The population dynamics of the western and northern corn rootworms in four tillage systems

Michael Eugene Gray
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THE POPULATION DYNAMICS OF THE WESTERN AND NORTHERN CORN ROOTWORMS IN FOUR TILLAGE SYSTEMS

Iowa State University

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The population dynamics of the western and northern corn rootworms in four tillage systems

by

Michael Eugene Gray

A Dissertation Submitted to the Graduate Faculty in Partial Fulfillment of the Requirements for the Degree of DOCTOR OF PHILOSOPHY

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Iowa State University
Ames, Iowa

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INTRODUCTION

Corn Rootworms

The northern corn rootworm, *Diabrotica barberi* Smith and Lawrence, and the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, are among the most important corn pests throughout the Corn Belt. Approximately 2,670,000 ha were treated with soil insecticides in Iowa during 1979 in an attempt to reduce root damage (Becker and Stockdale 1980). Rootworm populations may be dramatically reduced within a field by rotating to a nonhost crop. This control tactic was noted by Riley (1880) when he associated damaged corn roots to the northern corn rootworm. Gillette (1912) similarly recognized the western corn rootworm as a pest of corn in Colorado. For various economic and edaphic reasons much of the corn grown in the midwest is not rotated. In 1978, 91% of the continuous corn grown in Iowa was treated with soil insecticides in an attempt to reduce yield losses (Iowa Coop. Ext. Serv. 1978). Recently, Foster et al. (1986), indicated that a routine treatment of continuous corn every year was more economical than a scouting and prescribed application program over many seasons. This prophylactic use of soil insecticides accounts for the fact that corn is second in the United States in insecticide usage and first in the amount of land treated (Eichers et al. 1976).

The western and the northern corn rootworms are primarily univoltine species. Krysan (In press) reported that approximately 50% of northern
corn rootworm eggs were able to diapause for 2 years in areas where crop rotation is a dominant agronomic practice. The percentage of eggs capable of a 2-year diapause in contrast was much lower in continuous corn growing areas. The ability to diapause for 2 years has not been demonstrated for the western corn rootworm nor is it expected. Because of the northern corn rootworm's ability in certain areas to diapause for two years, the effectiveness of crop rotation will be diminished and a corresponding increase of insecticide use likely.

Overwintering is accomplished by the egg stage in the soil. Three larval instars undergo their development while feeding on corn roots. Branson and Ortman (1967, 1970) were able to demonstrate that 13 species of grass were also capable of supporting larval development. Destruction of root tissue leads to an overall loss of efficiency of the plant in conducting water and nutrients via the root system to the above-ground portion of the plant. If feeding is extensive, lodging may occur resulting in severe yield reductions at harvest. Adult rootworms begin emerging in early to mid-July in most Corn Belt states. As early as 1882 Forbes recognized adult rootworms reduced pollination by feeding on corn silks. Corn rootworms thus present themselves as a pest in two stages of their life cycle.

Soil Erosion and Adoption of Conservation Tillage Practices

Dubos (1972) credited the ancient Egyptians with introducing the "single technological innovation which has had the most profound and
lasting influence on the surface of the earth." The innovation referred to is the plow. Bagley (1973) maintained that "we are still following this ancient belief that cleanly tilled fields provide the best way to farm." The main reasons for tilling the land may be stated as follows (Willis and Amemiya 1973):

1. to establish a soil surface that prevents water and wind erosion, thus conserving both soil and water
2. to manipulate plant residues
3. to manage water
4. to prepare a seedbed
5. to control weeds

Largely as a result of this manipulation of the soil, 4 billion tons of sediment enter the streams and rivers of the United States annually (Bagley 1973).

Approximately two-thirds of the soil erosion is found on cropland. Cropland erosion is more severe in certain geographical areas (Crosson 1986). The Corn Belt, Appalachia, Southern Plains and the Mountain States constitute the areas most dramatically affected on a land area basis. Certain regions within each of these major geographical divisions are more prone to erosion problems. Sixteen percent of United States cropland and 31% of sheet and rill erosion are found within Illinois, Iowa and Missouri, all members of the Western Corn Belt. Amemiya (1977) reported that within the last three decades, "row crop areas have nearly doubled at the expense of small grains, hay and pasture. As a result of this, erosion has become more severe, because much of this land is not
suited for row crop production." Beyond the unmeasurable loss of a valuable resource, Crosson (1986) has identified the following costs of erosion:

1. costs of preventive measures like grassed waterways and strip cropping
2. costs of the production loss which occurs despite prevention efforts
3. costs of compensating for erosion damage by adding fertilizer to replace soil nutrients, liming to maintain adequate soil pH and tilling to restore soil tilth

In order to offset these losses, cropping systems are needed that will conserve water, soil and energy.

Allmaras and Dowdy (1985) defined a conservation tillage planting system as a cropping system where the surface of the soil was covered with at least 30% residue. Under this definition, 25% of United States cropland is under some form of conservation tillage. This portion is expected to grow to 50-80% by 2010. Conservation tillage is gaining impetus primarily because of reduced production costs. The benefits of reduced erosion are largely secondary.

Soil temperature, surface pH and aeration are generally lower in conservation tillage systems (Gebhardt et al. 1985). Recent technological gains have reduced the magnitude of many of the following problems formerly associated with the adoption of conservation tillage: weed pressure, seed-bed problems and tillage machinery function in
surface residue. Conservation tillage practices can produce yields that are comparable to conventional farming methods (Dick and VanDoren 1985, Eckert 1984, Hargrove 1985). The use of conservation tillage will, however, not be universally adopted. Soils that are high in clay content and found in areas prone to drainage problems are not likely to respond well to conservation tillage systems. Bhowmik and Doll (1982) reported reduced stands and corn yields in a no-till system. Yield losses were attributed to phytotoxicity. The cause of phytotoxicity was hypothesized as either allelochemicals being leached directly from residues, or were produced by microorganisms during residue decomposition. The response of plants and their subsequent yields to a particular tillage system will vary from location to location and tillage recommendations to growers should reflect this.

Factors likely to influence a farmer's decision to follow an extension recommendation to adopt conservation tillage practices have been the focus of many recent investigations. Growers with operations more extensive in size and scale typically are most likely to try new tillage techniques (Korsching et al. 1983, Lee and Stewart 1983, Magleby et al. 1985). Farmers within different geographical areas of the United States are switching to conservation tillage practices at different rates. This change is occurring most rapidly in the Corn Belt, with 39% of the growers choosing conservation tillage systems (Magleby et al. 1985).

The reasons for increasing farmer acceptance of these new and innovative techniques in tilling the land was investigated by Ladewig and
Garibay (1983). A survey of 1,200 farmers from Ohio was undertaken. Conservation tillage systems were employed by 43% of the growers. Environmental concerns and access to suitable equipment were primary factors in the decision process to adopt conservation practices. Reduced production costs of conservation tillage were secondary in importance. Farmers continuing to use conventional crop production systems indicated that lack of knowledge was the primary reason for failure to adopt new methods of farming. This implies that continuing extension efforts are needed to educate growers in this vital area.

Dudal (1982) reported that food and agricultural commodities requirements were expected to increase 50% in 20 years. To meet this growing demand, 200 million hectares of virgin soil will be brought into production by the year 2000. Much of this land will come from marginal areas not ideally suited for agricultural production. This will be especially true in developing countries where population growth will continually place pressure on these countries' resources. Currently, the world is capable of producing enough food for present and even future populations if resources were shared equitably. The reality is an uneven distribution of cultivable land, technological input and populations. Good stewardship of the land is vital worldwide if we are to safeguard our capacity to meet an increasing demand for vital requisites.

Recently, Gebhardt et al. (1985) reported that the use of conservation tillage practices "will have to increase much more in the next 15 years than it has in the past 15 if greater than 50% of U.S. cropland is to be farmed with conservation tillage by the year 2000."
Weeds, diseases and insects were identified as the major stumbling blocks in the adoption of conservation practices. Research directed at discovering how the population dynamics of these pests are affected in conservation tillage regimes is needed. This basic research approach is required before pest management strategies can be devised or improved when conservation practices are used.

Conservation Tillage and its Effects on Organisms

Influencing Crop Production

The increasing acceptance of conservation tillage has prompted many inquiries into the role these innovative crop production systems have on arthropod populations. Conservation tillage may have a direct, indirect or interactive influence on organisms inhabiting the epigeic or edaphic portions of the soil. The biotic potential of a species may be positively or negatively influenced by variations in soil physical or biological features among tillage practices. An organism's unique response to temperature, moisture, aeration, organic matter content and compaction difference among tillage regimes may be regarded as direct. Weed communities have been shown to produce an indirect influence on populations of arthropods in various agroecosystems. Stinner et al. (1984) indicated that poor weed control in no-tillage conditions produced an increase in stalk borer problems in corn. Corn production relying on no-tillage techniques was discontinued in some regions of Ohio due to the severity of stalk borer damage.
Much of the research concerning the role of tillage on arthropod populations in crop production systems has dealt with pests. Musick (1973) reported that damage inflicted by armyworms had increased significantly in no-tillage corn in Ohio. The interaction of crop rotation and tillage on black cutworm damage to corn was investigated by Johnson et al. (1984). Plots that had been tilled using a moldboard plow had reduced levels of damage under all rotation schemes. Cutworms have been implicated as serious pests in other crops utilizing conservation techniques. Cotton grown using conservation tillage practices in northern Alabama was not considered at a serious risk to increased insect pressure with the exception of cutworms (Gaylor et al. 1984). A 3-year study by Roach (1981) compared reduced and conventional tillages in cotton and tobacco produced in South Carolina. Populations of pests and nontarget organisms were monitored. The seasonal levels of insects inhabiting the surface area of vegetative tissue did not significantly differ between tillage treatments. The emergence of Heliothis spp. was greater in reduced tillage systems as compared to conventional operations. Differential emergence of teneral banded cucumber beetles, Diabrotica balteata (Le Conte), and bean leaf beetles, Cerotoma trifurcata (Forster), between conventional and no-till soybean systems was reported by Troxclair and Boethel (1984). Insect populations were monitored using sweep nets. This differential emergence was hypothesized to indicate "an ovipositional preference for the tilled soybeans or a higher egg/larval mortality in the no-till soybeans."

Certain pest populations may diminish in conservation tillage
regimes. Burton and Krenzer (1985) reported that greenbug populations in Oklahoma wheat were reduced when residue covering the surface of the soil was moderate to high. Their hypothesis for this phenomenon was as follows: "Wheat surface residues may serve as a reflective mulch that either repels the settling aphids or masks the existing attractancy of conventionally tilled plots." The reaction of different species of pests to different tillage systems is expected to be as diverse as the pest complex itself.

The influence of various tillage practices on nontarget organisms has been the focus of more recent research efforts. The effects of tillage on predator-black cutworm interactions was investigated by Brust et al. (1985) in cornfields located in Ohio. The use of phorate, a soil insecticide, and tillage caused a reduction in the density of predators. The decline in predators was related to a subsequent increase in plants cut by black cutworms. Parasitoids may be adversely affected also by increased tillage. A laboratory study revealed that females of a black cutworm parasitoid, *Meteropus rubens* (Nees von Esenbeck), if provided with flowering weeds common in reduced tillage corn, "lived longer, attacked more hosts, and produced more offspring than those lacking a food source" (Foster and Ruesink 1984). These flowering weeds served as nectar sources for the parasitoid population. It was speculated that increased black cutworm attacks in conservation tillage systems might in part be offset by the greater levels of parasitoids associated with an increase in the availability of nectar sources.

Ground beetles belong to the family Carabidae and are well
represented among the fauna of most agroecosystems. House and Stinner (1983) conducted an investigation into the community structure of conventional and no-tillage soybean practices in Georgia. Populations of arthropods in an old field nearby were compared to each tillage system. The ground beetle complex was greater in number, species diversity and biomass in the no-tillage crop production regime than in conventionally tilled soil. In a similar study, Blumberg and Crossley (1983) revealed that the diversity of soil inhabitants in sorghum was higher in a no-tillage system than in conventional or old field soils. Populations of ground beetles as reported in other studies have not shown any apparent reaction to tillage type (Tyler and Ellis 1979, Barney and Pass 1986).

The impact of new tillage systems on nematode populations has only recently been extensively studied by researchers. Results of these investigations are as varied as location and crop examined. Tyler et al. (1983) found fewer cyst nematodes in a no-till soybean cropping system in Tennessee. Research in Indiana on field corn by Bergeson and Ferris (1986) revealed that lesion nematodes, *Pratylenchus* spp., were more prevalent in roots of corn produced in moldboard tillage treatments than in no-till treatments. Fortnum and Karlen (1985) did not discover a relationship between tillage type and total nematode numbers in field corn grown in South Carolina. Individual species of nematodes were, however, variable in their population response to tillage type. A review of the literature concerning conservation tillage and its role on the population dynamics of nematodes was conducted by Minton (1986). An assessment of the literature is as follows: "The limited research on
conservation tillage indicates that its use may result in nematode problems never before encountered. Also the research has not been extensive and definitive enough to fully assess the impact of conservation tillage on nematode management.

Interest in the role tillage plays in the nutrient cycle and enhanced microbial degradation of pesticides (Kaufman and Edwards 1983) has led to many questions concerning how microbial populations are likely to respond to changing tillage practices. Linn and Doran (1984) examined the top 300 mm of soil in no-till and plowed treatments at several sites in the United States. The number of aerobic and anaerobic microbes from 0-75 mm was greater in no-tillage regimes than in soil subject to conventional practices. At depths below 75 mm aerobic microbes were more prevalent in conventional systems than no-tillage soil. Conventional practices tended to provide more total soil porosity from 0-150 mm within the soil profile. This generally allows for greater aeration of the soil.

Continued research on the influence of conservation tillage on a variety of soil organisms is vital. Successful pest management strategies are dependent upon a basic knowledge of how organisms interact with each other and the cropping system of which they are a part. The rate of acceptance of conservation tillage practices mandates continued research efforts in this direction.
The life cycle of corn rootworms is intimately linked to the soil they inhabit. It was recognized very early that a manipulation of the soil environment might exert an impact on the population dynamics of corn rootworms. Tate and Bare (1946) reported that fall plowing "was most effective in reducing losses" to rootworms. This conclusion was based upon lodging data collected at Lincoln, Nebraska in 1942 and 1943. Factors other than rootworm damage can account for lodging, such as shallow rooted corn plants exposed to strong winds. As sampling methodologies gradually improved, continued attempts were made to better understand the relationships involved between different tillage practices and rootworm dynamics.

The influence of tillage systems on the growth of corn and rootworm larval populations was examined by Matteson et al. (1965, 1972). The following tillage practices were evaluated: fall plowing, fall plowing and discing, fall discing and no fall tillage. Half of each plot was additionally disced in the spring. This was an attempt to further expose the eggs to harsher environmental conditions. Immediately prior to planting all plots were disced. An absolute no-till practice was not present in this experiment. As tillage increased stand density and the height of corn improved. Larval samples were taken by removing a 7-inch cube around the base of each corn plant. Results from this single-season experiment did not reveal any difference in the abundance of larvae among the tillage treatments.
A more extensive study concerning the influence of conservation practices on rootworms was conducted by Rasmussen (1967). Seven different combinations of tillage operations were evaluated. The egg, larval and adult stages were sampled. The western corn rootworm made up less than 10% of the population in this study. Egg samples were taken using a golf Par-Aide cup cutter and separated from soil with fine mesh screens. All egg samples were taken adjacent to the base of corn plants. Larval populations were estimated by the "5-quart method." This method is described as follows: "a hill of corn is dug up along with enough soil to fill a 5 quart pail." The soil was visually examined for larvae and pupae. Following this, the roots were placed over a pail of water. As the root system dried the larvae dropped into the water. Adults were sampled by taking ten-minute counts, ten-plant counts and using emergence cages covering a 3 by 3 feet area. Lodging counts were also taken as a measure of rootworm damage. The main conclusions from this study were as follows:

1. Fall plowing reduced corn rootworm populations more than did spring plowing.
2. The more the soil was disturbed in the fall, the more the rootworm population was reduced, possibly due to mechanical damage to the eggs.
3. Tillage practices which increase the exposure of soil to winter cold tend to reduce the rootworm population.

The impact of tillage systems on adult emergence and egg distribution of the western corn rootworm was explored by Pruess et al.
(1968). The Nebraska till-plant system and the conventional practice of discing and plowing before planting were compared. Corn was planted in the same rows as the previous season when the Nebraska till-plant system was used. This practice minimized soil disturbance as compared to conventional tillage regimes. The number of rootworm eggs recovered from each tillage system did not differ. A difference in egg distribution, however, was discovered between the tillages. In the conventional system western corn rootworm eggs were uniformly laid in the upper 6 inches of soil. More eggs were deposited in the furrow and ridge in the reduced strip tillage practice. Following planting more eggs were found in the seedling area in conventionally tilled corn. In the till-plant system eggs were most abundant in the furrow. Adult emergence was delayed 5-10 days in the till-plant corn.

Results obtained by Calkins and Kirk (1969) in 1965 and 1967 concerning the overwintering of western and northern corn rootworm eggs in fall plowed versus spring plowed plots differed from that previously reported by Tate and Bare (1946) and Rasmussen (1967). Larval samples were taken by removing 18 cm cubes of soil around the bases of corn plants. Ten samples were removed at random within each plot. Following the extraction, soil was sifted through 0.25 inch hardware cloth onto a dark surface. In 1965 and 1967 rootworm larvae were most abundant and larval damage greater in plots that had been fall plowed. In 1966 spring plowed plots suffered more larval damage. The percentage of plants that had lodged was used as an indicator of larval damage differences. Root ratings are currently the preferred method for evaluating root damage
(Hills and Peters 1971). Results obtained by Calkins and Kirk (1969) in 1965 and 1967 differ from that previously reported by Tate and Bare (1946) and Rasmussen (1967).

The role of ground cover and tillage on root damage and oviposition of the northern corn rootworm was reported by Musick and Collins (1971). The four treatments evaluated were as follows: (1) conventional, plow-disc-cultivate (2) no-tillage, zero ground cover (3) no-tillage, normal ground cover and (4) no-tillage, double ground cover. Plant residue was totally removed from treatment two and placed on treatment four to obtain desired levels of coverage. Egg samples taken the fall of 1969 indicated the mean number of eggs oviposited increased as the ground cover increased. Approximately four times as many eggs were laid in the no-tillage, double ground cover system compared to the conventionally tilled treatment. Larval damage was not significantly different between these two treatments in 1969. Musick and Collins (1971) made the assumption that "the same trend in oviposition occurred the previous year" and attempted to relate the 1969 oviposition data with the 1969 root ratings. Based on this assumption they suggested "that survival of the eggs or larvae is impeded in the no-tillage system." An additional study in 1970 indicated that larval populations were one-third less in no-tillage areas compared to conventional tillage systems. These tillage practices were performed in an area that had been corn the previous year. Egg samples were taken and supported the assumption that oviposition had been "equivalent" in all plots. Musick and Collins (1971) concluded that the suppression of corn rootworm populations in no-tillage systems was
related to egg or larval mortality.

Tyler and Ellis (1974) examined adult emergence, oviposition and lodging damage of the northern corn rootworm in three tillage systems. Eggs were sampled by taking random soil cores 15.2 cm deep by 1.9 cm in diameter from zero, minimum and full tillage fields. The number of eggs extracted did not differ significantly among the tillage treatments. Adult emergence was monitored using cages that enclosed 2-5 plants. The number of adults that emerged from the tillage operations was not significantly different. Emergence was earlier, however, in the full tillage field. The number of lodged plants was significantly greater in the full tillage system.

Musick and Beasley (1978) reported that corn rootworm ovipositional patterns did not differ significantly between no-till and conventional systems. This observation was based on unpublished data collected by G. J. Musick in 1974 for the northern corn rootworm. It was hypothesized that the western corn rootworm would not show an ovipositional preference for a particular tillage operation. Musick and Collins (1971) had earlier reported a four-fold increase in the number of eggs deposited by the northern corn rootworm in no-tillage, double ground cover plots as compared to conventionally tilled plots.

The impact of different levels of infested foxtail, *Setaria* spp., populations and tillage systems on corn rootworm oviposition was evaluated by Johnson and Turpin (1985). Both western and northern corn rootworm populations were studied. Eggs were sampled by using a Par-Aide golf-cup cutter. Cores of soil were removed to a depth of 10 cm between
plants and between rows following oviposition each fall. The influence of tillage system on oviposition for both species was not significant. Root damage ratings the following year did not reflect that each tillage operation had received comparable levels of rootworm eggs. Root damage ratings were generally lower in no-till plots than moldboard or chisel plow treatments despite roughly equivalent fall egg populations. Further investigations to explain this phenomenon were encouraged.

The role of conservation tillage systems on the population dynamics of the western and northern corn rootworms has been investigated by many researchers. The results of these numerous studies have not been consistent and much disagreement still remains concerning the influence of tillage practices on rootworm dynamics. The studies previously referred to relied upon sampling techniques that have been greatly improved upon in recent years. Sampling strategies for the egg, larval and adult stages devised by Foster et al. 1979, Bergman et al. 1981 and Hein et al. 1985, respectively, have enabled rootworm populations to be estimated with greater levels of precision than previously possible. The overall objective of this research, therefore, was to study the population dynamics of the western and northern corn rootworms in different conservation tillage systems utilizing these greatly improved sampling techniques for the egg, larval and adult stages. The specific objectives of this research were:

1. To determine the influence of tillage systems on western and northern corn rootworm oviposition and overwintering survival.
2. To determine if growing season survival of the western and northern corn rootworms differs among tillage systems.

3. To determine if emergence rates of the western and northern corn rootworms differ among tillage systems.

4. To determine the influence of tillage practices and the western and northern corn rootworm egg ratio on larval populations and damage.

Explanation of Dissertation Format

This dissertation is comprised of four manuscripts which will be submitted for publication in entomological journals. Research was conceived and conducted by myself as a member of the Corn Soil Insects Research Project at Iowa State University from 1983 through 1986. Co-authorship of Part 1 through Part 4 will be shared with Dr. Jon J. Tollefson my major professor.
Influence of Tillage Systems on Western and Northern Corn Rootworm (Coleoptera: Chrysomelidae) Oviposition and Overwintering Survival

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PART 1: INFLUENCE OF TILLAGE SYSTEMS ON WESTERN AND NORTHERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) OVIPOSITION AND OVERWINTERING SURVIVAL

Abstract

The influence of tillage systems on oviposition and overwintering survival was examined for the western and northern corn rootworms, *Diabrotica virgifera virgifera* LeConte (WCR) and *D. barberi* Smith and Lawrence (NCR), respectively, 1983 through 1985. Ovipositional depth preferences were evaluated for each rootworm species across all tillage systems. Fall and spring WCR and NCR egg populations were compared for two overwintering periods. No ovipositional preference for a tillage system was evident for either species. The preferred depth of oviposition for the NCR was the top 20 cm of soil with only 15% of the egg population occurring from 20 to 30 cm deep. One-third of WCR eggs were found from 20-30 cm, indicating that sampling for this species should be done to a depth of at least 30 cm. The influence of tillage practices on overwintering survival differed according to year. Egg populations of the WCR and NCR declined significantly from the fall of 1983 to the spring of 1984 in the paraplow and moldboard plow systems. No significant reductions in egg populations occurred in the no-till and chisel plow practices. Egg populations for the WCR and NCR were not significantly reduced from fall to spring in any tillage system the second overwintering period.
Introduction

The western and northern corn rootworms, *Diabrotica virgifera virgifera* LeConte (WCR) and *D. barberi* Smith and Lawrence (NCR), respectively, are serious pests to corn planted after corn. Eggs are laid during the summer, with oviposition 50% complete by mid-August (Hein and Tollefson 1985). The eggs overwinter in the soil and hatch the following summer. Eclosion occurs primarily in June and larvae begin feeding on corn roots. Development continues through three instars and pupation follows in an earthen cell. Adult emergence begins in late-July and continues through early-September. Beetles feed on corn silks and pollen and may reduce kernel set if feeding is intensive.

The importance of soil surface characteristics in influencing the ovipositional behavior of WCR adults was demonstrated by Kirk et al. (1968). Through the use of different tillage systems, various edaphic features may be greatly modified (Powers and Skidmore 1984, Sommerfeldt and Chang 1985, Mukhtar et al. 1985, Colvin et al. 1986). Although the epigeic and edaphic properties of tillage systems differ, several researchers have been unable to detect an ovipositional preference for a particular tillage practice (Pruess et al. 1968, Tyler and Ellis 1974, Johnson and Turpin 1985). In contrast Musick and Collins (1971) reported four times more NCR eggs were deposited in a no-till system than in a conventionally plowed area. This discrepancy in findings may largely reflect the considerable variation associated with egg sampling for the WCR and NCR. Recently, Hein et al. (1985) urged that WCR and NCR egg
samples be taken from soil comprising the entire interrow width to a depth of 20 cm to provide an absolute population estimate. Earlier attempts to quantify the relationship between oviposition and tillage practices used core sampling in which samples were taken to a depth of 10 cm by 10 cm in diameter. Sampling occurred at discrete points that did not reflect a uniform subunit of the ovipositional universe. With the exception of Pruess et al. (1968), these initial investigations did not sample deeply enough to provide an accurate assessment of the role tillage systems may have in influencing ovipositional patterns.

Most of the corn rootworm life cycle is spent in the egg stage. Some research has been devoted to examining egg survival throughout the winter. Chiang (1965) reported that NCR survival was reduced in eggs that were buried near the surface of the soil. Because tillage practices such as moldboard plowing exposed eggs that were deposited deeply in the soil, some researchers began investigating the importance of fall versus spring plowing in reducing populations of corn rootworms. Rasmussen (1967) reported that corn rootworm populations could be reduced more by fall plowing than spring plowing. With moderate temperatures and normal precipitation, Calkins and Kirk (1969) concluded that spring or fall plowing were equal in their effects on larval populations and damage. The importance of tillage on overwintering egg survival of the WCR was examined by Lawson (1986). Eggs were buried at different depths in four tillage systems. Survival was greater as depth of egg burial increased across tillage practices. A no-till system had the fewest negative-degree-day accumulations and had the least egg mortality.
The preceding studies describing tillage effects on overwintering survival of rootworm eggs have relied on artificially burying eggs or on indirect inferences of egg survival such as larval population estimates. Rasmussen (1967) based estimates of survival on egg samples taken in different tillage practices, but these samples were taken only to a depth of 10 cm.

The objectives of this research were to intensively investigate the influence of tillage systems on the ovipositional preferences and overwintering survival of natural populations of the WCR and NCR. Ovipositional depth preferences were also evaluated for each species of rootworm. Greatly improved sampling strategies (Foster et al. 1979, Hein et al. 1985) were used in an attempt to meet these objectives.

Materials and Methods

Agronomic practices

Four tillage systems were evaluated at the Iowa State University Agronomy and Agricultural Engineering Research Center near Ames, Iowa for their influence on oviposition and overwintering survival of WCR and NCR eggs from 1983 through 1985. Plots were 6.1 m wide by 27.4 m in length and consisted of eight 76-cm rows. The following tillage treatments were arranged in a randomized complete block design: (1) no-till (N), (2) fall chisel plow and spring disc, harrow, and field cultivate (C), (3) fall tillage by Paraplow (P), and (4) fall moldboard plow and spring disc, harrow, and field cultivate (M). The Paraplow® is a relatively novel
tillage instrument that uses a bent shank to lift and loosen soil without burying crop residue. Tillage practices were introduced in the fall of 1982. The entire experimental area encompassed ten replicates to be used cooperatively in a research program. Four to six replicates were devoted to this research project. The location of each tillage treatment remained the same for the duration of the study. Fall plowing was accomplished in late October or early November each year of the study, well after the ovipositional period. Spring discing, harrowing and field cultivations were performed in late April or early May. Corn (Pioneer 3720) was planted at a rate of 64,000 kernels per ha. Planting occurred on 6 and 10 May 1983 and 1984, respectively, and 29 April 1985. The application of herbicides and fertilizers was the same for all tillage practices. No insecticides were used in the experimental area.

Ovipositional preference study

The "frame method" described by Foster et al. (1979) was used to take egg samples in the falls of 1983-85. This sampling technique utilizes a metal frame that is pushed into the ground perpendicular to the corn row. The frame is 10.2 cm wide and the length is equal to the width between corn rows. Soil within the frame is completely removed with a spade to a desired depth and thoroughly sifted and mixed. Subsamples (0.47-1) are then removed from the main bulk of soil.

Egg sampling was performed before fall plowing and occurred from early to late October. Twenty frames of soil were removed randomly from each tillage treatment in 1983. Twenty-four frames per treatment were
taken the last two seasons in an effort to improve sampling precision (Hein et al. 1985). In 1983 and 1984, soil to a depth of 20 cm was removed from each frame; four and five 0.47-l subsamples per frame were analyzed each year, respectively. During the fall of 1985, soil was removed in three 10-cm depth increments, producing an upper, middle and bottom 10-cm sample of soil. Two 0.47-l subsamples were taken from each depth. Eggs were extracted from soil subsamples by using the extraction technique described by Shaw et al. (1976) and separated according to chorion sculpturing differences of Diabrotica (Atyeo et al. 1964).

All data were transformed to a $y = \log_{10} (X+1)$ relationship to reduce the dependence of the variance on the mean. Analysis of variance procedures were conducted to test for tillage influence on oviposition for each species of rootworm. In 1985, analysis of variance techniques were used to evaluate the interaction of tillage and depth on oviposition.

Overwintering study

Egg samples were taken from early- to mid-May the springs of 1984 and 1985. All sampling was performed after spring disking, harrowing and field cultivating had been conducted. Twenty frames of soil per tillage treatment were taken randomly in 1984; an additional four frames per treatment were removed in 1985. Five 0.47-l subsamples of soil were evaluated from each frame. Data were transformed ($y = \log_{10} (X+1)$) and analysis of variance procedures used to evaluate the influence of fall and spring tillage practices on WCR and NCR spring egg populations. T'-
tests (Snedecor and Cochran 1967) were used to compare fall and spring egg population means within each tillage system for both species of rootworms over the two winter seasons. This statistical technique allows for the comparison of two means that have different sample sizes and variances.

Results and Discussion

**Ovipositional preference study**

Egg sample means and 95% confidence intervals for the WCR and NCR across tillage systems, 1983-85, are illustrated in Fig. 1. Precision estimates (SE/X) for the egg-sampling methodology across tillage treatments for the WCR were 0.19, 0.39 and 0.28 from 1983-85, respectively. Sampling precision was better for the NCR with 0.15, 0.13 and 0.17 levels obtained each respective year. These estimates of precision are comparable to those obtained by Hein and Tollefson (1985) in an investigation using the frame method to examine WCR and NCR seasonal oviposition.

There was no significant tillage effect (P > 0.05) on WCR or NCR oviposition in each year of the experiment (Fig. 1). This agrees with most earlier studies (Pruess et al. 1968, Tyler and Ellis 1974, Johnson and Turpin 1985) but differs with the results reported by Musick and Collins (1971) from a 1-year study.

The preferred depth of oviposition for the WCR and NCR was evaluated in 1985 for each tillage regime. Western corn rootworms did not display
a strong ovipositional depth preference (Fig. 2). The upper 10-cm zone had numerically the fewest WCR eggs in relation to the other depths. Most NCR eggs were found from 0 to 10 cm; the bottom 10-cm layer had the fewest NCR eggs (Fig. 3). Previous research had shown that 85% of NCR eggs (Foster et al. 1979) and 66% of the WCR eggs (Hein et al. 1985) were in the top 10 cm of soil when the upper 20 cm of soil were sampled. Analysis of variance procedures revealed no tillage practice by depth interaction (P > 0.05) for WCR or NCR egg deposition. Because this interaction was nonsignificant, the main effect of depth was averaged across all tillage practices for each species of rootworm (Table 1). One-third of the WCR egg population was located in the bottom 10-cm level. This percentage of eggs was much greater than anticipated because very few drought cracks were observed in any tillage treatment in 1985. Deep cracks would allow for oviposition to occur at depths probably not feasible under wetter conditions. It was hypothesized that poorer precision estimates for the WCR relative to the NCR in 1983-84 were partly caused by failure to sample WCR eggs deeply enough. Previous studies that sampled only to a depth of 20 cm also may have underestimated the egg population of the WCR. Future researchers examining the population dynamics of the WCR are urged to sample to a depth of at least 30 cm with the frame method. Sampling to a depth of 20 cm is adequate for the NCR.
Overwintering study

The winter of 1983-84 was characterized by below normal snow-fall from December through February. The mean temperature for December was minus 13.0 C, approximately 9.0 C colder than average (National Oceanic Atmospheric Administration 1983-85). The following winter precipitation and temperatures were near average.

Precision (SE/\bar{x}) levels in the springs of 1984 and 1985 were 0.39 and 0.32 respectively, for the WCR. Sampling precision for the NCR was 0.14 each spring. Analysis of variance procedures were conducted on spring egg population data in 1984 and 1985 for the WCR and NCR. No significant differences (P > 0.05) were detected among the tillage treatments. A numerical reduction in WCR and NCR egg populations was observed in all tillage systems during both overwintering periods (Figs. 4 and 5). T'-tests were conducted between fall and spring egg population means within each tillage regime for the WCR and NCR. A significant reduction (P \leq 0.05) in the number of WCR and NCR eggs occurred with tillage by the Paraplow (WCR, t' = 2.97; df = 9) (NCR, t' = 2.72; df = 9) and moldboard plow systems (WCR, t' = 2.28; df = 9) (NCR, t' = 2.25; df = 9) from the fall of 1983 to the spring of 1984. Western and NCR eggs responded similarly in their ability to overwinter in the various tillage practices. Gustin (1983) previously reported that the NCR was more cold tolerant than the WCR.

During the winter of 1983-84, the no-till and chisel plow systems offered more protection to WCR and NCR eggs. Lawson (1986) similarly reported improved survival of eggs buried in a no-till system.
Overwintering survival of WCR and NCR eggs was expected to be similar in the treatment with the Paraplow and no-till system on the basis of the similarity in residue coverage between these two tillage practices. Other edaphic features must account for overwintering survival differences during severe winters for WCR and NCR eggs. On the basis of our findings for the winter of 1984-85, tillage differences are not expected to significantly affect WCR or NCR survival if winter conditions are characterized by moderate temperatures and normal snow cover.

Egg sampling data obtained during this study have revealed several relationships regarding oviposition and overwintering survival of WCR and NCR eggs. The influence of tillage type on WCR and NCR oviposition was not significant. Ovipositional data for the fall of 1985 revealed that roughly one-third of all WCR eggs sampled across tillage systems were located 20-30 cm deep. Future research concerning the population dynamics of the WCR should attempt to sample egg populations to a depth of at least 30 cm. The survival of WCR and NCR eggs during severe winters may be favored in certain tillage practices such as no-till and chisel plow systems. The influence of tillage type on corn rootworm survival during moderate winters seems negligible.
References Cited


Johnson, T. B., and F. T. Turpin. 1985. Northern and western corn rootworm (Coleoptera: Chrysomelidae) oviposition in corn as influenced by foxtail populations and tillage systems. J. Econ. Entomol. 78:57-60.


Table 1. Number of WCR and NCR eggs/ha ($10^6$) oviposited in the upper, middle and bottom 10 cm increments of soil removed to a depth of 30 cm across all tillage systems, 1985

<table>
<thead>
<tr>
<th>Depth</th>
<th>WCR Eggs</th>
<th>n</th>
<th>NCR Eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-10 cm</td>
<td>1.46</td>
<td>188</td>
<td>17.77</td>
</tr>
<tr>
<td>10-20 cm</td>
<td>3.07</td>
<td>191</td>
<td>9.50</td>
</tr>
<tr>
<td>20-30 cm</td>
<td>2.37</td>
<td>192</td>
<td>4.70</td>
</tr>
</tbody>
</table>

S. E.  

| b | 0.36 | 1.03 |
| L. S. D. | 1.04 | 2.93 |

\(a\) ns sub samples (0.47-1).

\(b\) L. S. D. = Least significant difference (P = 0.05).
Fig. 1. Western and northern corn rootworm oviposition, 1983-85. Means are bracketed by 95% confidence intervals. Tillages are: N = no-till, C = chisel plow system, P = Paraplow and M = moldboard plow system.
Fig. 2. Western corn rootworm oviposition, 1985. Means are bracketed by 95% confidence intervals. Tillages are: N = no-till, C = chisel plow system, P = Paraplow and M = moldboard plow system. Depths are: 1 = 0-10 cm, 2 = 10-20 cm and 3 = 20-30 cm.
Fig. 3. Northern corn rootworm oviposition, 1985. Means are bracketed by 95% confidence intervals. Tillages are: N = no-till, C = chisel plow system, P = Paraplow and M = moldboard plow system. Depths are: 1 = 0-10 cm, 2 = 10-20 cm and 3 = 20-30 cm.
NCR OVIPOSITION, 1985

EGGS/HA ($\times 10^5$)

TILLAGE SYSTEMS AND DEPTHS

DEPTHS
Fig. 4. Western and northern corn rootworm egg populations, fall 1983-spring 1984. Means are bracketed by 95% confidence intervals. Connected means within a tillage practice represent fall and spring egg populations, respectively. Tillages are: N = no-till, C = chisel plow system, P = Paraplow and M = moldboard plow system. Asterisk denotes \( P \leq 0.05 \) using a T'-test.
EGG SAMPLES, FALL 1983 SPRING 1984

EGGS/Ha (X10^6)

WCR

NCR

TILLAGE SYSTEMS

N  C  P  M

N  C  P  M

22.0
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
Fig. 5. Western and northern corn rootworm egg populations, fall 1984-spring 1985. Means are bracketed with 95% confidence intervals. Connected means within a tillage practice represent fall and spring egg populations, respectively. Tillages are: N = no-till, C = chisel plow system, P = Paraplow and M = moldboard plow system.
EGG SAMPLES, FALL 1984 SPRING 1985

EGGS/HA (X10^6)

TILLAGE SYSTEMS

WCR

NCR
Submitted To: Environmental Entomology

Survival of Western and Northern Corn Rootworms
(Coleoptera: Chrysomelidae) in Four Tillage Systems Throughout the Growing Season

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PART 2: SURVIVAL OF WESTERN AND NORTHERN CORN ROOTWORMS (COLEOPTERA: CHRYSOELIDAE) IN FOUR TILLAGE SYSTEMS THROUGHOUT THE GROWING SEASON

Abstract

The influence of tillage practices on growing season survival of the western and northern corn rootworms, *Diabrotica virgifera virgifera* LeConte (WCR) and *D. barberi* Smith and Lawrence (NCR), respectively, was examined from 1983-85. Absolute estimates of spring egg populations and emerging adult populations were made each year for both species across all tillage systems. Relative variation estimates (SE/\( \bar{X} \)) are presented for WCR and NCR egg and adult populations during each year of the experiment. Tillage practices did not significantly affect WCR or NCR survival throughout the growing season of corn. Western corn rootworm survival was significantly greater than that of the NCR in each tillage practice for the duration of the study. A quadratic equation is presented that describes the ratio of WCR to NCR adults likely to emerge based upon the spring WCR to NCR egg ratio.
Introduction

Western and northern corn rootworms, *Diabrotica virgifera virgifera* LeConte (WCR) and *D. barberi* Smith and Lawrence (NCR), respectively, may cause serious damage in fields planted continuously to corn. The majority of the rootworm life cycle is spent in the soil. Eggs are oviposited in the soil from mid-to-late summer and serve as the overwintering stage. Following eclosion in early June, feeding begins and continues through July. Root feeding and pruning by larvae which develop through three instars constitute the primary damage inflicted to the corn plant. Pupation occurs in the soil and adult emergence lasts from late July to early September. Adults feeding on corn silks during pollination may reduce kernel set. Thus, corn rootworms present themselves as a destructive pest during two stages of their life cycle.

Since the WCR and NCR life cycles are intimately linked to the soil, researchers have attempted to explain how different tillage systems may influence rootworm survival through modifications of the epigeic and edaphic features of the soil. Tyler and Ellis (1974) reported that NCR emergence and egg populations did not differ among several tillage practices. This implied that NCR survival among the tillage systems was comparable, however, these results were obtained from a single season. In contrast, Musick and Collins (1971) suggested that survival of NCR eggs or larvae in no-tillage regimes was reduced. This suggestion was based upon a comparison of root damage ratings and egg populations of various tillage treatments. Johnson and Turpin (1985) similarly
indicated that root damage was less in a no-till system than in moldboard or chisel plow plots. Fall WCR and NCR egg populations were equivalent or higher, however, in no-till plots as compared to the other treatments. Reduced survival of WCR and NCR eggs or larvae in the no-till system as earlier hypothesized by Musick and Collins (1971) may also help to explain these findings.

Previous investigations concerning the population dynamics of the WCR and NCR in different tillage systems have relied almost exclusively upon relative population estimates and root damage ratings. Conclusions from these studies are varied with respect to the role tillage systems have on rootworm survival. Sampling precisions have also been poor or unreported. Population dynamics research requires that absolute sampling techniques be employed in order to fully understand the response of an insect population to its biotic and abiotic environment. Recently developed absolute sampling procedures for the egg (Foster et al. 1979, Hein et al. 1985a) and adult (Hein et al. 1985b) stages of the WCR and NCR have enabled researchers to more intensively investigate the dynamics of each species.

This paper reports the results of a 3-year study of the survival of the WCR and NCR during the growing season of corn in four tillage systems. The primary objective was to assess the impact of different tillage operations on WCR and NCR survival. Absolute estimates of spring WCR and NCR egg populations were compared to absolute adult populations of each rootworm species in the various tillage regimes. The second objective was to compare survivorship of the WCR with that of the NCR.
It was hypothesized that the WCR would be competitively superior to the NCR based upon the WCRs closer evolutionary relationship with corn (Branson and Krysan 1981).

Materials and Methods

Agronomic practices

Four tillage systems were examined for their effect on WCR and NCR survival throughout the growing season from 1983-85. Experimental plots were located at the Iowa State University Agronomy and Agricultural Engineering Research Center near Ames, Iowa. Plots consisted of eight rows and were 6.1 m wide by 27.4 m in length. The following tillage treatments were arranged in a randomized complete block design: (1) no-till (N), (2) fall chisel plow, spring disc, harrow and field cultivate (C), (3) fall tillage by Paraplow (P) and (4) fall moldboard plow, spring disc, harrow and field cultivate (M). The Paraplow® is a tillage implement designed to promote favorable edaphic characteristics while maintaining large amounts of residue on the surface of the soil. Ten replicates of the tillage treatments were established in the fall of 1982 to be used cooperatively in a research program. Four replicates in 1983 through 1984 and six replicates in 1985 were devoted to this research project. Each tillage treatment remained in the same location throughout the 3-year experiment.

Fall tillage operations were performed in late October through November. Spring discing, harrowing and field cultivations took place in
late April or early May. Corn (Pioneer® 3720) was planted at a rate of 64,000 kernels per ha. Planting was accomplished on 6 and 10 May 1983 and 1984, respectively, and 29 April 1985. Fertilizer and herbicide use was the same for each tillage treatment. Insecticides were not used at any time during the investigation.

**Egg sampling**

Absolute estimates of the WCR and NCR egg populations were made each spring following tillage operations. Egg samples were taken by using the frame method described by Foster et al. (1979). This technique involves driving a metal frame into the soil perpendicular to the direction of the corn rows. The frame is 10.2-cm wide and the length of the row width (76 cm). Soil was removed to a depth of 20 cm within each frame with spades, sifted and thoroughly mixed. Two subsamples (0.47-l / subsample) of soil in 1983 and five subsamples in 1984-85 were taken from each frame. Twenty frames of soil were dug randomly per tillage treatment in 1983-84; four additional frames per treatment were removed in 1985 to improve sampling precision. Subsamples of soil were returned to the laboratory and eggs extracted according to procedures outlined by Shaw et al. (1976). Rootworm eggs were counted and separated by species based upon differences in chorionic sculpturing (Atyeo et al. 1964). Sampling to a depth of 20 cm was considered adequate. Hein et al. (1985a) reported that 82% of NCR eggs and 66% of WCR eggs were found in the upper 10.2 cm of soil when 20.3 cm of soil were sampled using the frame method. Sampling to a depth of at least 20 cm was recommended for both species.
All egg sampling data were transformed according to a \( y = \log_{10}(X+1) \) relationship to reduce the dependence of the variance on the mean. Analysis of variance techniques were used to examine the effect of tillage on spring WCR and NCR egg populations. \( T' \)-tests (Snedecor and Cochran 1967) were used to compare WCR and NCR egg populations within each tillage system. This test allows for two means to be compared that have different sample sizes and variances. Untransformed means are presented for WCR and NCR egg populations.

**Adult emergence**

Absolute estimates of WCR and NCR adult populations were made using a sampling technique described by Hein et al. (1985b). This procedure involved the use of emergence traps, each consisting of a wooden frame (76.2 cm X 35.6 cm) and attached aluminum screening approximately 50-cm high. Each trap was positioned over a corn plant that had been severed 50 cm above the soil surface. Soil disturbance within the trapping area was kept to a minimum. Traps were sealed by placing soil collected from outside the trapping area around the base of the trap frame. Within each trap a paper carton (0.47-l), coated internally with Tack Trap, was supported on the corn stalk by a nail driven through the stalk. As beetles emerged from the soil within the trapping area they moved upwards and were captured in the carton.

Forty traps per treatment were established at random in 1983; 60 traps per treatment were deployed the following two years. The seasonal sampling period in each tillage treatment was as follows: 8 July - 22
September 1983, 11 July - 18 September 1984 and 25 June - 20 September 1985. Emergence traps were monitored and paper cartons replaced when trapping efficiency diminished due to heavy rains that reduced the effectiveness of Tack Trap or when large numbers of rootworm beetles covered the interior surface of the cartons. Paper cartons within each emergence trap were replaced with freshly glued cartons five times in 1983 and 1985 and four times in 1984.

The number of WCR and NCR adults captured was summed by species over all sampling intervals each year for every tillage practice. Data describing total seasonal emergence from each tillage treatment for both species was transformed using the following relationship y = log_{10} (X+1). Analysis of variance procedures were conducted to determine the effect of different tillage regimes on WCR and NCR emergence. T' tests were used to contrast WCR and NCR populations emerging from within each tillage treatment.

Curvilinear regression was used to describe the relationship between the WCR and NCR spring egg ratio and the adult emergence species ratio. Data used for this regression procedure were combined over the 3-year period of this experiment across all tillage practices. A quadratic equation is presented to describe this relationship.

Results and Discussion

Relative variation estimates (SE/\bar{x}) (Southwood 1978) of WCR and NCR egg and beetle populations from 1983-85 reveal that sampling procedures
provided reasonably precise estimates of populations across tillage systems (Table 1). Northern corn rootworm egg and adult populations were sampled more precisely than WCR populations. The number of WCRs declined throughout the three years and higher relative variation values for 1984 and 1985 egg samples may have been due to low spring egg populations. Hein et al. (1985a) indicated that the WCR was more likely to oviposit at deeper depths than the NCR. Reduced levels of precision for WCR eggs relative to NCR egg populations in 1984 and 1985 may have been improved upon if samples had been taken below 20 cm.

The influence of different tillage practices on WCR and NCR survival throughout the growing season of corn was evaluated by comparing absolute estimates of egg and emerging beetle populations. Analysis of variance procedures conducted each season revealed no significant difference (P > 0.05) in WCR or NCR spring egg populations among the tillage treatments from 1983-85 (Figs. 1-3). Analysis of variance techniques similarly revealed no significant tillage effect (P > 0.05) with regard to the number of WCR or NCR beetles that emerged each year. I conclude that tillage practices do not influence rootworm survival during the growing season. These results differ from those reported by Musick and Collins (1971) in which survival of NCR eggs or larvae was reduced in a no-tillage system. Johnson and Turpin (1985) also reported less damage in a no-till system than was expected based upon WCR and NCR egg samples. Each of these previous studies relied on relative estimates of egg populations and root damage ratings. To fully evaluate the influence of tillage on rootworm survival during the growing season, however, absolute
estimates such as used in this study, of spring egg populations and emerging adult populations must be made.

Although different tillage practices were shown not to influence WCR or NCR survival, survivorship between rootworm species differed significantly each year of the experiment. In 1983, T'-tests were conducted between WCR and NCR egg population means within each tillage practice. No significant differences (P > 0.05) were detected between WCR and NCR egg populations within each tillage treatment. Numerically more WCR than NCR eggs were found within each tillage operation (Fig. 1). T'-tests were used also to compare emerging WCR and NCR populations within each tillage system. Western corn rootworm emergence was significantly greater (P ≤ 0.05) in every tillage regime as compared to the NCR: [(N) T' = 4.80, df = 9; (C) T' = 2.92, df = 9; (P) T' = 6.14, df = 9; and (M) T' = 3.56, df = 9]. Since spring egg populations did not differ between rootworm species for any tillage practice the magnitude of this differential emergence was not expected. Survival of the WCR was much greater than that of the NCR. This competitive advantage occurred in each tillage treatment.

In 1984, T'-tests revealed no significant differences (P ≥ 0.05) between the WCR and NCR spring egg populations in each tillage practice. Numerically more NCR than WCR eggs were found when populations were compared within a tillage treatment (Fig. 2). T'-tests again were used to test for differences between average WCR and NCR emergence. Significantly (P ≤ 0.05) more WCR than NCR adults emerged in the no-till, chisel plow and Paraplow systems: [(N) T' = 2.87, df = 9; (C) T' =
2.34, df = 9; and (P) T' = 2.53, df = 9]. No significant difference (P > 0.05) in emergence between the WCR and NCR was observed in the moldboard plow treatment. With the exception of the moldboard plow system, NCR survival was much reduced compared to the WCR.

The WCR spring egg population was very low in 1985 (Fig. 3). T'-tests indicated that significantly more (P < 0.01) NCR eggs were found in every tillage practice: (C) T' = 4.37, df = 15; (C) T' = 3.70, df = 15; (P) T' = 6.02, df = 15; and (M) T' = 4.29, df = 15]. This was the first time in which spring egg populations differed between the species. Significantly more NCR beetles were expected to emerge compared to the WCR across all tillage systems because of the large difference in spring egg populations. This hypothesis was rejected, because emergence data revealed no significant difference (P > 0.05) between WCR and NCR adult populations within each tillage system according to T'-tests.

Evidence collected during this experiment overwhelmingly indicate that the WCR is better able to survive than the NCR in a continuous corn system regardless of tillage type. Results similar to these findings were reported by Piedrahita et al. (1985) in a greenhouse experiment. Survivorship of the NCR was reduced by the WCR in root systems of potted corn seedlings. The NCR did not influence the spatial distribution or survival of the WCR.

In order to better understand survivorship differences between the species, the emergence ratio (WCR/NCR) was regressed against the spring egg ratio (WCR/NCR). Spring egg population and adult emergence means for all tillage practices, 1983-85, were used in this analysis. Survival
differences between species were consistent across years and tillage systems. Curvilinear regression significantly reduced the residual sum of squares ($P = 0.05$) over a linear model. A significant quadratic relationship ($R^2 = 0.91$, $n = 12$, $P < 0.01$) was used to describe the ratio of WCR to NCR adults likely to emerge from spring egg populations of the two species (Fig. 4). Approximately four times as many WCRs may emerge than NCR beetles when comparable spring egg populations of each species are present according to this quadratic formula. This analysis and previous T'-tests conducted each year indicate that NCR survival is less than that of the WCR in continuous corn production systems regardless of tillage regime.

In summary, the use of different tillage practices does not influence WCR or NCR survival during the growing season of corn. This conclusion was based upon comparisons of absolute egg and adult populations for each species among the various tillage treatments from 1983-85. Survivorship between the WCR and NCR, however, was significantly different. The original hypothesis proposed concerning the competitive superiority of the WCR over the NCR was accepted. Reasons for the apparent difference in survival between the species may reflect greater WCR competitiveness for resource requisites and/or greater efficiency in assimilating them.
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Johnson, T. B., and F. T. Turpin. 1985. Northern and western corn rootworm (Coleoptera: Chrysomelidae) oviposition in corn as influenced by foxtail populations and tillage systems. J. Econ. Entomol. 78:57-60.


Table 1. Relative variation (SE/X) for WCR and NCR egg and adult populations across tillage systems, 1983-1985

<table>
<thead>
<tr>
<th></th>
<th>1983</th>
<th>n\textsuperscript{a}</th>
<th>1984</th>
<th>n</th>
<th>1985</th>
<th>n</th>
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<td>WCR, Eggs</td>
<td>0.20</td>
<td>20</td>
<td>0.39</td>
<td>20</td>
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<td>24</td>
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<td>0.12</td>
<td>60</td>
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<td>60</td>
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<td>20</td>
<td>0.14</td>
<td>20</td>
<td>0.14</td>
<td>24</td>
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<tr>
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<td>40</td>
<td>0.11</td>
<td>60</td>
<td>0.09</td>
<td>60</td>
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</tbody>
</table>

\textsuperscript{a}n = number of samples per tillage treatment.
Fig. 1. Seasonal survival of the WCR and NCR in four tillage systems for 1983. Means are bracketed by 95% confidence intervals. Tillages are, N = no-till, C = chisel plow system, P = Paraplow and M = moldboard plow system.
Fig. 2. Seasonal survival of the WCR and NCR in four tillage systems for 1984. Means are bracketed by 95% confidence intervals. Tillages are, N = no-till, C = chisel plow system, P = Paraplow and M = moldboard plow system.
1984 SEASONAL SURVIVAL

EGGS/HA (X10^6)

WCR NCR
EGGS

BEETLES

WCR NCR
BEETLES/HA (X10^6)
Fig. 3. Seasonal survival of the WCR and NCR in four tillage systems for 1985. Means are bracketed by 95% confidence intervals. Tillages are, N = no-till, C = chisel plow system, P = Paraplow and M = moldboard plow system.
Fig. 4. Relationship between the emergence ratio, WCR/NCR, to the spring egg ratio, WCR/NCR, across tillage systems, 1983-85
SPECIES RATIO, 1983-1985

\[ Y = 0.905 - 0.028X + 3.246X^2 \]

\[ R^2 = 0.91 \]

EMERGENCE RATIO (WCR/NCR)

SPRING EGG RATIO (WCR/NCR)
Submitted To: Environmental Entomology

Emergence of Western and Northern Corn Rootworms (Coleoptera: Chrysomelidae) from Four Tillage Systems

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PART 3: EMERGENCE OF WESTERN AND NORTHERN CORN ROOTWORMS
(COLEOPTERA: CHRYSOMELIDAE) FROM FOUR TILLAGE SYSTEMS

Abstract

Emergence of the western (WCR) and northern corn rootworm (NCR), Diabrotica virgifera virgifera LeConte and D. barberi Smith and Lawrence, respectively, was evaluated in four tillage systems near Ames, Iowa from 1983-85. Linear regression equations and coefficients of determination are presented that describe cumulative emergence (probit scale) on Julian date. Emergence was generally delayed in conservation tillage treatments for the WCR. The rate of WCR emergence in these tillage systems was greater than in more conventional practices. Because of increased rates of WCR emergence from conservation tillage practices cumulative beetle emergence by mid-August through early September was comparable among tillage treatments despite delayed emergence associated with conservation practices. The NCR was less responsive in its emergence pattern to the different tillage operations. Adult sampling should not be delayed in conservation tillage systems to correspond with delayed emergence.
The western (WCR) and northern corn rootworms (NCR), *Diabrotica virgifera virgifera* LeConte and *D. barberi* Smith and Lawrence, respectively, are serious pests of corn-following-corn production systems. Eggs are laid during late summer and serve as the overwintering stage. Eclosion occurs the following spring and larvae develop through three larval instars while feeding on root tissue. Adults emerge from late July through mid-September. Beetles may reduce kernel set if feeding on silks is intensive. Thus, corn rootworms are pests of corn during two stages of their univoltine life cycle.

Bergman and Turpin (1986) found that soil heat units didn't offer any advantage over Julian date in estimating the phenology of field populations of corn rootworms. Quantification of variables likely to influence soil temperatures and hence rootworm development, was encouraged to increase the potential usefulness of soil heat unit models.

The influence of tillage systems on soil thermal properties has been reported. Potter et al. (1985) demonstrated that tillage practices, in addition to altering residue cover on the soil surface, change the thermal properties of the soil, both of which influence soil temperature. Conservation tillage systems reduced soil temperatures in the 5-15 cm layer during the early portion of the growing season (Johnson and Lowery 1985). Hein et al. (1985a) reported that 82% of NCR eggs and 66% of WCR eggs were found in the upper 10 cm of soil when samples to a depth of 20 cm were taken. Foster et al. (1979) similarly indicated that 85% of NCR
eggs are found at depths in which soil temperatures are likely to be influenced by tillage practices.

The influence of temperature on corn rootworm development has been discussed (Chiang and Sisson 1968, Apple et al. 1971, Wilde 1971). The role of tillage systems in influencing the rate of development of corn rootworms has not been intensively investigated. Patel and Apple (1967) observed that prior to plowing 88% of NCR eggs were found in the top 7.5 cm of soil, however, after plowing no eggs were discovered at this level. It was suggested that deep plowing would delay eclosion by subjecting eggs to cooler temperatures in the lower soil profile. Pruess et al. (1968) reported that WCR beetle emergence was delayed 5-10 days in till-plant corn compared to a conventional system. Emergence cages used during this experiment did not sample the entire interrow width and thus, adult emergence cannot be considered as representative of an absolute measure of the emerging beetle population. Emergence patterns from soil located near the base of a plant in contrast to soil midway between rows are likely to differ due to differences in soil temperatures. The exposed soil surface between rows is subject to more sunlight consequently resulting in higher temperatures until canopy closure.

The number of cages utilized by Pruess et al. (1968) per tillage treatment was well below the recently reported number of samples required to achieve estimates of WCR emerging beetle populations with a standard error within 10% of the mean (Hein et al. 1985b).

Tyler and Ellis (1974) monitored the emergence of NCR in three tillage systems in a one year study. Fifty percent emergence was 5 days
earlier in the conventional tillage practice compared to conservation treatments. The emergence traps used in this experiment were described by Musick and Fairchild (1970). These traps provided only relative estimates of the emerging beetle population and the number used per tillage treatment was low considering recent findings concerning sample sizes required for desired precision levels (Hein et al. 1985b).

In order to better understand the phenology of corn rootworm populations in the field, factors which may influence the seasonal occurrence of life stages must be quantified. The objectives of this research were to determine the influence of tillage systems on the emergence rates of the WCR and NCR and to compare emergence patterns between the rootworm species. These data may be useful in phenological models that attempt to predict the seasonal dynamics of corn rootworms. Until the influence of many variables such as tillage practices are understood regarding development of field populations, Julian date may continue to serve as the best estimate of rootworm phenology.

Materials and Methods

Agronomic practices

Emergence of the WCR and NCR was monitored at the Iowa State University Agronomy and Agricultural Engineering Research Center near Ames, Iowa from 1983–85. Four tillage systems were arranged in a randomized complete block design. Ten replicates of each tillage treatment were established and used in a cooperative research effort.
Four replicates in 1983 and 1984, and six replicates in 1985 were used to examine beetle emergence. Each plot was comprised of eight rows spaced 76 cm apart and was 6.1-m wide by 27.4-m long. The tillage treatments evaluated were as follows: (1) no-till, (N), (2) fall chisel plow, spring disc, harrow and field cultivate, (C), (3) fall tilled with Paraplow, (P) and (4) fall moldboard plow, spring disc, harrow and field cultivate, (M). The Paraplow is a tillage implement with bent shanks designed to reduce soil compaction while minimizing residue disturbance. Tillage practices were initiated during the fall of 1982 and each treatment remained in the same location for the duration of the experiment. Fall plowing was performed in late October or November and spring tillage operations were accomplished in late April or early May. Corn (Pioneer 3720) was planted on 6 and 10 May 1983 and 1984, respectively, and 29 April 1985 at the rate of 64,000 kernels per ha. Fertilizer and herbicide practices were uniform for all tillage treatments. No insecticides were applied during the experiment.

Adult sampling

Emergence cages that sampled the entire interrow width were used to provide an absolute estimate of WCR and NCR beetle emergence (Hein et al. 1985b). Forty cages per tillage treatment were used in 1983 and sixty cages per treatment were utilized the last two years of the study. Cages were comprised of a wooden frame (35.6 cm by 76.2 cm internally) to which aluminum screening was attached. Within each cage a paper carton (0.47-1) was supported on a corn stalk that had been severed approximately 50
cm above the soil surface. Tack Trap was used to coat each paper carton internally. As beetles emerged they moved upwards and were captured in the carton. Soil outside the sampling area was used to seal the wooden frame to the soil surface.

In 1983, traps were positioned randomly in the field on 8 July and cartons replaced on the following dates: 22 and 29 July, 5 and 16 August and 1 September. All traps were removed from the field on 22 September. During the second year traps were deployed in each tillage treatment on 11 July. Carton replacement dates were as follows: 27 July and 3, 10 and 20 August. Emergence traps were taken from the field on 18 September. In 1985, traps were established on 25 June. Cartons were replaced on 16 and 23 July and 1, 12 and 21 August. On 20 September traps were removed. Each trap remained in the same location throughout the emergence season.

Beetles captured were counted and separated according to species. The relative variation (SE/\bar{X}) across tillage treatments was determined for each species. Accumulated emergence on each sampling date was calculated for each tillage treatment as a proportion of the total emergence over the season. Cumulative proportions were transformed to a probit scale (Sokal and Rohlf 1981). Cumulative proportions of 1.0 and 0.0 were not used because these values are undefined for a probit transformation.

Linear regression was used to express cumulative emergence (probit scale) on Julian date for each species of rootworm for each tillage practice. Regression equations and coefficients of determination are presented. Analysis of variance procedures were conducted to determine
if significant differences occurred between the slopes (rate) and intercepts (emergence initiation) of each tillage for WCR and NCR emergence. Least significant difference values ($P = 0.05$) are presented for slope and intercept estimates for each regression equation.

Results and Discussion

To understand the population dynamics of an organism it is desirable that its universe be sampled with a high degree of precision. Southwood (1978) estimated that a precision level of 0.10 was necessary for intensive natural population studies. Relative variation estimates ($SE/\bar{x}$) were calculated across tillage treatments for each species of rootworm. Sampling precision from 1983-85 for the WCR was 0.21, 0.12 and 0.13, respectively. Precision was slightly better for the NCR with estimates of 0.15, 0.11 and 0.09 determined from 1983-85, respectively. Sampling procedures described by Hein et al. (1985b) and used in this investigation, thus provided absolute estimates of WCR and NCR emerging adult populations with high levels of precision.

In 1983, analysis of variance procedures revealed a significant tillage by linear interaction for cumulative emergence (probit scale) for the WCR ($F = 5.76$, df = 12, $P < 0.05$). Western corn rootworm emergence was significantly delayed in the no-till and paraplow treatments, however the rate of emergence in each of these systems was greater than in chisel or moldboard plow practices (Table 1). The initiation and rate of
emergence of the WCR were similar for the Paraplow and no-till systems and between the moldboard and chisel plow practices (Fig. 1).

Analysis of variance techniques did not indicate a significant tillage by linear interaction (P > 0.05) for cumulative NCR emergence in 1983. Emergence initiation or rate did not significantly differ among the tillage practices (Table 1). Because intercept and slope values describing NCR emergence did not significantly differ among tillage practices a single line is presented to represent emergence of the NCR in 1983 (Y = -19.56 + 0.088 X, n = 20, R² = 0.91, P < 0.01) (Fig. 2). Cumulative emergence of the NCR was delayed in comparison to the WCR. A delay in NCR emergence relative to the WCR had been reported earlier by Hein (1984).

A significant tillage by linear interaction for cumulative emergence was not observed in 1984 (P > 0.05) for either species of rootworm. A comparison of slope and intercept values, however, revealed that WCR emergence followed trends witnessed in 1983 (Table 1). Emergence in no-till and paraplow treatments was delayed in relation to the more conventional tillage practices (Fig. 3).

Northern corn rootworm cumulative emergence was not influenced by tillage in 1984. Slope and intercept values across tillage treatments reveals the similarity of emergence (Table 1). The following equation describes NCR cumulative emergence in 1984 (Fig. 4): Y = -18.73 + 0.087 X (N = 16, R² = 0.89, P < 0.01). Emergence of the NCR was not delayed in relation to the WCR. This was in contrast to 1983 findings.
In the final year of the experiment analysis of variance procedures indicated a significant tillage by linear interaction for WCR cumulative emergence \((F = 4.47, df = 20, P < 0.05)\). Western corn rootworm emergence was delayed in the no-till and paraplow treatments (Table 1). Emergence rates in these tillage practices were also high in relation to chisel and moldboard plow regimes. Because slope and intercept values between no-till and Paraplow treatments were not significantly different a single line was empirically fit to represent WCR emergence in 1985 for these two systems (Fig. 5). Western corn rootworm emergence began earlier in the moldboard tillage practice and proceeded at a reduced rate. Emergence initiation and rate was intermediate for the chisel plow treatment among tillage operations.

A significant tillage by linear interaction for NCR cumulative emergence was not observed in 1985 \((P > 0.05)\). Slope and intercept values for the no-tillage treatment (Table 1) indicated, however, that emergence was delayed and rate of emergence increased in relation to other tillage systems. Emergence from the no-tillage and moldboard practices represented extremes in NCR emergence in 1985 (Fig. 6). Cumulative emergence for the WCR and NCR was comparable in 1985 across Julian date.

Hein and Tollefson (1985) reported that rootworm populations from mid-August through early September are responsible for greater than 50% of the cumulative oviposition in fields devoted to continuous corn production. A thorough monitoring of adult populations during this period is vital in order to assess the potential of larval damage the
following season. Results from this experiment indicate that emergence is often delayed in conservation tillage systems. This delay in emergence was seen most consistently with the WCR throughout the 3-year period. Northern corn rootworms were less responsive to tillage practices with regard to their emergence behavior, however, NCR emergence was delayed in the no-till regime in 1985. Despite delayed emergence in conservation tillage treatments, emergence rates are generally greater in these tillage practices compared to conventional operations. By mid-August through early September, cumulative emergence is generally comparable across tillage systems. Therefore, scouting programs should not delay scouting procedures for WCR or NCR adults in fields farmed with conservation tillage techniques.

In summary, conservation tillage treatments delay corn rootworm emergence in comparison to conventional systems. Western corn rootworms were more likely to display this delayed response relative to the NCR. Emergence rates were greatest in conservation tillage treatments. Cumulative emergence by mid-August through early September is generally comparable regardless of tillage for both species of corn rootworms. These data describing the impact of tillage systems on WCR and NCR emergence may be used to improve future phenological models for natural populations of corn rootworms.
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systems. J. Econ. Entomol. 61:1424-1427.
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and lodging damage of northern corn rootworm (Coleoptera:
Chrysomelidae) under three tillage systems. Proc. Entomol. Soc.
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Table 1. Regression equations and coefficients of determination ($R^2$) for relationships between cumulative proportion emergence (probit) and Julian date for the WCR and NCR in each tillage treatment, 1983-85

<table>
<thead>
<tr>
<th>Tillage Treatment</th>
<th>Probit of Proportion</th>
<th>Equation</th>
<th>$n$</th>
<th>$R^2$</th>
<th>S. E.</th>
<th>$a^a$</th>
<th>$b^b$</th>
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</thead>
<tbody>
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<td><strong>WCR, 1983</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>No-till</td>
<td>$-20.12 + 0.092 \text{ (JDATE)}$</td>
<td>5</td>
<td>0.97**</td>
<td>2.15</td>
<td>0.010</td>
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<tr>
<td>Chisel Plow</td>
<td>$-15.66 + 0.072 \text{ (JDATE)}$</td>
<td>5</td>
<td>0.93**</td>
<td>2.52</td>
<td>0.011</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paraplow</td>
<td>$-19.53 + 0.091 \text{ (JDATE)}$</td>
<td>5</td>
<td>0.98**</td>
<td>1.43</td>
<td>0.007</td>
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<tr>
<td>Moldboard Plow</td>
<td>$-14.85 + 0.070 \text{ (JDATE)}$</td>
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<td>0.97**</td>
<td>1.47</td>
<td>0.007</td>
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<tr>
<td>*L. S. D.$^c$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.68</td>
<td>0.012</td>
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<tr>
<td><strong>NCR, 1983</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>No-till</td>
<td>$-18.60 + 0.084 \text{ (JDATE)}$</td>
<td>5</td>
<td>0.92**</td>
<td>3.26</td>
<td>0.015</td>
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<td>$-19.80 + 0.088 \text{ (JDATE)}$</td>
<td>5</td>
<td>0.89*</td>
<td>4.03</td>
<td>0.018</td>
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<td>0.94**</td>
<td>3.22</td>
<td>0.015</td>
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</tr>
<tr>
<td>Moldboard Plow</td>
<td>$-18.09 + 0.082 \text{ (JDATE)}$</td>
<td>5</td>
<td>0.96**</td>
<td>2.25</td>
<td>0.010</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*L. S. D.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4.48</td>
<td>0.020</td>
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$^a$ $a = \text{intercept.}$  
$^b$ $b = \text{slope.}$  
$^c$ $\text{L. S. D. = least significant difference (P = 0.05).}$  

* Significant at the 0.05 probability level.  
** Significant at the 0.01 probability level.
Table 1 continued.

<table>
<thead>
<tr>
<th></th>
<th>Equation</th>
<th>n</th>
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<th>S.E.</th>
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<td>Cumulative Emergence</td>
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<td>Probit of Proportion</td>
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**WCR, 1984**

<table>
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<th>Equation</th>
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<th>$R^2$</th>
<th>S.E.</th>
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<tbody>
<tr>
<td>No-till</td>
<td>$-23.53 + 0.108 \text{(JDATE)}$</td>
<td>4</td>
<td>0.99**</td>
<td>2.04</td>
<td>0.009</td>
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<tr>
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<td>$-21.15 + 0.098 \text{(JDATE)}$</td>
<td>4</td>
<td>0.99**</td>
<td>1.31</td>
<td>0.006</td>
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<tr>
<td>Paraplow</td>
<td>$-24.35 + 0.111 \text{(JDATE)}$</td>
<td>4</td>
<td>0.99**</td>
<td>1.70</td>
<td>0.008</td>
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<td>Moldboard Plow</td>
<td>$-20.93 + 0.096 \text{(JDATE)}$</td>
<td>4</td>
<td>0.99**</td>
<td>0.10</td>
<td>0.001</td>
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<td>L. S. D.</td>
<td>2.42</td>
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**NCR, 1984**

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<th>Equation</th>
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<th>$R^2$</th>
<th>S.E.</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
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<td>No-till</td>
<td>$-19.88 + 0.092 \text{(JDATE)}$</td>
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<td>0.94*</td>
<td>3.65</td>
<td>0.017</td>
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<tr>
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<td>0.95*</td>
<td>3.38</td>
<td>0.015</td>
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<td>0.96*</td>
<td>3.16</td>
<td>0.014</td>
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</tr>
<tr>
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<td>$-15.20 + 0.072 \text{(JDATE)}$</td>
<td>4</td>
<td>0.95*</td>
<td>2.60</td>
<td>0.012</td>
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<td>L. S. D.</td>
<td>5.25</td>
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Table 1 continued.

<table>
<thead>
<tr>
<th></th>
<th>Equation</th>
<th>n</th>
<th>$R^2$</th>
<th>S. E.</th>
<th>a</th>
<th>b</th>
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<td><strong>WCR, 1985</strong></td>
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<tr>
<td>No-till</td>
<td>$-22.66 + 0.104 (\text{JDATE})$</td>
<td>5</td>
<td>0.99**</td>
<td>1.24</td>
<td>0.006</td>
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<tr>
<td>Chisel Plow</td>
<td>$-18.87 + 0.090 (\text{JDATE})$</td>
<td>5</td>
<td>0.99**</td>
<td>1.24</td>
<td>0.006</td>
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<tr>
<td>Paraplow</td>
<td>$-23.07 + 0.107 (\text{JDATE})$</td>
<td>5</td>
<td>0.97**</td>
<td>2.25</td>
<td>0.011</td>
<td></td>
</tr>
<tr>
<td>Moldboard Plow</td>
<td>$-15.43 + 0.074 (\text{JDATE})$</td>
<td>5</td>
<td>0.95**</td>
<td>2.03</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td></td>
<td>L. S. D. $^c$</td>
<td>2.41</td>
<td>0.011</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>NCR, 1985</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No-till</td>
<td>$-18.22 + 0.083 (\text{JDATE})$</td>
<td>5</td>
<td>0.96**</td>
<td>2.21</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td>Chisel Plow</td>
<td>$-14.46 + 0.068 (\text{JDATE})$</td>
<td>5</td>
<td>0.96**</td>
<td>1.64</td>
<td>0.008</td>
<td></td>
</tr>
<tr>
<td>Paraplow</td>
<td>$-14.90 + 0.070 (\text{JDATE})$</td>
<td>5</td>
<td>0.96**</td>
<td>1.63</td>
<td>0.008</td>
<td></td>
</tr>
<tr>
<td>Moldboard Plow</td>
<td>$-12.83 + 0.062 (\text{JDATE})$</td>
<td>5</td>
<td>0.96**</td>
<td>1.48</td>
<td>0.007</td>
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<tr>
<td></td>
<td>L. S. D.</td>
<td>2.43</td>
<td>0.011</td>
<td></td>
<td></td>
<td></td>
</tr>
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</table>
Fig. 1. Cumulative WCR emergence (probit scale) on Julian date, 1983. Tillages are, (N) = no-till, (C) = chisel plow system, (P) = Paraplow and (M) = moldboard plow system. Line 'a' represents C and M tillage practices. Line 'b' represents N and P tillage systems.
1983, WCR EMERGENCE

CUM. WCR EMERGE. (probit scale)

JULIAN DATE
Fig. 2. Cumulative NCR emergence (probit scale) on Julian date, 1983. Tillages are, (N) = no-till, (C) = chisel plow system, (P) = Paraplow and (M) = moldboard plow system.
1983, NCR EMERGENCE

CUM. NCR EMERGE. (probit scale)

JULIAN DATE
Fig. 3. Cumulative WCR emergence (probit scale) on Julian date, 1984. Tillages are, (N) = no-till, (C) = chisel plow system, (P) = Paraplow and (M) = moldboard plow system. Line 'a' represents C and M tillage practices. Line 'b' represents N and P tillage systems.
1984, WCR EMERGENCE

CUM. WCR EMERG. (probit scale)

JULIAN DATE

[Graph showing cumulative WCR emergence across different dates, with probit scale on the y-axis and Julian dates on the x-axis.]
Fig. 4. Cumulative NCR emergence (probit scale) on Julian date, 1984. Tillages are, (N) = no-till, (C) = chisel plow system, (P) = Paraplow and (M) = moldboard plow system.
Fig. 5. Cumulative WCR emergence (probit scale) on Julian date, 1985. Tillages are, (N) = no-till, (C) = chisel plow system, (P) = Paraplow and (M) = moldboard plow system. Line 'a' represents the M tillage treatment. Line 'b' represents the N and P tillage practices.
Fig. 6. Cumulative NCR emergence (probit scale) on Julian date, 1985. Tillages are, (N) = no-till, (C) = chisel plow system, (P) = Paraplow and (M) = moldboard plow system. Line 'a' represents the M tillage practice. Line 'b' represents the N treatment.
Influence of Tillage Systems and Western and Northern Corn Rootworm (Coleoptera: Chrysomelidae) Egg Ratio On Larval Populations and Damage

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PART 4: INFLUENCE OF TILLAGE SYSTEMS AND WESTERN AND NORTHERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) EGG RATIO ON LARVAL POPULATIONS AND DAMAGE

Abstract

The influence of tillage systems on larval populations and root damage was examined for the western and northern corn rootworms, *Diabrotica virgifera virgifera* LeConte (WCR) and *D. barberi* Smith and Lawrence (NCR), respectively. Larval populations and root damage were lower than expected in the no-till treatment relative to other tillage practices based upon absolute estimates of WCR and NCR spring egg populations. Root weights were least in the no-till regime and may have resulted in failure of early instar larvae to locate root tissue. The ratio of WCR to NCR eggs was shown to be an important factor in establishing larval populations and precipitating root damage across tillage systems. Rootworm populations comprised primarily of the NCR are less capable of causing as much root damage as a comparable population of WCRs. Linear regression equations are presented to describe this relationship.
Introduction

The western corn rootworm (WCR), *Diabrotica virgifera virgifera* LeConte, and the northern corn rootworm (NCR), *D. barberi* Smith and Lawrence, are economic pests of corn following corn production systems. Eggs are oviposited in the soil from mid-to-late summer and serve as the overwintering stage. Eclosion occurs primarily in June and larvae begin feeding on developing corn roots. Damage sustained by root systems may lead to an overall loss of efficiency and vigor of the corn plant. Extensive root pruning may result in lodging with an associated reduction in the harvestability of the crop. There are three larval instars and pupation occurs in an earthen cell. Beetles emerge from late July to early September and may cause reductions in kernel set if feeding on corn silks and pollen is intense.

The impact of different tillage systems on corn rootworm larval populations is unclear. Previous research has not produced consistent results regarding the role of tillage on larval dynamics. Calkins and Kirk (1969) evaluated the influence of fall versus spring plowing on WCR and NCR populations. The percentage of plants that had lodged was used as an indicator of root damage differences. In two out of three years larvae were most abundant and damage greater in plots that had been fall plowed. Spring plowed plots suffered the most damage in the other year of the experiment. The percentage of plants that had lodged was used as an indicator of root damage differences. Root ratings are currently the preferred method for evaluating root damage (Hills and Peters 1971).
Musick and Collins (1971) suggested that NCR egg or larval survival was reduced in a no-tillage treatment. Four times as many eggs in the no-tillage system were required to cause comparable root damage to that in a conventional tillage practice. Matteson et al. (1972) did not find any difference in the abundance of larvae among tillage systems in a one-year study. Tyler and Ellis (1974) evaluated lodging damage caused by the NCR in three tillage systems. The number of lodged plants was significantly greater in the full tillage treatment for this single season trial. The influence of different levels of infested foxtail, Setaria spp., and tillage practices on WCR and NCR oviposition and root damage were evaluated by Johnson and Turpin (1985). Root damage was generally lower in no-till plots than moldboard or chisel plow treatments despite roughly equivalent fall egg populations. Further investigations to explain this phenomenon were encouraged.

The size of larval populations within any tillage system is likely to be dependent upon the total spring egg population. More eggs typically yield more larvae until intraspecific and interspecific competition negate the effect of additional eggs. Previous field research concerning WCR and NCR larval populations and root damage has not recognized, however, the importance of the ratio of WCR to NCR eggs in influencing the severity of damage to corn roots. Prior to recent greenhouse investigations, the total number of rootworm eggs was primarily the only factor considered in predicting the magnitude of root damage likely to occur. Piedrahita et al. (1985) reported that WCR larvae reduced the survival and influenced the spatial distribution of
NCR larvae in root systems of potted corn seedlings. The NCR was unable to influence survival of WCR larvae. Artificial infestation techniques (Sutter and Branson 1980) were used by Fisher (1985) to evaluate root damage caused by the WCR and NCR independently from each other. The NCR was less able to inflict as much root damage as a comparable WCR population.

The objectives of this research were to evaluate the impact of different tillage systems on larval populations and to determine the importance of the WCR to NCR spring egg ratio in establishing larval populations and subsequent root damage. Root weights from each tillage system were also examined in an effort to further explain differences in larval dynamics among the tillage systems.

Materials and Methods

Agronomic practices

Research for this experiment was conducted at the Iowa State University Agronomy and Agricultural Engineering Research Center near Ames, Iowa from 1983-85. Four tillage treatments were arranged in a randomized complete block design. Ten replicates of each tillage practice were established during the fall of 1982. The entire research area was jointly used with other researchers in a cooperative experimental program. Four replicates in 1983 and 1984, and six replicates in 1985 were used to monitor egg and larval populations and evaluate root damage. Plots were 6.1 m wide by 27.4 m long and were
comprised of eight rows spaced 76 cm apart. The tillage operations were: (1) no-till (N), (2) fall chisel plow and spring disc, harrow and field cultivate (C), (3) fall tilled by Paraplow (P), and (4) fall moldboard plow and spring disc, harrow and field cultivate (M). The Paraplow® is a tillage implement with bent shanks that loosens soil and reduces compaction while leaving crop residue on the soil surface. Each tillage treatment remained in the same location throughout the experiment. Fall tillage operations were conducted in late October to early November. Spring tillage practices were carried out in late April or early May. Corn (Pioneer® 3720) was planted on 6 and 10 May 1983 and 1984, respectively, and 29 April 1985 at a rate of 64,000 kernels per ha. Insecticides were not used during the experiment and fertilizer and herbicide applications were uniform for all tillage systems.

Egg sampling

Absolute estimates of WCR and NCR egg populations were made using the frame method described by Foster et al. (1979). This sampling technique involves the use of a metal frame 10.2 cm wide by the row-width long. The frame is positioned perpendicular to the row direction and driven into the soil. Hein et al. (1985) recommended that sampling for WCR or NCR eggs should occur to a depth of at least 20 cm and include the complete inter-row width because of the variable horizontal and vertical aggregations of WCR and NCR eggs.

Sampling for WCR and NCR eggs was conducted on 1-3 June 1983, 23-24 May 1984 and 9-13 May 1985. Soil to a depth of 20 cm was removed from
within the frame and thoroughly mixed and subsamples taken. Twenty frames of soil per tillage treatment were randomly removed in 1983 and 1984; 24 frames per treatment were evaluated in 1985. Two 0.47 l subsamples of soil were taken from each frame in 1983; five 0.47 l subsamples were examined for each frame in 1984 and 1985. Eggs were separated from soil using procedures outlined by Shaw et al. (1976). Eggs were identified to species based upon differences in the sculpturing of the chorion (Atyeo et al. 1964) and counted.

Data were transformed according to the following relationship, $y = \log_{10} (X + 1)$, to reduce the dependence of the variance on the mean. Analysis of variance procedures were conducted on spring egg population data for each year. A least significant difference value ($P = 0.05$) for each year is presented with untransformed WCR and NCR egg population means of each tillage system. The mean number of WCR and NCR eggs were contrasted within each tillage treatment by year using $T'$-tests (Snedecor and Coohran 1967). This test allows for the direct comparison of two means with different variances and sample sizes. Relative variation ($SE/X$) estimates are given for the WCR and NCR across tillage treatments for each year. Linear regression was used to describe the dependence of larval populations and root damage on the ratio of WCR to NCR eggs. Regression equations are presented to quantify these relationships.

**Larval sampling**

Relative estimates of larval populations were made for each tillage treatment using procedures similar to those described by Bergman et al.
Each larval sample was comprised of an 18-cm cube of soil that contained a portion of the corn root system found at the base of the plant. Approximately 140 samples were removed at random from each tillage treatment on 6-7 July 1983, 6-9 July 1984 and 26 June-2 July 1985. All samples were frozen until they were processed.

The extraction of larvae from each sample involved a washing and screening technique. After thawing cubes were individually placed in a pail and flooded with pressurized water. The solution was mixed by hand. The liquid portion was decanted into a second pail. This procedure was repeated again with the liquid portion poured into a third pail. The original pail was flooded and stirred for a third time after which the liquid portion of each pail was poured through two sieves. The top and bottom sieves had openings of 600 μm and 180 μm, respectively. Larvae were hand picked from organic debris that collected on the sieves and placed in alcohol. The number of larvae from each larval cube was recorded. Larval sampling data were transformed by $Y = \log_{10}(X + 1)$. These data were analyzed by analysis of variance procedures. Untransformed means for each tillage treatment, a least significant difference value ($P = 0.05$) and relative variation ($SE/X$) estimates are presented each year across tillage systems.

The root system from every cube was rated for damage using a 1-9 root damage scale described by Apple et al. (1977). This scale was used to quantify the percentage of pruning more precisely than the familiar 1-6 rating scale (Hills and Peters 1971). Roots were oven dried (% moisture < 10%) and weighed. Root damage and dry weight data were
analyzed using analysis of variance techniques. Least significant difference values ($P = 0.05$) are presented along with root rating and dry root weight means for each year.

Results and Discussion

Egg samples

Orthogonal contrasts among tillage systems revealed significantly ($P < 0.05$) more WCR and NCR eggs in the no-till treatment compared to the chisel plow and spring disc practice in 1983 (Table 1). In 1984, the WCR egg population was significantly greater ($P < 0.05$) in the no-till system than in the moldboard plow and spring disc treatment. With the exception of these significant contrasts, spring WCR and NCR egg populations were comparable among the tillage regimes each year. Sampling precision ($SE/\bar{X}$) was 0.20, 0.39 and 0.32 for the WCR from 1983-85, respectively. Northern corn rootworm eggs were sampled more precisely with estimates of relative variation approximately 0.15 each year. Hein et al. (1985) noted that the WCR was more likely to oviposit deeper in soil than the NCR. Reduced sampling precision for the WCR each year relative to the NCR may have resulted from not sampling deeply enough for WCR eggs.

Western and NCR egg population means were contrasted within each tillage system for each year using $T'$-tests (Table 1). In 1983 and 1984, WCR and NCR egg populations did not significantly differ within any tillage system. Each tillage system had numerically more WCR eggs than NCR eggs in 1983, however, this pattern was reversed in 1984. In 1985,
the NCR egg population was significantly greater (P < 0.01) than the WCR population in each tillage practice: [ N (T' = 4.37, df = 15), C (T' = 3.70, df = 15), P (T' = 6.02, df = 15) and M (T' = 4.29, df = 15) ]. The significant decline in the WCR egg population relative to the NCR may reflect the behavioral tendency of WCR female beetles to move out of corn following corn systems more readily than male WCR adults (Hill and Mayo 1980). Godfrey and Turpin (1983) similarly reported higher densities of female WCR adults in first year corn fields than in continuous corn fields and suggested using different economic thresholds for each system. Higher densities of females in first year cornfields may result in increased oviposition and subsequent root damage. Movement of NCR females appears to be more dependent upon food quality and availability (Cinereski and Chiang 1968) with ovipositional behavior not as greatly influenced by cropping sequence. Based upon differences in WCR and NCR ovipositional behavior, NCR populations may remain more stable in continuous corn production systems relative to the WCR.

Larval samples

Sampling for larvae using 18-cm cubes provides a relative estimate of the population since only a portion of the total larval universe is sampled. Distribution of larvae may be different among the tillage practices reflecting differences in root proliferation (Bauder et al. 1985). Sampling for larvae using 18-cm cubes, however, provides a good estimate of the larval population most likely to cause economic root damage.
In 1983 and 1984, analysis of variance procedures revealed no significant tillage effect on larval populations (Table 2). The influence of tillage on larval populations in 1985 was significant \((F = 7.93, \text{df} = 15, P < 0.002)\) with fewer larvae detected in the no-tillage treatment. Higher WCR and NCR spring egg populations in the no-till regime did not yield corresponding larval populations in 1983 or 1984. Sampling precision \((\text{SE}/\bar{X})\) for larvae was 0.08 in 1983 and 0.09 for each of the remaining two years. Southwood (1978) reported that high levels of accuracy, standard errors of within 10% of the mean, are desirable when working with natural populations.

Root damage among the tillage practices paralleled the larval population estimates very closely each year. Damage ratings were low because larval samples were taken before peak root feeding occurred. This was necessary in order to sample larvae before pupation or early emergence. Root damage was significantly greater in the Paraplow system in 1983 compared to other tillage treatments \((F = 10.94, \text{df} = 9, P < 0.0023)\). No significant differences in root damage were observed in 1984. Damage in 1985, was significantly influenced by tillage \((F = 10.07, \text{df} = 15, P < 0.0007)\) with pressure the least in the no-till treatment.

Root damage throughout the experiment was less in the no-till treatment than expected. In 1983, WCR and NCR egg populations were significantly greater in the no-till regime than in the chisel plow treatment, however, root damage between the two systems was comparable. The following year significantly more WCR eggs were detected in the no-
till practice as compared to the moldboard plow treatment. Root ratings were not significantly different between these tillage operations. Western and NCR egg populations did not significantly differ in 1985 among tillage treatments, however, root damage in the no-till practice was significantly less in relation to other systems.

Lower damage in the no-till regime may be related to the availability of root tissue for early larval feeding. Dry root weights were evaluated to determine if the amount of root tissue within 18-cm cubes differed among the tillage treatments. Root weights were significantly influenced by tillage in 1983 (\(F = 3.60, \text{df} = 9, P < 0.05\)) and 1985 (\(F = 5.79, \text{df} = 15, P < 0.0078\)). In 1983 and 1985, root systems in the no-till regime weighed significantly less than roots from the moldboard plow practice. While not significant, this pattern was also followed in 1984. Smaller root systems within the no-tillage treatment may be due to lower soil temperatures encountered by seedlings (Johnson and Lowery 1985, Potter et al. 1985). I hypothesize that reduced root damage in a no-till field may be directly related to increased starvation of early instar larvae.

An increase in the proportion of NCRs relative to the total egg population was observed from 1983 through 1985. Due to this proportional population shift, the ratio of WCR to NCR eggs was examined for its possible influence on larval populations and root damage over the three year period. Using artificial infestation techniques Fisher (1985) reported that the NCR was less able to cause as much root damage as a comparable level of WCRs. It was hypothesized that larval populations
and root damage ratings in 1984 and 1985 were reduced across all tillage practices from 1983 partially because of the increasing dominance of the NCR population. The total (WCR + NCR) egg population in 1983 was greater in each tillage treatment and also accounts for the higher larval population and root damage.

To evaluate the impact of the WCR and NCR spring-egg ratio and total on larval populations and root damage, data were combined across tillage practices and years to represent the proportional dominance of each species observed during this experiment. Significant relationships between the total number of eggs with larval populations \( r = 0.84, n = 12, P < 0.0007 \) and with root damage \( r = 0.73, n = 12, P < 0.007 \) were determined. These relationships indicate that larval populations and subsequent root damage are responsive to the total spring-egg population as expected. Regression analyses yielded significant linear relationships for the number of larvae per 18-cm cube \( Y = 1.22 + 0.898 X, R^2 = 0.70, n = 12, P < 0.0007 \) and root damage \( Y = 1.53 + 0.191 X, R^2 = 0.53, n = 12, P < 0.007 \) regressed on the spring-egg total.

Significant correlations between the WCR and NCR spring-egg ratio with larval populations \( r = 0.87, n = 12, P < 0.0002 \) and with root damage \( r = 0.84, n = 12, P < 0.0006 \) were detected. Regression techniques were used to quantify these observations. Significant linear relationships for larval populations \( P < 0.0002 \) and root damage \( P < 0.0006 \) were noted when these variables were regressed independently on the WCR and NCR egg ratio (Figs. 1 and 2). Results from these analyses indicate that the severity of root damage across tillage systems is
closely linked to the proportion of WCR to NCR eggs with which each field begins the growing season. Egg populations that are predominantly NCR do not produce as many larvae or as much root damage within an 18-cm cube around the base of a corn plant as a comparable WCR population.

In summary, relative estimates of larval populations and root damage in a no-tillage system were lower than expected based upon absolute WCR and NCR spring egg population estimates. Smaller root systems in the no-till treatment may have resulted in increased mortality of early instar larvae due to the greater difficulty in locating root tissue. The ratio of WCR to NCR eggs in the spring significantly influenced larval populations and root damage across tillage systems. A population comprised primarily of NCR eggs is less likely to produce as many larvae or as much root damage as an equivalent population of WCR eggs.
References Cited


Fisher, J. R. 1985. Comparison of controlled infestations of *Diabrotica virgifera virgifera* and *Diabrotica barberi* (Coleoptera: Chrysomelidae) on corn. *J. Econ. Entomol.* 78:1406-1408.


Johnson, T. B., and F. T. Turpin. 1985. Northern and western corn rootworm (Coleoptera: Chrysomelidae) oviposition in corn as influenced by foxtail populations and tillage systems. *J. Econ. Entomol.* 78:57-60.


Table 1. Mean number of WCR and NCR eggs/ha ($10^6$) in each tillage treatment for the springs of 1983-85

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>No-Till</td>
<td>28.63</td>
<td>21.03</td>
<td>6.74</td>
<td>7.20</td>
<td>1.85</td>
<td>11.33**</td>
</tr>
<tr>
<td>Chisel Plow</td>
<td>15.57</td>
<td>12.35</td>
<td>3.67</td>
<td>6.42</td>
<td>2.35</td>
<td>10.28**</td>
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<tr>
<td>Paraplow</td>
<td>22.97</td>
<td>13.96</td>
<td>2.74</td>
<td>6.33</td>
<td>1.95</td>
<td>14.87**</td>
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<td>Moldboard Plow</td>
<td>18.14</td>
<td>17.18</td>
<td>1.30</td>
<td>5.77</td>
<td>1.34</td>
<td>10.72**</td>
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<td>1.28</td>
<td>0.54</td>
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<tr>
<td>L. S. D. a</td>
<td>12.74</td>
<td>7.53</td>
<td>5.31</td>
<td>4.09</td>
<td>1.62</td>
<td>6.29</td>
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</table>

*L. S. D. = least significant difference (P = 0.05).

** P < 0.01, T'-test comparison between WCR and NCR means, within tillage systems for 1985.
Table 2. Mean number of larvae per 18-cm cube, root damage rating means, 1-9 scale, and root dry weight (grams) means across tillage treatments, 1983-1985

<table>
<thead>
<tr>
<th>Tillage Treatment</th>
<th>1983</th>
<th>1984</th>
<th>1985</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$L^a$</td>
<td>$RR^b$</td>
<td>$WT^c$</td>
</tr>
<tr>
<td>No-till</td>
<td>8.89</td>
<td>2.94</td>
<td>5.53</td>
</tr>
<tr>
<td>Chisel Plow</td>
<td>8.73</td>
<td>2.92</td>
<td>5.93</td>
</tr>
<tr>
<td>Paraplow</td>
<td>13.12</td>
<td>4.74</td>
<td>5.84</td>
</tr>
<tr>
<td>Moldboard Plow</td>
<td>7.77</td>
<td>2.68</td>
<td>7.07</td>
</tr>
<tr>
<td>S. E.</td>
<td>1.81</td>
<td>0.29</td>
<td>0.36</td>
</tr>
<tr>
<td>L. S. D.</td>
<td>5.80</td>
<td>0.92</td>
<td>1.14</td>
</tr>
</tbody>
</table>

$L^a$ = number of larvae per 18-cm cube.

$RR^b$ = root rating, 1-9 damage scale.

$WT^c$ = dry weight of root systems (grams).

$L. S. D.$ = least significant difference (P = 0.05).
Fig. 1. Relationship between the number of larvae per 18-cm cube and the spring WCR to NCR egg ratio.
Egg and Larval Samples, 1983–1985

\[ Y = 1.80 + 5.45X \]

\[ R^2 = 0.76 \]
Fig. 2. Relationship between root damage (1-9 scale) and the spring WCR to NCR egg ratio
ROOT and EGG SAMPLES, 1983-1985

\[ Y = 1.56 + 1.29X \]

\[ R^2 = 0.71 \]
SUMMARY

Research concerning the influence of conservation tillage systems on corn rootworm population dynamics and damage prior to this study, relied primarily on relative sampling techniques. Sampling precision in these earlier investigations was often poor or unreported. Absolute sampling strategies for the egg and adult stages were utilized in this experiment to monitor intensively the population fluctuations of the WCR and NCR in different tillage systems. Relative estimates of the larval population along with root damage and root weights were also evaluated.

The influence of tillage type on oviposition and overwintering survival were evaluated by sampling for the WCR and NCR egg stage during the fall and spring of each year. Western corn rootworm and NCR oviposition were not influenced by the tillage practice used. Survival of WCR and NCR eggs was favored in the no-till and chisel-plow systems during the severe winter of 1983-84. The following winter was more moderate and rootworm egg survival was not affected by the tillage treatments. Egg samples should be taken at a depth of at least 30 cm in future population studies of the WCR.

Survivorship of the WCR and NCR throughout the growing season of corn was examined by comparing absolute estimates of spring egg populations with adult emergence later in the season. Tillage systems did not affect WCR or NCR survival. Western corn rootworm survivorship was significantly greater than that of the NCR during the growing season.
Emergence rate and initiation were evaluated for the WCR and NCR in each tillage practice. These data may be useful in improving phenological models for each species of rootworm. Conservation tillage operations delayed corn rootworm emergence in comparison to conventional systems. Northern corn rootworms were less likely to display this delayed response. Emergence rates were greatest in conservation tillage treatments for the WCR and NCR.

The effect of the ratio of WCR to NCR eggs on larval populations and root damage was investigated. This ratio significantly influenced larval population size and root damage across tillage systems. A population comprised primarily of NCR eggs did not produce as many larvae or as much root damage as an equivalent population of WCR eggs. Larval populations and root destruction in a no-tillage system were lower than expected based upon absolute WCR and NCR spring egg population estimates. Future research efforts concerning larval populations should concentrate on developing absolute techniques to better evaluate larval survival.
ADDITIONAL REFERENCES CITED


Johnson, T. B., and F. T. Turpin. 1985. Northern and western corn rootworm (Coleoptera: Chrysomelidae) oviposition in corn as influenced by foxtail populations and tillage systems. J. Econ. Entomol. 78:57-60.


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There are many people to be recognized for their encouragement and assistance throughout this research project. Jim Oleson deserves a special thanks for his patience and untiring devotion to the research conducted by graduate students. James Gifford's incredible ability to give of himself will not be forgotten. Barb Spike provided a spark of enthusiasm and humor that made long days in the field more enjoyable. Dr. Gary Hein offered many helpful suggestions and insights that strengthened this research effort. Dr. Joel R. Coat's guidance and sincere interest in my development is especially appreciated. Dr. Coats was instrumental in smoothing my transition into graduate school for which I am very thankful. Dr. Donald C. Erbach is due a special thanks for his assistance and cooperation.

Finally and most importantly, I thank my wife Ellen for her constant devotion and sacrifices during my studies. Ellen and my daughter Kendra provided tireless love and support throughout this endeavor for which I shall always be grateful.