi.org/10.1017/S1742758400022268>
- Haggis, M. J. (1986). Distribution of the African armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae), and the frequency of larval outbreaks in Africa and Arabia. *Bulletin of Entomological Research*, *76*, 151–170.
- Harrington, R., Fleming, R. A., & Woiwod, I. P. (2001). Climate change impacts on insect management and conservation in temperate regions: Can they be predicted? *Agricultural and Forest Entomology*, *3*, 233–240. <https://doi.org/10.1046/j.1461-9555.2001.00120.x>
- Hatting, J. L., Humber, R. A., Poprawski, T. J., & Miller, R. M. (1999). A survey of fungal pathogens of aphids from South Africa, with special reference to cereal aphids. *Biological Control*, *16*, 1–12. <https://doi.org/10.1006/bcon.1999.0731>
- Hatting, J. L., Poprawski, T. J., & Miller, R. M. (2000). Prevalence of fungal pathogens and other natural enemies of cereal aphids (Homoptera: Aphididae) in wheat under dryland and irrigated conditions in South Africa. *BioControl*, *45*, 179–199.
- Hatting, J. L., Wraight, S. P., & Miller, R. M. (2004). Efficacy of *Beauveria bassiana* (Hyphomycetes) for the control of Russian wheat aphid (Homoptera: Aphididae) on resistant wheat under field conditions. *Biocontrol Science and Technology*, *14*, 459–473.
- Heinrich, B. (1993). *The hot-blooded insects: Strategies and mechanisms of thermoregulation*, p. 601. Cambridge, MA: Harvard University Press.
- Held, M., & Baldwin, I. T. (2005). Soil degradation slows growth and inhibits jasmonate-induced resistance in *Artemisia vulgaris*. *Ecological Applications*, *15*, 1689–1700.
- Himanen, S. J., Nissinen, A., Dong, W. X., Nerg, A. M., Stewart, C. N., Poppy, G. M., & Holopainen, J. K. (2008). Interactions of elevated carbon dioxide and temperature with aphid feeding on transgenic oilseed rape: Are *Bacillus thuringiensis* (Bt) plants more susceptible to nontarget herbivores in future climate? *Global Change Biology*, *14*, 1437–1454. <https://doi.org/10.1111/j.1365-2486.2008.01574.x>
- Huang, Y., Chen, Y., Zeng, B., Wang, Y., James, A. A., Gurr, G. M., ... You, M. (2016). CRISPR/Cas9 mediated knockout of the abdominal-A homeotic gene in the global pest, diamondback moth (*Plutella xylostella*). *Insect Biochemistry and Molecular Biology*, *75*, 98–106. <https://doi.org/10.1016/j.ibmb.2016.06.004>
- Hughes, R. D., & Maywald, G. F. (1990). Forecasting the favourableness of the Australian environment for the Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae), and its potential impact on Australian wheat yields. *Bulletin of Entomological Research*, *80*, 165–175.

- Hunter, M. D. (2001). Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Agriculture and Forest Entomology*, 3, 153–159.
- Ingber, D. A., Mason, C. E., & Flexner, L. (2018). Cry1 Bt susceptibilities of fall armyworm (Lepidoptera: Noctuidae) host strains. *Journal of Economic Entomology*, 111(1), 361–368. <https://doi.org/10.1093/jee/tox311>
- IPCC (2014). Summary for policymakers. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, ... L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1–32). Cambridge, UK and New York: Cambridge University Press.
- ISAAA (2017). *Global status of commercialized Biotech/GM Crops: 2017*. ISAAA Brief No. 53. Ithaca, NY: ISAAA. Retrieved from <http://www.isaaa.org>
- ISAAA (2018). *Scientists recommend Bt maize as solution to fall armyworm infestation in Kenya*. Retrieved from <http://www.isaaa.org/kc/cropbiotechupdate/article/default.asp?ID=16136>
- Jankielsohn, A. (2011). Distribution and diversity of Russian Wheat Aphid (Hemiptera: Aphididae) biotypes in South Africa and Lesotho. *Journal of Economic Entomology*, 104, 1736–1741. <https://doi.org/10.1603/EC11061>
- Jankielsohn, A. (2016). Changes in the Russian wheat aphid (Hemiptera: Aphididae) biotype complex in South Africa. *Journal of Economic Entomology*, 109, 907–912. <https://doi.org/10.1093/jee/tov408>
- Kahn, B. (2010). Intercropping for field production of peppers. *Horticulture Technology*, 20, 530–532. <https://doi.org/10.21273/HORTTECH.20.3.530>
- Khadioli, N., Tonnang, Z. E., Muchugu, E., Ong'amo, G., Achia, T., Kipchirchir, I., ... B., (2014). Effect of temperature on the phenology of *Chilo partellus* (Swinhoe) (Lepidoptera, Crambidae); simulation and visualization of the potential future distribution of *C. partellus* in Africa under warmer temperatures through the development of life-table parameters. *Bulletin for Entomological Research*, 104, 809–822. <https://doi.org/10.1017/S0007485314000601>
- Kinama, J. M., Habineza, M., & Jean Pierre, H. M. (2018). A review on advantages of cereals-legumes intercropping system: Case of promiscuous soybeans varieties and maize. *International Journal of Agronomy and Agricultural Research*, 12, 155–165.
- Klapwijk, M. J., Ayres, M. P., Battisti, A., & Larsson, S. (2012). Assessing the impact of climate change on outbreak potential. In P. Barbosa, D. K. Letourneau, & A. A. Agrawal (Eds.), *Insect outbreaks revisited* (pp. 429–450). Chichester, UK: John Wiley & Sons Ltd.
- Knops, J. M. H., Tilman, D., Haddad, N. M., Naeem, S., Mitchell, C. E., Haarstad, J., ... Groth, J. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, 2, 286–293. <https://doi.org/10.1046/j.1461-0248.1999.00083.x>
- Konar, A., Singh, N. J., & Paul, R. (2010). Influence of intercropping on population dynamics of major insect pests and vectors of potato. *Journal of Entomological Research*, 3, 151–154.
- Koutroumpa, F. A., Monsempes, C., François, M. C., De Cian, A., Royer, C., Concordet, J. P., & Jacquin-Joly, E. (2016). Heritable genome editing with CRISPR/Cas9 induces anosmia in a crop pest moth. *Scientific Reports*, 6, 29620. <https://doi.org/10.1038/srep29620>
- Kremen, C., Iles, A., & Bacon, C. (2012). Diversified farming systems: An agroecological, systems-based alternative to modern industrial agriculture. *Ecology and Society*, 17, 44. <https://doi.org/10.5751/ES-05103-170444>
- Kriticos, D. J., Maywald, G. F., Yonow, T., Zurcher, E. J., Herrmann, N. I., & Sutherst, R. W. (2015). *CLIMEX version 4: Exploring the effects of climate on plants, animals and diseases*. Canberra: CSIRO.
- Letourneau, D. K., Armbrrecht, I., Rivera, B. S., Lerma, J. M., Carmona, E. J., Daza, M. C., ... Trujillo, A. R. (2011). Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, 21, 9–21. <https://doi.org/10.1890/09-2026.1>
- Liebhald, A. M., Berec, L., Brockerhoff, E. G., Epanchin-Niell, R. S., Hastings, A., Herms, D. A., ... Yamanaka, T. (2016). Eradication of invading insect populations: From concepts to applications. *Annual Review of Entomology*, 61, 335–352. <https://doi.org/10.1146/annurev-ento-010715-023809>
- Liu, X., Marshall, J. L., Stary, P., Edwards, O., Puterka, G., Dolatti, L., & ... Smith, C. M. (2010). Global phylogenetics of *Diuraphis noxia* (Hemiptera: Aphididae), an invasive aphid species: evidence for multiple invasions into North America. *Journal of Economic Entomology*, 103, 958–965.
- Macfadyen, S., & Kriticos, D. J. (2012). Modelling the geographical range of a species with variable lifehistory. *PLoS ONE*, 7(7), e40313. <https://doi.org/10.1371/journal.pone.0040313>
- Macfadyen, S., McDonnald, G., & Hill, M. P. (2018). From species distributions to climate change adaptation: Knowledge gaps in managing invertebrate pests in broad-acre grain crops. *Agriculture, Ecosystems & Environment*, 253, 208–219.
- Macharia, M., Gethi, M., Ngari, C. M., & Njuguna, M. (2012). Impact of climate change on wheat insect pests in Kenya. In E. Quilligan, P. Kosina, A. Downs, D. Mullen, & B. Nemcova (Eds.), *Wheat for food security in Africa conference*. October 8-12, Addis Ababa, Ethiopia.
- Maffei, M. E., Mithofer, A., & Boland, W. (2007). Before gene expression: early events in plant–insect interaction. *Trends in Plant Sciences*, 12, 310–316.
- Malézieux, E. (2012). Designing cropping systems from nature. *Agronomy for Sustainable Development*, 32, 15–29. <https://doi.org/10.1007/s13593-011-0027-z>
- Malik, H. J., Raza, A., Amin, I., Scheffler, J. A., Scheffler, B. E., Brown, J. K., & Mansoor, S. (2016). RNAi-mediated mortality of the whitefly through transgenic expression of double-stranded RNA homologous to acetylcholinesterase and ecdysone receptor in tobacco plants. *Scientific Reports* 6, Article number. *Brown & Shahid Mansoor*, 6, 38469. <https://doi.org/10.1038/srep38469>
- Malinga, J. N., Kinyua, M. G., Kamau, A. W., Wnjama, J. K., Awalla, J. O., & Pathak, R. S. (2007). Biotypic and genetics variation within tropical populations of Russian wheat aphid, *Diuraphis noxia* (Kurdjumov)(Homoptera: Aphididae) in Kenya. *Journal of Entomology*, 4, 350–361.
- Martins, C. M., Beyene, G., Hofs, J.-L., Krüger, K., Van der Vyver, C., Schlüter, U., & Kunert, K. J. (2008). Effect of water deficit stress on cotton plants expressing the Bt-toxin. *Annals of Applied Biology*, 152, 255–262.
- Mattson, W., & Haack, R. (1987). Role of drought in outbreaks of plant-eating insects. *BioScience*, 37, 110–118.
- Mhamdi, A., & Noctor, G. (2016). High CO₂ primes plant biotic stress defences through 1 redox-linked pathways. *Plant Physiology*, 172, 929–942. <https://doi.org/10.1104/pp.16.01129>

- Mondor, E. B., Tremblay, M. N., Awmack, C. S., & Lindroth, R. L. (2005). Altered genotypic and phenotypic frequencies of aphid populations under enriched CO₂ and O₃ atmospheres. *Global Change Biology*, *11*, 1990–1996. <https://doi.org/10.1111/j.1365-2486.2005.1054.x>
- Mugerwa, H., Seal, S., Wang, H.-L., Patel, M. V., Kabaalu, R., Omongo, C. A., ... Colvin, J. (2018). African ancestry of New World, *Bemisia tabaci*-whitefly species. *Scientific Reports*, *8*(1), 2734. <https://doi.org/10.1038/s41598-018-20956-3>
- Mugo, S., Murenga, M. G., Karaya, H., Tende, R., Taracha, C., Gichuki, S., ... Chavangi, A. (2011). Control of *Busseola fusca* and *Chilo partellus* stem borers by *Bacillus thuringiensis* (Bt)- δ -endotoxins from Cry1Ab gene event MON810 in greenhouse containment trials. *African Journal of Biotechnology*, *10*, 4719–4724.
- Nagoshi, R. N., Meagher, R. L., & Hay-Roe, M. (2012). Inferring the annual migration patterns of fall armyworm (Lepidoptera: Noctuidae) in the United States from mitochondrial haplotypes. *Ecology and Evolution*, *2*(7), 1458–1467. <https://doi.org/10.1002/ece3.268>
- Navarro, M., & Hautea, R. (2011). Communication challenges in crop biotechnology. The Asia Pacific experience. *Asia Pacific Journal of Molecular Biology and Biotechnology*, *19*, 131–136.
- Newbery, F., Qi, A., & Fitt, B. D. L. (2016). Modelling impacts of climate change on arable crop diseases: progress, challenges and applications. *Current Opinion in Plant Biology*, *32*, 101–109.
- Ngenya, W., Malinga, J., Tabu, I., & Masinde, E. (2016). Reproduction and population dynamics as biotypic markers of Russian wheat aphid *Diuraphis noxia* (Kurdjumov). *Insects*, *7*(2), 1–12. <https://doi.org/10.3390/insects7020012>
- Niang, I., Ruppel, O. C., Abdrabo, M. A., Essel, A., Lennard, C., Padgham, J., & Urquhart, P. (2014). Africa. In *Climate change 2014: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Niassy, S., & Subramanian, S. (2018). *Exploring the best tactics to combat fall armyworm outbreaks in Africa*. The Conversation. Retrieved from <https://theconversation.com/exploring-the-best-tactics-to-combat-fall-armyworm-outbreaks-in-africa-95451>
- Njuguna, M. N., Macharia Mwangi, M. H. G., Kamundia, J. K., Koros, I., & Ngotho, G. (2016). Cultural management of Russian wheat aphid infestation of bread wheat varieties in Kenya. *African Crop Science Journal*, *24*(Suppl. S1), 101–107.
- Noctor, G., & Mhamdi, A. (2017). Climate change, CO₂, and defense: The metabolic, redox, and signaling perspectives. *Trends in Plant Science*, *22*(10), 857–870. <https://doi.org/10.1016/j.tplan.2017.07.007>
- Organisation for Economic Co-operation and Development/United Nations (2011). *Economic diversification in Africa. A review of selected countries*. Paris, France: Organisation for Economic Co-operation and Development/United Nations.
- Overholt, W. A., Ngi-Song, A. J., Kimani, S. K., Mbatia, J., Lammers, P., & Kioko, E. (1994). Ecological considerations of the introduction of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) for biological control of *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in Africa. *Biocontrol News and Information*, *15*, 19N–24N, ref.77.
- Paarlberg, R. L. (2010). *Food politics: what everybody needs to know*. Oxford, England: Oxford.
- Paini, D. R., Sheppard, A. W., Cook, D. C., De Barro, P. J., Worner, S. P., & Thomas, M. B. (2016). Global threat to agriculture from invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 7575–7579. <https://doi.org/10.1073/pnas.1602205113>
- Parker, J. E., Rodriguez-Saona, C., Hamilton, G. C., & Snyder, W. E. (2013). *Companion planting and insect pest control*. Copenhagen, Denmark: INTECH Open Access Publisher.
- Perkins, A., Xu, X., Higgs, D. R., Patrinos, G. P., Arnaud, L., Bieker, J. J., & Philipson, S. (2016). Krüppeling erythropoiesis: An unexpected broad spectrum of human red blood cell disorders due to *KLF1* variants. *Blood*, *127*, 1856–1862. <https://doi.org/10.1182/blood-2016-01-694331>
- Pfeiffer, D., Muniappan, R., Sall, D., Diatta, P., Diongue, A., & Dieng, E. O. (2013). First record of *Tuta absoluta* (Lepidoptera: Gelechiidae) in Senegal. *Fla Entomology*, *96*, 661–662.
- Pimentel, D., Hepperly, P., Hanson, J., Douds, D., & Seidel, R. (2005). Environmental, energetic, and economic comparisons of organic and conventional farming systems. *BioScience*, *55*, 7–15. [https://doi.org/10.1641/0006-3568\(2005\)055\[0573:EEAECO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0573:EEAECO]2.0.CO;2)
- Plant Health Australia (2017). *Russian Wheat Aphid* (Diuraphis noxia). Retrieved from <https://portal.biosecurityportal.org.au/rwa/Documents/Russian%20Wheat%20Aphid%20Distribution%20Map.pdf>
- Pogue, M. (2002). A world revision of the genus *Spodoptera* Guenée (Lepidoptera: Noctuidae). *Memoirs of the American Entomological Society*, *43*, 1–202.
- Prasanna, B. M., Huesing, J. E., Eddy, R., & Peschke, V. M. (Eds). (2018). *Fall armyworm in Africa: A guide for integrated pest management, first edition*. Mexico, CDMX: CIMMYT. USAID and CIMMYT. Retrieved from https://reliefweb.int/sites/reliefweb.int/files/resources/FallArmyworm_IPM_Guide_forAfrica.pdf
- Pratt, C. F., Constantine, K. L., & Murphy, S. T. (2017). Economic impacts of invasive alien species on African smallholder livelihoods. *Global Food Security*, *14*, 31–37.
- Prinsloo, G. J. (1998). *Aphelinus hordei* (Kurdjumov) (Hymenoptera: Aphelinidae) a parasitoid released for control of *Diuraphis noxia* (Kurdjumov)(Homoptera: Aphididae) in South Africa. *African Entomology*, *6*, 147–156.
- Prinsloo, G. J. (2000). Host and host instar preference of *Aphelinus* sp.nr. *varipes* (Hymenoptera: Aphelinidae), a parasitoid of cereal aphids (Homoptera: Aphididae) in South Africa. *African Entomology*, *8*, 57–61.
- Prinsloo, G. J., & Du Plessis, U. (2000). Temperature requirements of *Aphelinus* sp. nr. *varipes* (Foerster) (Hymenoptera: Aphelinidae) a parasitoid of the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Homoptera: Aphididae). *African Entomology*, *8*, 75–79.
- Ramirez-Cabarel, N. Y. Z., Kumar, L., & Shabani, F. (2017). Future climate scenarios project a decrease in the risk of fall armyworm outbreaks. *The Journal of Agricultural Science*, *155*, 1219–1238. <https://doi.org/10.1017/S0021859617000314>
- Rao, M. S., Manimanjari, D., Vanaja, M., Rama Rao, C. A., Srinivas, K., Rao, V. U. M., & Venkateswarlu, B. (2012a). Impact of elevated CO₂ on tobacco caterpillar, *Spodoptera litura* on peanut, *Arachis hypogaea*. *Journal of Insect Science*, *12*, 103.
- Rao, M. S., Rama Rao, C. A., Srinivas, K., Pratibha, G., Vidya Sekhar, S. M., Sree Vani, G., & Rizk, A. M. (2012b). Effect of strip-management on the population of the aphid, *Aphis craccivora* Koch and its associated predators by intercropping *Faba bean*, *Vicia faba* L. with coriander, *Coriandrum sativum* L. *Egyptian Journal of Biological Pest Control*, *21*, 81–87.
- Rebers, J. E., & Willis, J. H. (2001). A conserved domain in arthropod cuticular proteins binds chitin. *Insect Biochemistry and Molecular Biology*, *31*, 1083–1093.
- Ryalls, J. M. W., Moore, B. D., Riegler, M., Gherlenda, A. N., & Johnson, S. N. (2015). Amino-acid mediated impacts of elevated

- carbon dioxide and simulated root herbivory on aphids are neutralized by increased air temperatures. *Journal of Experimental Botany*, *66*, 613–623. <https://doi.org/10.1093/jxb/eru439>
- Sasson, A. (2012). Food security for Africa: An urgent global challenge. *Agriculture & Food Security*, *1*(1), 2. <https://doi.org/10.1186/2048-7010-1-2>
- Savary, S., Willocquet, L., Pethybridge, S. J., Esker, P., McRoberts, N., & Nelson, A. (2019). The global burden of pathogens and pests on major food crops. *Nature Ecology & Evolution*, *3*(3), 430–439. <https://doi.org/10.1038/s41559-018-0793-y>
- Schlenker, W., & Lobell, D. B. (2010). Robust negative impacts of climate change on African agriculture. *Environ Research Letters*, *5*(1), 014010. <https://doi.org/10.1088/1748-9326/5/1/014010>
- Selale, H., Dağlı, F., Mutlu, N., Doğanlar, S., & Frary, A. (2017). *Cry1Ac*-mediated resistance to tomato leaf miner (*Tuta absoluta*) in tomato. *Plant Cell, Tissue and Organ Culture (PCTOC)*, *131*, 65–73. <https://doi.org/10.1007/s11240-017-1262-z>
- Serdeczny, O., Adams, S., Baarsch, F., Coumou, D., Robinson, A., Hare, W., ... Reinhard, J. (2016). Climate change impacts in Sub-Saharan Africa: From physical changes to their social repercussions. *Regional Environmental Change*, *17*, 1585–1600. <https://doi.org/10.1007/s10113-015-0910-2>
- Sharaby, A., Abdel-Rahman, H., & Sabry, S. (2015). Moawad1 intercropping system for protection the potato plant from insect infestation. *Ecologia Balkanica*, *7*, 87–92.
- Sisay, B., Simiyu, J., Malusi, P., Likhayo, P., Mendesil, E., Elibariki, N., ... Tefera, T. (2018). First report of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), natural enemies from Africa. *Journal of Entomology*, *142*, 800–804.
- Smyth, S. J. (2017). Genetically modified crops, regulatory delays, and international trade. *Food Energy Security*, *6*, 78–86. <https://doi.org/10.1002/fes3.100>
- Song, B., Tang, G., Sang, X., Zhang, J., Yao, Y., & Wiggins, N. (2013). Intercropping with aromatic plants hindered the occurrence of *Aphis citricola* in an apple orchard system by shifting predator-prey abundances. *Biocontrol Science and Technology*, *3*, 381–395. <https://doi.org/10.1080/09583157.2013.763904>
- Storer, N. P., Babcock, J. N., Schlenz, M., Meade, T., Thompson, G. D., Bing, J. W., & Huckaba, R. M. (2010). Discovery and characterization of field resistance to Bt Maize: *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Puerto Rico. *Journal of Economic Entomology*, *103*, 1031–1038. <https://doi.org/10.1603/EC10040>
- Strydom, E., Erasmus, A., du Plessis, H., & Van den Berg, J. (2019). Resistance status of *Busseola fusca* (Lepidoptera: Noctuidae) populations to single- and stacked-gene Bt Maize in South Africa. *Journal of Economic Entomology*, *112*, 305–315. <https://doi.org/10.1093/jeet/toy306>
- Sulvai, F., Chaúque, B. J. M., & Macuvele, D. L. P. (2016). Intercropping of lettuce and onion controls caterpillar threat, *Agrotis ipsilon* major insect pest of lettuce. *Chemical and Biological Technologies in Agriculture*, *3*, 28. <https://doi.org/10.1186/s40538-016-0079-z>
- Sun, D., Guo, Z., Liu, Y., & Zhang, Y. (2017). Progress and prospects of CRISPR/Cas systems in insects and other Arthropods. *Frontiers in Physiology*, *8*, 608. <https://doi.org/10.3389/fphys.2017.00608>
- Sutherst, R. W., Maywald, G. F., & Kriticos, D. J. (2007). *CLIMEX version 3: User's guide* (p. 131). Melbourne, Vic.: Hearne Scientific Software.
- Tabashnik, B. E., Fabrick, J. A., Unnithan, G. C., Yelich, A. J., Masson, L., Zhang, J., & Soberón, M. (2013). Efficacy of genetically modified Bt toxins alone and in combinations against pink bollworm resistant to Cry1Ac and Cry2Ab. *PLoS one*, *8*(11), e80496. <https://doi.org/10.1371/journal.pone.0080496>
- Tefera, T., Mugo, S., Mwimali, M., Anani, B., Tende, R., Beyene, Y., ... Prasanna, B. M. (2016). Resistance of Bt-maize (MON810) against the stem borers *Busseola fusca* (Fuller) and *Chilo partellus* (Swinhoe) and its yield performance in Kenya. *Crop Protection*, *89*, 202–208.
- Thornton, P. K., Jones, P. G., Ericksen, P. J., & Challinor, A. J. (2011). Agriculture and food systems in sub-Saharan Africa in a 4 °C world. *Philosophical Transactions of the Royal A Mathematical and Physical Engineering Sciences*, *369*, 117–136. <https://doi.org/10.1098/rsta.2010.0246>
- Tolmay, V. L., Lindeque, R. C., & Prinsloo, G. H. (2007). Preliminary evidence of a resistance-breaking biotype of the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Homoptera: Aphididae), in South Africa. *African Entomology*, *15*, 228–230. <https://doi.org/10.4001/1021-3589-15.1.228>
- Tolmay, V. L., Prinsloo, G. H., & Hattling, J. L. (2000). Russian wheat aphid resistant wheat cultivars as the main component of an integrated control programme. In CIMMYT [Centro Internacional de Mejoramiento de Maiz y Trigo (International Maize and Wheat Improvement Centre)] (Ed.), *The Eleventh Regional Wheat Workshop for Eastern, Central and Southern Africa* (pp. 190–194). Addis Ababa, Ethiopia: CIMMYT.
- Tonnang, H. E. Z., Hervéc, H. D. B., Biber-Freudenberger, L., Salifub, D., Subramanian, S., Ngowi, V. B., ... Christian Borgemeister, C. (2017). Advances in crop insect modelling methods—Towards a whole system approach. *Ecological Modelling*, *354*, 88–103. <https://doi.org/10.1016/j.ecolmodel.2017.03.015>
- Tonnang, H. E. Z., Mohamed, S. F., Khamis, F., & Ekesi, S. (2015). Identification and Risk Assessment for Worldwide Invasion and Spread of *Tuta absoluta* with a Focus on Sub-Saharan Africa: Implications for Phytosanitary Measures and Management. *PLoS ONE*, *10*(8), e0135283. <https://doi.org/10.1371/journal.pone.0135283>
- Traynor, P., Adonis, M., & Gil, L. (2007). Strategies approaches to informing the public about Biotechnology in Latin America. *Electronic Journal of Biotechnology*, *10*(2), 169–177.
- Vaiyapuri, K., Amanullah, M. M., Rajendran, K., & Sathyamoorthi, K. (2010). Intercropping unconventional green manures in cotton: An organic approach for multiple benefits: A review. *Asian Journal of Plant Sciences*, *9*, 223–226. <https://doi.org/10.3923/ajps.2010.223.226>
- Vandegheuchte, M. L., de la Peña, E., & Bonte, D. (2010). Relative importance of biotic and abiotic soil components to plant growth and insect herbivore population dynamics. *PLoS ONE*, *5*(9), e12937. <https://doi.org/10.1371/journal.pone.0012937>
- Van Niekerk, H. A. (2001). Southern Africa wheat pool. In A. P. Bonjean & W. J. Angus (Eds.), *The world wheat book: The history of wheat breeding* (pp. 923–936). Paris, France: Lavoisier Publishing.
- Walters, M. C. (1984). *Progress in Russian wheat aphid (Diuraphis noxia Mordvilko) research in the Republic of South Africa*. Pretoria, South Africa: South African Department of Agriculture, Technical Communication 191.
- Walters, M. C., Penn, F., du Toit, F., Botha, T. C., Aalbersberg, Y. K., Hewitt, P. H., & Broodryk, S. W. (1980). *The Russian wheat aphid*. Farming in South Africa Leaflet Series, Wheat G.3/1980, Pretoria.

- Wan, F. H., & Yang, N. W. (2016). Invasion and management of agricultural alien insects in China. *Annual Review of Entomology*, *61*, 77–98.
- Wang, J., Zhang, H., Wang, H., Zhao, S., Zuo, Y., Yang, Y., & Wu, Y. (2016). Functional validation of cadherin as a receptor of Bt toxin Cry1Ac in *Helicoverpa armigera* utilizing the CRISPR/Cas9 system. *Insect Biochemistry and Molecular Biology*, *76*, 11–17. <https://doi.org/10.1016/j.ibmb.2016.06.008>
- Ward, N. L., & Masters, G. J. (2007). Linking climate change and species invasion: An illustration using insect herbivores. *Global Change Biology*, *13*, 1605–1615. <https://doi.org/10.1111/j.1365-2486.2007.01399.x>.
- Wild, S. (2017). African countries mobilize to battle invasive caterpillar. *Nature*, *543*, 13–14. <https://doi.org/10.1038/nature.2017.21527>
- Xie, H., Liu, K., Sun, D., Wang, Z., Lu, X., & He, K. (2015). A field experiment with elevated atmospheric CO₂-mediated changes to C4 crop-herbivore interactions.
- Yazdani, M., Baker, G., DeGraaf, H., Henry, K., Hill, K., Kimber, B., ... Nash, M. A. (2017). First detection of Russian wheat aphid *Diuraphis noxia* Kurdjumov, 1913 (Hemiptera: Aphididae) from Australia: A major threat to cereal production. *Austral Entomology*, *57*, 410–417. <https://doi.org/10.1111/aen.12292>
- Yu, S. J. (1991). Insecticide resistance in the fall armyworm, *Spodoptera frugiperda* (Smith, J.E.). *Pesticide Biochemistry and Physiology*, *39*, 84–91. [https://doi.org/10.1016/0048-3575\(91\)90216-9](https://doi.org/10.1016/0048-3575(91)90216-9)
- Zerbe, N. (2004). Feeding the famine? American food aid and the GMO debate in Southern Africa. *Food Policy*, *29*, 593–608. <https://doi.org/10.1016/j.foodpol.2004.09.002>
- Zhang, L., van der Werf, W., Zhang, S., Li, B., & Spiertz, J. H. J. (2007). Growth, yield and quality of wheat and cotton in relay strip intercropping systems. *Field Crops Research*, *103*, 178–188. <https://doi.org/10.1016/j.fcr.2007.06.002>
- Zhang, R. J., Yu, D. J., & Zhou, C. Q. (2000). Effects of temperature on certain population parameters of *Liriomyza sativae* Blanchard (Diptera: Agromyzidae). *Entomologica Sinica*, *7*, 185–192.
- Zhu, G. H., Xu, J., Cui, Z., Dong, X. T., Ye, Z. F., Niu, D. J., ... Dong, S. L. (2016). Functional characterization of *SlitPBP3* in *Spodoptera litura* by CRISPR/Cas9 mediated genome editing. *Insect Biochemistry and Molecular Biology*, *75*, 1–9. <https://doi.org/10.1016/j.ibmb.2016.05.006>
- Ziska, L. H., Blumenthal, D. M., Runion, G. B., Hunt, E. R. Jr, & Diaz-Soltero, H. (2011). Invasive species and climate change: An agronomic perspective. *Climate Change*, *105*, 13–14. <https://doi.org/10.1007/s10584-010-9879-5>
- Ziter, C., Robinson, E. A., & Newman, J. A. (2012). Climate change and voltinism in Californian insect pest species: Sensitivity to location, scenario and climate model choice. *Global Change Biology*, *18*, 2771–2780. <https://doi.org/10.1111/j.1365-2486.2012.02748.x>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Botha A-M, Kunert KJ, Maling'a J, Foyer CH. Defining biotechnological solutions for insect control in sub-Saharan Africa. *Food Energy Secur.* 2020;9:e191. <https://doi.org/10.1002/fes3.191>