



Postharvest insect resistance in maize

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ABSTRACT

One of the main challenges for the 21st century is ensuring global food security. Today, maize is the largest staple crop produced worldwide. Postharvest primary insect pests, especially the maize weevil (*Sitophilus zeamais*) and the large grain borer (*Prostephanus truncatus*) cause food-grain losses during storage up to 40% of total production, mainly in developing countries. Alternatives for pest management have been explored, including the implementation of hermetic storage structures and the application of chemical insecticides. Nevertheless, in low-income regions, both strategies are rarely accessible to smallholders. Modern breeding programs have endeavored to develop insect-resistant varieties, which diminish postharvest pest losses. In this review, we report the current status and advances in maize kernel-pest interactions, the bases and mechanisms of kernel resistance and their biotechnological perspectives. We demonstrate that the comprehension of resistance mechanisms has been fundamental for the development of new productive and resistant varieties, representing a sustainable alternative for developing countries. Finally, we analyse the biotechnological perspectives of natural kernel resistance in global food security.

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1. Introduction

Maize (*Zea mays* L. (Poaceae)), is the staple crop with the largest production worldwide, with an estimated of 1026 million tons (Cerquiglini et al., 2016). This cereal is the basic food in developing countries in terms of calories and protein intake, ranging from 61% in Mesoamerica, 45% in Eastern and Southern Africa, 29% in the Andean region, to 25% in West and Central Africa (Shiferaw et al., 2011). In the cited regions, maize is mainly cultivated by small-holder farmers, who take advantage of corn adaptability, high yields and valuable by-products (Rosegrant et al., 2009; Shiferaw et al., 2011). However, biotic and abiotic factors cause losses ranging 30–60% of global yield (Gitonga et al., 2013; Lesk et al., 2016; Ronald, 2011; Shiferaw et al., 2011). Abiotic stress is mainly caused by extreme environmental conditions, which are enhanced by climate change (Lesk et al., 2016; Ronald, 2011; Shiferaw et al., 2011). Biotic stress caused by diseases, weeds, and insects lead to losses of 54% of attainable yield in Africa, 48% in Central and South America, whereas in Asia reached 42% (Oerke, 2006; Shiferaw et al., 2011). Pre-harvest pests represent an average of 35% of potential yield loss worldwide (Oerke, 2006; Popp et al., 2013), whereas postharvest losses range between 14 and 36%. These losses could be observed along the whole food chain, including transport, pre-processing, storage, processing, packaging, marketing and plate waste (Kumar and Kalita, 2017; Popp et al., 2013; Tefera, 2012; Serna-Saldivar and García-Lara, 2016). Postharvest losses caused by insect pests represent 12–36% of grain weight worldwide (Gitonga et al., 2013; Tefera et al., 2016), affecting mainly low-income developing countries, due to poor postharvest management and inappropriate grain storage conditions (Gitonga et al., 2013; Midega et al., 2016; Tefera et al., 2016; García-Lara and Serna-Saldivar, 2016). Furthermore, significant losses in terms of product quality has been observed when infested kernels by insects were used for manufacture end products such as tortillas (García-Lara et al., 2013a,b).

Management programs have explored diverse alternatives to reduce insect postharvest losses, including chemical crop protection and the implementation of hermetical storage structures (Boyer et al., 2012; García-Lara et al., 2013a,b; Gitonga et al., 2013; Mlambo et al., 2017; Tefera et al., 2011a). International breeding efforts have endeavored to develop high yield insect-resistant maize varieties (Abebe et al., 2009; Tefera et al., 2013, 2016), using maize landraces as natural sources of resistance, which are also adapted to the farming conditions of the target regions. (Arnason et al., 1994; Abebe et al., 2009; García-Lara and Bergvinson, 2013; Midega et al., 2016; Mikami et al., 2012; Tefera et al., 2016). Thus, the knowledge of the mechanisms and molecular bases of the natural resistance is crucial to the identification of resistance traits, which can be used in high-yield insect-resistant varieties. In this review, we discuss the current knowledge about the natural resistance to main storage pests in maize.

2. Distribution and impact of post-harvest insect pests

Postharvest maize insect pests include many species from the orders Coleoptera and Lepidoptera, which are distributed worldwide, causing yield and quality losses of grains and by-products, with important economic repercussions (García-Lara and Bergvinson, 2014; Sallam, 1999). However, most of the insect postharvest losses are caused by populations of a single pest, depending of the region and the agroecology, as observed in Table 1. Species such as *Sitophilus zeamais*, *Prostephanus truncatus*, *Sitotroga cerealella*, *Rhyzopertha dominica* and *Tribolium castaneum* are considered major pests and are a serious concern in global agriculture (CABI, 2017; García-Lara and Bergvinson, 2014; Gitonga et al., 2013; Mohandass et al., 2007; Sallam, 1999; Tefera et al., 2016). In this review we will focus mainly in two species: *Sitophilus zeamais* and *Prostephanus truncatus*.

2.1. Maize weevil (*Sitophilus zeamais* Motschulsky)

Sitophilus zeamais (Coleoptera: Curculionidae) has an ancient origin, about 8.7 million years ago, and has been recognized as predator of modern maize (Corrêa et al., 2016). This pest has been detected in 112 countries worldwide (Fig. 1 and Table 1) (CABI, 2017). *Sitophilus zeamais* is responsible for 12–36% grain weight loss worldwide (García-Lara and Bergvinson, 2014; Gitonga et al., 2013; Tefera et al., 2016), reaching 65–80% in vulnerable zones from tropical and subtropical regions. In western Kenya, 67% of farmers reported very severe losses caused by this pest (Midega et al., 2016), whereas in Ethiopia losses reached 80% (Sori and Ayana, 2012). These scenarios lead to extreme food insecurity and poverty in vulnerable regions (Abass et al., 2014; Affognon et al., 2015; Kumar and Kalita, 2017).

2.2. Large grain borer (*Prostephanus truncatus* Horn)

Prostephanus truncatus (Coleoptera: Bostrichidae) is a pest originated in meso-America and accidentally introduced to Africa in the late 1970s (Hodges, 1986). This pest has been detected in tropical and subtropical regions in 26 countries (Table 1 and Fig. 1) (APHIS, 2017; CABI, 2017; EPPPO, 2017). *P. truncatus* has an enormous impact on the agriculture due to its voracious behavior (Abass et al., 2014; García-Lara and Bergvinson, 2013; Midega et al., 2016). In Latin America, losses caused by this pest can be as high as 50–80% (García-Lara and Bergvinson, 2013; Kumar and Kalita, 2017). In Western Kenya, 84% of farmers experienced severe losses in stored maize caused by *P. truncatus* (Midega et al., 2016), while in Tanzania these losses reached 56.7% (Abass et al., 2014). Thus, this pest is also a major concern in food security of tropical and dry regions.

Table 1
Geographical distribution of economically important postharvest insect pests.

Species	Distribution	References
<i>Sitophilus oryzae</i>	Warm, tropical and temperate regions worldwide	Sallam, 1999; Mason and McDonough 2012; CABI, 2017; EPPO, 2017
<i>Sitophilus zeamais</i>	Warm and tropical regions worldwide	Sallam, 1999; Mason and McDonough, 2012; CABI, 2017; EPPO, 2017
<i>Sitophilus granarius</i>	Temperate regions in Asia, Africa, North and South America, Europe and Australia	Sallam, 1999; Mason and McDonough, 2012; CABI, 2017; EPPO, 2017
<i>Tribolium castaneum</i>	Tropical and subtropical regions worldwide. Secondary pest.	Sallam, 1999
<i>Tribolium confusum</i>	Tropical and subtropical regions worldwide. Secondary pest.	Sallam, 1999
<i>Tenebrio molitor</i>	Worldwide	Sallam, 1999
<i>Rhyzopertha dominica</i>	Tropical and temperate regions worldwide	Sallam, 1999; Mason and McDonough, 2012; CABI, 2017
<i>Prostephanus truncatus</i>	Southern USA, Mexico, Central and South America, Africa, Italy. Categorized as quarantine pest in Israel (2009), Jordan (2007) and New Zealand (2000)	Sallam, 1999; CABI, 2017; APhIS, 2017; EPPO, 2017
<i>Trogoderma granarium</i>	Temperate regions in South Asia, Africa, former USSR and Spain	Sallam, 1999; CABI, 2017; EPPO, 2017
<i>Tenebroides mauritanicus</i>	Worldwide. Categorized as quarantine pest in Jordan (2007)	Sallam, 1999; EPPO, 2017
<i>Ephesia cautella</i>	Tropical and subtropical regions worldwide	Sallam, 1999
<i>Plodia interpunctella</i>	Tropical, subtropical and temperate regions worldwide	Mohandass et al., 2007; Sallam, 1999
<i>Sitotroga cerealella</i>	Worldwide	Sallam, 1999; CABI, 2017; EPPO, 2017
<i>Cryptolestes ferrugineus</i>	Worldwide. Categorized as quarantine pest in Jordan (2007)	Mason and McDonough, 2012; EPPO, 2017

2.3. Strategies for reduction of postharvest food-grain losses

Integrated pest management programs have explored diverse alternatives to reduce pest postharvest losses, considering the taxonomy, behavior, ecology and biology of the insects and the effective use of monitoring and management tools (Trematerra, 2013). Chemical protection of stored crops has been successfully used to control insect populations, being phosphine the most widely used insecticide (Boyer et al., 2012). However, this strategy have demonstrated hazardous effects to the environment and toxic effects on human and animal health (Boyer et al., 2012; Bumbrah et al., 2012). Besides pesticide toxicity, development of insecticide resistance has been recorded for at least 28 species (Boyer et al., 2012), such as phosphine-resistant populations of *Rhyzopertha dominica* in Australia (Collins et al., 2017) or pyrethroid-resistant populations of *Sitophilus zeamais* in Brazil (Corrêa et al., 2011). Thus, it is necessary to explore less toxic and more sustainable alternatives (García-Lara and Serna-Saldivar, 2016).

Hermetic storage structures, including metal silos and portable hermetic bags have been successfully tested under laboratory conditions against diverse pests, including *S. zeamais*, *P. truncatus* and *S. cerealella* (García-Lara et al., 2013a,b; Tefera et al., 2011). Consequently, these structures were tested at field-scale in vulnerable regions, with successful results (Gitonga et al., 2013; Ng'ang'a et al., 2016). In Kenya, the usage of metal silos and super grain bags lead to reduction of losses caused by *S. zeamais* and *P. truncatus* to less than 5% (De Groote et al., 2013). However, the associated costs are often unaffordable to low-income farmers (Midega et al., 2016).

In vulnerable regions, farmers have explored more accessible alternatives, such as the application of ground powders from repellent native plants to stored kernels (Midega et al., 2016) and the use of local varieties with some degree of natural resistance. Native maize landraces have been identified as some of the best natural sources of resistance, leading to loss reduction to less than 10% without cost increment (Daiki et al., 2017; García-Lara and Bergvinson, 2013; Mwololo et al., 2012). However, their yield is often very low. International breeding programs have therefore

considered native landraces for the development of high yield genotypes with insect resistance (Abebe et al., 2009; Tefera et al., 2016). Population 84 is an example of an insect-resistant genotype, derived from 20 Caribbean accessions with high resistance to *S. zeamais* and moderate resistance to *P. truncatus* (Bergvinson and García-Lara, 2011; García-Lara et al., 2004, 2007). This genotype displayed loss reduction to 30% of grain weight loss caused by *P. truncatus* infestation in comparison with a susceptible (Bergvinson and García-Lara, 2011). For *S. zeamais*, loss reduction reached up 75% of grain weight loss in comparison with a susceptible genotype (García-Lara et al., 2007). Thus, the development of insect-resistant genotypes would be a sustainable alternative for pest control.

Additionally, biological control strategies based on pest/predator or pest/parasitic species have been tested for several pests, including *S. zeamais* and *P. truncatus* (Schöller and Flinn, 2000). Parasitic species, such as *Lariophagus distinguendus* have demonstrated high potential for *S. zeamais* control, leading to population reduction between 34 and 74% in bulk maize and 81% in bag stored maize (Adarkwah et al., 2012). In Kenya, interaction between *P. truncatus* and *Teretrius nigrescens* (predator) led to reduction of 84% of the *P. truncatus* population in a time lapse of 5 years (Hill et al., 2003). In addition, combination of insect-resistant genotypes and *Teretrius nigrescens* displayed synergistic effects on *P. truncatus* control, leading to adult progeny reduction of 80%, whereas grain weight losses were diminished 80% in 28 weeks (Bergvinson and García-Lara, 2011).

Transgenic avidin maize was considered as a possible alternative to reduce insect postharvest losses. This GMO was tested at laboratory scale, showing demonstrated toxic effects against diverse storage pests, including *S. zeamais* and *Sitotroga cerealella*. However, this technology is not applicable to *P. truncatus*, which displayed tolerance to avidin (Kramer et al., 2000). Moreover, the development and application of GMO has been a serious concern in the last years, due to rigid regulations and low social acceptance (Araki and Ishii, 2015; Azadi et al., 2017).

Thus, the identification of resistance traits in natural sources is crucial to the development of new varieties adapted to smallholder

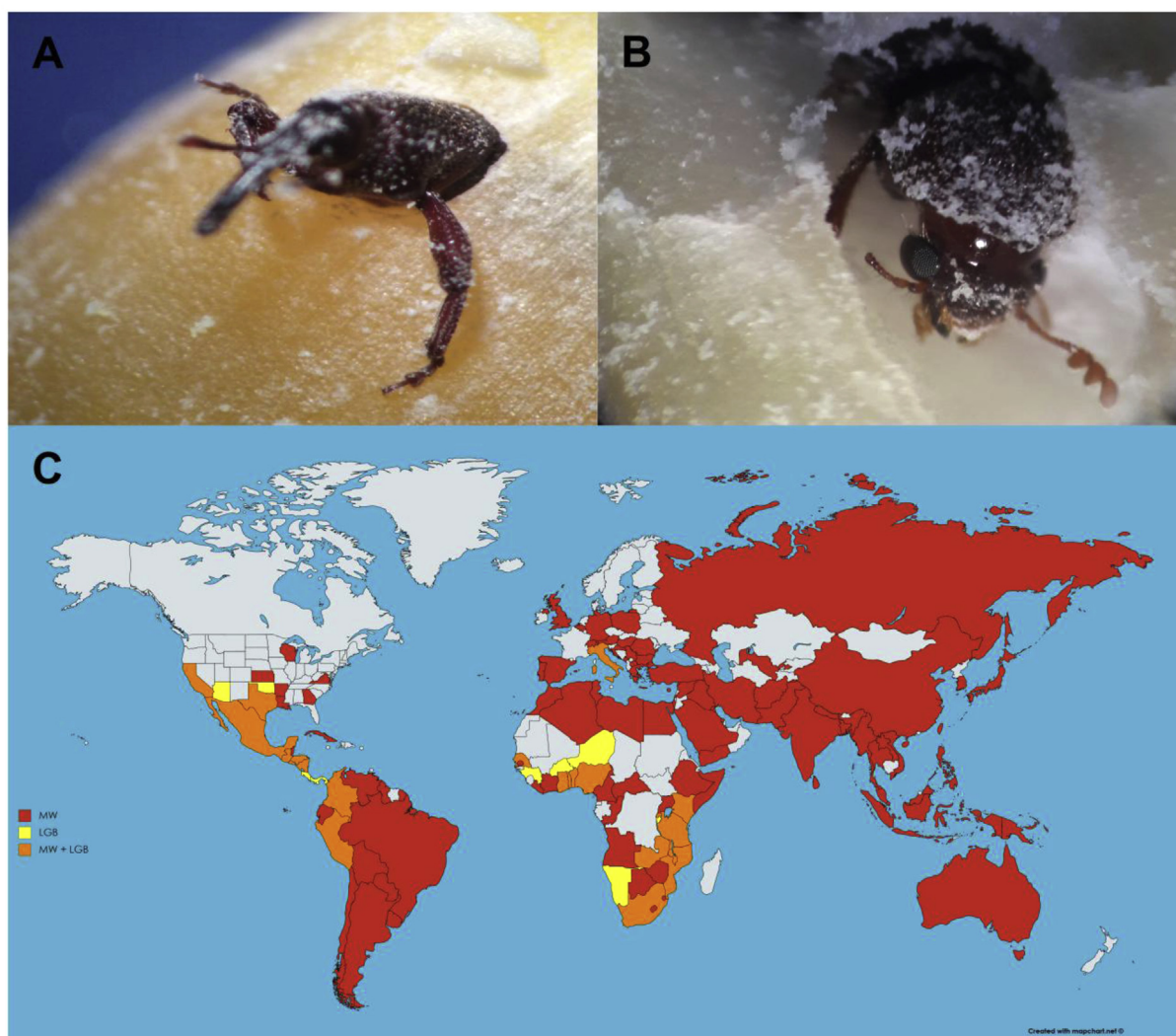


Fig. 1. Global distribution of the main storage pests. **A.** Maize weevil (*S. zeamais*) emerging from an infested maize kernel **B.** Large grain borer (*P. truncatus*) in a maize kernel. **C.** World map showing countries where presence of maize weevil (red), large grain borer (yellow) or both species (orange) have been detected. Data were compiled from CABI (2017), EPPO (2017) and APHLIS (2017) databases. Map was created using the web tool mapchart in the website <https://mapchart.net/>.

requirements, with the aim to contribute substantially to the assessment of food security of vulnerable regions.

3. Host plant resistance

In terms of plant and insect interactions, host plant resistance has been defined as the property by which plant species avoid, tolerate or recover from injury by insect populations, reducing their successful use for insect feeding and/or reproduction (Beck, 1965; Sharma and Ortiz, 2002; Tefera et al., 2016; Thomas and Waage, 1996). This response is determined by heritable plant characters and physicochemical characteristics, which influence insect behavior and biology (Bruce, 2015; Sharma and Ortiz, 2002; Tefera et al., 2016). Plant species could be divided in host and non-host plants. Host plants offer propitious conditions for insect feeding and reproduction, whereas non-host plant do not support insect feeding and/or reproduction (Bruce, 2015). Host plant response could be manifested as immunity (when the plant is not affected by the insect under any condition) high resistance, moderate resistance, low resistance and susceptibility, depending on the impact of

insect damage (Beck, 1965; Wiseman, 1985). In maize kernels, host resistance against *S. zeamais* and *P. truncatus* has been observed in several landraces (Mwololo et al., 2012; García-Lara and Bergvinson, 2013). This resistance is influenced by biophysical, biochemical and genetic factors, including kernel hardness, pericarp thickness/thoughness, phenolic compounds, enzymes and structural components of the kernel (Akpodiete et al., 2015; García-Lara et al., 2004, 2007; López-Castillo et al., 2018; Saulnier and Thibault, 1999; Sen et al., 1994). The level of resistance is often assessed by the Dobie Index of susceptibility, which defines a cultivar as highly resistant, moderately resistant or susceptible (Demissie et al., 2015; Dobie, 1974; García-Lara et al., 2007). From an evolutionary perspective, resistance traits are influenced by plant and insect coevolution and/or artificial plant selection (Sharma and Ortiz, 2002; Simms and Fritz, 1990).

3.1. Co-evolution of plants and insects

According to the “classic theory”, proposed by Ehrlich and Raven (1964), coevolution is a dynamic process whereby plant and insect

species exhibit reciprocal selective pressure (Agosta, 2006; Ehrlich and Raven, 1964; Jermy, 1984). Along this evolutionary process, insects diversify their feeding habits and behaviors, whereas plants develop defense strategies against insect herbivory, leading to plant and insect diversification (Ehrlich and Raven, 1964; Hogenhout and Bos, 2011; Jermy, 1984; Rausher, 2001; Thompson, 1999). Plant defense strategies are based on physical barriers, constitutive chemical defenses and indirect inducible defenses including volatiles (Ehrlich and Raven, 1964; Hogenhout and Bos, 2011). In the model of kernel-pest interactions, development of maize landraces resistant to insect pests is a good example of co-evolution. During this process (assisted by artificial plant selection), insect pressure induces the development of resistance factors, which are manifested by the bioaccumulation of insect-deterrent compounds, the development of physical barriers and genotypical modifications (Classen et al., 1990; García-Lara and Bergvinson, 2013; Ignjatović-Mićić et al., 2013; Serratos et al., 1987; Tamiru et al., 2015). However, insect pressure is often caused by diverse species, and resistance could be broken by the introduction of new colonizing species, as the case of *P. truncatus* in Africa (Hodges, 1986; Bosque-Pérez and Buddenhagen, 1992). Insect survival is also influenced by their sophisticated host selection strategies, mediated by olfactory recognition of semiochemicals coming from adult-infested kernels of the same species and attractant or repellent compounds from the kernel (Danho et al., 2015; Piesik and Wenda-Piesik, 2015; Trematerra et al., 2007, 2013). The knowledge of co-evolution of kernels and insects is important to the understanding of host plant response and to the development of successful breeding programs, considering the agroecological conditions, including the interaction with predator species (Tefera et al., 2016; Bosque-Pérez and Buddenhagen, 1992). Breeding strategies based in co-evolutionary mechanisms, such as the high-dose/refuge strategy have been implemented to delay evolution of insect virulence, and the consequent loss of plant resistance (Rausher, 2001; Lamb et al., 2016). In brief, this strategy consists in the interspersation of susceptible (refuge) plants in a resistant cultivar. Numerous insects will emerge from refuge plants, whereas few resistant insects are expected, preventing the production of homozygous insect progeny adapted to the resistant plants (Rausher, 2001). This strategy has contributed to effective pest control, as observed in the interaction between Bt corn and various pests, including the European corn borer, *Ostrinia nubilalis*, the southwestern corn borer, *Diatraea grandiosella* and the tobacco budworm, *Heliothis virescens* (Huang et al., 2011). Another successful example has been reported for the resistance of spring wheat (*Triticum aestivum*, L.) to the wheat midge (*Sitodiplosis mosellana*) in Canada (Lamb et al., 2016).

3.2. Plant selection

Artificial selection started with plant domestication for agricultural purposes. During this process, farmers selected resistant plants, which were able to deal with environmental stress, including insects and diseases (Sharma and Ortiz, 2002; Tefera et al., 2016). Modern breeding strategies for the development of insect-resistant maize genotypes (landraces, recurrent selection populations, hybrids) are based on formal plant selection methods, such as artificial infestation or genetic mediation by biotechnological means (García-Lara and Bergvinson, 2013; Sharma and Ortiz, 2002; Tefera et al., 2011b, 2016).

4. Mechanisms of resistance

Host plant resistance to insect pests comprises a wide set of genetically inherent qualities (biophysical and biochemical) manifested by three possible mechanisms: antibiosis, antixenosis and

tolerance (Beck, 1965; Smith, 1997; Tefera et al., 2016).

4.1. Antibiosis

Antibiosis is a mechanism by which host plant constituents causes adverse effects in the pest life cycle (Derera et al., 2001; Mihm, 1985; Tefera et al., 2016; Wiseman, 1994). It results in reduction in insect fertility and fecundity, delayed development, reduced size and weight, malformations, abnormal behavior and/or death (Wiseman, 1994; Khan, 1997). In maize, antibiosis against *S. zeamais* and *P. truncatus* has been found in several maize genotypes and landraces (Derera et al., 2001; Nwosu et al., 2015; García-Lara and Bergvinson, 2013). This mechanism has been closely associated to the action of allelochemicals such as phenolic acid amides (Fig. 2) (Sen et al., 1994; Arnason et al., 1997). However, the specific mechanisms and their effects on the insect lifecycle remain unknown.

4.2. Tolerance

Tolerance has been defined as the genetic ability of plants to grow, reproduce or repair and recover from insect damage (Wiseman, 1994; Smith, 1997; Tefera et al., 2016). In other words, it works as a compensation mechanism, since it does not prevent pest infestation and damage. In postharvest insect resistance, this mechanism does not occur, considering that stored kernels are dormant structures, with temporary suspension of growth and reduced metabolic activity (Amen, 1968; García-Lara et al., 2003).

4.3. Antixenosis (non-preference)

Antixenosis or non-preference is an effect on insect behavior, forcing the selection of alternative hosts (Tefera et al., 2016; Cardona and Sotelo, 2005; Khan, 1997; Wiseman, 1994). Antixenotic factors include physical barriers and phytochemical repellents (Smith, 1997). In kernel-insect interactions, antixenosis is usually manifested through mechanical resistance (Fig. 2) through kernel hardness and pericarp thickness/toughness. Both biophysical traits influence kernel accessibility, limiting insect feeding and oviposition (Arnason et al., 1992, 1994; García-Lara et al., 2004; García-Lara and Bergvinson, 2014).

5. Bases of resistance

Insect resistance in maize kernels is based in complex interactions between anatomical, biochemical and genetic factors, as observed in Fig. 2. All these factors are considered as bases of resistance, and may have diverse roles in antibiosis and antixenosis (Bergvinson and García-Lara, 2004; Tefera et al., 2016).

5.1. Biophysical factors

Biophysical bases of the resistance against *S. zeamais* and *P. truncatus* are involved in the antixenosis mechanism (Akpodiète et al., 2015; García-Lara and Bergvinson, 2014; Serratos et al., 1987). Anatomical barriers of the kernel, such as the pericarp thickness/toughness, kernel hardness and endosperm vitreous have been directly correlated with the level of resistance (Akpodiète et al., 2015; Classen et al., 1990; García-Lara et al., 2004; Serratos et al., 1987). Studies performed in QPM varieties concluded that kernel hardness *per se* is not a sole factor influencing susceptibility to *S. zeamais* infestation (Demissie et al., 2015; Oloyede-Kamiyo and Adetumbi, 2017). Pericarp thickness/toughness is a biophysical trait closely associated with cell wall reinforcement. This reinforcement (Fig. 2A, Table 2) is caused by complex interactions

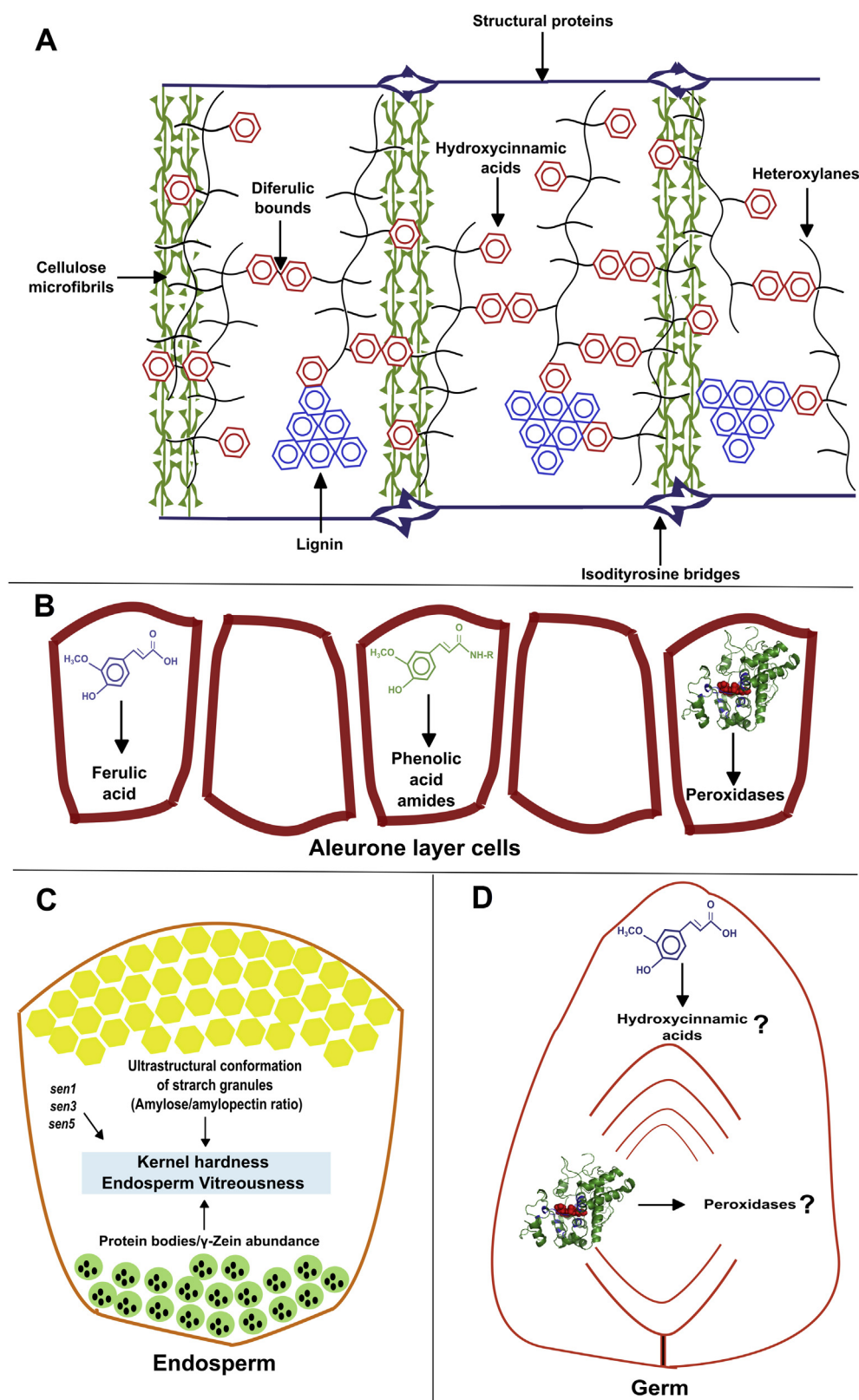


Fig. 2. Bases of postharvest insect resistance in maize kernels. **A.** Model of the pericarp cell wall, representing the linkage among structural proteins, cellulose microfibrils, heteroxylanes, lignin and hydroxycinnamic acids. **B.** Bases of resistance in aleurone layer cells. Resistance in aleurone layer is mainly attributed to the presence of ferulic acid, diferulates, phenolic acid amides and the action of peroxidases. **C.** Resistance factors in endosperm. Endosperm resistance has been associated with kernel hardness and endosperm vitreousness. Both traits are closely linked to the ultrastructural conformation of starch granules (influenced by amylose/amylopectin proportion) and protein bodies (influenced by γ -zein abundance). Genetic factors, including the genes *soft endosperm 1, 3 and 5* (*sen1*, *sen3* and *sen5*) have been also associated with kernel resistance. **D.** Possible resistance factors in germ. Presence of hydroxycinnamic acids and peroxidases has been detected, however, correlation among these biochemical compounds and the resistance has not been established in this kernel structure.

Table 2
Principal factors involved in maize kernel postharvest pest resistance.

Bases of resistance	Description	References
a) Anatomical		
Kernel hardness	Implicated in resistance against <i>P. truncatus</i> and <i>S. zeamais</i> . Mainly influenced by the ultrastructural arrangement of starch granules	Demissie et al., 2015; Dombink-Kurtzman and Knutson, 1997; García-Lara and Bergvinson, 2014; Gaytán-Martínez et al., 2006; Mwololo et al., 2013; Narváez-González et al., 2006; Siwale et al., 2009
Pericarp thickness/thoughness	Implicated in resistance against <i>P. truncatus</i> and <i>S. zeamais</i> . Influenced by phytochemical compounds implicated in cell-wall reinforcement mechanisms.	Classen et al., 1990; García-Lara et al., 2004; Oloyede-Kamiyo and Adetumbi, 2017; Santiago et al., 2013; Saulnier and Thibault, 1999
Vitreous endosperm	Implicated in resistance against <i>P. truncatus</i> and <i>S. zeamais</i> . Influenced by structural arrangement of starch granules and by γ -zein content.	García-Lara and Bergvinson, 2014; Landry et al., 2004; Mestres and Matencio, 1996; Narváez-González et al., 2006
b) Biochemical		
Hydroxycinnamic acids	Localized in the pericarp and aleurone layer. Implicated in resistance against <i>P. truncatus</i> and <i>S. zeamais</i> . Contribution in pericarp cell-wall reinforcement. Identified as possible insect deterrent compounds.	Classen et al., 1990; García-Lara et al., 2004, 2010a,b; Iiyama et al., 1994; Ndolo et al., 2013; Santiago et al., 2013; Serratos et al., 1987
Hydroxyproline-rich glycoproteins, extensins	Implicated in resistance against <i>S. zeamais</i> . Contribution in pericarp cell-wall reinforcement.	García-Lara et al., 2004, 2010a,b; Hood et al., 1991; Santiago et al., 2013
Zeins	Accumulated in endosperm protein bodies. Implicated in kernel hardness and endosperm vitreousness	Lopes and Larkins, 1993; Mestres and Matencio, 1996; Robutti et al., 1997
Arabinoxylans	Implicated in resistance against <i>S. zeamais</i> and <i>P. truncatus</i> . Contribution in pericarp cell-wall reinforcement	Arnason et al., 1994; García-Lara et al., 2004; Iiyama et al., 1994; Santiago et al., 2013; Saulnier and Thibault, 1999
Peroxidases	Implicated in resistance against <i>S. zeamais</i> and <i>P. truncatus</i> . Contribution in cell-wall reinforcement by oxidative coupling of hydroxycinnamic acids. Contribution in antibiosis mechanism against <i>S. zeamais</i>	Arnason et al., 1994; Barros-Rios et al., 2015; García-Lara et al., 2007; Iiyama et al., 1994; López-Castillo et al., 2018.
Phenolic acid amides	Localized in the aleurone layer. Implicated in antibiosis mechanism by possible inhibition of insect neuron receptors	Arnason et al., 1994; Fixon-Owoo et al., 2003; García-Lara et al., 2010a,b; Sen et al., 1994
c) Genetic		
Biophysical factors (grain weight, soft endosperm, grain dry matter, floury grain)	Associated with soft endosperm genes (<i>sen 1</i> , <i>sen3</i> and <i>sen5</i>) and QTL grain weight, which co-localized in chromosome 1.09, 2.04, 3.01, and 8.05 with QTL of susceptibility traits. Cellulose synthases involved in cell wall reinforcement have been also identified.	García-Lara et al., 2009; 2010a,b; 2015; Castro-Álvarez et al., 2015; Holland et al., 2000; Meyer et al., 2007; Yencho et al., 2000.
Biochemical factors (peroxidase, pectin methyltransferase and sugar content)	Related with Peroxidase gene (<i>px1</i>), Pectin methyltransferase gene (<i>pme1</i>), and QTL for leaf reductor sugars, which co-localized in chromosome 2.05, 8.05, 10.04 and 10.07 with susceptibility traits	Davis et al., 1999; García-Lara et al., 2009; 2010a,b; 2015; Holland et al., 2000; Meyer et al., 2007; Yencho et al., 2000.
Response to fungus attack and other insect pests	Linked with QTL for response to <i>Cercospora zeae-maydis</i> , QTL for European Corn Borer response, QTL for European Corn Borer response, QTL for Sugarcane borer response, and QTL for Corn Earworm response, which co-localized in chromosome 2.05, 4.08, 8.08, 10.04 and 10.07 with susceptibility traits	Bergvinson and García-Lara, 2006; Castro-Álvarez et al., 2015; Cardinal and Lee, 2005; García-Lara et al., 2009; 2010a,b; 2015; Krakowsky et al., 2007; Meyer et al., 2007.
Biochemical factors with undefined function in resistance	Genes of chalcone synthase, phenylalanine ammonium lyase, caffeate o-methyltransferase, arginine decarboxylase, ornithine decarboxylase and spermidine synthase	Davis et al., 1999; Meyer et al., 2007; Rodríguez-Kessler et al., 2006

between structural factors (proteins and polysaccharides) and phytochemicals (hydroxycinnamic acids) (Akpodiete et al., 2015; Arnason et al., 1992; García-Lara et al., 2004; Mwololo et al., 2013; Saulnier and Thibault, 1999; Sen et al., 1994). Kernel hardness and endosperm vitreous (Fig. 2C, Table 2) have been associated with the ultrastructural arrangement of starch granules (determined by the amylose/amylopectin ratio) and the content of γ -zein in protein bodies (Dombink-Kurtzman and Knutson, 1997; Gaytán-Martínez et al., 2006; Narváez-González et al., 2006).

5.2. Biochemical factors

Diverse biochemical factors are involved in antibiosis and antixenosis. Cell-wall reinforcement (Fig. 2A) is a complex antixenotic trait, which involves the crosslinking of proteins (extensins and hydroxyproline-rich glycoproteins) and esterified cell wall hemicellulose (heteroxylans, such as feruloyl and *p*-coumaroylarabinoxylans) which surround cellulose microfibrils (García-Lara et al., 2004; Santiago et al., 2013; Saulnier and Thibault, 1999). This process is under metabolic control of esterification reactions (Barros-Rios et al., 2015; García-Lara et al., 2007; Iiyama et al.,

1994). Peroxidase-mediated oxidative coupling of hydroxycinnamic acids form diferulate cross links in hemicelluloses also occur. However, some details about this mechanism remain unknown, such as the identity of specific genes and role of peroxidases implicated in oxidative coupling, although possible candidates have been suggested (López-Castillo et al., 2015; Winkler and García-Lara, 2010). In the antibiosis mechanism, phenolic acid amides localized in aleurone layer cells (Fig. 2B), such as diferuloylputrescine and di-*p*-coumaroylputrescine have been also suggested as insect-deterrent compounds (Arnason et al., 1997; Bily et al., 2003; Sen et al., 1994). However, their mechanism of action is not clear, although possible inhibition of insect neuroreceptors has been suggested (Fixon-Owoo et al., 2003). Recently, peroxidases from the aleurone layer have been suggested as part of the antibiosis mechanism against *S. zeamais*, performing a biochemical response by catalyzing the oxidation of soluble phenolic compounds located at this layer (López-Castillo et al., 2018). Presence of hydroxycinnamic acids and peroxidases has been detected in maize germ (Fig. 2D). However, their function has not been associated yet to insect resistance (García-Lara et al., 2007, 2015).

5.3. Genetic factors

Postharvest insect resistance inheritance has been extensively studied in tropical maize, confirming the polygenic (quantitative) inheritance of resistance, the importance of the pericarp (Tipping et al., 1989), main maternal effects (Serratos et al., 1997) and specific genetic effects for additive and non-additive gene action (Dhaliwayo et al., 2005). However, the relatively low heritability of these traits leads to relatively slow progress in trait transference into elite germplasm via phenotypic selection. Therefore, molecular markers are now used to accelerate the transfer of genes or genetic regions associated with resistance in a modern breeding program through marker-assisted selection (MAS). Recent molecular breeding efforts have focused on the identification of genomic areas and genes involved in resistance to the major pests. The principal quantitative trait loci (QTL) and specific associated genes in maize for lepidopteran insect resistance have been elucidated. Loci and genes associated with resistance are clustered in regions co-localized with biochemical resistance factors, as observed in Table 2. Major associations for *S. zeamais* resistance are located in chromosome 2, 6, 7 and 10, which may be candidate regions for further fine mapping. (Cardinal and Lee, 2005; Castro-Álvarez et al., 2015; García-Lara et al., 2009, 2010a,b; Krakowsky et al., 2007; Yencho et al., 2000). Recently, QTLs for *S. zeamais* resistance have been detected in an F₂ population (García-Lara et al., 2009). In addition, when QTLs of phytochemical grain composition were added to the F₂ map, close association of insect resistance loci with structural cell wall components, key enzymes, and phenolic acid biosynthesis pathways were identified, as observed in Table 2 (García-Lara et al., 2010a,b). Comparing QTL from F₂ reports on biophysical (García-Lara et al., 2009) and phytochemical (García-Lara et al., 2010a,b) resistance parameters, with the RIL mapping population (Castro-Álvarez et al., 2015) there are several common genomic regions. Major QTL areas of cell wall phenolic acids and amides clustered to specific genomic areas that carry genes involved in cell wall biochemistry and phenylpropanoid biosynthesis. These genes include cellulose synthases (Holland et al., 2000), chalcone synthase (Meyer et al., 2007), phenylalanine ammonium lyase, caffeate O-methyltransferase genes (Davis et al., 1999), arginine decarboxylase, ornithine decarboxylase and spermidine synthase (Rodríguez-Kessler et al., 2006). QTL mapping is important for the identification of new sources of resistance associated to tissue-specific genes, such as peroxidases (García-Lara et al., 2007; Winkler and García-Lara, 2010; López-Castillo et al., 2015, 2018).

There is clearly a functional relationship between genes and QTL for insect resistance and genes for resistance factors which can now be exploited in the development of resistant maize varieties (Cardinal and Lee, 2005; Krakowsky et al., 2007; Meyer et al., 2007; Castro-Álvarez et al., 2015). Genes and QTLs for disease resistance have now also been associated with insect pest resistance areas in genomic maps. This clustering may be advantageous in the identification of multifunctional markers, which can be used to stack multiple stress resistances into a single variety (Bergvinson and García-Lara, 2006). A disadvantage that needs to be considered is the fact that most of QTLs associated with *S. zeamais* resistance traits show significant QTL × E interactions. Identification of novel QTL associated with postharvest resistance in maize enables breeders to exploit the genetic variation and increase the efficiency in delivering maize lines resistant to storage pests.

6. Biotechnological perspectives and conclusions

Maize kernel resistance to postharvest pests is manifested by antibiosis and antixenosis mechanisms. Both involve complex interactions between biophysical, genetic and biochemical factors, manifested as kernel modifications which lead to limited

accessibility or toxicity to the invading pest. Progress has been made that has informed breeding programs and led to the development of resistant cultivars such as the as the Population 84 which have displayed drastic reduction of grain weight losses caused by *S. zeamais* (up to 75%) and *P. truncatus* (up to 30%).

However, our knowledge about natural resistance is still limited. The specific function of biochemical factors, such as peroxidases and phenolic acid amides remains undiscovered. Wider and deeper research in this area is necessary in order to better inform future breeding programs. Modern GMO technologies, such as specific gene editing systems will contribute substantially to elucidate the specific function of resistance genes and the development of new resistance markers. This knowledge will be fundamental in future breeding programs, contributing to reduction of postharvest insect losses of food and global food security, with special interest in vulnerable countries.

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Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be considered as a potential conflict of interest.

Author contribution statement

All authors contributed equally to this work in terms of writing and conception. All authors wrote and reviewed the latest version of this manuscript.

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