ABSTRACT - Since the early 1990s, maize producers in Europe and North America have shared management challenges with two formidable insect foes: the European corn borer (Ostrinia nubilalis Hübner) and the western corn rootworm (Diabrotica virgifera virgifera LeConte). Although considerable progress has been made in the management of European corn borer via the use of commercially available maize hybrids that offer some degree of conventional host plant resistance, the deployment of resistant (antibiosis) alleles in maize for corn rootworm has been disappointing. Producers in the United States have relied largely upon crop rotation and the prophylactic use of soil insecticides in an effort to prevent economic losses caused by corn rootworm larvae. In some areas of the western Corn Belt, an over reliance on insecticides to suppress egg laying by corn rootworm adults has led to the development of insecticide resistance to methylparathion and carbaryl. Since the mid-1990s, the non-diversified agroecosystem of the US eastern Corn Belt has led to the development of a variant western corn rootworm that is able to circumvent the cultural management tactic of rotating maize and soybean. The integration of many management strategies (IPM) is critical in prolonging the usefulness of individual control tactics for both of these important insect pests of maize. The receptiveness to transgenic hybrids by producers on each continent remains strikingly different. Although we believe transgenic hybrids offer producers yet another management tool to deploy within an IPM framework for European corn borers and western corn rootworms, they should not be viewed as the ultimate solution for either species. Like all insects, these two pests are versatile and will adapt to any technology if it is abused.

KEY WORDS: European corn borer; Corn rootworm; Pest management; Ostrinia nubilalis; Diabrotica virgifera virgifera; Invasive species.

INTRODUCTION

To commemorate the 50th anniversary of Maydica, we will reflect upon the impact of two invasive insect pests and the evolution of tactics to manage them. One is an old nemesis in Europe and the United States: the European corn borer (Ostrinia nubilalis Hübner). The other, an old nemesis in the United States, has become a new nemesis in Europe: the western corn rootworm (Diabrotica virgifera virgifera LeConte).

It is somewhat ironic that following the introduction of a major insect pest from Europe to the US (European corn borer) almost a hundred years ago, Europeans find themselves facing a new challenge (western corn rootworm) as the result of a recent introduction from the US. Many articles about both pests have occurred throughout the history of Maydica. The first mention of European corn borer (ECB) was by CAVAZZA (1956) in the first year of this publication. He discussed the cultivation of maize in the Calabria region of Italy and mentioned it was “rare to find the harvest that is not attacked by the larvae of this greedy insect (translation”). ROGERS et al. (1977) published the first Maydica article about corn rootworm (CRW) wherein they discussed the expected gains in selection for resistance in maize to CRW.

European Corn Borer, Ostrinia nubilalis Hübner

Before the introduction of Zea maize L. from the American continent, ECB probably infested wild hops and grasses in Eurasia (BARCOCK and VANCE, 1929). The earliest published European accounts indicated ECB was a pest of broomcorn millet (Panicum miliaceum), hops (Humulus lupulus), and hemp (Cannabis sativa). Christopher Columbus was the first to introduce maize into Europe, bringing it from the Caribbean to Spain in 1492. Recent
molecular studies by 

Rebourg et al. (2003) have suggested further introductions into northern Europe were made by Giovanni Verrazano and Jacques Cartier in 1524 and 1535, respectively. As the cultivation of maize spread throughout Europe, ECB began to adapt to this new host. The first widespread outbreak in Europe was reported in 1879, followed by another in 1915-1917 (Babcock and Vance, 1929).

In 1914, the European corn borer was first discovered on the North American continent infesting corn fields near Boston, Massachusetts (Vinal, 1917). The exact origin of this pest introduction is unknown, but circumstantial evidence, based on voltinism, suggests diapausing larvae may have been present within the discarded stalks of broom corn imported from southern Europe (Caffrey and Worthley, 1927). By the late 1940’s, the ECB had spread into the heart of the US corn belt and was firmly established as a major pest despite efforts to control its spread. Currently, the ECB is established in most of the continental US east of the Rocky Mountains (Showers, 1979).

Following its introduction, state and federal governmental agencies enlisted a two-pronged approach to managing the pest: prevention of spread into new areas and control of existing populations. Quarantines on the movement of corn and corn products were implemented during the late 1920’s, but they failed to contain the expansion of the pest. The most likely reason for the failure lies in the relatively mobile nature of the adult moth, capable of flying several kilometers, which circumvented the quarantine barriers. Also, isolation within the rural agricultural community prevented the proper communication and enforcement of quarantine zones, leading to transportation of ECB-containing ears of corn from quarantined areas into new areas (Worthley and Caffrey, 1927). Control of existing populations was attempted through a series of innovative technologies including heat treatment of stalk debris to kill overwintering larvae, deep plowing intended to bury stalk debris and prevent emergence the following spring, and truck-mounted stalk crushers to mechanically kill overwintering larvae. Biological control with diseases and insects was investigated and introductions of the fungal pathogen Beauveria bassiana and several native and foreign dipteran parasites were initiated (Caffrey and Worthley, 1927). Chemical control technologies were limited to the few organic pesticides in existence. Despite the attempts at using current technology, the ECB became firmly established throughout the major corn growing regions of the US and Canada by the late 1950’s (Chiang and Wendels, 1972).

Beginning in the early 1950’s, attention turned to controlling endemic populations of the European corn borer. In 1948, the North Central Regional Association of Directors of Agricultural Experiment Stations directed the establishment of a North Central Regional Technical Committee on Entomology (Brindle and Showers, 1978). Representatives from each of the North Central Region states (Illinois, Indiana, Iowa, Kansas, Kentucky, Michigan, Minnesota, Missouri, Nebraska, North Dakota, Ohio, South Dakota, and Wisconsin) and one from the USDA’s Bureau of Entomology and Plant Quarantine constituted the original committee. A sub-project, “The Effect of Time of Planting, Weather Conditions, and Character of Plant Growth on Corn Borer Populations,” was initiated in 1953 with the participation of Iowa, Minnesota, and Ohio in cooperation with the USDA’s newly established European Corn Borer Laboratory at Ankeny, Iowa. In 1954, the USDA upgraded the sub-project to a fully-funded North Central Regional Project relating to ECB that exists to the present day as NC-205. Committee members of this Regional Project have been responsible for most of the research on ECB biology and management in the United States since the 1950’s.

Insecticides and resistant varieties were promoted as the best methods for ECB control from the 1950’s through the mid-1990’s. DDT sprays and dusts were the principle means of chemical control of ECB in the 1950’s (USDA, 1955). By the early 1960’s, the insecticide arsenal included DDT, endrin, EPN, and toxaphene (USDA, 1962). Although very efficacious, the environmental persistence of these pesticides led to their banishment from use by the 1970’s. They were replaced by various formulations of organophosphates, carbamates, pyrethroids, and to a much lesser extent, Bacillus thuringiensis – based microbials (Foster et al., 1985).

In the U.S., plant resistance research for ECB has been conducted since its introduction (Caffrey and Worthley, 1927). Until the early 1960’s, plant breeders and entomologists relied upon natural infestations of ECB in breeding nurseries. The erratic and unpredictable nature of feral populations made it difficult to identify resistant sources of maize and hindered the deployment of resistant alleles. Between 1950 and the mid-1960’s, Beck (Beck et al. 1949; Beck and Stauffer, 1950) and other re-
searchers (Surany, 1957; Brindley and Dicke, 1963; Guthrie et al, 1965) developed and refined methods for mass-rearing of ECB on a meridic diet. This significant achievement enabled plant breeders to uniformly infest nurseries with ECB and readily identify the presence of plant resistance alleles.

Throughout the 1960s, 1970s, and 1980s, many advances were made in identifying and characterizing the genetic basis of maize resistance to ECB (Brindley and Dicke, 1963; Russell et al, 1974; Brindley et al, 1975; Mihm, 1997). Duvick (1984) reported significant improvements in the resistance of maize to both first and second generation ECB when examining hybrids from different eras, an indication that plant breeders and entomologists were successful in deploying enhanced levels of resistance to ECB in commercially available corn hybrids.

Koziel et al. (1993) reported on the successful transformation of maize with an insecticidal gene from Bacillus thuringiensis and its field expression in commercial hybrids. The expressed protein was very efficacious against the early larval stages of ECB and this event ushered in a new era of ECB control. Since the first commercial introduction in 1996, there have been six transgenic events registered with the U.S. Environmental Protection Agency, the final regulating authority in the U.S. Of the six, three remain in the marketplace: Bt11 marketed by Syngenta, MON810 marketed by Monsanto, and TC1507 marketed jointly by Dow Agro-Sciences and Pioneer Hi-Bred International, Inc. Bt corn offers unparalleled protection from ECB and this event ushered in a new era of ECB control. Since the first commercial introduction in 1996, there have been six transgenic events registered with the U.S. Environmental Protection Agency, the final regulating authority in the U.S. Of the six, three remain in the marketplace: Bt11 marketed by Syngenta, MON810 marketed by Monsanto, and TC1507 marketed jointly by Dow Agro-Sciences and Pioneer Hi-Bred International, Inc. Bt corn offers unparalleled protection from ECB and this event ushered in a new era of ECB control.

Western corn rootworms, Diabrotica virgifera virgifera LeConte

Krysan and Smith (1987) speculated that Diabrotica virgifera (sensu lato) evolved with maize in Mexico and Central America. Based upon archeological records, they also suggested that maize was grown in the southwestern United States approximately 3,000 years ago. Melhus et al. (1954) indicated that growers, for centuries, have “hilled” their maize in an effort to reduce lodging caused by corn rootworm larvae. Smith and Lawrence (1967) speculated that densities of the western corn rootworm may have increased when the Spanish introduced the European system of maize production, plowing fields and using large monocultures. Greater densities may have contributed to greater root injury in maize fields. These practices were in sharp contrast to the more diversified agricultural culture of Mesoamerica where plots were smaller, ever changing, and occasionally abandoned. Branson and Krysan (1981) maintained that the genus Diabrotica is largely neotropical with adults serving primarily as leaf feeders and larvae as root tissue consumers. They also hypothesized that diapause, within this genus, evolved as an adaptation to the wet and dry seasons of the tropics. In addition, these authors argued that the western corn rootworm evolved in the tropics or subtropics of Mesoamerica in association with progenitorial maize. Progenitorial maize was never abundant, growing in association with other wild plants such as grasses (Setaria spp.) and cucurbits (Cucurbita spp.).

There are many thorough review articles on western corn rootworms that include the following: Chang (1973), Krysan (1986), and Levine and Oloymi-Sadeghi (1991). Scientific citations regarding western corn rootworms date back to the 1800s attesting early on to the importance of this pest to maize production. Chang (1973) indicated that western corn rootworms were first recorded in Kansas in 1868. LeConte (1868) described the western corn rootworm as the Colorado corn rootworm from specimens collected in Colorado. Damage by the Colorado corn rootworm was reported in 1909, 1910, and 1911 (Gillette, 1912). It was from Colorado that the western corn rootworm began its eastward migration across Nebraska. Tate and Bube (1946) indicated the Colorado species was first observed in Nebraska in 1929 and 1930 with injury occurring in approximately five counties in the southwestern portion of the state. The greatest infestations of the “Colorado” species were noted in irri-
gated fields. The introduction of irrigation systems throughout Nebraska facilitated the rapid movement of western corn rootworms across the state and into less arid regions of the United States Corn Belt. Prior to 1955, the distribution of this species was limited to Nebraska, eastern Colorado and Kansas, and smaller more isolated areas of South Dakota and Iowa (Chiang, 1973). Expansion of the geographic range throughout much of the Corn Belt was extensive from 1955 through 1970. By the mid-1980s, the dispersal of this species continued to the eastern edge of the United States and western corn rootworms could be found in fields of maize in southwestern Virginia (Youngman and Day, 1993).

Metcalf (1986) suggested the corn rootworm complex (Diabrotica spp.) costs producers in the United States $1 billion (due to crop losses and $'s spent on insecticides) each growing season. During the last two decades, the effects of corn rootworm damage have been quantified more precisely; however, fluctuations in weather (particularly precipitation), hybrid selection, larval densities, and other agronomic and economic variables greatly influence the economic importance of western corn rootworms from year to year. Many entomologists have sought to clarify the elusive relationship between corn rootworm larval injury and yield. Gray and Steffey (1998) evaluated root injury, root volumes (July and August) and yield data for 12 maize hybrids in two Illinois locations over a 4-year period (1993-1996) and determined that yield responses were highly dependent upon the interactions of soil moisture, level of root injury, and root regeneration characteristics of hybrids. The research of Godfrey et al. (1993) reinforces the variability in the economic impact of western corn rootworms each season. They reported western corn rootworm larval injury reduced grain yields of maize by 15.0% and 40.7% in 1989 and 1990, respectively. On-farm studies have increased our knowledge of the frequency of economic infestations of western corn rootworms. Gray et al. (1993) reported that during a 2-year period (1990 and 1991), only 26 of 58 (45%) on-farm experiments had root injury that equaled or exceeded a root rating of 3.0 (Hills and Peters, 1971), a level considered of potential economic importance. On-farm research conducted (1993-94) in Virginia on 32 non-rotated maize sites revealed that only 19% of the fields had economic losses due to corn rootworm damage (Kuhar et al., 1997). The authors concluded that much of the soil insecticide use is unnecessary on the continuous corn acres within Virginia. Davis and Coleman (1997) determined that only 30 and 50% of New York maize fields had positive economic benefits from an insecticide treatment in 1993 and 1994, respectively (cost of soil insecticide $39.54 per hectare).

Within the past decade, significant developments within the crop production and protection arenas have occurred that affect the management of the European corn borer and western corn rootworm. These profound events include: 1) the discovery of western corn rootworms near Belgrade, Serbia, and Montenegro, in Europe during during 1992 (Kiss et al., 2005), 2) the commercialization of Bt insectidal maize hybrids for European corn borers (1996) and corn rootworms (2003), 3) the loss of crop rotation as an effective cultural management tactic (1995) for western corn rootworms in some portions of the eastern Corn Belt of the United States, and 4) the development of insecticide resistance in the western Corn Belt (Nebraska) to methyl-parathion and carbaryl. A brief description of each event is provided.

Western corn rootworms now inflict injury to maize in many countries throughout Europe (> 14 countries) (EPPO, 2003). Igric Barčić et al. (2003) provided a review of the current research on western corn rootworms in Croatia from 1994 through 2003 and also featured a distribution map of western corn rootworm infestations in Europe showing dispersal of this species into maize producing regions of Italy (2001), France (2002), Netherlands (2003), and Great Britain (2003). The mechanism by which this species was introduced into Europe is not known. However, international flights that depart from airports within major corn production regions of the United States to European countries could unintentionally accommodate a few gravid western corn rootworm adults. Baca (1994) reported that in mid-July of 1992, an infestation of the western corn rootworm was identified in a small field (0.5 ha) near the Belgrade airport. Subsequent surveys in 1993 indicated a spreading infestation from the Surchin Plateau to the northwest into lower Srem, beetles having crossed the Sava and Danube rivers. Berger (1998) provided a more complete description of the distribution of western corn rootworms in Croatia, Hungary, Romania, Bulgaria, Serbia, Bosnia, and Herzegovina. The economic importance of western corn rootworms to maize is now a reality on two continents (Edwards et al., 1998, 1999). The use of crop rotation practices in more diverse European agricultural settings will
most likely provide the main pest management strategy to reduce larval injury to maize roots. In some European countries, such as Croatia and Serbia and Montenegro, maize grown in rotation with other crops may still receive some larval injury, particularly in border rows because of the common practice of producing crops in long and narrow strips. Corn rootworm injury in strip-intercropping systems has been reported previously in the United States (Tonhasca and Stinner, 1991; Ellsbury et al., 1999). In large monocultures of non-rotated maize produced in some European countries such as France and Italy, annual use of soil insecticides delivered at planting may be required to reduce economic losses.

In 1996, producers in the U.S. Corn Belt began to plant genetically transformed maize hybrids in which a gene from the bacterium, *Bacillus thuringiensis*, had been inserted (event 176) to encode for the production of the Cry1Ab protein endotoxin that is toxic to European corn borer larvae, especially first instars (Shelton et al., 2002). These first transgenic maize hybrids expressed the Cry1Ab endotoxin exclusively in green plant tissue and pollen and were more susceptible to injury caused by second generation European corn borer larvae (Ostlie et al., 1997). As of October 2003, three Bt events had been approved for use in maize against the European corn borer (USEPA, 2003a). These events along with their registration and expiration dates, respectively, are as follows: 1) Bt11 (Cry1Ab), Syngenta, August 1996 - October 2008; 2) MON 810 (Cry1Ab), Monsanto, December 1996 - October 2008; and 3) TC 1507 (Cry1F), Pioneer/DuPont and Dow AgroSciences LLC, May 2001 - October 2008. The transgenic insecticidal cultivars that are currently registered for European corn borers produce a high dose of their respective Bt endotoxin (either Cry1Ab or Cry1F) causing high levels of mortality among first instars. By combining the high dose effects of the transgenic insecticidal cultivars with the planting of a structured refuge, a high dose - refuge management strategy (Gould, 1998) has been implemented by U.S. producers to reduce the likelihood of resistance development (USEPA, 1998). In February 2003, the USEPA approved the use of a new Bt event (MON 863) that encodes for the expression of the endotoxin Cry3Bb1 in maize plants with activity against corn rootworm larvae. Unlike the high dose events currently registered for European corn borer control, transgenic insecticidal cultivars (event MON 863, Cry3Bb1) designed to control corn rootworm larvae have been characterized as non-high dose events (USEPA, 2003b). To date, there is no evidence of any control problems associated with the use of Bt maize hybrids for European corn borers. However, in only the second season of commercialization (2004), performance problems have been documented for some corn rootworm Bt hybrids. Gray and Steffe (2004) reported significant root pruning and subsequent lodging had occurred with a Bt corn hybrid (MON 863, Cry3Bb1) used in an experiment near Urbana, Illinois. The MON863 event has not been approved for use in Europe, dampening the interest of USA producers who might otherwise be more inclined to plant these corn rootworm Bt hybrids (Gray, 2001). This is particularly true for producers in eastern areas (Illinois, Indiana, Ohio) of the Corn Belt that rely upon a strong export market for their maize and associated by products (gluten). If resistance to a Bt endotoxin expressed in maize hybrids occurs, Gray (2001) speculated that it would most likely occur first in a transgenic insecticidal cultivar designed to provide protection against corn rootworm larvae. Many modeling studies have been published regarding the potential occurrence of resistance to Bt maize hybrids by European corn borer (Onstad et al., 2002) and corn rootworms (Onstad et al., 2001; Storer, 2003). To date, no insect resistance has been confirmed for either of these species with respect to the use of Bt transgenic maize hybrids.

During the summer of 1995, producers in east central Illinois suffered widespread and significant yield losses in maize that had been rotated with soybeans the previous season (Levine and Gray, 1996). The insect responsible for this destruction was a variant of the western corn rootworm (O’Neal et al., 1999) that had adapted to crop rotation by shifting its ovipositional behavior to include crops (soybean, alfalfa, oat stubble) other than maize (Rondon and Gray, 2004, 2003). Prior to the mid-1990s, with the exception of severe larval injury to six maize seed-production fields in 1987 (east central Illinois), the rotation of maize with soybeans had provided effective control of western corn rootworms for most Illinois producers (Gray et al., 1998). A review of this unique adaptation by western corn rootworms and hypotheses explaining its occurrence are provided by Levine et al. (2002). Scouting procedures and economic thresholds have been devised (O’Neal et al., 2001) that rely upon the use of Pherocon AM traps in soybean to estimate densities of western corn rootworm adults in
an effort to predict potential egg laying and subsequent larval damage in rotated maize fields. Producers are encouraged to consider the use of a soil insecticide or seed treatment in those maize fields where densities of western corn rootworm adults in soybean the preceding season reached or exceeded the threshold (six beetles per trap per day). ONSTAD et al. (2003) reported that the western corn rootworm variant had expanded its range to include much of east central and northeastern Illinois, northern Indiana, southern Michigan, and the western edge of Ohio. They also hypothesized that as landscape diversity increases, the rate of range expansion for the western corn rootworm variant should decrease. If this model (ONSTAD et al., 2003) is accurate, evolution of a variant western corn rootworm in Europe seems less likely, particularly in more eastern countries of the continent. Considerable speculation has occurred regarding whether or not the variant western corn rootworm occurs in Europe. To date, no such positive confirmation exists.

As the western corn rootworm became an entrenched and dominant insect pest of continuous maize in Nebraska, the use of organochlorine cyclodiene insecticides (e.g., BHC, aldrin, heptachlor) escalated throughout the 1950s (METCALF, 1986). BALL and WEEKMAN (1963) documented high levels of resistance to aldrin by western corn rootworms. Because of its impressive dispersal abilities, the resistant strain spread rapidly across much of the Corn Belt by the early 1970s (METCALF, 1986). Even though chlorinated hydrocarbons have not been used since the early 1970s for corn rootworm control, resistance to this class of insecticides persists (SIEGFRIED and MULLIN, 1989). Because of control failures associated with the use of organochlorine soil insecticides in the late 1950s and 1960s, producers in south-central Nebraska began to increasingly rely (1970s to 1990s) upon aerial applications of organophosphate and/or carbamate insecticides to suppress egg laying by corn rootworm adults. These adult-control programs were often managed by crop consultants and their popularity flourished in west central Nebraska states such as Kansas and Nebraska. Not unexpectedly, MEINKE et al. (1998) confirmed that resistance to methyl parathion and/or carbaryl had developed in several areas of Nebraska. Other investigations have confirmed subsequently the development of insecticide resistance to methyl parathion and carbaryl by western corn rootworms (SCHARF et al., 1999; ZHU et al., 2001; PARMI et al., 2003). Although resistance to methyl parathion and carbaryl appears to be limited to areas in which adult control programs have been used for decades, there is concern that this resistance could cross over to soil insecticides and spread to other areas of the Corn Belt such as occurred in the 1960s and 1970s with the organochlorine resistant strain. If this occurred, coupled with the frustrated utility of crop rotation as a cultural management strategy in the eastern Corn Belt, producers would increasingly rely upon transgenic insecticidal maize hybrids as the mainstay of their corn rootworm protection program. Increased use of these transgenic insecticidal cultivars for corn rootworms would eventually intensify the selection pressure for resistance development. Perhaps, as never before, the integration of various management strategies for this insect pest is of paramount importance. Entomologists, policy makers, crop production specialists, producers, and others who are charged with developing and implementing IPM strategies for western corn rootworms in Europe can learn much from the mistakes we have repeated in the United States regarding the management of this impressive insect foe.

Defining the host range of western corn rootworms continues to be an area of fertile research that began in earnest during the 1960s. BRANSON and ORTMAN (1967a) recovered viable western corn rootworm eggs from adults that had been reared as immatures on green foxtail, Setaria viridis (L.), and yellow foxtail, Setaria pumila (Poir.) Roem. & Schult. In other experiments, BRANSON and ORTMAN (1967b, 1970) observed that western corn rootworm larvae survived 10 days on 18 graminaceous species, and completed immature stages on 13 species. BRANSON (1971) noted that western corn rootworm larvae survived on 21 graminaceous species (not including maize); however, adults reared from some graminaceous species were significantly smaller than those reared on maize, suggesting some deleterious effects. In BRANSON’s and ORTMAN’S experiments (1967b, 1970), western corn rootworm larvae failed to survive on 27 species of broadleaves (12 species of broadleaf weeds, 15 species of broadleaf crops). With respect to crops, BRANSON and ORTMAN (1970) indicated that oats, Avena sativa L.; sorghum, Sorgbhum bicolor (L.) Moench; soybeans, Glycine max (L.); flax, Linum usitatissimum L.; alfalfa, Medicago sativa L.; and sunflowers, Helianthus annuus L. were not larval hosts and could be rotated with maize for pest man-
agement purposes against western corn rootworms. More recent research on the suitability of non-maize hosts, including prairie grass species, has been conducted by entomologists at the University of Missouri and the USDA Agricultural Research Unit in Columbia, Missouri (Clark and Hibbard, 2004; Oyediran et al., 2004; Wilson and Hibbard, 2004). Oyediran et al. (2004) evaluated the suitability of 21 prairie grass species believed to be prominent in the western Great Plains of North America 200 years ago. Western corn rootworm adults were produced from 14 of these species. Research on alternative hosts for western corn rootworms has attracted considerable interest from scientists developing and improving resistance management models for this species in relation to the effective deployment of transgenic rootworm-resistant maize hybrids (Onstad et al., 2001; Storber, 2003).

As western corn rootworms expand their range across Europe, many entomologists and plant breeders in European countries are beginning to search for potential sources of resistance that can be crossed into conventional maize hybrids that are adapted to local growing conditions. Moeser and Vidal (2004) evaluated the responses of western corn rootworm larvae to 17 maize hybrids obtained from six European countries. They detected significant differences among the maize hybrids with respect to larval growth, levels of ingestion, and root tissue conversion efficiencies. They further categorized maize hybrids into suitable and unsuitable categories based upon the development of western corn rootworm larvae, presumably related to their responses to root phytosterols. For many decades, entomologists and plant breeders have attempted to discover host plant resistant traits against corn rootworm larvae and successfully breed these characteristics, particularly antibiotic features, into maize hybrids. Unfortunately, these research pursuits have been largely futile despite the knowledge that some close relatives to maize, such as eastern gamagrass, Tripsacum dactyloides, have antibiotic or extreme non-preference properties against corn rootworm larvae (Branson, 1971).

Although DIMBOA, a plant aglucone, has provided resistance to first-generation European corn borers (Bary and Darrah, 1991), and to a lesser extent the second-generation in the United States, less is known about the influence of this compound on corn rootworm larval densities across a wide array of commercial maize hybrids. Xie et al. (1990) evaluated the influence of 2,4-dihydroxy-7-methoxy-1,4-benoxazin-3-one (DIMBOA), a hydroxamic acid present in many commercial hybrids, on western corn rootworm larvae. In a greenhouse experiment, a hybrid that produced high concentrations of DIMBOA in roots resulted in fewer emerging adults, lower adult weights, and smaller head-capsule widths. Xie et al. (1992a) investigated the response of western corn rootworm larvae to roots that had been treated with hydroxamic acids. Results from behavioral trials suggested that these acids could potentially serve as feeding deterrents. Xie et al. (1992b) screened thirty-three maize lines with diverse geographical origins and found a considerable range in the concentrations of four hydroxamic acids in roots: 1) DIMBOA, 2) DIM$_2$BOA - 2,4-dihydroxy-7,8-dimethoxy-1,4-benzoxazin-3-one, 3) HM-BOA - 2-hydroxy-7-methoxy-1,4-benzoxazin-3-one, and 4) MBOA - 6-methoxy-benzoxazolinone. Inbreds that had greater levels of resistance to western corn rootworm larvae had larger root systems and greater concentrations of hydroxamic acids. A weak correlation was evident regarding concentrations of DIMBOA in roots and leaf tissue. Xie et al. (1992b) suggested that hydroxamic acids may contribute to corn rootworm larval resistance in some maize hybrids. The hydroxamic acid content of 18 maize hybrids grown in Ontario, Canada, was determined using high performance liquid chromatography (Assabgui et al., 1993). Based upon low concentration levels of this acid, the antibiotic effect of the maize hybrids was expected to be minimal under field conditions. Abou-Fakhr et al. (1994) determined that MBOA had no toxic effects on western corn rootworm larvae. Moellenbeck et al. (1995) evaluated T. dactyloides, for potential antibiosis or antixenosis traits against western corn rootworm larvae. This species is closely related to maize. Reduced numbers and size of larvae that had fed on T. dactyloides seedlings (50 - 56 days old) suggested that resistance traits should be further evaluated for potential use in commercial maize hybrids. Assabgui et al. (1995) evaluated the relationship of hydroxamic acid concentrations in the roots of nine inbreds and western corn rootworm larval injury. Yields were less affected by rootworm injury in maize inbreds with greater concentrations of hydroxamic acids. They concluded that mid-whorl stage inbreds had some antibiotic properties, possibly because of hydroxamic acids.

For over 50 years, differences in tolerance to rootworm larval injury have been observed among corn cultivars (Tate and Bare, 1946). In 1992 and
1993, Allee and Davis (1996) conducted an experiment in New York in which they examined the potential effect of manure on the tolerance of two maize hybrids. They concluded that manure enhanced the tolerance of both hybrids by improving root recovery capabilities. Gray and Steffey (1998) evaluated the compensatory root regeneration characteristics of 12 maize hybrids over a 4-year period at two sites in Illinois. They suggested the level of root regeneration and the availability of soil moisture are critical factors in determining yield. Some hybrids suffered yield losses in wet summers due to the regrowth of excessive amounts of root tissue following larval injury. Conversely, those same hybrids characterized as having good root regeneration qualities, generally had superior yields during a dry summer. Riedell and Evenson (1993) suggested that large root systems provide tolerance to maize hybrids grown in the northern United States. The hybrids Riedell and Evenson (1993) evaluated were primarily developed in the 1980s as were those used by Gray and Steffey (1998). Despite the considerable host plant resistance research to date, commercial hybrids feature “resistance” to corn rootworm larval injury primarily in the form of tolerance. This has been achieved by providing producers with maize hybrids that have large root systems and good root regeneration characteristics. The search for non-transgenic maize hybrids with antibiotic or antixenotic properties against corn rootworm larvae continues; however, the search for highly effective sources of resistance remains a challenge to entomologists and plant breeders.

SUMMARY

Since the early 1990s, maize producers in Europe and North America have shared management challenges with these two formidable insect foes. Although considerable progress has been made in the management of European corn borer via the use of commercially available maize hybrids that offer some degree of conventional host plant resistance, the deployment of resistant (antibiosis) alleles in maize for corn rootworms has been disappointing. Producers in the United States have relied largely upon the prophylactic use of soil insecticides in an effort to prevent economic losses caused by corn rootworm larvae. In some areas of the western Corn Belt, an over reliance on insecticides to suppress egg laying by corn rootworm adults has led to the development of insecticide resistance to methyl-parathion and carbaryl. Since the mid-1990s, the non-diversified agroecosystem of the US eastern Corn Belt has led to the development of a variant western corn rootworm that is able to circumvent the cultural management tactic of rotating maize and soybean. The integration of many management strategies (Integrated Pest Management or IPM) is critical to prolonging the usefulness of individual control tactics for both of these important insect pests of maize. The receptiveness to transgenic hybrids by producers on each continent remains strikingly different. Although we believe transgenic hybrids offer producers yet another management tool to deploy with an IPM framework for European corn borers and western corn rootworms, they should not be viewed as the ultimate solution to management of these two species. Like all insects, these two pests are versatile and will adapt to any technology if it is abused.

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