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REVIEW

Fall armyworm (*Spodoptera frugiperda*) (J. E. Smith) (Lepidoptera: Noctuidae) infestation: maize yield depression and physiological basis of tolerance

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Abstract

Fall armyworm (*Spodoptera frugiperda)* (FAW) is an important invasive pest of maize. The young FAW larva disrupts the photosynthetic system by feeding on the leaves. The older caterpillar interferes with pollination and fertilization processes, destroying the tassel and silks, or it bores into the maize cob, reducing harvest quality and predisposing the cob to secondary infections. The infested plant responds by channeling or converting the primary metabolites into secondary metabolites for plant defense, further reducing crop yield. The devastating feeding effect on maize becomes even more severe when maize plants are exposed to prolonged drought, during which the production of secondary metabolites is optimum. These secondary metabolites are food for herbivorous insects like the fall armyworm. Naturally, plants possess several adaptive features which enable them to cope and survive herbivorous insect attacks without compensating yield for plant defense. Such features include: thickening of the leaf cuticle of the epidermal cell walls, production of certain allelochemicals, defense proteins and the toxic chemical compound, favone glycoside (silk maysin). This review attempts to critically appraise the physiological implications of fall armyworm damage on developmental processes and maize yield. Understanding the mechanisms of various adaptive traits that confer resistance to maize against herbivorous insect damage would assist greatly in crop improvement processes.

Keywords: allelochemicals, crop yield, herbivory, plant defense, secondary metabolites

Introduction

Maize is an important cereal crop in the diet and livelihood of most inhabitants of Sub-Saharan Africa. Apart from being a major staple, maize form an important raw material for the production of confectioneries, livestock feed formulations and syrups for pharmaceuticals. Globally, there has been more demand for maize than other cereals, due to a major shift towards higher protein food necessitated by increased personal income and urbanization (FAO 2015).

Despite the numerous highlighted benefits of maize in the daily livelihood of inhabitants of Sub-Saharan African countries, a very wide margin still exists between the actual maize demand and production in the Sub-Saharan region. The low maize production could be attributed to several biotic and abiotic factors which include erratic rainfall patterns, declined soil fertility (Ngetich *et al*. 2012) and emergence and resurgence of pests and diseases (Akinbode *et al*. 2014). The devastating effects of fall armyworm, an alien pest on maize production in the Sub-Sahara and the entire African continent, cannot be underestimated.

Fall armyworm (FAW), a Lepidopteran pest, is a native of tropical and subtropical regions of the Americas (Nagoshi *et al.* 2012; Early *et al.* 2018). On arrival in Africa, this invasive pest was first noticed in some West African countries (Benin, Nigeria, Sao Tome and Principe, and Togo) in 2016 (Abrahams *et al.* 2017; FAO 2018). Subsequently, FAW has continued to spread across the entire African continent with occurrences reported and confirmed in 44 African countries (Rwomushana *et al.* 2018). Fall armyworm is a highly polyphagous insect that feeds on more than 80 crops and plant species which include sorghum, millet, vegetables and others (Prasanna 2018; Birhanu *et al.* 2018). In Africa, FAW prefers maize over any other crop. Presently, fall armyworm invasion has become the biggest threat to maize production and maize's value chain in Africa. In Nigeria, many maize farmers are switching from maize farming to production of cassava and other crops.

The fall armyworm causes crop growth distortion, reduced crop yield and total crop failure in the absence of effective management intervention. In the absence of effective control measures, FAW has the potential to cause an estimated yield loss of about 8.3 to 20.6 million tonnes of maize per annum (valued at US$ 2,481–6,187 million) in 12 maize producing countries in Sub-Saharan Africa, which accounts for approximately 20% of the total production in the region (Abrahams *et al.* 2017). Rwomushana *et al.* (2018) gave an estimated production loss of between 4.1 and 17.7 million tonnes (US$ 1,088 and US$ 4,661 million) due to fall armyworm compared with the total expected production of 39.3 million tonnes (US$ 10,343 million) across Africa. The influx of FAW on the continent indicates that there is a serious threat to food security considering the importance of maize as a major staple crop in the daily livelihood of the continent's increasing population.

Therefore, a better understanding of the mechanisms of yield loss and physiological basis of host plant resistance would assist in developing a FAW tolerant maize genotype, alongside other sustainable intervention protocols. This review has tried to appraise the impact of fall armyworm infestation on maize growth and development, yield losses and contribution of various identified adaptive features for FAW tolerance.

Factors affecting the survival of fall armyworm in Africa

Food availability

Fall armyworm is a voracious pest that shows great adaptation to diverse environments and survives on a wide range of hosts. The quality and quantity of food available to a large extent determine the rate of insect growth, survival and reproduction (Abbott 2012). Therefore, insect fecundity and rapid population growth in a new area of invasion could be enhanced by low defense and high food quality of the host (Awmack and Leather 2002; Yanchuk *et al.* 2008; Cudmore *et al.* 2010). The FAW, being a polyphagous pest, can easily switch hosts and survive on an alternative crop/plant in the absence of the preferred host. The African continent has diverse weeds and alternative crops that could serve as reservoirs for FAW survival during off planting seasons. The FAW shows vast genetic variability and two races of FAW have been identified; the 'rice strain' (R strain) which prefers feeding on rice and grasses while the 'corn strain' (C strain) feeds on maize, cotton and sorghum (Lu and Adang 1996; Lewter *et al.* 2006; Nagoshi *et al.* 2007).

Temperature

Fall armyworm was regarded as an occasional pest when it was first sighted in Africa in 2016. However, reports from farmers and other stake-holders in maize's value chain have realistically shown that FAW is an evil that we may have to contend with for a very long time. This is because even though Africa is the hottest continent, warming has been on the increase as was earlier predicted. The continent is expected to be 1.5 times warmer than the global average, according to the UN Intergovernmental Panel on Climate Change (IPCC).

Fall armyworm requires suitable climatic conditions for its reproductive and developmental processes. The FAW is a tropical species and has shown great adaption to warmer parts of South America. All aspects of insect pest out-breaks are expected to intensify as the climate warms. Hot, dry weather patterns have been found to be responsible for increased insect pest outbreaks in some parts of America (Logan *et al.* 2003). According to Dale and Frank (2017) the rise in air and host plant temperature associated with drought conditions provides a favorable thermal environment for the growth of phytophagous insects. Hence, the successful thriving of FAW on the continent of Africa could be linked to the availability of conducive and favorable climatic/weather conditions. The ideal temperature for FAW caterpillar development is 28°C (Rwomushana *et al.* 2018), whereas, temperatures can be as high as 40°C during the year in some places in Africa. Temperature plays an important role in insect metabolism, metamorphosis, mobility, and host availability, which determines the chances of changes in pest populations and dynamics (Shrestha 2019).

Recently, a research study was conducted in the United States of America, led by Deutsch in 2018, to investigate the impact of increased temperature on insects' feeding habits. The outcome of the study showed that insects tend to feed more under warmer environmental conditions (Petersen *et al.* 2000; Irlich *et al.* 2009; Dillon *et al.* 2010). Based on the outcome of the study, it was predicted that pests are expected to eat 10–25% more wheat, rice and maize across the globe for each degree rise in climate temperature. In organisms such as fall armyworm where body temperature is determined by the environment, the development rate generally changes with temperature (Garcia *et al.* 2017). Warm conditions drive insect energy and prompt them to eat more (Deutsch *et al.* 2018), thereby enhancing insect growth and fecundity. The findings of the study also presented empirical evidence that pests would show greater resistance to pesticides in warmer (similar to what exists today in the tropics) climates. Increases in temperature are expected to accelerate insect metabolism and boost an insect's appetite at a predictable rate. Conducive and favorable high temperatures provide ample potential for continuous insect breeding, resulting in four to six generations per year (population increase) (Garcia *et al.* 2017).

Plant nutrition

Plant nutritional levels and allelochemicals are very important factors determining plant suitability and resistance to insect herbivores (Chen *et al.* 2008). Greater growth rates, coupled with higher feed conversion efficiency are observed in insects that feed on diets or host plants that are high in nitrogen than on host plants with low nitrogen content (Woods 1999; Chen *et al.* 2008). According to Fox *et al.* (1990), Prudic *et al.* (2005), Bede *et al.* (2007), and Chen *et al.* (2008), herbivorous insect pests have the inherent ability to distinguish qualitatively among host plants for diet and oviposition.

Natural enemies

These are biological agents that play great roles in the development of sustainable integrated pest management of fall armyworm. Types of vegetation or landscape have been greatly influenced by intensive agricultural production. Natural habitats have been transformed and simplified leading to land fragmentations, dispersal and abundance of natural enemies (Letourneau 1998; Zabel and Tscharntke 1998; Landis *et al.* 2000; Altieri and Nicholls 2004; Tscharntke *et al.* 2005).

Unlike African armyworm, a native of Africa, that has encountered complex challenges from natural biological enemies such as predators, parasitoids and diseases which have kept the population very low. Fall armyworm is alien to Africa and was not accompanied by its natural enemies, allowing the population to increase unabatedly and unchecked (FAO 2018). However, a natural enemy (black ant) was observed feeding on the young larva of FAW on a maize field at the Institute of Agricultural Research and Training (I.A.R&T), Ibadan, in 2018. Similarly, a few new species of FAW natural enemies were recorded in maize fields in Ethiopia, Kenya and Tanzania in 2017 (Sisay *et al.* 2018). This serves as a good indicator for possible biological control of FAW in Africa.

Maize phenology and fall armyworm infestation

Maize growth and developmental stages can be classified into vegetative and reproductive stages. The vegetative growth stage can be further categorized based on the number of uppermost leaves with a visible collar (Darby and Lauer 2000). The vegetative growth stage can be further subdivided into different stages starting from VE (emergence), V1, V2 …Vn where "n" represents the last stage before Vt (tasseling).

Fall armyworm infestation could resume very early on maize, even at a very tender age after plant emergence. Fall armyworm affects maize plants at all developmental stages, but the effect of damage is more severe at the young growing phase, besides maize cobs can be severely damaged under heavy infestation. One begins to notice some degree of damage as the egg hatches into larva between 3–6 days creating windows, while constant feeding results in skeletonized leaves and heavily windowed whorls loaded with larval frass patches on the leaves (Goergen *et al.* 2016).

The period of active photosynthesis in maize begins at V3, V5 or five leaf stages (21 days after planting) when cob and tassel initiation commence (Bell 2017). During this period a new leaf appears every 3 days, while the yield potential and the number of kernel rows per cob are pre-determined (Grant 2020). At this stage, each internode is expected to develop a cob, however, only one or two internodes at the top produce cobs for harvest. The period from V7 (seven leaf) to V8 (eight leaf) represents the stage of rapid plant and cob development, while the numbers of kernel per row are also determined. The number of ovules (potential kernels) and kernel rows on each ear and the size of the ear are also pre-determined at V12 (twelve stage) (Darby and Lauer 2000; Nielson 2018). During the vegetative growth periods, the larvae of FAW feed on the leaves, move to the growing points of a young maize plant and destroy it. The large caterpillar destroys the young plant by cutting the stem at the base. The small caterpillars hide in the joints between the leaves and the stem and whorl of the maize plant during the day but feed ferociously on the leaves at night (nocturnal), thereby reducing the leaf area and the general photosynthetic system. The feeding of herbivorous insects on host plants significantly induces quite a number of biochemical and physiological changes which in turn affect the host plant (Gomez *et al.* 2012). The VT which is the stage of tassel emergence marks the end of the vegetative growth period. This period is followed by the reproductive growth stage with the emergence of the silk. The FAW destroys the tassel and clip the silk, thereby interfering with pollination and fertilization processes. Herbivorous feeding habits of FAW limit photosynthate availability due to loss of photosynthetic leaf area especially during grain filling, resulting in kernel abortion and reduced crop yield potential (Darby and Lauer 2000; Nielson 2018).

The FAW caterpillar burrows into the side of the cob, exposing the cob to secondary infections by pathogens (ear rot), consequently reducing grain yield and harvest quality. Once the maize leaves are eaten up by FAW, the leaves cannot perform the roles of trapping sunlight energy for food formation and onward translocation to the growing points and grains. Apart from reducing the photosynthetic potential of maize leaves, the laceration and wound openings formed during caterpillar feeding can become infected by disease causal organisms.

The ability of the host plant to recover from insect damage depends on the (i) severity of damage (ii) physiological age of the host plant at infestation and the (iii) effectiveness of insect control measures. For instance, young maize damaged during the early vegetative growth stage may stand a better chance of recovering when appropriate control measures are applied. The ability of the damaged plant to recover may be minimal if nothing is done quickly as the plant proceeds to maturity. The time interval at which a plant is exposed to insect infestation and the amount of tissue damage that occurs during feeding are additional parameters that significantly affect plant metabolic responses (Frost *et al.* 2008; Bruce 2015). Within an hour after exposure of a plant to herbivore feeding, expression of genes encoding for diverse plant metabolic pathways is altered (Fürstenberg-Hägg *et al.* 2013).

Variation in the genetic response of maize to fall armyworm infestation has been reported in many maize genotypes. Therefore, the level of crop damage under FAW infestation depends on (i) the phenological stage of plant development (ii) severity of infestation (iii) environmental suitability and (iv) inherent maize plant resistance.

Physiological implications of fall armyworm feeding on growth and yield of maize

Chlorophyll degradation

Chlorophyll degradation is a major consequence of herbivorous insect damage on host leaves (Ni *et al.* 2001). The leaf chlorophyll content is one of the most important factors in determining a crop's rate of photosynthesis and remains a useful indicator of both potential photosynthetic productivity and general plant vigor (Zarco-Tejada *et al.* 2002; Mao *et al.* 2007). The feeding of *Bemisia tabaci* Gennadius reduced leaf photosynthesis in tomato leaves by decreasing the content and photosynthetic capacity of chlorophyll (Buntin *et al.* 1993). In a related development, infestation by scale herbivorous insects was reported to cause significant decreases in chlorophyll *a*, *b* and carotenoid levels in plant leaves (Golan *et al.* 2015). The extent of insect damage depends on the inherent properties of the plants under infestation and the severity of infestation. Feeding injury by *Stephanitis pyrioides* (Scott) has been implicated for reduction in chlorophyll content, rate of net leaf photosynthesis and transpiration in azalea (Buntin *et al.* 1996).

Excessive and uncontrolled water loss

Evaporation occurs at damaged sites when water travels directly to the cut edge through the apoplasm or symplasm of epidermal and mesophyll cells of the damaged leaves (Canny 1990; Barbour and Farquhar 2003). The evidence of excessive and uncontrolled water loss from cut edges of leaves or injured cuticles of maize leaves by herbivorous feeding habits of FAW was well documented and reported by Ostlie and Pedigo (1984) and Welter (1989).

Nutritional deficiencies

Fall armyworm like any other insect derives its nutrients from the host plant, thereby depriving the plant of its essential nutrients. Nutritional deficiency in plants in response to insect feeding was earlier reported by Ni *et al.* (2001, 2002), Heng-Moss *et al.* (2003), Nykänen and Koricheva (2004) and Goławska *et al.* (2010).

Nutritional requirements of insects include carbohydrates, proteins, amino acids, fatty acids, minerals and vitamins (Kiran *et al.* 2018). Sugars constitute the sole food of certain adult insects and play a significant role in the feeding behavior and orientation of certain phytophagous insects on their host plants (Kiran *et al.* 2018). During drought periods, a plant produces secondary metabolites which are mainly free sugars and amino acids during osmotic adjustment (Hummel *et al.* 2010; Showler 2013; Anjorin *et al.* 2016). The production of secondary metabolites offers rich nutrition for herbivorous insects and enhances their proliferation and general performances (Huberty and Denno 2004; White 2009; Ximénez-Embún *et al.* 2017). The plant stress hypothesis (PSH) states that moderate environmental stress on plants decreases plant resistance to insects by changing the biochemical source–sink relationship and foliar chemistry, thus providing better nutrition for the insects (Behmer and Joerm 2012).

It is therefore not surprising that FAW voraciousness is usually at its peak during drought periods in a maize field. During drought periods, there is greater production of secondary metabolites. The higher the level of drought tolerance, the higher the production of secondary metabolites which are produced to prevent plant cells from oxidation death. Incidentally, these secondary metabolites are principally sugars and amino acids which are preferred by herbivorous insects like fall armyworm. Therefore, one can infer that a very high drought-tolerant crop genotype may not be a good candidate for fall armyworm resistance.

Harmful effects of an insect's salivary components and waste products

Components of saliva and waste products of most Lepidopteran and Orthopteran herbivorous insects secreted on the host plant have been found to contain certain metabolites that could influence a plant's primary metabolism and trigger defense in the host plant (Alborn *et al.* 1997, 2000, 2007; Hodge *et al.* 2013).

Aphids and other Hemiptera secrete sugar-rich honeydew known as trehalose (Hodge *et al.* 2013). Both trehalose and trehalose-6-phosphate have been identified as important plant-signaling molecules responsible for regulating the relative allocation of carbon into starch and sugar as well as plant growth and development (Cortina and Culiáñez-Macià 2005; Satoh-Nagasawa *et al.* 2006). Zhou *et al.* (2015) were of the view that insect attacks often affect reallocations of existing and newly formed primary metabolites between attacked and systemic tissues. Holland *et al.* (1996) and Lee *et al.* (2012) felt that metabolites transported in response to herbivore attack, are perhaps not stored within plants but rather exuded. An increase in carbon release and respiration was observed in the rooting system when grasshoppers fed on maize leaves. Millard and Grelet (2010) ascribed reallocation of metabolites by plants under insect attack to a recovery tolerance strategy after infestation.

Production of trichomes/thickened cell walls

Part of an induced plant response to herbivorous insect attack is the production of trichomes or thickened cell walls which confer physical defenses against insect feeding. Hedins *et al.* (1996) studies on FAW on maize reported that resistant maize lines contain more hemicellulose and cellulose in whorls than susceptible maize lines as the major difference lie in the thickness of the cuticle and the epidermal cell walls.

The cell wall of plants is made up of cellulose microfibrils which are embedded in a lignin-hemicellulosic macromolecule, to which the acetyl and phenolic acid groups are bound (Morrison 1979; Heldt and Piechulla 2011). Arabinoxylans are the characteristic hemicelluloses of cereals (Fry 1989), while p-coumaric and ferulic acids make up the phenolic constituents (Hartley and Jones 1978; Sosulski *et al.* 1982).

Increased production of secondary metabolites

Naturally, when a plant is exposed to external stress, a host of survival mechanisms to annul the consequences of such stress is presented. The damaging effects of fall armyworm on maize leaves could initiate complex processes that may affect gaseous exchange in the remaining part of the leaf tissue.

The damaged plant diverts carbon and nitrogen away from the primary metabolism into the production of secondary metabolites which consequently alter the leaf photochemical status (Karban and Myers 1989; Leon *et al.* 2001; Kessler and Baldwin 2001). The production of secondary metabolites such as reactive oxygen species may reduce photosystem II operating efficiency (PSII) and carbon assimilation rates in damaged leaves (Bi and Felton 1995; Thordal-Christensen *et al.* 1997; Leon *et al.* 2001; Bown *et al.* 2002).

At the molecular level, Schenk *et al.* (2000) inferred that herbivores may regulate defense genes at the expense of genes coding for rate-limiting constituents of photosynthetic metabolism. A similar production of reactive oxygen species (superoxides) by injured soy bean leaves under herbivorous insect damage was reported by Leon *et al.* (2001) and Bown *et al.* (2002). This results in detoxification of superoxide into hydrogen peroxide in the chloroplast thylakoid-bound superoxide dismutase in a Mehler ascorbate peroxidase pathway. The hydrogen peroxide produced withdraws electrons from the photosynthetic electron transport chain in a reaction mediated by monodehydroascorbate reductase which uses NADPH (Ort and Baker 2002). The activity of this pathway may explain the transient increase in FPSII in damaged leaves, while carbon gain either decreased or remained constant.

Production of semiochemicals

Host plants under herbivorous insect attack produce a number of volatile compounds known as "semiochemicals" which serve numerous physiological and ecological functions (Hilker and Meiners 2006). The defense volatiles which are emitted are also referred to as herbivores induced volatiles (HIPVs). The HIPVs serve as a call for natural enemies (predatory and parasitic arthropods) and alert neighboring plants of impeding attack (Kost and Heil 2006; Dicke 2009; Degenhardt 2009). Maize plants emit large quantities of different HIPVs above and below ground in response to insect feeding and egg deposition (Tamiru *et al.* 2011).

Certain defense proteins are also produced in response to herbivorous insect attacks. These include (i) proteinases (which have been recognized as defense proteins through DNA technology gene expression analyses), (ii) 33 kDa cysteine proteinase (iii) Mirl-cp, associated with chitin binding activity in damaged foliage sites in FAW resistant maize lines. These proteins move through vascular tissues and confers defense to maize (Pechan *et al.* 2000; Lopez *et al.* 2007).

Maize silk produces a toxic chemical compound, favone glycoside, known as "silk maysin" which also creates a form of resistance to Lepidoptera insects when consumed (Waiss *et al.* 1979; Snook *et al.* 1994). Ni *et al.* (2008) studied FAW resistance in seedlings of four CML inbred maize lines with varying silk maysin levels. The study revealed that inbred maize lines CML333 (with moderate silk maysin), CML336 (with low silk maysin) and CML338 (with high silk maysin) were resistant to FAW feeding at the seedling stage, compared to CML335 (without silk maysin) which was highly susceptible.

Fall armyworm damage and maize yield loss

Maize yields are greatly impaired by damages incurred from FAW feeding at virtually all developmental growth stages. Feeding of FAW larva destroys the photosynthetic apparatus of maize leaves, thereby disrupting the process of photosynthesis. Consequently, the photoassimilates generated in the mesophyll cells become significantly or totally reduced.

The source capacity or availability of photoassimilates primarily depends on the efficacy of the photosynthetic system. The source capacity to a large extent determines the rate of photoassimilate partitioning into various sinks (Ho 1988). Photoassimilate partitioning between different organs is the major determinant of plant growth and development (Tymowska--Lalanne and Kreis 1998). Feeding of FAW on maize not only interferes with the growth processes but also disrupts the development of plant yield potentials. When leaves of maize are destroyed by FAW during the grain filling stage, partitioning of assimilates into the "sinks" becomes seriously affected. Clipping of maize tassel and silk by FAW can result in poor pollination, reduced fertilization, kernel abortion and reduced grain yield. Plants respond naturally by producing a host of defensive mechanisms to counter the stress imposed by herbivorous insect attacks. This involves the production of myriads of defensive mechanisms such as reactive oxygen species also known as compatible solutes or secondary metabolites. These secondary metabolites are classified as hydroxyl (sucrose, polyhydric alcohols and oligosaccharides) and nitrogen containing groups (compounds include proline, other amino acids, quaternary ammonium compounds and polyamines). Resources for the production of primary metabolites are diverted to the biosynthesis of secondary metabolites, thereby reducing crop yield.

Damage to cobs may lead to fungal infection and aflatoxins resulting in significant yield loss and maize grain quality. Earlier reports have shown that bacteria and viruses are among the major factors reducing maize yields in Africa (Fajemisin *et al.* 1984; Fajemisin 1985; Mihm 1994). Bacteria, fungi and virus enter plants through wounds caused by insects consequently affecting crop yield and economic value (Nazarov *et al.* 2020). Evidence of insect (plant hopper) transmitting maize stripe virus (MStV) was well documented and reported by Falk and Tsai (1998) and Ramirez (2008). The adult moths of FAW are strong flyers and migrate quickly. There is great chance of plant disease transmission across borders, though presently information on fall armyworm disease transmission is very scarce.

Conclusions

Fall armyworm, an invasive herbivorous insect feeds on maize plants virtually at all developmental stages. The extent of damage depends on the maize phenological growth phase at the time of infestation, the severity of infestation which is subject to insect population, environmental suitability and inherent maize plant resistance. The herbivorous feeding habits of fall armyworm negatively influenced processes that are directly or indirectly associated with maize yield. FAW feeding causes chlorophyll degradation, excessive and uncontrolled water loss, disruption of photosynthetic processes, nutrient deficiency and an increased rate of respiration. Conversion of the plant primary metabolites into secondary metabolites towards plant resistance limits crop yield.

Fall armyworm constitutes an important pest of maize across Africa and several parts of the world. This review has critically appraised the impact of FAW damage on maize physiology, crop responses and yield depression. This information can assist in developing sustainable intervention protocols for modifying maize morphology, biochemistry and genetic composition towards fall armyworm resistance/ tolerance while crop yield is stabilized.

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