

Pest Status and Management of Corn Earworm (Lepidoptera: Noctuidae) in Field Corn in the United States

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Abstract

The corn earworm, *Helicoverpa zea* (Boddie), is a common lepidopteran pest of corn (*Zea mays* L.) in the United States. This article provides an overview of the life history, ecology, plant injury, and management of *H. zea* in corn. Leaf injury by *H. zea* feeding can occur in vegetative stage corn, though this type of injury is rare. The most common type of injury is caused by larval feeding in ears. Because kernel injury is typically limited to the tip of the ear, *H. zea* is generally not considered an economic pest. The use of transgenic corn hybrids expressing insecticidal Cry proteins from *Bacillus thuringiensis* (Bt) Berliner can reduce injury from *H. zea*, though complete control is not achieved with most Bt traits. Resistance has been reported to several Bt toxins. Because *H. zea* is a major economic pest in cotton (*Gossypium hirsutum* L.) and because *H. zea* moths that developed on corn can migrate to cotton, selection pressure on *H. zea* in Bt corn has major implications for the pest status and injury to Bt cotton. Although the impact of *H. zea* on yield of field corn is generally negligible, the selection pressure exerted by Bt corn has led to management issues in cotton.

Key words: *Helicoverpa zea*, transgenic crop, *Bacillus thuringiensis*, maize

The corn earworm, *Helicoverpa zea* (Boddie), is the most common lepidopteran pest of corn (*Zea mays* L.) in the southern United States (Cartwright 1939; Buntin et al. 2001, 2004; Reisig et al. 2015; Reay-Jones et al. 2016). While the insect is not thought to overwinter at latitudes greater than 40° (Hardwick 1965), *H. zea* is also a common pest in northern regions of the United States as a result of yearly migration. The insect is also a common pest other field crops such as cotton, *Gossypium hirsutum* L., soybean, *Glycine max* (L.) Merr., sorghum, *Sorghum bicolor* (L.), and many vegetable crops. The insect is present in temperate and tropical regions of the Americas as well as Hawaii (Zimmerman and Fletcher 1956). As a polyphagous pest, *H. zea* has three common names approved by the Entomological Society of America (corn earworm, tomato fruitworm, and bollworm), in addition to being known as sorghum headworm, soybean podworm, and vetchworm. Formerly thought to be part of one species with the Old World bollworm, *Helicoverpa armigera* (Hübner), the taxonomy was clarified by Hardwick (1965) with a description of the two distinct species. Noted as a pest of corn as early as 1905 in the United States (Quaintance and Brues 1905), the insect has since received considerable attention, particularly as a pest susceptible to transgenic corn hybrids and cotton cultivars expressing *Bacillus thuringiensis* (Bt) Berliner toxins. While a recent review was published on management in sweet corn (Olmstead et al.

2016), this article aims to provide an overview of *H. zea* as a pest in field corn.

Life Cycle

The number of generations per year varies with latitude, with one to two generations in Ontario, two generations in Massachusetts and Oregon, two to three generations in Delaware, the Sacramento and San Joaquin Valleys of California, and Ohio, three generations in Illinois, up to four generations per year in North Carolina and northern Texas, five generations in Alabama and Louisiana, six generations along the Gulf Coast of Texas, and seven generations in south Texas (Quaintance and Brues 1905, Brazzel et al. 1953, Neunzig 1969, Hoffmann et al. 1991, Coop et al. 1992). The life cycle of egg, larva, pupa, and adult can be completed in about 30 d (Butler 1976, Hardwick 1965). The insect overwinters as a pupa in the soil, though this occurs only in the southern United States, since *H. zea* is not thought to overwinter at latitudes greater than 40° (Hardwick 1965). After eclosion in the spring, moths can migrate throughout most of the United States and southern Canada.

The adult moth (Fig. 1) is highly variable in color and wing markings. Wing expanse averaged 38.6 ± 2.9 mm in the Americas (Hardwick 1965), with males being more variable in size than

females (Quaintance and Brues 1905). Males are paler (light yellow to brown) in color than females (brown to pinkish-brown) (Quaintance and Brues 1905). Longevity ranges from 7.5 to 14.5 d for males and from 9.5 to 18 d for females. Moths can feed on nectar on a range of plants (Nuttycombe 1930).

Laid singly, eggs are dome-shaped or spherical with a diameter of 0.60 ± 0.05 mm in diameter and 0.52 ± 0.04 mm in height, with a pale green color shortly after oviposition turning to a more pale yellow color over time (Hardwick 1965). The egg stage can vary from 80 to 90 h at 25°C (Hardwick 1965) and from 2 d in mid-summer to 8 d in the spring (Quaintance and Brues 1905). In corn, eggs are laid mainly on silks (Ditman and Cory 1931), though oviposition can occur on the upper leaf surface and on the stalk, particularly if silks are not available (McColloch 1920).

Larvae typically develop through six instars, though a range of five to eight instars has been noted (Quaintance and Brues 1905). With the general appearance of a typical noctuid (Fig. 2), larval head plates are orange to light brown, and the body color can be more variable, ranging from green, brown, pink to yellow, with four pairs of pale prolegs and darker thoracic legs. Development is completed in 13.2 d for five-stadia larvae and 16.3 d for six-stadia larvae (Hardwick 1965). Head capsule width ranges from 0.292 ± 0.017 mm for first instars to 3.10 ± 0.11 mm for the last instar (Hardwick 1965). Body length ranges across instars from 1.5 mm at hatching to 42.2 mm for a fully grown sixth instar (Quaintance and Brues 1905). Newly hatched larvae first feed on their eggshell (Quaintance and Brues 1905), followed by migration to the ear in corn along the silks where feeding continues. Up to half of a larva's growth can result from silk feeding alone (Quaintance and Brues 1905), though ear tip feeding often occurs earlier during larval growth.

The pupa (Fig. 3) is also similar to many other Noctuid species, with a shiny red to dark brown body (14 to 23 mm in length) (Quaintance and Brues 1905). The pupal stage lasts 13.5 d for males and 12.6 d for females (Hardwick 1965). Fully grown larvae drop to the ground where they burrow to create a pupal cell, with an average depth of 46 mm (Quaintance and Brues 1905), although pupal depth is likely a function of soil type, moisture, and pupal size. The insect overwinters in the soil as diapausing pupae (Hardwick 1965).

Host Plants and Seasonal Dynamics

As a polyphagous pest, *H. zea* larvae feed and reproduce on both cultivated and wild hosts, though wild hosts are considered to be of lesser importance in southeastern United States agroecosystems (Neunzig 1969). Feeding on both wild and cultivated hosts occurs primarily on the reproductive structures. Surveys showed common weed hosts to include toadflax, *Nuttallanthus canadensis* (L.) D. A. Sutton, in North Carolina (Neunzig 1963) and crimson clover, *Trifolium incarnatum* L., and cutleaf geranium, *Geranium dissectum* L. in Mississippi (Stadelbacher 1981). Among crop hosts, *H. zea* can feed on soybean, peanuts, *Arachis hypogaea* L., cotton, okra, *Abelmoschus esculentus* (L.), sweet potato, *Ipomoea batatas* (L.), tomato, *Solanum lycopersicum* L., alfalfa, *Medicago sativa* L., tobacco, *Nicotiana tabacum* L., green beans, *Phaseolus vulgaris* L. sorghum, *Sorghum bicolor* (L.) Moench, and strawberries, *Fragaria* spp. (Neunzig 1969). For at least two initial generations following overwintering in the southern United States, *H. zea* feed on wild hosts and corn; corn is a preferred host, with oviposition occurring on the silks during June-July across the southern United States (Roltsch and Mayse 1984, Bradley 1993). After corn silks dry, *H. zea* prefer to oviposit in other plant hosts during their blooming stages (Hardwick

1965; Terry et al. 1987a, b; Jackson et al. 2008; Head et al. 2010), with large numbers emerging from corn that inundate the landscape across an extensive region (Gould et al. 2002, Jackson et al. 2008). One of the most comprehensive datasets on *H. zea* dynamics in the southern United States is summarized in Jackson et al. (2008), which was a 2-yr study across five southern states examining *H. zea* larval infestations in several crops to determine the contribution of non-Bt and non-cotton hosts to a refuge for Bt cotton. The study showed that larval populations in corn, soybean, grain sorghum, and peanut were substantially greater than in cotton, with populations being mainly confined to corn in July followed by other non-cotton crops later in the year. Host usage by *H. zea* across four southern states has also been inferred by stable carbon isotope ratios and gossypol residues in moths (Head et al. 2010); the study showed that C_4 hosts were the main source of moths from mid-June to early September. Starting in August, C_3 hosts (cotton, soybean, and peanut) became a more dominant source of *H. zea* moths until mid-September when C_4 hosts were again the overriding source. Gossypol analysis also showed that *H. zea* moths from cotton represented <1% of total moths from June to early August, followed by a peak in September at 19%, indicating that cotton was a minor source of moths. These studies clearly show the major role that corn plays in the seasonal dynamics of *H. zea*, and the importance of non-Bt corn for Bt resistance management. In the northern United States, *H. zea* generally infests crops later in the season after migration from southern regions, and can be a serious pest of sweet corn (Bartels and Hutchison 1995), in addition to infesting field corn (Pilcher et al. 1997).

Migration

The widespread pest status of *H. zea* is greatly aided by the capability of moths to move both short and long distances (Fitt 1989). Movement of *Heliothis* and *Helicoverpa* moths has been hypothesized to belong to three categories (Farrow and Daly 1987), although the distinction between the three can sometimes be unclear (Fitt 1989): 1) short-range movement within habitats close to plant hosts to meet appetitive needs, 2) long-range movement between habitats at heights of 1–10 m to meet appetitive needs, and 3) migratory movement



Fig. 1. *Helicoverpa zea* adult. Photo: Mark Dreiling, Bugwood.org.

downwind at heights greater than 30 m that are less associated with appetitive needs. Migration distances of at least 750 km from Texas to Arkansas were shown using pollen on *H. zea* (Hendrix et al. 1987). *Citrus* sp. pollen was collected on *H. zea* in Oklahoma, suggesting migration from Florida, the Caribbean, Mexico, or Central America (Lingren et al. 1994). Moth migration from Mexico and south Texas to more northern parts of the United States is strongly supported by a lack of synchrony between traps catches of moths and emergence from overwintering (Stadelbacher and Pfrimmer 1972, Hartstack et al. 1982, Head et al. 2010). Timing of first appearance of *H. zea* in the United States varies with latitude, with emergence in April–June in the Carolinas (Caron et al. 1978, Roach 1981), May–June in Arkansas (Slosser et al. 1975), April in North Texas (Eger et al. 1983), and January–February in South Texas (Graham and Fife 1972). The first appearance in many parts of the United States likely results from migration, because *H. zea* is not thought to overwinter at latitudes greater than 40° (Hardwick 1965). The physiological potential for migratory flight was shown in a flight mill study using *H. zea* male moths caught in pheromone traps in Texas, with a total flight distance of 32.5 km (Beerwinkle et al. 1995). Migration plays an important role in the dispersal of *H. zea*, with movement strongly affected by weather patterns (Sandstrom et al. 2007).

Injury to Corn and Impact on Yield

Leaf injury by *H. zea* feeding can occur in vegetative stage corn, though this type of injury is rare (Quaintance and Brues 1905). The most common type of injury is caused by larval feeding in ears (Fig. 2) and has been reported across all corn-growing regions in the United States (Bohnenblust et al. 2013, Reay-Jones et al. 2016). Larvae begin feeding on the silks and move down the silk channel, where feeding generally occurs on the ear tip before larvae move into the ear (Wiseman et al. 1978). Complete development of *H. zea* can occur with only silk and tip feeding, with limited or no injury to kernels, as the tip of corn ears generally contains unpollinated kernels that do not develop. Because injury is typically limited to the tip of the ear, *H. zea* is generally not considered an economic pest when corn is planted within recommended planting windows (Reay-Jones and Reisig 2014). Although there is one report of *H. zea* causing average yield losses from 1.5 to 16.7% in the United States (Widstrom et al. 1989), this publication does not report data that support this statement or how such experiments were conducted. When kernel injury does occur, intraear compensation can sometimes further reduce any impact on yield (Steckel and Stewart 2015). Despite applications of insecticide every 1–2 d (Bibb et al. 2018) or every 3–4 d (Reay-Jones and Reisig 2014) from R1 for *H. zea* control, yields were not affected by insecticide treatment compared to the untreated control. While *H. zea* is a major economic pest of sweet corn (Olmstead et al. 2016) though primarily because for aesthetic reasons rather than yield loss, *H. zea* injury generally does not lead to yield loss in field corn, including when comparing hybrids expressing insecticidal Cry proteins from Bt to non-Bt near isolines (Buntin et al. 2004, Bowen et al. 2014, Reay-Jones and Reisig 2014, Reay-Jones et al. 2016). However, late-planted corn can sometimes benefit from protection, as the risk of damage from *H. zea* is greater (Buntin et al. 2001, 2004). In addition to impacts on yield, corn earworm injury to ears may provide a pathway for fungal colonization, leading to greater levels of the two major types of mycotoxins, fumonisins and aflatoxins, which are a major concern for human and animal health (Widstrom 1996, Munkvold 2003). However, association between ear injury and concentrations of fumonisins and aflatoxins are generally weak (Bibb et al. 2018).

Non-transgenic Control Tactics

Host Plant Resistance

Tolerance, non-preference, and antibiosis have been identified as mechanisms of resistance to *H. zea* in corn (Wiseman and Davis 1990). A long tight silk channel with silk that is able to maintain a high level of moisture, husk tightness, and short husk length have been shown to reduce kernel injury by preventing *H. zea* larvae from moving onto the ear (Wiseman et al. 1977, Rector et al. 2002, Ni et al. 2007). Levels of antibiosis against *H. zea* can vary considerably among corn hybrids (e.g., Knapp et al. 1967, Wiseman and Snook 1996). Waiss et al. (1979) reported that maysin, a flavone lycoside, slowed growth of *H. zea* and was associated with antibiotic resistance in corn. Non-preference was reported for some corn genotypes for silk feeding (Wiseman et al. 1983) and oviposition (Widstrom et al. 1979). More recent work identified corn genotypes resistant to *H. zea* despite having low levels of maysin, indicating a new mechanism of resistance (Abel et al. 2000). While resistant genotypes and mechanisms have been identified, transgenic corn traits expressing Bt toxins currently dominate genetic resistance in corn to *H. zea*, though combining Bt traits with innate resistant germplasm to multiple pests would benefit corn production (Ni et al. 2007).

Cultural Practices

Only a limited number of studies have been published on cultural practices as a management tactic for *H. zea* in corn. However, the status of corn as a preferred host for *H. zea* in the landscape makes any kind of cultural practice based on habitat manipulation a major challenge. This is underlined by the fact that corn has been used as the trap crop itself for *H. zea* in other crops, including soybean (Javaid



Fig. 2. *Helicoverpa zea* larva feeding on corn ear. Photo: Thomas Bilbo, Clemson University.

et al. 2005) and cotton (Lincoln and Isely 1947). Among cultural practices in field corn, planting early can help to avoid high *H. zea* pressure later in the season (Buntin et al. 2004). Ear infestations of *H. zea* decreased with increasing rates of nitrogen fertilizer, which was attributed to reduced moth pressure during the earlier silking that occurred with higher nitrogen rates, in addition to increased husk tightness (Klostermeyer 1950). Because *H. zea* overwinters in the soil as pupae (Phillips and Barber 1929), tillage has been investigated as a cultural practice to reduce populations by either disrupting emergence tunnels or causing direct mortality (Barber and Dicke 1937). This approach dubbed ‘pupae busting’ has been successfully adopted to manage the closely related species *Helicoverpa armigera* Hübner after harvest of cotton in Australia (Fitt 1994). However, the complexity of the landscape in the southern and southeastern United States with a multitude of *H. zea* host plants suggest the use of tillage may not be feasible as a control tactic to reduce significant proportions of the pest population, in addition to widespread tillage leading to substantial increases in soil erosion (Montgomery 2007). Furthermore, tillage would be impossible to manage *H. zea* infestations developing in corn ears, as this would need to be done prior to harvest.

Biological Control

Several species of egg parasitoids have been reported in the United States, including *Trichogramma pretiosum* Riley, *Trichogramma exiguum* Pinto and Platner (Hymenoptera: Trichogrammatidae), and *Telenomus heliothidis* Ashmead (Hymenoptera: Scelionidae) (Puterka et al. 1985, Kauffman and Kennedy 1989). Corn earworm larvae are relatively protected from natural enemies within corn ears relative to other crops such as cotton and soybean (Manley et al. 1991). Only 6% of *H. zea* larvae collected in corn ears in trials in South Carolina were parasitized, with the main species being the tachinid larval-pupal parasitoid *Archytas marmoratus* (Townsend) (Diptera: Tachinidae) (Manley et al. 1991). Inundative releases of *A. marmoratus* in Georgia showed potential as a component of an IPM program (Proshold et al. 1998). Other larval parasitoids of *H. zea* include *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae) and *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) (Puterka et al. 1985, Manley et al. 1991). Kring et al. (1993) showed that pupal mortality from natural enemies was limited in trials in Arkansas and recommended that classical biological control programs therefore be implemented. Predators include *Harpalus pennsylvanicus* DeGeer (Lesiewicz et al. 1982) and *Orius insidiosus* (Say) (Reid 1991), in addition to birds (Mott and Stone 1973). Entomopathogenic nematodes have been suggested to be important natural enemies of *H. zea*, including *Steinernema riobravis* Cabanillas, Poinar, and Raulston in Arkansas (Feaster and Steinkraus 1996) and Texas (Cabanillas and Raulston 1996). Nucleopolyhedroviruses (NPV) can infect *H. zea* and be applied as biopesticides to reduce pest populations (Pingel and Lewis 1999, Lacey et al. 2001). Advantages of NPVs can include specificity for target pests and elevated rates of infection, and field trials in Mississippi showed the potential of this method to reduce *H. zea* populations (Hardee et al. 1999). While widespread adoption of NPVs holds potential as a tool to reduce populations of *H. zea*, current use of transgenic Bt crops has likely hindered the development and use of microbial control methods. While a complex of natural enemies can affect *H. zea*, the impact on *H. zea* dynamics are generally not sufficient to prevent it from being the most common Lepidopteran pest of corn in many parts of the United States.

Insecticides

The use of foliar insecticides to manage this pest in corn is challenging, as larvae quickly burrow into the silks and become protected within the ears (Widstrom et al. 1976). Kernel injury still occurred in non-Bt corn hybrids despite intensive applications (13–18 per trial) of chlorantraniliprole (a highly effective insecticide in other crops) in trials in North and South Carolina (Reay-Jones and Reisig 2014). Similarly, applications of flubendiamide or chlorantraniliprole from silk emergence to silk senescence every 1–2 d only reduced kernel injury from ~7.1 kernels per ear in untreated plots to ~2.5 kernels per ear in treated plots in trials in Mississippi and Georgia with a Bt hybrid expressing Cry1F (Bibb et al. 2018). Intensive insecticide usage is undoubtedly cost prohibitive for field corn producers intending to eliminate corn earworm injury, and, as such, published data are limited on insecticide efficacy for *H. zea* control. In contrast, tolerance for *H. zea* injury to ears in sweet corn is low, particularly for fresh market sweet corn (Shelton et al. 2013). Timing of insecticides is crucial, as insecticides need to be applied at short intervals during silking to prevent *H. zea* larvae from reaching the ear. Synthetic (carbamate, diamide, oxadiazines, pyrethroids, and spinosyns) and biologically based insecticides (mainly Bt) are used in sweet corn to manage *H. zea* (Shelton et al. 2013).

Management Using Transgenic Bt Hybrids

History and Efficacy

The use of transgenic Bt corn hybrids can reduce injury from *H. zea*, though complete control is not achieved with most Bt traits (Buntin et al. 2004, Reay-Jones and Reisig 2014). Bt corn was first introduced in 1996 to control the European corn borer, *Ostrinia nubilalis* (Hübner), and other stalkboring species (Koziel et al. 1993). The first Bt corn hybrids expressed a single toxin (Cry1Ab or Cry1F) and provided excellent control of stalkborers, but only poor to fair levels of control of *H. zea* (Buntin et al. 2004, Reay-Jones et al. 2009, Reay-Jones and Reisig 2014). For example, hybrids expressing Cry1Ab reduced kernel injury by 67% in South Carolina in 2007–2009 (Reay-Jones et al. 2009), 30% across 12 southern states in 2010–2011 (Reisig et al. 2015), and 51% in trials in North and South Carolina in 2012–2013 (Reay-Jones and Reisig 2014). Hybrids expressing Cry1F reduced kernel injury by 39% in trials across four southern states in 2007–2009 (Siebert et al. 2012), 14% across 12 southern states in 2010–2011 (Reisig et al. 2015), and 30% control in trials in North and South Carolina in 2012–2013 (Reay-Jones and Reisig 2014).



Fig. 3. *Helicoverpa zea* pupa. Photo: Sturgis McKeever, Georgia Southern University, Bugwood.org.

More recent Bt traits in corn, known as ‘pyramids’, include events that express several toxins (Table 1), which can have the following advantages: 1) increasing the range of activity against multiple pests (Rule et al. 2014), 2) delaying the development of resistance by assuming that resistance to one toxin does not provide cross-resistance to other toxins included in the pyramid (Carrière et al. 2016), and 3) decreasing the size of the non-Bt refuge (Storer et al. 2012). The first Bt pyramid for above ground pests was commercialized in 2010 and expressed Cry1A.105 + Cry2Ab2; control of *H. zea* was improved compared with single-toxin hybrids, with 95% control in trials across four southern states in 2007–2009 (Siebert et al. 2012), 83% control in trials in South Carolina in 2007–2009 (Reay-Jones et al. 2009), and 97% control in trials in North and South Carolina in 2012–2013 (Reay-Jones and Reisig 2014). Bt hybrids expressing Cry1Ab + Cry1F do not provide better suppression of *H. zea* injury than either toxin alone, with 55% control in trials in North and South Carolina in 2012–2013 (Reay-Jones and Reisig 2014), and 46% across 12 southern states in 2010–2011 (Reisig et al. 2015). Only the Vip3A20 toxin is rated as providing excellent levels of control of *H. zea*, and is considered to approach a ‘high dose’ (Burkness et al. 2010), i.e., a dose that kills >95% of heterozygotes for single-allele Bt resistance (Gould 1998). Because Vip3A20 has no activity on stalk borers, Bt hybrids expressing this toxin are included in pyramids with either Cry1Ab, Cry1Ab + Cry1F, or Cry1A.105 + Cry2Ab2.

In addition to *H. zea*, a number of insects are targeted by Bt corn, including *O. nubilalis*, fall armyworm, *Spodoptera frugiperda* (J. E. Smith), lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller), sugarcane borer, *Diatraea saccharalis* (F.), western bean cutworm, *Striacosta albicosta* (Smith), and southwestern corn borer, *Diatraea grandiosella* Dyar. Yields of Bt corn hybrids can be substantially higher than yields of non-Bt corn hybrids in the presence of corn borers (Rice and Pilcher 2001). However, infestations of *H. zea* alone in Bt corn trials only rarely result in significant differences in yield between Bt and non-Bt hybrids (Buntin et al. 2004, Bowen et al. 2014, Reay-Jones and Reisig 2014, Reay-Jones et al. 2016). However, in addition to yield, grain quality can be improved by protecting ears from *H. zea* injury using Bt corn. Fumonisin contamination in corn ears can be reduced in Bt hybrids compared with non-Bt isolines (Dowd 2001, Wu 2006). Reduction in fumonisin concentrations in Bt corn hybrids expressing Cry1Ab has been shown to occur when *O. nubilalis* is the predominant pest (Munkvold et al. 1999, Clements et al. 2003). Such a reduction does not occur when *H. zea* is the predominant pest, likely because Bt hybrids expressing

Cry1Ab provide only limited suppression of *H. zea* injury to ears (Clements et al. 2003). The effect of Bt corn on aflatoxin contamination is inconsistent (Buntin et al. 2004, Bowen et al. 2014, Bibb et al. 2018), although most published studies examined single-toxin Bt hybrids and more data are needed on the potential role of pyramided Bt corn hybrids in reducing aflatoxin concentrations (Abbas et al. 2013). Insect injury to corn ears is only one of many factors that can impact the epidemiology of *Aspergillus flavus*, a common pathogen that produces aflatoxins (Diener et al. 1987). Suppression of aflatoxin therefore should not be considered a benefit of planting Bt corn in the southern United States. While beneficial impacts of Bt corn on yield are difficult to quantify when *H. zea* is the only pest, a widespread benefit of planting Bt corn has been the regional suppression of both *O. nubilalis* and *H. zea*, as demonstrated by 30 yr of trapping data in the mid-Atlantic region of the United States (Dively et al. 2018).

Resistance to Bt Corn

While major resistance genes have not yet been identified in *H. zea*, evidence for minor resistance genes has been reported (Burd et al. 2003), indicating that evolution of resistance may occur gradually with multiple alleles with minor effects involved (Caprio and Sumerford 2007). Recent work has identified a decrease in Cry1Ac activation as a mechanism of resistance to Cry1Ac (Zhang et al. 2019). Resistance monitoring for many years among *H. zea* populations collected in cotton across the southeastern United States documented a range of susceptibility to Cry1Ac and Cry2Ab2, with some populations being significantly more resistant than a laboratory colony (Ali et al. 2006, Luttrell and Ali 2009). Populations collected across the southeastern and southern United States in corn have shown resistance to Cry1A.105 and Cry2Ab2 (Bilbo et al. 2019, Kaur et al. 2019). Recent reports of resistance to Bt cotton expressing two Cry toxins for *H. zea* control have led to recommendations by extension entomologists to consider the need for supplemental foliar insecticide sprays (Reisig et al. 2018). *Helicoverpa zea* is a major economic pest of cotton in the United States (Luttrell and Jackson 2012). While Bt cotton is still effective in managing the tobacco budworm, *Chloridea virescens* (Fabricius), field-evolved resistance to Cry toxins in *H. zea* is a major concern for cotton production.

A recent study documented a decline in efficacy of sweet corn expressing Cry1Ab from 1996 to 2016 and Cry1A.105 + Cry2Ab2 from 2010 to 2016 in Maryland, and resistance to Cry1Ab was

Table 1. Bt corn products with efficacy on above-ground pests, including *H. zea*

Bt events in single and multiple toxin Bt hybrids	Bt toxins	Structured refuge ^d	
		Non-cotton counties (%)	Cotton counties (%)
Bt11	Cry1Ab	20	50
Bt11, MIR162	Cry1Ab + Vip3A	5	20
Bt11, MIR162, TC1507	Cry1Ab + Vip3A +Cry1F	5	20
TC1507	Cry1F	20	50
TC1507, MON810	Cry1F + Cry1Ab	5	20
TC1507, MON810, MIR162	Cry1F + Cry1Ab + Vip3A	5	20
MON810	Cry1Ab	20	50
MON89034	Cry1A.105 + Cry2Ab2	5	20
MON89034, TC1507	Cry1A.105 + Cry2Ab2 + Cry1F	5	20
MON89034, TC1507, MIR162	Cry1A.105 + Cry2Ab2 + Vip3A	5	20

^dIn non-cotton growing counties, bags of blended refuges of 5% non-Bt are available for selected Bt traits.

confirmed using laboratory bioassays (Dively et al. 2016). In field corn, evidence of resistance evolving to Cry1Ab in *H. zea* has also been shown in North and South Carolina (Reisig and Reay-Jones 2015). Kernel damage by *H. zea* feeding has also increased in recent years in Bt corn expressing Cry1A.105 and Cry2Ab2 in the southeastern United States (F.P.F. Reay-Jones and D. D. Reisig, unpublished data). With only Vip3A20 expressed at a near-high dose for *H. zea* in corn (Burkness et al. 2010), the development of resistance to this toxin is a major concern in both corn and cotton, where the toxin is included in recent triple-toxin varieties (Reisig and Kurtz 2018). This concern was recently substantiated by the recovery of *H. zea* pupae from corn expressing Cry1Ab + Cry1F + Vip3A20 in North Carolina (Bilbo et al. 2018) and South Carolina (F.P.F. Reay-Jones and D. D. Reisig, unpublished data).

The development of resistance by target pests is a major threat to Bt crops (Onstad 2008, Carrière et al. 2010). Insect resistance management (IRM) practices have been developed to delay the development of resistance to among target pests. The United States Environmental Protection Agency (EPA) defines IRM as a ‘practices aimed at reducing the potential for insect pests to become resistant to a pesticide’ (USEPA 2001). Among tactics proposed for IRM of Bt crops, the following have been suggested: 1) moderate toxin dosage levels to lead to the survival of a fraction of susceptible insects; 2) high-dose toxin to kill insects heterozygous for resistance; 3) pyramiding toxins with independent modes of action; 4) temporal or tissue-specific toxin expression; and 5) use of nontoxic refuge plants (Bates et al. 2005). In practice, many of these tactics are combined to form an IRM strategy. IRM for Bt corn products in North America targeting *O. nubilalis* initially implemented the ‘high dose/refuge’ strategy which involves expression of a high dose toxin to kill insects heterozygous for resistance combined with the use of nontoxic (refuge) plants to provide susceptible individuals to mate with rare resistant individuals emerging from the Bt crop (Gould 1998, Tabashnik 2008). The refuge in non-cotton growing areas currently consists of 20% for single-toxin Bt hybrids or 5% for pyramids. In cotton growing counties, the refuge consists of 50% for single-toxin Bt hybrids or 20% for pyramids. All Bt products targeting *O. nubilalis* still provide excellent levels of control, with no indication of resistance (Huang et al. 2011). Two major factors that led to this success are 1) the high dose of commercial Bt traits against *O. nubilalis* and 2) the low initial Bt resistance allele frequency.

For *H. zea*, IRM has been confronted with several issues that are likely reasons for widespread resistance currently observed to several Cry toxins. First, the high-dose criteria that was successfully used for *O. nubilalis* was never met with *H. zea* (Storer et al. 2001, Tabashnik et al. 2013), as the insect is inherently more tolerant of Cry toxins. Another issue is that pyramids of Bt corn and cotton that express multiple Bt toxins contain Cry toxins that were either widely used in single-toxin Bt traits for many years (such as Cry1Ab and Cry1F) or are similar and/or cross-resistant to these Cry toxins (Cry1A.105 and Cry2Ab) (Welch et al. 2015). The value of using pyramids that express Bt toxins with different modes of action has never fully been realized, even though Vip3A20 was never included in single-toxin Bt corn prior to being included in pyramids. In addition, a lack of compliance with non-Bt corn refuge has further jeopardized IRM (Reisig 2017, Reisig and Kurtz 2018). Finally, the majority of cotton planted in the United States expressed Bt toxins that are either the same or very similar as those in corn (Von Kanel et al. 2016), which prolongs exposure of the polyphagous *H. zea* to Bt toxins during a growing season and increases the risk of resistance development.

Conclusion

A number of studies have shown that *H. zea* is generally not considered an economic pest when corn is planted within recommended planting windows (Buntin et al. 2001, 2004; Bowen et al. 2014; Reay-Jones and Reisig 2014; Reay-Jones et al. 2016; Bibb et al. 2018). Because *H. zea* is a major economic pest in cotton and because *H. zea* moths that developed on corn can migrate to cotton, selection pressure on *H. zea* in Bt corn has major implications for the pest status on injury to Bt cotton. Practical resistance in *H. zea* was recently documented in pyramided Bt cotton expressing two Cry toxins, with increased insecticidal applications in fields with increased boll injury (Reisig et al. 2018). New triple-toxin cotton varieties express combinations of two Cry proteins and Vip3A, and their adoption should lead to a reduction in injury and the need to use supplemental applications of insecticides. However, widespread selection pressure with Vip3A with increased usage of this toxin across two major crops will likely lead to reduced durability, and underlines the importance of adopting IRM practices such as planting of non-Bt corn refuge. While *H. zea* remains a minor pest in field corn, this crop plays a major role in the landscape contribution of moths with widespread selection pressure to multiple Bt toxins. Another concern for the pest status of *H. zea* is the potential establishment of the invasive *H. armigera* in the United States (Kriticos et al. 2015). Native to the Old World, the insect was found in South America in 2013, and in Puerto Rico in 2014. As *H. armigera* and *H. zea* are morphologically similar related species that both cause damage to reproductive tissue of cultivated plants, the introduction of *H. armigera* into the Americas presents challenges for management and IRM. *Helicoverpa armigera* has a greater genetic diversity than *H. zea* and has developed resistance to several Bt toxins (Bird and Downes 2014, Anderson et al. 2018). Furthermore, a point mutation conferring resistance to Cry1Ac in *H. armigera* in China was recently shown to have single-allele dominant resistance (Jin et al. 2018). Hybridization between the two species could lead to new ecotypes with enhanced pest status and resistance levels to insecticides (Anderson et al. 2018).

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