

Biology, Ecology, and Evolving Management of *Helicoverpa zea* (Lepidoptera: Noctuidae) in Sweet Corn in the United States

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Abstract

The corn earworm, *Helicoverpa zea* (Boddie), is a polyphagous pest found throughout the United States, where it attacks many field and vegetable crops. Although *H. zea* has long been a traditional pest of sweet corn, its importance to this crop has increased dramatically over the past two decades. In this review, we summarize information critical for current and future management of *H. zea* in sweet corn production in the United States. First, we discuss the pest status of *H. zea* and its life history, including migration, infestation and larval development, diapause, overwintering, and abiotic factors that affect its biology. Next we describe monitoring methods, crop protection decision-making processes, chemical control options, and the use of genetic technologies for control of *H. zea*. Alternative *H. zea* management options including biological control, cultural controls, host plant resistance, and pheromone disruption are also reviewed. The role of climate change and its effects on *H. zea* and its ecology are discussed, as well as the recent invasion of its relative, *Helicoverpa armigera* (Hübner), which is a major pest of corn in other parts of the world. To conclude, we suggest future research opportunities for *H. zea* and *H. armigera* management in sweet corn.

Key words: corn earworm, *Helicoverpa armigera*, *Zea mays* L., development, host interaction

The corn earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), is a key pest of many field and vegetable crops and is found throughout the western hemisphere (Cohen et al. 1988, CABI 2016). This review focuses on *H. zea* in sweet corn, *Zea mays* L. convar. *saccharata* Koern, in the United States. Although *H. zea* is a traditional pest of sweet corn in the United States, its significance has increased over the past two decades. The importance of understanding *H. zea* and its close relationship with sweet corn is vital for pest management of this valuable crop.

Despite the considerable body of work on *H. zea* in sweet corn that has been published over the past 100 years, we are unaware of a comprehensive review or synthesis of this information. Thus, a review is timely and, we hope, will stimulate discussion on future work with this key pest. In this review, we highlight key information on the biology, ecology, and management of *H. zea* in sweet corn in the United States. First, we briefly provide context by describing sweet corn production in the United States. We follow this by describing the life history of *H. zea*, including its migration, infestation and larval development, diapause, overwintering, and abiotic factors affecting its life history. We discuss monitoring methods, crop treatment decision-making processes, chemical control options, and the use of genetic technologies for *H. zea* management in sweet corn. Also covered are tactics of biological control, cultural controls, host plant resistance, and pheromone

disruption. We conclude by discussing the role of climate change and its potential effects on *H. zea* biology and the implications of the recent arrival of *Helicoverpa armigera* (Hübner) in the continental United States on sweet corn insect pest management.

Sweet Corn Production

Sweet corn is an important specialty crop and is grown in 158 countries for fresh-market and processing purposes (USDA ERS 2015). In the United States, sweet corn was harvested on >28,000 farms representing all 50 states, with Minnesota, Washington, Wisconsin, Florida, and New York harvesting the largest combined acreage of fresh-market and processing sweet corn in 2013 (USDA NASS 2016). Florida, Georgia, New York, and California produce the most fresh-market sweet corn annually by weight, whereas Minnesota, Washington, Wisconsin, and New York produce the most processing sweet corn. Sweet corn added US\$1.2 billion in 2013 to the U.S. economy. In the same year, 96,591 ha of sweet corn were harvested for fresh market, with a value of US\$842.3 million and a per ha value of US\$8,720; 127,510 ha were harvested for processing, with a value of US\$357.8 million and a per ha value of US\$2,806 (USDA NASS 2016).

Sweet corn is closely related to field corn, but only the sweet corn ear or its kernels are marketed for human consumption. In contrast, many parts of a field corn plant are used for diverse purposes, ranging from animal feed and processed foods to ethanol production. Although both corn types are attacked by *H. zea*, pest management strategies for the two types of corn vary considerably.

All sweet corn varieties contain variations of *Su*, *Se*, and *Sb-2* genotypes. *Su* causes the pericarp to produce water-soluble polysaccharides instead of starches and results in desirable eating characteristics (James et al. 1995, Tracy et al. 2006). *Su* sweet corn varieties were the first modern lines to be developed in the early 1900s and have moderate sugar levels in the kernel. *Se*, when activated, enhances the activity of *Su*, causing the production of additional sugars (Ferguson et al. 1978). Homozygous *Sb-2* varieties produce kernels with higher sugar content than *Su* homozygous varieties (Najeeb et al. 2011). *Se* and *Sb-2* genes have been bred into modern Triplesweet sweet corn lines, where 100% of ear kernels express the *Se* phenotype and 25% also express *Sb-2* characteristics (Grubinger 2004).

Modern sweet corn varieties have been bred for kernel traits desirable for human consumption. These characteristics also make the developing sweet corn ear an ideal source of nutrition for *H. zea* (Cohen et al. 1988). Corn kernels have multiple nutritional components, and *H. zea* larvae take advantage of these different parts to satisfy their developmental requirements (Waldbauer et al. 1984). For this reason, *H. zea* will preferentially choose corn over other plant hosts (Johnson et al. 1975) because there is a higher likelihood of completing development.

Pest Description

Helicoverpa zea has many common names, including, but not limited to, corn earworm, cotton bollworm, bollworm, tomato fruitworm, soybean podworm, and sorghum headworm (CABI 2016). Adults are 20–25 mm in length and have brown (females) to brown-green (males) coloration (CABI 2016). Small spots are sometimes visible on the forewings, while dark outer-marginal bands and brown disc-shaped spots are found on the dorsal surfaces of the underwings (Hardwick 1965). Eggs are laid singly, have an approximate dimension of 0.5 mm length by 0.5 mm width, and vary in color from white after they are laid to yellow near larval hatch (CABI 2016). First instars are small gray caterpillars, 1–2 mm in length, with a black head capsule. Third instars undergo a change in color to either brown or green morphs and develop distinct white or yellow longitudinal lines. Fifth and sixth instars change to pink, orange, brown, or green morphs that average 40 mm in length (CABI 2016). Pupae are reddish-brown and are approximately 20 mm in length.

Life History

Dispersal and Migration

Infestation of corn by *H. zea* is influenced by dynamic population movements by moths at landscape, regional, and continental scales (Fitt 1989, Latheef et al. 1993, Westbrook et al. 1997, Gould et al. 2002, Westbrook and Lopez 2010). Landscape-level movements occur when moths seek nectar or search for mates and oviposition sites (Latheef et al. 1993, Lingren et al. 1993). An adult *H. zea* sustains its energy by nectar-feeding, but must do so by visiting flowering plants other than corn. When females are ready to lay eggs, they

are attracted to corn silks (Cantelo and Jacobson 1979, Fitt 1989, Raina et al. 1992).

Helicoverpa zea is widespread throughout North America (CABI 2016), but populations are not permanent or ubiquitous in all areas. *Helicoverpa zea* is often migratory, and airborne radar observations have revealed that mass migrations can occur over long distances in a single night (Wolf et al. 1990) at altitudes up to 900 m (Beerwinkle et al. 1994). Studies examining pollen on *H. zea* moths also support the idea that migrations occur over hundreds of kilometers (Hendrix et al. 1987, Westbrook et al. 1997). Furthermore, Gould et al. (2002) have argued that reverse migration might occur in the fall from northern states to overwintering sites in Texas and Louisiana.

The ability of *H. zea* moths to travel long distances in a short period can complicate local field-level management. In a short period, *H. zea* adults can theoretically migrate from a remote location >400 km away (Westbrook et al. 1997). For this reason, *H. zea* moth activity in sweet corn fields must be monitored (described in sections that follow), so that local population levels are checked on a regular basis.

Regional moth activity data and meteorological forecasting can be used to provide knowledge about impending immigrations of *H. zea* into regional and local landscapes (Beerwinkle et al. 1994). For example, Pest Watch (www.pestwatch.psu.edu) provides a regional view of *H. zea* over time and space in the northeastern and mid-Atlantic United States based on weekly catches from a network of pheromone and black light traps (Fleischer 2016). Other sites (www.insectforecast.com) predict *H. zea* migrations using meteorological forecasting (Sandstrom 2016). If source locations for *H. zea* migrations and the history of chemical controls used to manage them could be determined, the timing of immigrating populations may be predicted and management improved by avoiding similar chemical controls.

Host range and Landscape Considerations

Successful development of *H. zea* can occur on large acreage field crops such as field corn, soybean, and cotton (Kennedy and Storer 2000), but corn earworms also feed on many important vegetable crops such as snap bean, sweet corn, and tomato. A variety of weedy, uncultivated plants can also serve as hosts to *H. zea* (Nuenzig 1963, Hardwick 1965, Sudbrink and Grant 1995, Kennedy and Storer 2000). However, corn is the preferred host (Hardwick 1965, Johnson et al. 1975).

The ability of *H. zea* to utilize a wide range of cultivated and wild hosts complicates its management in sweet corn. As host diversity within an agricultural landscape increases, the probability of successful *H. zea* development is likely to increase because there are more host choices. Moreover, the availability and attractiveness of these hosts change through space and time, and this impacts *H. zea* populations (Kennedy and Storer 2000). Consequently, regional and temporal differences in landscape composition and natural areas harboring wild host species likely influence *H. zea* population structure at the field level during the growing season in any given area of the United States.

Sweet corn as a Host

Female *H. zea* moths are attracted to ethylene, one of many volatiles produced by corn silks. When a virgin female detects ethylene, she is stimulated to produce sex pheromones for attraction of males (Raina et al. 1991, 1992). Although females can oviposit on any part of the sweet corn stalks or leaves and may do so as early as the

whorl stage (Barber 1943, Johnson et al. 1975), they prefer to oviposit on silks.

A single *H. zea* female can lay 800 to 1,500 eggs in her lifetime (Akkawi and Scott 1984, Fitt 1989). Although movement of *H. zea* larvae to the ear from other plant parts is possible, most ear damage originates from caterpillars that hatch from eggs laid on silk (Hardwick 1965, Coop et al. 1992). Thus, silks play a critical role in infestation, and this knowledge may be exploited in pest management strategies.

After hatching, *H. zea* larvae consume the egg chorion and corn silk, and then move quickly downward into the husk of a developing ear (Barber 1941). Inside the husk, they feed exclusively on corn kernels and do not exit the husk until they prepare for pupation (Waldbauer et al. 1984, Cohen et al. 1988). At the prepupal stage, *H. zea* larvae exit the husk, drop to the ground, and burrow 5 to 13 cm into the soil, where a pupal cell is constructed (Roach and Hopkins 1979).

Helicoverpa zea larvae may be cannibalistic within the husk. If a harvested ear of corn is infested by *H. zea*, there is usually only a single larva. In contrast, earlier in ear development, two or more early instars may feed on the same ear (D.L.O., and A.M.S. unpublished data). Interestingly, Joyner and Gould (1985) showed that *H. zea* larvae given a low-moisture diet supplemented with other *H. zea* larvae as prey took less time to develop, had lower mortality rates, and were significantly heavier as pupae compared with larvae reared on a low-moisture diet alone. In contrast, there were no differences between cannibalistic and noncannibalistic larvae when offered a standard high-moisture diet. Joyner and Gould (1985) concluded that there is a benefit to cannibalism among *H. zea* when subjected to adverse growing conditions.

Although it has been demonstrated that sweet corn silk is very attractive to female *H. zea* and that silk volatiles stimulate them to produce sex pheromones (Raina et al. 1992), we are unaware of any studies that have exploited this plant-insect relationship for pest management purposes. The communication that occurs between the plant and *H. zea* could possibly be exploited in the future for deterrence, avoidance, or confusion in an effort to reduce damage.

Diapause

Helicoverpa zea diapauses in the pupal stage for up to 20 months as a strategy to avoid adverse conditions (Phillips and Newsom 1966). Photoperiod and temperature have strong interactive effects on the induction of diapause in *H. zea* larvae. Photoperiods >13 h per day completely suppress diapause (Benschoter 1968), while photoperiods ≤10 h per day maximize diapause (Phillips and Newsom 1966, Benschoter 1968). Diapause rates are optimized during a short photophase and low temperature (Wellso and Adkisson 1966). However, the effect of a shorter photoperiod on diapause induction can be counteracted if temperatures increase, and a longer photoperiod can be counteracted by low temperatures (Phillips and Newsom 1966).

Overwintering

Helicoverpa zea overwinters in the pupal stage, and its ability to survive the winter depends on whether the pupa is in diapause. An *H. zea* pupa that is in diapause has a lower supercooling point (SCP) and a lower lethal temperature (LT₅₀) and can also survive for longer periods at temperatures near LT₅₀ (Bale 1987, Morey et al. 2012). Pupae in diapause survive at significantly lower soil temperatures and have lower SCP than nondiapausing pupae (Eger et al. 1982, Morey et al. 2012). Morey et al. (2012) reported SCP values

of -19.3°C and -16.4°C for diapausing and nondiapausing *H. zea* pupae, respectively. LT₅₀ values for diapausing and nondiapausing pupae were -13.0°C and -10.0°C, respectively. The difference in time to mortality between diapausing and nondiapausing *H. zea* pupae is significant, with the former surviving much longer than the latter. For example, at 0°C, time to 50% mortality of nondiapausing pupae and diapausing pupae is 474 h and 1,127 h, respectively (Morey et al. 2012).

Soil moisture, soil type, and duration of exposure to low temperatures influence pupal overwintering survival (Slosser et al. 1975). Direct contact with soil moisture increases pupal mortality at sub-freezing temperatures due to nucleation of water to ice within pupal tissues (Eger et al. 1982). Increased soil temperature during pupal diapause is also positively associated with mortality due to increased respiration and drowning (Williams and Stinner 1987).

Overwintering survival of diapausing pupae drops considerably north of the 40° N latitude (Hardwick 1965, Westbrook and Lopez 2010, Morey et al. 2012). Analysis of soil temperature profiles in Texas, Missouri, Kansas, Iowa, and Minnesota were compared with laboratory-derived lethal time (LT₅₀) values. Results from that study revealed that soil temperatures were lethal in states above the 40° parallel because the period at which pupae were exposed to extreme low temperatures was much greater than the average period experienced among locations below the 40° parallel.

Abiotic Factors

Abiotic factors, including temperature, relative humidity (RH), moisture, day-length, and lunar phase, influence *H. zea* populations. Increased temperature and RH decrease larval development time, increase pupation rate, and improved adult eclosion rates of *H. zea* (Harrell et al. 1979). High soil moisture can reduce pupal survival by >50% (Roach and Hopkins 1979, Williams and Stinner 1987). Lunar phase also influences adult flight behavior and plant host-seeking by adult *H. zea* moths (Parajulee et al. 1998).

Temperature influences mating, larval development, feeding behavior, flight capacity, and diapause induction (Callahan 1958, Mangat and Apple 1966, Phillips and Newsom 1966, Wellso and Adkisson 1966, Eger et al. 1982, Westbrook et al. 1997, Morey et al. 2012). The developmental rate of *H. zea*, like other poikilotherms, is dependent on the temperature of its immediate surroundings (Wagner et al. 1984). Day-degree models have been constructed to estimate development of *H. zea* in sweet corn (Mangat and Apple 1966, Stinner et al. 1974, Butler 1976) and economic loss that occurs as a result of infestations (Butler and Scott 1976, Coop et al. 1993). The lower developmental temperature threshold has been calculated as 12.5°C for *H. zea* reared on sweet corn (Mangat and Apple 1966). Maximum developmental threshold temperatures for eggs, larvae, pupae, and adults are 34°C, 36°C, 35°C, and 42°C, respectively (Butler 1976). Mangat and Apple (1966) calculated that 690.2 day-degrees are required from oviposition to 75% adult emergence, using a base 12.5°C model.

Management

Current management practices for *H. zea* in most sweet corn fields rely on foliar applications of insecticides, use of insect-resistant genetically engineered sweet corn, or a combination of both (Flood et al. 2005). Insecticide management decisions are based on the frequency of adults captured in black light traps or pheromone traps during silking (Flood et al. 2005). At the time of publication, we were unaware of any peer-reviewed research establishing an

economic injury level or economic threshold for *H. zea* infestations in sweet corn. When sweet corn is destined for processing, there is a greater tolerance for infested ears because only the ear tip is typically infested and it can be mechanically removed. As a result, growers may be less constrained in their insecticide spray program for processing sweet corn than fresh-market sweet corn. More research-based treatment guidelines are needed for both markets.

Monitoring

Monitoring *H. zea* populations is an important step for making informed control decisions. Because of the high labor requirements and difficulty in monitoring eggs on the silks, pheromone traps have been used since the 1980s to monitor adult male *H. zea* populations. Research has suggested correlations between pheromone traps capturing male moths and corresponding abundance of female *H. zea* moths caught using traditional black light or net catch methods in the same vicinity (Chowdhury et al. 1987a, Latheef et al. 1993). The relationship between pheromone-trapped males and free-flying female moths has formed the basis for current decision-making strategies. However, whether there is a direct relationship between pheromone trap catches and subsequent ear damage remains unclear.

Trap type and lure composition–brand can have a significant impact on the efficacy of monitoring *H. zea* populations. Research shows the attraction of male *H. zea* to different lure brands is variable and that trap design (Hartstack vs. Heliothis) is also important (Drapek et al. 1990, Gauthier et al. 1991). Nonetheless, pheromone traps are an important tool for sweet corn growers. The New York State Integrated Pest Management Program (NYSIPM) Sweet Corn Pheromone Trap Network Report provides weekly local counts across New York State through the growing season using Heliothis traps baited with Hercon (Hercon Environmental, Emigsville, PA, USA) earworm pheromone lures that are checked by growers and cooperators and are accessible online anytime (<http://sweetcorn.nysipm.cornell.edu/>). Pest Watch integrates both field collection and pheromone trap data from state-level cooperators across the northeast United States to provide growers and researchers a regional perspective of earworm population trends in real time (<http://www.pestwatch.psu.edu/sweetcorn/tool/tool.html>).

Sweet corn planting date, frequency of insecticide applications, and pheromone trap catches have all been used in predictive models to understand when and how infestation by *H. zea* occurs. Chowdhury et al. (1987b) found that the sum of *H. zea* males captured in pheromone traps on all pesticide-free days during ear development best predicted yield loss at harvest in Georgia. In Texas, statistical modeling showed that male *H. zea* abundance in pheromone traps was significantly correlated with the emergence of fresh green silks on the ear (Latheef et al. 1991). However, the literature still has not provided a reliable predictor of ear damage based on pheromone trap catch.

Chemical Control

Synthetic Insecticides

Synthetic insecticides used against *H. zea* in sweet corn have evolved since the 1940s, when they first became available (Johnson 1944). As of 2016, synthetic insecticides that are currently registered for use against *H. zea* in sweet corn represent several different modes of action (IRAC 2016), including carbamates (IRAC group 1A), diamides (IRAC group 28), oxadiazines (IRAC group 22A), pyrethroids (IRAC group 3A), and spinosyns (IRAC group 5; IRAC 2016). Field testing has shown diamides provide consistent high levels of *H. zea* control, whereas pyrethroids are more variable and spinosyns

generally provide less control of *H. zea* (Musser and Shelton 2003, McLeod 2010, Shelton and Olmstead 2010). Research shows that insecticidal compounds developed within the past 20 yr may have lower toxicity to nontarget beneficial insects. For example, indoxacarb, spinosad, and chlorantraniliprole are less toxic to the most abundant naturally occurring predators in sweet corn compared with pyrethroid insecticides (Musser and Shelton 2003, Gradish et al. 2011).

Pyrethroid insecticides are commonly used against *H. zea* in many major agricultural crops of the United States. *Helicoverpa zea* adult populations were surveyed throughout the United States, and widespread but variable levels of pyrethroid resistance were observed during the 1997 and 1998 growing seasons (Martin et al. 1999). Martin et al. (1999) sampled and tested male moth populations using two pyrethroid doses (5 µg and 10 µg) and found variable levels of resistance in Alabama (12 and 2%, respectively), Louisiana (22 and 18%, respectively), North Carolina (13 and 2%, respectively), South Carolina (17 and 6%, respectively), Tennessee (6 and 1%, respectively), and Texas (6% for both). Because *H. zea* migrates from southern regions, where they may have been subjected to intense use of insecticides, to northern regions, growers in northern regions are often concerned that *H. zea* that arrive in their fields may already be resistant to insecticides they intend to use. Preliminary screening of migratory *H. zea* adult males caught in 2011 and 2012, using a discriminating dose of lambda-cyhalothrin vial test protocol (Payne et al. 2006), showed higher than expected levels of resistance that varied yearly (D.L.O., and A.M.S. unpublished data).

Biologically Based Insecticides

The most commonly used biologically based group of insecticides for *H. zea* management in sweet corn includes the active ingredient *Bacillus thuringiensis* (Bt). Bt insecticides are frequently used in organic sweet corn production, sometimes in combination with Zea-later II application methods (Cook et al. 2003), and are less commonly used in conventional systems utilizing traditional varieties (i.e., non-Bt cultivars; Hall and Dunn 1958, Bartels and Hutchison 1995). As of 2016, Deliver (Certis USA, Columbia, MD) and DiPel (Valent Biosciences, Libertyville, IL), both of which contain the 'kurstaki' Bt isolate, are the two formulated Bt products available for use against *H. zea* in the United States.

Viruses known to infect *H. zea* include lepidopteran-specific baculoviruses that are classified into alphabaculoviruses (nucleopolyhedroviruses; NPV) and betabaculoviruses (granuloviruses; Jehle et al. 2006, Chiu et al. 2012). Most research has focused on the potential control of *H. zea* with "cytoplasmic polyhedral virus" (Ignoffo and Adams 1966, Bong and Sikorowski 1991, Lua and Reid 2000), which Chiu et al. (2012) include as a member of the genus *Cypovirus* within the family Reoviridae.

Variable rates of control using NPV against *H. zea* have been achieved when applied directly to larvae or to infested corn silks (Ignoffo and Adams 1966, Hamm and Young 1971, Bell and Romine 1986, Bong and Sikorowski 1991, Lua and Reid 2000, Granados et al. 2001). Applications of NPV alone and in combination with other insecticides to early-season sweet corn significantly improved yield by 18.3 and 28.4%, respectively (Hamm and Young 1971). Granuloviruses have been evaluated to a lesser extent in combination with Bt for control of *H. zea* (Bell and Romine 1986, Granados et al. 2001). The use of these two pathogens together was antagonistic and resulted in lower overall mortality of *H. zea* compared with either one used separately. Gemstar (Certis, Columbia, MD) is the only NPV product commercially available in the United States.

Genetically Engineered Sweet Corn

Field corn expressing insecticidal crystal (Cry) proteins from *Bacillus thuringiensis* (Bt) was first commercialized in 1997 (Naranjo et al. 2008) to provide systemic plant protection against the European corn borer, *Ostrinia nubilalis* (Hübner), another lepidopteran caterpillar pest of sweet corn. Bt field corn has been widely adopted (>80% in 2015 in the United States, Fernandez-Cornejo and Wechsler 2016) and has proven so successful that *O. nubilalis* populations in the “Midwestern Corn Belt” of the United States have declined to the point of not being a significant corn pest (Hutchison et al. 2010).

Bt sweet corn varieties have piggy-backed on the development and registration of Bt field corn (Naranjo et al. 2008, Shelton 2012). Bt event 11, responsible for the expression of Cry1Ab, was the first to be bred into sweet corn for control of *O. nubilalis* and was marketed by Novartis Seeds in 1998 (Shelton 2012). Now marketed by Syngenta, Cry1Ab sweet corn hybrids containing this protein use the trade name Attribute and have been further enhanced by combining the original Bt event 11 with a second protein called Vip3A. Vip3A is an exotoxin also derived from Bt, but produced during vegetative bacterial growth. The Vip3A protein has a different target site than Cry toxins (Burkness et al. 2010). In the Attribute line of sweet corn, pyramided Cry1Ab and Vip3A proteins provide more complete control of *H. zea* due to different modes of action compared with plants that expressed a single gene, or none at all. In Minnesota and Maryland, pyramided (Cry1Ab and Vip3A) sweet corn hybrids provided almost complete control of *H. zea* as well as *O. nubilalis* and fall armyworm, *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) (Burkness et al. 2010). When plants expressed either protein alone, neither performed as well as when they were combined (Burkness et al. 2010).

Seminis (St. Louis, MO, USA) offers sweet corn hybrids that use Performance series technology to express pyramided Cry1A.105 and Cry2Ab2 insecticidal proteins. Shelton et al. (2013) reported results from multi-state field trials of sweet corn pyramided with Cry1A.105 and Cry2Ab2 compared with a sweet corn variety expressing only Cry1Ab and a non-Bt isolate, with and without the use of foliar insecticides. Sweet corn expressing two proteins (Cry1A.105 + Cry2Ab2) or a single protein (Cry1Ab) provided high marketability, and both Bt varieties significantly outperformed the traditional non-Bt isolines in nearly all cases regardless of insecticide application frequency. When comparisons for marketability in the same state were made between Cry1A.105 + Cry2Ab2 versus Cry1Ab plants for fresh-market standards, plants expressing Cry1A.105 + Cry2Ab2 provided better protection and resulted in less variability in control.

Insect resistance management strategies are mandatory in Bt field corn, but sweet corn represents only a very small fraction of total corn production in the United States (Burkness et al. 2011, Edwards et al. 2013), representing less than 1% of total corn planted in 2012 (USDA NASS 2016). For this reason, Bt sweet corn is exempt from United States Environmental Protection Agency rules requiring a proportion of corn acreage to be planted with a non-Bt corn refuge to delay resistance in *H. zea* or other Lepidoptera (Bates et al. 2005, Edwards et al. 2013). However, crop destruction soon after harvest is required, although this is primarily to control *O. nubilalis*, which overwinters in corn stalks. Bt sweet corn is also compatible with biological control because proteins expressed in these varieties have no adverse effects on nontarget beneficial organisms that are important for control of *H. zea* (Bartsch et al. 2008; Tian et al. 2012, 2013, 2014a,b; Liu et al. 2014). The conservation of biological control

agents can help control secondary pests of sweet corn, including aphids (Musser et al. 2006), and can help delay the evolution of resistance to Bt plants (Onstad et al. 2013, Liu et al. 2014).

In 2013, it was estimated that Seminis sweet corn hybrids using Performance series technology captured 5–10% of the fresh market in the United States (Shelton et al. 2013). Bt sweet corn has the capacity to significantly reduce the use of conventional insecticides used against lepidopteran pests and reduce occupational and environmental risks that arise from intensive insecticide use. Whether this will be fully realized will depend on consumer acceptance.

Additional Management Options

Biological Control

Many insects have been identified in the literature as control agents of *H. zea* in sweet corn fields. Species of Coccinellidae, Diptera, Hemiptera, and Hymenoptera either parasitize or are predators of eggs and larval stages.

Predators

Harmonia axyridis (Pallas) and *Coleomegilla maculata* (De Geer) (Oatman 1966, Pfannenstiel and Yeagan 2002, Musser et al. 2004) are commonly found on sweet corn. Pfannenstiel and Yeagan (2002) attributed 45% of all observed predation events to *C. maculata* in their study in Kentucky. Musser et al. (2004) documented that *C. maculata* and *H. axyridis* were the most abundant predators in New York State sweet corn. Exact predation levels of *H. zea* by these predators are not known.

Hemipteran predators observed on sweet corn include *Geocoris* spp. (Oatman 1966), *Lygus lineolaris* (Pfannenstiel and Yeagan 2002), and *Orius insidiosus* (Say) (Oatman 1966, Reid 1991, Pfannenstiel and Yeagan 2002). *Geocoris* spp. were not as abundant as *Orius* spp. in a study by Oatman (1966), but were still significant predators of *H. zea*. Pfannenstiel and Yeagan (2002) showed that *O. insidiosus* and *L. lineolaris* each accounted for >10% of overall predation of *H. zea* in their sweet corn studies. Reid (1991) showed >75% predation on *H. zea* eggs in corn silk at an artificial infestation rate of 12 *O. insidiosus* per plant. *Orius insidiosus* were also twice as abundant as all other predators combined (Oatman 1966).

Parasitoids

Hymenopteran parasitoids of *H. zea* eggs and larvae have been reported. *Campoletis* spp., *Hyposoter* spp., and *Meloborus juscifemora* (Graf) (Ichneumonidae) (Oatman and Platner 1970) have been recovered from *H. zea* larvae, whereas *Trichogramma pretiosum* (Trichogrammatidae) (Oatman 1966) have been collected from *H. zea* eggs. Oatman and Platner (1970) reported that *Campoletis* spp. were the most common species among all observed parasitoids.

Work has been done using the parasitoid *Archytas marmoratas* (Diptera: Tachinidae) against *H. zea* in sweet corn. Gross and Young (1984) achieved a rate of 40% larval parasitism in controlled cage studies. A follow-up field study achieved a parasitism rate of 58% when adult female *A. marmoratas* were released in fields with low-density *H. zea* larval populations (Gross 1990). Oatman and Platner (1970) collected the tachinids *Eucelatoria armigera* (Coquillett) and *Lespesia archippivora* (Riley) from *H. zea* larvae grown on sweet corn. We are unaware of any commercial inundative releases of biological control agents for control of *H. zea*,

although programs of releases of *Trichogramma* spp. for *O. nubilalis* may also impact *H. zea*.

Cultural Control

Pest avoidance is a cultural control strategy that utilizes knowledge of interactions between the host, the pest, and environment. Research shows that *H. zea* oviposition rates peak during fresh silk production, compared with later reproductive and earlier vegetative stages of sweet corn development (Mitchell 1978, Latheef et al. 1991, Coop et al. 1992, Archer and Bynum 1994). Utilizing knowledge of this insect–plant–environment relationship to minimize *H. zea* infestations may be helpful for pest management in specific situations.

Cultural options to manage *H. zea* in sweet corn via the use of either a trap crop or push–pull strategy, however, have been limited. The success of a trap cropping or a push–pull strategy is contingent on including a host that is more attractive than the cash crop itself (Shelton and Badenes-Perez 2006). Corn is the most attractive host for *H. zea* (Johnson et al. 1975), and therefore poses a great challenge for trap cropping. However, differences in sweet corn attraction could be created by manipulating the planting date or using early maturing cultivars. For example, smaller plantings of non-cash-crop sweet corn could be planted in proximity to the larger plantings of cash-crop sweet corn. Earlier plantings of the non-cash-crop corn would produce silks earlier and be more attractive than those in the later plantings of cash-crop sweet corn, thereby luring ovipositing *H. zea* away from the cash crop. In regions planted with large areas of field corn, it may be possible to time sweet corn plantings so they are less attractive than the nearby field corn. More research is warranted for evaluating the effectiveness, feasibility, and economics of such cultural control practices.

Host-plant Resistance

Traditional breeding for insect-resistant traits to manage *H. zea* in sweet corn has a long history, but minimal commercial success. Experiments have shown that silks of different corn varieties have significant differences in cuticular lipids, maysin, and isomaysin content, all of which significantly hinder larval development (Wiseman and McMillian 1982, Wiseman and Isenhour 1990, Wiseman et al. 1992, Yang et al. 1992). Anti-feeding compounds such as these may have a negative effect on *H. zea* fecundity and cause reductions in overall larval size and extend larval development time. Wiseman and Carpenter (1995) determined that growth inhibition factors in silk decrease protein absorption in *H. zea*, leading to malnutrition. However, we are unaware of any traditionally bred sweet corn varieties on the market that are effective in controlling *H. zea*.

Pheromone Disruption

In small corn fields, mating has been reduced using a disruption strategy called the air-permeation technique (mating disruption) with synthetic pheromones that impede males from finding and mating with females (Mitchell et al. 1975, Mitchell and McLaughlin 1982). The success of this strategy may have little utility in northern regions if *H. zea* moths mate in southern regions before migrating north to infest sweet corn fields. While a reduction in pest pressure might be possible at the field level where *H. zea* is a resident, using mating disruption in a coordinated area-wide effort across the agricultural landscape would have the highest likelihood of area-wide pest suppression (Cardé and Minks 1995). This strategy must also be carefully considered if more than one pest moth species is present.

A New Invasive Threat

While *H. zea* has become a major threat to sweet corn production in the United States in the past two decades, its newly invasive relative, *H. armigera*, will likely exacerbate problems. Like *H. zea*, *H. armigera* is a heliothine moth (Lepidoptera: Noctuidae: Heliethinae) and many of its close relatives are notorious for causing severe injury and economic losses in major agricultural crops worldwide (Cho et al. 2008). Cho et al. (2008) evaluated the ancestry of *H. zea* and other heliothines using a three-gene marker maximum likelihood analysis (EF-1 α , DDC, COI) and concluded that *H. zea* is most closely related to *H. armigera* (Old World origin) and *H. armigera* (New Zealand origin). *Helicoverpa zea* is separated from *H. armigera* by a single phylogenetic division with a low bootstrap score of 60 (Cho et al. 2008).

Tay et al. (2013) provided genetic evidence for the presence of *H. armigera* in Brazil, and this was the first such report of established *H. armigera* populations anywhere in the New World. Kritikos et al. (2015) warned of the damage it could cause if it invaded North America. As of 2014, *H. armigera* has been intercepted at U.S. ports of entry >800 times (Sullivan and Molet 2014), and its presence was confirmed in San Germán Puerto Rico the same year (USDA APHIS 2014), representing the first detection of *H. armigera* within U.S. political boundaries. In July 2015, live male specimens were captured in Manatee County, Florida (USA), the first occurrence in the continental United States (USDA APHIS 2015).

If *H. armigera* undergoes further range expansion in North America, the similarity in behavior and biology to *H. zea* will complicate management of the lepidopteran complex in sweet corn production. For instance, these sister species can vary in their susceptibility to insecticide chemistries; therefore, knowledge of insecticides that will kill both species will be critical (McCaffery 1998). Until now, there has been little need to develop rapid genetic identification techniques for *H. zea*. However, sweet corn growers and researchers alike should learn to differentiate the two species and make appropriate management decisions.

In conclusion, the large body of literature on *H. zea* in sweet corn provides valuable insights about the biology, ecology, and management of this important insect pest and should be used to refine our existing management programs. Strategies that include resistant sweet corn varieties, biological control, and cultural control can give growers the flexibility to reserve insecticide use as a supplemental or curative control tactic. With recent confirmation of *H. armigera* in the continental United States, and the fact that this species is well-known for its ability to develop resistance to insecticides, biotechnology may be an important component to successful management of sympatric *Helicoverpa* spp. in sweet corn.

Sweet corn containing insect-resistant traits, whether developed through traditional breeding or genetic engineering, should be the foundation of any integrated pest management (IPM) program (Kennedy 2008). The introduction of Bt field corn in the mid-1990s and subsequent area-wide adoption ultimately led to regional declines of *O. nubilalis* (Hutchison et al. 2010), and Bt technology also may bode well for control of heliothine pests in sweet corn. Efforts by public and private entities should continue to focus on *H. zea*, but attention must also be paid to *H. armigera* so that plant resistance technologies are in place when and wherever these insects co-occur in the future.

Little is known about the defensive responses by sweet corn to herbivory, especially those caused by *H. zea*. Current ecological

research shows that a complex system of chemical communication exists between a plant host, the herbivore, and natural enemies (Heil and Bueno 2007, Howe and Jander 2008, Hermann and Thaler 2014). The chemical responses, or lack thereof, within sweet corn to *H. zea* herbivory could generate new candidate mechanisms of control.

Traditional plant breeding and genetic engineering techniques present opportunities to tailor sweet corn lines for enhanced resistance to *H. zea* and *H. armigera*. Modification of traits such as husk length, silk density, and silk maysin content, or inhibition of silk ethylene production may hold promise as mechanisms for future control of *H. zea*. Other insecticidal molecules derived from Bt or other organisms, use of RNAi technology, or behavioral modifying traits may become realities in the future; however, this approach could also suffer from negative public acceptance (Shelton 2012). Most importantly, any insect-resistant plants expressing insecticidal or behavioral modifying compounds should be implemented in the overall framework of an ecologically and economically sustainable IPM program.

Use of “softer” technologies such as Bt sweet corn or “softer” insecticides like IRAC class 28 diamide chemistries may improve the prospects for conserving biological control agents, leading to more broadly integrated management tactics for *H. zea* and *H. armigera* in the future. Use of more IPM-compatible insecticides will also need to be coupled with better monitoring strategies and identification of a more precise and reliable relationship between the presence of insects and damage to the crop. The use of softer insecticides and genetically engineered insect-resistant plants should also encourage natural biological control in sweet corn.

The southern United States has long dealt with high pest pressure from *H. zea*, not only in sweet corn, but across a wide variety of vegetable and field crops. As producers elsewhere in the United States face growing *H. zea* management challenges in sweet corn, they should look to management strategies implemented by growers and researchers in the southern United States, where *H. zea* abundance is historically high. The agricultural community in these southern areas is also likely to first confront the arrival of *H. armigera* in the United States. Adequate resources should be provided now to growers and researchers in the southern states to better understand and manage *H. armigera* in sweet corn. By doing so, growers and researchers elsewhere in North America will be better prepared to deal with *Helicoverpa* spp. threats to sweet corn in the coming years.

There is broad consensus among scientists that climate change is no longer a question of “if or when” (Oreskes 2004), but where climate change impacts will be most pronounced. The impacts of such changes on lepidopteran species around the world (Parmesan et al. 1999, Hill et al. 2002, Both et al. 2009) demonstrate the coming challenges to managing *H. zea* and *H. armigera* in sweet corn. Commercial sweet corn plantings are usually grown in monocultures, but cropping patterns for sweet corn could change and may include more diverse crops, including other nonhost crops in the landscape that might lower populations of *H. zea*. Likewise, long- and short-distance movement patterns of *H. zea* may shift due to changing weather patterns or cropping systems in regions where *H. zea* overwinters. The probability of successful overwintering by *H. zea* in northern regions may increase due to warmer soil temperatures and decreased exposure to lethal low temperatures. Larval development rates will increase as the accumulation of developmental heat units accelerates. The potential for climate change to increase the number of *H. zea* generations within a single season has broad implications for *H. zea* management in sweet corn.

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Literature Cited

- Akkawi, M. M., and D. R. Scott. 1984. The effect of age of parents on the progeny of diapaused and non-diapaused *Heliothis zea*. Entomol. Exp. Appl. 35: 235–239.
- Archer, T. L., and E. D. Bynum. 1994. Corn earworm (Lepidoptera: Noctuidae) biology on food corn on the high plains. Environ. Entomol. 23: 343–348.
- Bale, J. S. 1987. Insect cold hardiness: freezing and supercooling—an ecophysiological perspective. J. Insect Physiol. 33: 899–908.
- Barber, G. W. 1941. Observations on the egg and newly hatched larva on the corn earworm on corn silk. J. Econ. Entomol. 34: 451–456.
- Barber, G. W. 1943. Oviposition habits of the earworm moth in relation to infestation in the ears and to control. J. Econ. Entomol. 36: 611–618.
- Bartels, D. W., and W. D. Hutchison. 1995. On-farm efficacy of aerially applied *Bacillus thuringiensis* for European corn borer (Lepidoptera: Pyralidae) and corn earworm (Lepidoptera: Noctuidae) control in sweet corn. J. Econ. Entomol. 88: 380–386.
- Bartsch, D., F. Bigler, M. P. Candolfi, M. M. Gielkens, S. E. Hartley, R. L. Hellmich, J. E. Huesing, P. C. Jepson, R. Layton, H. Quemada, et al. 2008. Assessment of risk of insect-resistant transgenic crops to nontarget arthropods. Nat. Biotechnol. 26: 203–208.
- Bates, S. L., J. Z. Zhao, R. T. Roush, and A. M. Shelton. 2005. Insect resistance management in GM crops: past, present and future. Nat. Biotechnol. 23: 57–62.
- Beerwinkle, K. R., J. D. Lopez, J. A. Witz, P. G. Schleider, R. S. Eyster, and P. D. Lingren. 1994. Seasonal radar and meteorological observations associated with nocturnal insect flight at altitudes to 900 meters. Environ. Entomol. 23: 676–683.
- Bell, M. R., and C. L. Romine. 1986. *Heliothis virescens* and *H. zea* (Lepidoptera: Noctuidae): dosage effects of feeding mixtures of *Bacillus thuringiensis* and a nuclear polyhedrosis virus on mortality and growth. Environ. Entomol. 15: 1161–1165.
- Benschoter, C. A. 1968. Diapause and development of *Heliothis zea* and *H. virescens* in controlled environments. Ann. Entomol. Soc. Am. 61: 953–956.
- Bong, C.F.J., and P. P. Sikorowski. 1991. Effects of cytoplasmic polyhedrosis virus and bacterial contamination on growth and development of the corn earworm, *Helicoverpa zea* (Lepidoptera: Noctuidae). J. Invertebr. Pathol. 57: 406–412.
- Both, C., M. van Asch, R. G. Bijlsma, A. B. van den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? J. Anim. Ecol. 78: 73–83.
- Burkness, E. C., G. Dively, T. Patton, A. C. Morey, and W. D. Hutchison. 2010. Novel Vip3A *Bacillus thuringiensis* (Bt) maize approaches high-dose efficacy against *Helicoverpa zea* (Lepidoptera: Noctuidae) under field conditions: Implications for resistance management. GM Crops 1: 337–343.
- Burkness, E. C., P. K. O'Rourke, and W. D. Hutchison. 2011. Cross-pollination of nontransgenic corn ears with transgenic Bt corn: efficacy against lepidopteran pests and implications for resistance management. J. Econ. Entomol. 104: 1476–1479.
- Butler, G. D. 1976. Bollworm: development in relation to temperature and larval food. Environ. Entomol. 5: 520–522.
- Butler, G. D., and D. R. Scott. 1976. Two models for development of the corn earworm on sweet corn in Idaho. Environ. Ent. 5: 68–72.
- CABI. 2016. *Helicoverpa zea*. In: Invasive Species Compendium. (www.cabi.org/isc) (accessed 08 March 2016).
- Callahan, P. S. 1958. Behavior of the imago of the corn earworm, *Heliothis zea* (Boddie), with special reference to emergence and reproduction. Ann. Entomol. Soc. Am. 51: 271–283.
- Cantelo, W. W., and M. Jacobson. 1979. Corn silk volatiles attract many pest species of moths. J. Environ. Sci. Health Part Environ. Sci. Eng. 14: 695–707.

- Cardé, R. T., and A. K. Minks. 1995. Control of moth pests by mating disruption: Successes and constraints. *Annu. Rev. Entomol.* 40: 559–585.
- Chiu, E., F. Coulbaly, and P. Metcalf. 2012. Insect virus polyhedra, infectious protein crystals that contain virus particles. *Curr. Opin. Struct. Biol.* 22: 234–240.
- Cho, S., A. Mitchell, C. Mitter, J. Regier, M. Matthews, and R. Robertson. 2008. Molecular phylogenetics of heliothine moths (Lepidoptera: Noctuidae: Heliothinae), with comments on the evolution of host range and pest status. *Syst. Entomol.* 33: 581–594.
- Chowdhury, M. A., R. B. Chalfant, and J. R. Young. 1987a. Comparison of sugarline sampling and pheromone trapping for monitoring adult populations of corn earworm and fall armyworm (Lepidoptera: Noctuidae) in sweet corn. *Environ. Entomol.* 16: 1241–1243.
- Chowdhury, M. A., R. B. Chalfant, and J. R. Young. 1987b. Ear damage in sweet corn in relation to adult corn earworm (Lepidoptera: Noctuidae) populations. *J. Econ. Entomol.* 80: 867–869.
- Cohen, R. W., G. P. Waldbauer, and S. Friedman. 1988. Natural diets and self-selection: *Heliothis zea* larvae and maize. *Entomol. Exp. Appl.* 46: 161–171.
- Cook, R., A. Carter, P. Westgate, and R. Hazzard. 2003. Direct silk applications of corn oil and *Bacillus thuringiensis* as a barrier to corn earworm larvae in sweet corn. *HortTechnology* 13: 509–514.
- Coop, L. B., R. J. Drapek, B. A. Croft, and G. C. Fisher. 1992. Relationship of corn earworm (Lepidoptera: Noctuidae) pheromone catch and silking to infestation levels in Oregon sweet corn. *J. Econ. Entomol.* 85: 240–245.
- Coop, L. B., B. A. Croft, and R. J. Drapek. 1993. Model of corn earworm (Lepidoptera: Noctuidae) development, damage, and crop loss in sweet corn. *J. Econ. Entomol.* 86: 906–916.
- Drapek, R. J., L. B. Coop, B. A. Croft, and G. C. Fisher. 1990. *Heliothis zea* pheromone trapping: studies of trap and lure combinations and field placement in sweet corn. *Southwest. Entomol.* 15: 63–69.
- Edwards, K. T., M. A. Caprio, K. C. Allen, and F. R. Musser. 2013. Risk assessment for *Helicoverpa zea* (Lepidoptera: Noctuidae) resistance on dual-gene versus single-gene corn. *J. Econ. Entomol.* 106: 382–392.
- Eger, J. E. J., J. A. Witz, A. W. J. Hartstack, and W. L. Sterling. 1982. Survival of pupae of *Heliothis virescens* and *Heliothis zea* at low temperatures. *Can. Entomol.* 114: 289–301.
- Ferguson, J. E., A. M. Rhodes, and D. B. Dickinson. 1978. The genetics of sugary enhancer (se), an independent modifier of sweet corn (su). *J. Hered.* 69: 377–380.
- Fernandez-Cornejo, J., and S. J. Wechler. 2016. Adoption of genetically engineered crops in the United States, 1996–2015. United States Department of Agriculture Economic Research Service. (<http://www.ers.usda.gov/data-products/adoption-of-genetically-engineered-crops-in-the-us/recent-trends-in-ge-adoption.aspx>) (accessed 10 March 2016).
- Fitt, G. P. 1989. The ecology of *Heliothis* species in relation to agroecosystems. *Annu. Rev. Entomol.* 34: 17–53.
- Fleischer, S. 2016. Pest Watch. (<http://www.pestwatch.psu.edu/index.html>) (accessed 08 March 2016).
- Flood, B. R., R. Foster, W. D. Hutchison, and S. Pataky. 2005. Sweet corn. pp. 39–61. *In* R. Foster and B. R. Flood (eds.), *Vegetable insect management*. Meister Media Worldwide, Willoughby, OH.
- Gauthier, N. L., P. A. Logan, L. A. Tewksbury, C. Hollingsworth, D. C. Weber, and R. G. Adams. 1991. Field bioassay of pheromone lures and trap designs for monitoring adult corn earworm (Lepidoptera: Noctuidae) in sweet corn in southern New England. *J. Econ. Entomol.* 84: 1833–1836.
- Gould, F., N. Blair, M. Reid, T. L. Rennie, J. Lopez, and S. Micinski. 2002. *Bacillus thuringiensis*-toxin resistance management: Stable isotope assessment of alternate host use by *Helicoverpa zea*. *Proc. Natl. Acad. Sci. USA.* 99: 16581–16586.
- Gradish, A. E., C. Scott-Dupree, L. Shipp, R. C. Harris, and G. Ferguson. 2011. Effect of reduced risk pesticides on greenhouse vegetable arthropod biological control agents. *Pest Manag. Sci.* 67: 82–86.
- Granados, R. R., Y. Fu, B. Corsaro, and P. R. Hughes. 2001. Enhancement of *Bacillus thuringiensis* toxicity to lepidopterous species with the enhancer from *Trichoplusia ni* granulovirus. *Biol. Control* 20: 153–159.
- Gross, H. R. 1990. Field release and evaluation of *Archytas marmoratus* (Diptera: Tachinidae) against larvae of *Heliothis zea* (Lepidoptera: Noctuidae) in whorl stage corn. *Environ. Entomol.* 19: 1122–1129.
- Gross, H. R., and O. P. Young. 1984. *Archytas marmoratus* (Diptera: Tachinidae): Screened-cage evaluations of selected densities of adults against larval populations of *Heliothis zea* and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on whorl and tassel stage corn. *Environ. Entomol.* 13: 157–161.
- Grubinger, V. 2004. Sweet corn genotypes. University of Vermont Extension Vegetable and Berry Program. (<https://www.uvm.edu/vtvegandberry/fact-sheets/corngenotypes.html>) (accessed 08 March 2016).
- Hall, I. M., and P. H. Dunn. 1958. Susceptibility of some insect pests to infection by *Bacillus thuringiensis* Berliner in laboratory tests. *J. Econ. Entomol.* 51: 296–298.
- Hamm, J. J., and J. R. Young. 1971. Value of virus presilk treatment for corn earworm and fall armyworm control in sweet corn. *J. Econ. Entomol.* 64: 144–146.
- Hardwick, D. F. 1965. The corn earworm complex. *Mem. Entomol. Soc. Can.* 97: 5–247.
- Harrell, E. A., W. D. Perkins, and B. G. Mullinix. 1979. Effects of temperature, relative humidity, and air velocities on development of *Heliothis zea*. *Ann. Entomol. Soc. Am.* 72: 222–223.
- Heil, M., and J. C. Silva Bueno. 2007. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *Proc. Natl. Acad. Sci. USA.* 104: 5467–5472.
- Hendrix, W. H., T. F. Mueller, J. R. Phillips, and O. K. Davis. 1987. Pollen as an indicator of long-distance movement of *Heliothis zea* (Lepidoptera: Noctuidae). *Environ. Entomol.* 16: 1148–1151.
- Hermann, S. L., and J. S. Thaler. 2014. Prey perception of predation risk: Volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. *Oecologia* 176: 669–676.
- Hill, J. K., C. D. Thomas, R. Fox, M. G. Telfer, S. G. Willis, J. Asher, and B. Huntley. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proc. R. Soc. B Biol. Sci.* 269: 2163–2171.
- Howe, G. A., and G. Jander. 2008. Plant immunity to insect herbivores. *Annu. Rev. Plant Biol.* 59: 41–66.
- Hutchison, W. D., E. C. Burkness, P. D. Mitchell, R. D. Moon, T. W. Leslie, S. J. Fleischer, M. Abrahamson, K. L. Hamilton, K. L. Steffey, M. E. Gray, et al. 2010. Areawide suppression of European corn borer with Bt maize reaps savings to non-Bt maize growers. *Science* 330: 222–225.
- Ignoffo, C. M., and J. R. Adams. 1966. A cytoplasmic-polyhedrosis virus, *Smithiavirus pectinophorae* sp. n. of the pink bollworm, *Pectinophora gossypiella* (Saunders). *J. Invertebr. Pathol.* 8: 59–66.
- IRAC. 2016. Insecticide Resistance Action Committee MoA classification scheme. (<http://www.irac-online.org/documents/moa-classification/?ext=pdf>) (accessed 08 March 2016).
- James, M. G., D. S. Robertson, and A. M. Myers. 1995. Characterization of the maize gene sugary1, a determinant of starch composition in kernels. *Plant Cell* 7: 417–429.
- Jehle, J. A., G. W. Blissard, B. C. Bonning, J. S. Cory, E. A. Herniou, G. F. Rohrmann, D. A. Theilmann, S. M. Thiem, and J. M. Vlak. 2006. On the classification and nomenclature of baculoviruses: A proposal for revision. *Arch. Virol.* 151: 1257–1266.
- Johnson, G. V. 1944. DDT for the control of the tomato fruitworm. *J. Econ. Entomol.* 37: 151–152.
- Johnson, M. W., R. E. Stinner, and R. L. Rabb. 1975. Ovipositional response of *Heliothis zea* (Boddie) to its major hosts in North Carolina. *Environ. Entomol.* 4: 291–297.
- Joyner, K., and F. Gould. 1985. Developmental Consequences of Cannibalism in *Heliothis zea* (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 78: 24–28.
- Kennedy, G. G. 2008. Integration of insect-resistant genetically modified crops within IPM programs. pp. 1–26. *In* J. Romeis, A. M. Shelton, and G. G. Kennedy (eds.), *Integration of insect-resistant genetically modified crops within IPM programs*. Springer Netherlands.
- Kennedy, G. G., and N. P. Storer. 2000. Life systems of polyphagous arthropod pests in temporally unstable cropping systems. *Annu. Rev. Entomol.* 45: 467–493.
- Kritikos, D. J., N. Ota, W. D. Hutchison, J. Beddow, T. Walsh, W. T. Tay, D. M. Borchert, S. V. Paula-Moreas, C. Czapak, and M. P. Zalucki. 2015.

- The potential distribution of invading *Helicoverpa armigera* in North America: is it just a matter of time? PLoS ONE 10: e0119618.
- Latheef, M. A., J. A. Witz, and J. D. Lopez. 1991. Relationships among pheromone trap catches of male corn earworm moths (Lepidoptera: Noctuidae), egg numbers, and phenology in corn. Can. Entomol. 123: 271–281.
- Latheef, M. A., J. D. Lopez, and J. A. Witz. 1993. Capture of corn earworm (Lepidoptera: Noctuidae) in pheromone traps and hand nets: relationship to egg and adult densities in field corn, Texas Brazos River Valley. J. Econ. Entomol. 86: 407–415.
- Lingren, P. D., V. M. Bryant, J. R. Raulston, M. Pendleton, J. Westbrook, and G. D. Jones. 1993. Adult feeding host range and migratory activities of corn earworm, cabbage looper, and celery looper (Lepidoptera: Noctuidae) moths as evidenced by attached pollen. J. Econ. Entomol. 86: 1429–1439.
- Liu, X., M. Chen, H. L. Collins, D. W. Onstad, R. T. Roush, Q. Zhang, E. D. Earle, and A. M. Shelton. 2014. Natural enemies delay insect resistance to Bt crops. PLoS ONE 9: e90366.
- Lua, L. H. L., and S. Reid. 2000. Virus morphogenesis of *Helicoverpa armigera* nucleopolyhedrovirus in *Helicoverpa zea* serum-free suspension culture. J. Gen. Virol. 81: 2531–2543.
- Mangat, B. S., and J. W. Apple. 1966. Corn earworm development in relation to temperature. J. Econ. Entomol. 59: 1005–1006.
- Martin, S. H., R. D. Bagwell, M. L. Boyd, B. L. Freeman, G. A. Herzog, D. R. Johnson, M. B. Layton, B. R. Leonard, N. Liu, G. T. Payne, et al. 1999. Status of bollworm, *Helicoverpa zea*, susceptibility to pyrethroids: IRAC-US 1998 update. (<http://www.westga.edu/~gpayne/Research/Insecticide%20Resistance%20Monitoring/irac-us1999data.htm>) (accessed 08 March 2016).
- McCaffery, A. R. 1998. Resistance to insecticides in heliothine Lepidoptera: A global view. Philos. T. R. Soc. B. 353: 1735–1750.
- McLeod, P. 2010. Evaluation of foliar insecticides for corn earworm management on sweet corn, 2009. Arthropod Manag. Tests 35: E27.
- Mitchell, E. R. 1978. Relationship of planting date to damage by earworms in commercial sweet corn in north central Florida. Fla. Entomol. 61: 251–255.
- Mitchell, E. R., and J. R. McLaughlin. 1982. Suppression of mating and oviposition by fall armyworm and mating by corn earworm in corn, using the air permeation technique. J. Econ. Entomol. 75: 270–274.
- Mitchell, E. R., M. Jacobson, and A. H. Baumhover. 1975. *Heliothis* spp.: Disruption of pheromonal communication with (Z)-9-tetradecen-1-ol formate. Environ. Entomol. 4: 577–579.
- Morey, A. C., W. D. Hutchison, R. C. Venette, and E. C. Burkness. 2012. Cold hardiness of *Helicoverpa zea* (Lepidoptera: Noctuidae) pupae. Environ. Entomol. 41: 172–179.
- Musser, F. R., and A. M. Shelton. 2003. Bt sweet corn and selective insecticides: Impacts on pests and predators. J. Econ. Entomol. 96: 71–80.
- Musser, F. R., J. P. Nyrop, and A. M. Shelton. 2004. Survey of predators and sampling method comparison in sweet corn. J. Econ. Entomol. 97: 136–144.
- Musser, F. R., J. P. Nyrop, and A. M. Shelton. 2006. Integrating biological and chemical controls in decision making: European corn borer (Lepidoptera: Crambidae) control in sweet corn as an example. J. Econ. Entomol. 99: 1538–1549.
- Najeeb, S., F. A. Sheikh, M. A. Ahanger, and N. A. Teli. 2011. Popularization of sweet corn (*Zea mays* L. Saccharata) under temperate conditions to boost the socioeconomic conditions. Maize Genet. Coop. Newsl. 85.
- Naranjo, S. E., J. R. Ruberson, H. C. Sharma, L. Wilson, and K. Wu. 2008. The present and future role of insect-resistant genetically modified cotton in IPM, pp. 159–194. In J. Romeis, A. M. Shelton, and G. G. Kennedy (eds.), Integration of insect-resistant genetically modified crops within IPM Programs. Springer, Dordrecht, The Netherlands.
- Neunzig, H. H. 1963. Wild host plants of the corn earworm and the tobacco budworm in eastern North Carolina. J. Econ. Entomol. 56: 135–139.
- Oatman, E. R. 1966. Parasitization of corn earworm eggs on sweet corn silk in southern California, with notes on larval infestations and predators. J. Econ. Entomol. 59: 830–835.
- Oatman, E. R., and G. R. Platner. 1970. Parasitization of corn earworm larvae infesting sweet corn tassels in southern California. J. Econ. Entomol. 63: 326–327.
- Onstad, D. W., X. Liu, M. Chen, R. Roush, and A. M. Shelton. 2013. Modeling the integration of parasitoid, insecticide, and transgenic insecticidal crop for the long-term control of an insect pest. J. Econ. Entomol. 106: 1103–1111.
- Oreskes, N. 2004. The scientific consensus on climate change. Sci. New Ser 306: 1686.
- Parajulee, M. N., J. E. Slosser, and E. P. Boring. 1998. Seasonal activity of *Helicoverpa zea* and *Heliothis virescens* (Lepidoptera: Noctuidae) detected by pheromone traps in the Rolling Plains of Texas. Environ. Entomol. 27: 1203–1219.
- Parmesan, C., N. Ryrholm, C. Stefanescu, and J. K. Hill. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579–583.
- Pfannenstiel, R. S., and K. V. Yeargan. 2002. Identification and diel activity patterns of predators attacking *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs in soybean and sweet corn. Environ. Entomol. 31: 232–241.
- Phillips, J. R., and L. D. Newsom. 1966. Diapause in *Heliothis zea* and *Heliothis virescens* (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am. 59: 154–159.
- Raina, A. K., J. C. Davis, and E. A. Stadelbacher. 1991. Sex pheromone production and calling in *Helicoverpa zea* (Lepidoptera: Noctuidae): Effect of temperature and light. Environ. Entomol. 20: 1451–1456.
- Raina, A. K., T. G. Kingan, and A. K. Mattoo. 1992. Chemical signals from host plant and sexual behavior in a moth. Sci. New Ser. 255: 592–594.
- Reid, C. D. 1991. Ability of *Orius insidiosus* (Hemiptera: Anthoridae) to search for, find, and attack European corn borer and corn earworm eggs on corn. J. Econ. Entomol. 84: 83–86.
- Roach, S. H., and A. R. Hopkins. 1979. *Heliothis* spp.: behavior of prepupae and emergence of adults from different soils at different moisture levels. Environ. Entomol. 8: 388–391.
- Sandstrom, M. 2016. Insectforecast.com. (<http://www.insectforecast.com>) (accessed 08 March 2016).
- Shelton, A. M. 2012. Genetically engineered vegetables expressing proteins from *Bacillus thuringiensis* for insect resistance: successes, disappointments, challenges and ways to move forward. GM Crops Food Biotechnol. Agric. Food Chain 3: 175–183.
- Shelton, A. M., and F. R. Badenes-Perez. 2006. Concepts and applications of trap cropping in pest management. Annu. Rev. Entomol. 51: 285–308.
- Shelton, A. M., and D. L. Olmstead. 2010. Control of lepidoptera on sweet corn, 2010. Arthropod Manag. Tests 36: E78.
- Shelton, A. M., D. L. Olmstead, E. C. Burkness, W. D. Hutchison, G. Dively, C. Welty, and A. N. Sparks. 2013. Multi-state trials of Bt sweet corn varieties for control of the corn earworm (Lepidoptera: Noctuidae). J. Econ. Entomol. 106: 2151–2159.
- Slosser, J. E., J. R. Phillips, G. A. Herzog, and C. R. Reynolds. 1975. Overwinter survival and spring emergence of the bollworm in Arkansas. Environ. Entomol. 4: 1015–1024.
- Stinner, R. E., R. L. Rabb, and J. R. Bradley. 1974. Population dynamics of *Heliothis zea* (Boddie) and *H. virescens* (F.) in North Carolina: a simulation model. Environ. Ent. 3: 163–168.
- Sudbrink, D. L., and J. F. Grant. 1995. Wild host plants of *Helicoverpa zea* and *Heliothis virescens* (Lepidoptera: Noctuidae) in eastern Tennessee. Environ. Entomol. 24: 1080–1085.
- Sullivan, M., and T. Molet. 2014. CPHST pest datasheet for *Helicoverpa armigera*. USDA-APHIS-PPQ-CPHST. (https://www.aphis.usda.gov/plant_health/plant_pest_info/owb/downloads/owb-factsheet.pdf) (accessed 2 January 2016).
- Tay, W. T., M. F. Soria, T. Walsh, D. Thomazoni, P. Silvie, G. T. Behere, C. Anderson, and S. Downs. 2013. A Brave New World for an Old World Pest: *Helicoverpa armigera* (Lepidoptera: Noctuidae) in Brazil. PLoS ONE 8: e80134. (doi: 10.1371/journal.pone.0080134)
- Tian, J.-C., H. L. Collins, J. Romeis, S. E. Naranjo, R. L. Hellmich, and A. M. Shelton. 2012. Using field-evolved resistance to Cry1F maize in a lepidopteran pest to demonstrate no adverse effects of Cry1F on one of its major predators. Trans. Res. 21: 1303–1310.
- Tian, J.-C., X.-P. Wang, L.-P. Long, J. Romeis, S. E. Naranjo, R. L. Hellmich, P. Wang, E. D. Earle, and A. M. Shelton. 2013. Bt crops producing Cry1Ac, Cry2Ab and Cry1F do not harm the green lacewing, *Chrysoperla rufilabris*. PLoS ONE 8: 1–6.

- Tian, J.-C., L.-P. Long, X.-P. Wang, S. E. Naranjo, J. Romeis, R. L. Hellmich, P. Wang, and A. M. Shelton. 2014a. Using resistant prey demonstrates that Bt plants producing Cry1Ac, Cry2Ab, and Cry1F have no negative effects on *Geocoris punctipes* and *Orius insidiosus*. *Environ. Entomol.* 43: 242–251.
- Tian, J.-C., X.-P. Wang, L.-P. Long, J. Romeis, S. E. Naranjo, R. L. Hellmich, and A. M. Shelton. 2014b. Eliminating host-mediated effects demonstrates Bt maize producing Cry1F has no adverse effects on the parasitoid *Cotesia marginiventris*. *Trans. Res.* 23: 257–264.
- Tracy, W. F., S. R. Whitt, and E. S. Buckler. 2006. Recurrent mutation and genome evolution: Example of Sugary1 and the origin of sweet maize. *Crop Sci.* 46: S49–S54.
- (USDA APHIS) United States Department of Agriculture Animal and Plant Health Inspection Service. 2014. Detection of old world bollworm (*Helicoverpa armigera*) in Puerto Rico (corrected). USDA-APHIS-PPQ. (https://www.aphis.usda.gov/plant_health/plant_pest_info/owb/downloads/DA-2014-45.pdf) (accessed 08 March 2016).
- (USDA APHIS) United States Department of Agriculture Animal and Plant Health Inspection Service. 2015. Detection of old world bollworm (*Helicoverpa armigera*) in Florida. USDA-APHIS-PPQ. (https://www.aphis.usda.gov/plant_health/plant_pest_info/owb/downloads/DA-2015-43.pdf) (accessed 08 March 2016).
- (USDA ERS) United States Department of Agriculture Economic Research Service 2015. U.S. phytosanitary regulation of sweet corn imports. (http://www.ers.usda.gov/datafiles/Phytosanitary_Regulation/Individual_Commodity_Files/Vegetables/veg-sweetcorn.xls) (accessed 08 March 2016).
- (USDA NASS) United States Department of Agriculture National Agricultural Statistics Service. 2016. 2013 sweet corn production totals for the United States. (<http://www.nass.usda.gov>) (accessed 08 March 2014).
- Wagner, T. L., H.-I. Wu, P.J.H. Sharpe, R. M. Schoolfield, and R. N. Coulson. 1984. Modeling insect development rates: A literature review and application of a biophysical model. *Ann. Entomol. Soc. Am.* 77: 208–225.
- Waldbauer, G. P., R. W. Cohen, and S. Friedman. 1984. Self-selection of an optimal nutrient mix from defined diets by larvae of the corn earworm, *Heliothis zea* (Boddie). *Physiol. Zool.* 57: 590–597.
- Wellso, S. G., and P. L. Adkisson. 1966. A long-day short-day effect in the photoperiodic control of the pupal diapause of the bollworm, *Heliothis zea* (Boddie). *J. Insect Physiol.* 12: 1455–1465.
- Westbrook, J. K., and J. D. Lopez. 2010. Long-distance migration in *Helicoverpa zea*: What we know and need to know. *Southwest. Entomol.* 35: 355–360.
- Westbrook, J. K., W. W. Wolf, P. D. Lingren, J. R. Raulston, J. D. Lopez, J. H. Matis, R. S. Eyster, J. F. Esquivel, and P. G. Schleider. 1997. Early-season migratory flights of corn earworm (Lepidoptera: Noctuidae). *Environ. Entomol.* 26: 12–20.
- Williams, D. W., and R. E. Stinner. 1987. Respiration and drowning in overwintering pupae of *Heliothis zea* (Boddie). *Can. Entomol.* 119: 329–338.
- Wiseman, B. R., and J. E. Carpenter. 1995. Growth inhibition of corn earworm (Lepidoptera: Noctuidae) larvae reared on resistant corn silk diets. *J. Econ. Entomol.* 88: 1037–1043.
- Wiseman, B. R., and D. J. Isenhour. 1990. Effects of resistant maize silks on corn earworm (Lepidoptera: Noctuidae) biology: A laboratory study. *J. Econ. Entomol.* 83: 614–617.
- Wiseman, B. R., and W. W. McMillian. 1982. Alterations in corn earworm larval feeding behavior and corn ear penetration. *J. Ga. Entomol. Soc.* 17: 321–327.
- Wiseman, B. R., M. E. Snook, R. L. Wilson, and D. J. Isenhour. 1992. Allelochemical content of selected popcorn silks: Effects on growth of corn earworm larvae (Lepidoptera: Noctuidae). *J. Econ. Entomol.* 85: 2500–2504.
- Wolf, W. W., J. K. Westbrook, J. Raulston, S. D. Pair, S. E. Hobbs, J. R. Riley, P. J. Mason, and R. J. V. Joyce. 1990. Recent airborne radar observations of migrant pests in the United States. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 328: 619–630.
- Yang, G., B. R. Wiseman, and K. E. Espelie. 1992. Cuticular lipids from silks of seven corn genotypes and their effect on development of corn earworm larvae *Helicoverpa zea* (Boddie). *J. Agric. Food Chem.* 40: 1058–1061.