A Descriptive Study of the Population Dynamics of Adult *Diabrotica Virgifera Virgifera* (Coleoptera: Chrysomelidae) in Artificially Infested Corn Fields

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ABSTRACT

The influence of corn plant phenology on the dynamics of adult western corn rootworm, *Diabrotica virgifera virgifera,* populations was studied during 1988 and 1989 in corn fields artificially infested with eggs. Fifty percent of adult emergence from the soil occurred by day 194 in 1988 and day 203 in 1989. In both years, adult emergence was synchronized with corn flowering, eggs were recovered in soil samples approximately four days after reproductive females were first observed in the population, and oviposition was essentially complete about 25 days after it began. The number of reproductive female beetle-days accumulating per m^2 was similar in both years. Approximately two times as many eggs were laid in 1988 (1239 eggs /m^2) as in 1989 (590 eggs /m^2). The difference in egg density may have been caused by differences among years in the temporal synchrony of reproductive beetles with flowering corn. Daily survival rates of adults were high while corn was flowering; exhibited a gradual decline during grain filling; and decreased rapidly during the grain drying stage.

The western corn rootworm, *Diabrotica virgifera virgifera* LeConte, is among the most destructive insect pests of corn, *Zea mays,* grown in the midwestern United States. The species is univoltine and overwinters in the egg stage. Eggs, larvae, and pupae are subterranean. Eggs hatch in the spring, and larvae feed on the roots of corn plants. Larval feeding reduces the ability of corn plants to absorb nutrients and moisture from the soil and makes them susceptible to lodging. Adults emerge from the soil in the summer and feed primarily on the leaves, silks, and pollen of corn.

The potential for large, damaging, larval populations in fields is generally determined by the number of eggs laid there the previous summer; however highly variable and unpredictable mortality during the immature life stages makes prediction of damage difficult. The number of eggs laid per unit area in a field is related to the density of female beetles, their fecundity, and residence time in the field. Beetles of both sexes feed on a variety of corn tissues, but survival and fecundity rates vary with the tissues upon which they feed, and consequently, on the growth stage of corn plants in the field (Elliott et al. 1990a). Dispersal rates of adults are also influenced by corn plant phenology. Beetles are attracted to fields of silking and pollinating

corn, but tend to leave fields in which corn has advanced to more mature stages of growth (Hill and Mayo 1974, Godfrey and Turpin 1983).

Recent advances in laboratory rearing methods for *D. virgifera* that permit production of large numbers of *D. virgifera* eggs (Jackson 1986) have made it possible to infest relatively large field plots with eggs at densities similar to those encountered in naturally infested fields. Field tests conducted over several years have failed to demonstrate differences in the biology of beetles developing from eggs laid by colony beetles and those developing from eggs laid by field collected beetles (J. R. Fisher unpublished data). Thus, artificial infestation may be a useful method for initiating *D. virgifera* field populations with dynamics similar to those of naturally occurring populations.

Previous studies of the seasonal population dynamics of adult *D. virgifera* related patterns of adult emergence from the soil, oviposition, and population change to calendar date and heat units (Hein and Tollefson 1985, Hein et al. 1988). There have been no studies of adult *D. virgifera* field populations in which the processes of emergence from the soil, reproductive development, oviposition, and mortality were studied in relation to corn plant phenology. Our objectives were to measure beetle emergence from the soil, sex ratio, reproductive development, mortality, and oviposition in relation to time during the growing season and corn plant phenology. Because extreme annual variation in the climate of eastern South Dakota (particularly during winter) makes natural infestations of *D. virgifera* sporadic and unpredictable, we chose to conduct our studies in artificially infested fields.

MATERIALS AND METHODS

Field studies were conducted in eastern South Dakota during 1988 and 1989. Each year, a single 0.4 ha field on a research farm located adjacent to the USDA, ARS Northern Grain Insects Research Laboratory, Brookings, South Dakota, that had been planted to wheat the previous year (1988) or fallowed (1989) was infested with *D. virgifera* eggs obtained from a laboratory colony maintained by the methods of Jackson (1986). Corn ('Pioneer 3978') was planted and fields were infested with eggs on 12 May each year. The entire length of each row of corn in a field was infested with eggs at population densities of 2612 and 2275 eggs per m^2 in 1988 and 1989, respectively, using methods described by Sutter and Branson (1986). Corn was planted at densities of 5.22 and 4.77 plants per m^2 in 1988 and 1989, respectively.

To facilitate sampling each year, the field was partitioned into 12 rectangular sub-plots of equal size. Two emergence traps similar to those described by Fisher (1984) were positioned at random locations within each sub-plot (total 24 traps). The emergence traps used were 0.91 m wide in 1988 and 1.0 m wide in 1989 (one row width) and were 0.61 m in length (three times the plant spacing within rows). Each trap was centered over three plants within a row. Emerged beetles were collected from traps three times weekly on alternate days. The number and sex of beetles in each collection were recorded.

The population density of adult beetles in the field was determined three times each week by counting all beetles on an entire corn plant and the soil surface and weeds surrounding the plant. Beetles were counted on each of four plants selected in a haphazard fashion from within each sub-plot (total 48 plants). Hanway's (1966) 0–10 numeric rating system was used to estimate the growth stage of each sampled corn plant. We combined plant phenology data into three groups. We considered corn plants in the field to be in the flowering stage from the date at which 10% of plants had advanced at least to stage 4 (tassel visible) to the date at which 90% of plants had advanced beyond stage 5.5 (pollination complete, silks beginning to turn brown), plants to be in the grain filling stage from the date at which more than 90% of plants had progressed beyond stage 5.5 to the date at which 90% of plants had

advanced beyond stage 8 (a few kernels with dents), and plants to be in the grain drying stage from the date at which more than 90% had advanced to stage 9 (all kernels with dents).

Soil samples were taken once each week beginning approximately one week after beetles began to emerge from the soil and continuing until the study was terminated. Each soil sample consisted of 12 subsamples (one from each sub-plot). A subsample consisted of 10 cylindrical cores taken with a 5.4 cm diameter bulb-setter to a depth of 15 cm. Each core was taken directly within a row at the base of a corn plant selected in a haphazard fashion from within the sub-plot. The 10 cores were sifted through a 1 cm screen, thoroughly mixed, and 0.47 l of soil was removed for processing. Eggs were washed from each subsample using the method of Shaw et al. (1976) and floatation in magnesium sulphate. All *D. virgifera* eggs were counted and identified to species by chorion sculpturing (Atyeo et al. 1964).

On the date the study was terminated each year, an estimate of the absolute population density of eggs was obtained using the frame method (Foster et al. 1979). The frame was one-half the row width long and one-half the plant spacing in rows wide. A sample consisted of 24 subsamples (two subsamples from each sub-plot); each subsample consisted of the soil dug to a depth of 20 cm within a single frame placed at the base of a plant chosen at random from within the sub-plot. Soil from each subsample was sifted and mixed as described above, and 0.47 l of soil was removed for processing. Eggs were washed from the soil, counted, and identified to species as described above.

Twice weekly, 50–75 female beetles were collected from within the field, taken to the laboratory, and dissected to determine their reproductive status. A 1 to 5 scale was used to rate ovarian stage of development (Cinereski and Chiang 1968). Beetles with ovaries rating 1–2 were considered reproductively immature, beetles rating 3–4 were reproductively mature, and beetles rating 5 were post-reproductive (Short and Hill 1972).

Survival rates of beetles were estimated once each week. One-hundred female and 50 male beetles were collected from within the field and placed in screen cages described by Elliott et al. (1990a). Each cage enclosed a single plant, and 5 male and 10 female beetles were placed in a cage. Growth stages of the 10 caged plants were representative of those in the field. Cages were left in place for 48 hours after which the number of surviving beetles of each sex was determined. A proportional daily survival rate was calculated from survival data for each 48 hour period. In making calculations we assumed that the survival rate of beetles was constant each day during the 48 hour period.

Total beetle-days per m^2 over the season were calculated for components of the adult population by fitting a cubic spline function to observed time series of population density data and calculating the area under the curve using numerical integration.

RESULTS

Adult Emergence. Dates of completion of 50% of adult emergence varied by about 10 days among years, from day 191 for males and day 196 for females in 1988, to day 199 for males and day 206 for females in 1989 (Fig. 1). In both years emergence was synchronized with the time period during which corn in the field was flowering. About 70% of males and females emerged while corn was flowering in 1988 and about 85% of males and 90% of females emerged during flowering in 1989. Shapes of cumulative emergence curves were similar among sexes (Fig. 1), but emergence of males began and was completed about 5 days earlier than emergence of females. Adult emergence extended over a longer time period in 1988 than in 1989.

Approximately 1.5 times as many beetles emerged in 1988 as in 1989 (Table 1). The difference in total emergence probably resulted from a combination of differ-
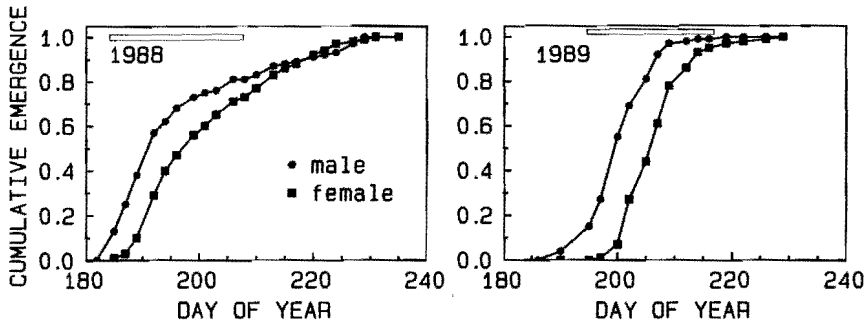
Figure 1. Cumulative emergence of adult male and female *D. v. virgifera* from the soil. Horizontal bars at the top of each figure represent the time period during which corn was flowering (>10% of plants flowering to > 90% post-flowering).

Table 1. —— Beetle-days accumulated per m^2 and number of beetles emerging per m^2 by various components of *D. v. virgifera* populations in corn fields in 1988 and 1989.

	Year	
	1988	1989
Beetle-days/m^2		
total (male + female)	765.8	697.0
female	455.4	390.7
pre-reproductive female	222.7	168.0
reproductive female	230.3	219.3
post-reproductive female	2.4	3.4
Beetles emerging/m^2		
total (male + female)	72.1	49.5
female	50.6	30.2

ences in initial egg densities (2612 eggs per m^2 in 1988 versus 2275 eggs per m^2 in 1989) and immature survival (2.8% in 1988 versus 2.2% in 1989).

More females than males emerged both years, 70% in 1988 and 61% in 1989. Due to the higher total emergence and larger proportion of females emerging in 1988, about 1.7 times as many female beetles emerged per m^2 in 1988 as in 1989.

Population Structure. The population density of adults in the field increased rapidly in both years and peaked about two weeks after emergence began (Fig. 2). Males were more abundant initially, reflecting their earlier emergence, while females became increasingly dominant as the season progressed. Populations of both males and females peaked while corn was flowering (Fig. 2).

The total number of beetle-days per m^2 accumulating during the season by various components of the adult population in 1988 and 1989 are listed in Table 1. Slightly more total beetle-days accumulated in 1988 (765.8 beetle-days/m^2) than in 1989 (697.0 beetle-days/m^2). This observation is consistent with the fact that beetle emergence was greater in 1988 than in 1989 (Table 1). However, the ratio of beetle-days per m^2 in 1988 to that in 1989 equals 0.91, and is considerably greater than the corresponding ratio of the numbers of beetles emerging per m^2 among the two years
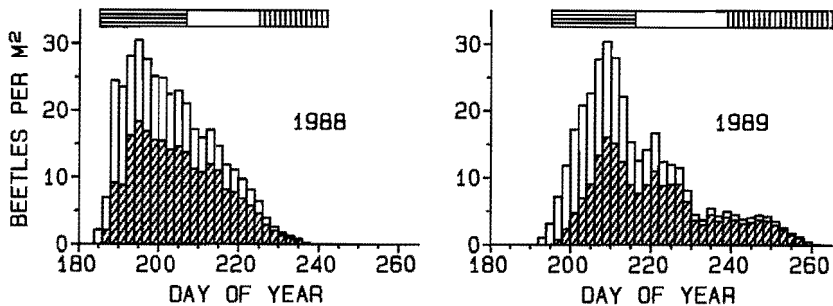
Figure 2.   Population density of adult *D. v. virgifera*. Cross-hatched vertical bars represent female beetle density and empty vertical bars are total beetle density. Horizontal bars at the top of each figure represent corn plant growth stage (horizontal striped bar, >10% of plants flowering to >90% of plants post-flowering; empty bar, >90% of plants post-flowering to > 90% of plants in grain drying stage; vertical striped bar, >90% of plants in grain drying stage.

(0.69), indicating that mortality, emigration, immigration, or a combination of these factors occurred at different rates in 1988 and 1989.

The proportion of females in the population, based on the ratio of female beetle-days to total beetle-days, was smaller in both years (59% in 1988 and 56% in 1989) than the proportion of females emerging in the field (70% in 1988 and 61% in 1989). Naranjo (1990a, 1990b) demonstrated that from 14 to 24% of pre-reproductive adult females migrate, and that the migration rate of young adult males is only about one-half that of females of similar age. The most plausible explanation for the discrepancy in sex ratios calculated from emergence and total seasonal occurrence is differential emigration of male and female beetles from the field. However, other explanations include differences in the sampling efficiency of plant counts for males and females, and sampling error in determining sex ratios based on numbers of emerging beetles and from beetles collected from plants.

Estimates of reproductive female beetle-days per m^2 were similar in both years (Table 1). In both years, reproductive females began to appear in the population approximately five days after the appearance of the first females in the field (Fig. 3). The proportion of reproductively mature females in the population increased steadily as the season progressed. In 1988 the population density of reproductive females peaked while corn was in the flowering stage, in 1989 the peak was less well defined, but appeared to occur during grain filling (Fig. 3). In 1988, 112.9 out of a total of 230.3 reproductive female beetle-days accumulated during flowering (49% of the total), while in 1989 only 49.9 out of a total of 219.3 reproductive female beetle-days accumulated during flowering (23% of the total). Post-reproductive females were not collected until late in the season each year, and did not constitute a significant proportion of the female population until the last few sampling dates each year (Fig. 3).

Oviposition. The first soil sample containing eggs each year was collected approximately four days after the appearance of reproductive females in the field. Egg densities plateaued by day 222 in 1988 and between days 220 and 230 in 1989. Thus, in both years there were approximately 25 days from the onset to the completion of oviposition.

Frame sampling yielded estimates of the mean number of eggs per m^2 of 1239 (SE = 219.8) and 590 (SE = 116.7) in 1988 and 1989, respectively. Based on a two sample t-test, the two means differed significantly ($t = 2.6$; $P = 0.006$). End-of-
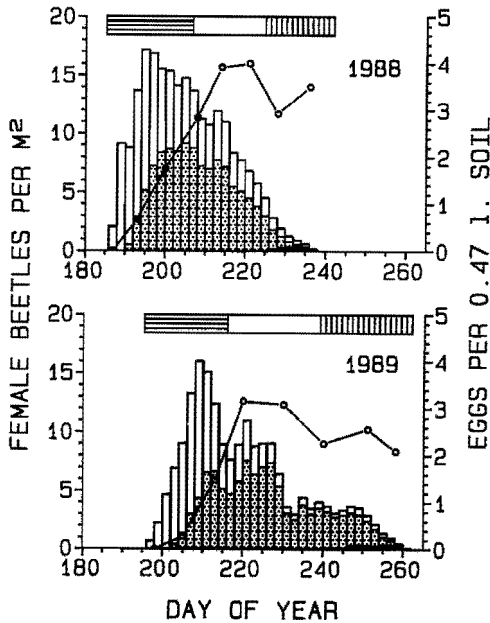
Figure 3.   Population density of adult female *D. v. virgifera*. Solid vertical bars represent the density of post-reproductive females, stippled bars represent the density of reproductive females and empty bars represent total female density. Horizontal bars at the top of each figure represent corn plant growth stage (horizontal striped bar, >10% flowering to >90% post-flowering; empty bar, >90% post-flowering to >90% in grain drying stage; vertical striped bar, >90% in grain drying stage.

season egg densities were approximately 1/2 in 1988 and 1/4 in 1989 of initial densities.

Adult Survival. A two sample z-test was used to compare proportional survival rates of males and females calculated from data pooled over all sampling dates within each year. Proportional survival did not differ significantly among the sexes in 1988 ($z = 1.1$; $P = 0.28$) or in 1989 ($z = 1.6$; $P = 0.11$). Therefore, we pooled survival data for the two sexes to assess seasonal survival patterns. Patterns in daily survival rates during the season differed somewhat among years (Fig. 4). However, a general trend in daily survival rates was apparent; survival rates were near 1 each year while corn was flowering, exhibited a gradual decline during grain-filling, and decreased at a more rapid rate during the grain drying stage (Fig. 4).

DISCUSSION

Immature development of *D. virgifera* is primarily dependent on temperature (Jackson and Elliott 1988), although development may be retarded slightly in extremely dense immature populations (Elliott et al. 1989), apparently as a result of competition for food. We found that when time was expressed on a calendar scale,
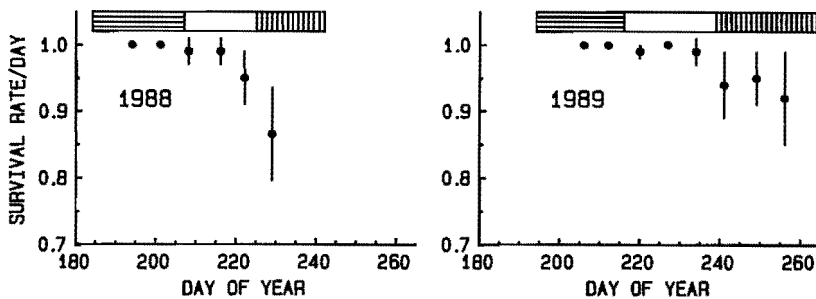
Figure 4. Survival rate per day of adult *D. v. virgifera*. Vertical bars on each data point are standard errors. Horizontal bars at the top of each figure represent corn plant growth stage (horizontal striped bar, >10% flowering to >90% post-flowering; empty bar, >90% post-flowering to >90% in grain drying stage; vertical striped bar, >90% in grain drying stage.

emergence of adult *D. virgifera* from the soil differed markedly among years in spite of identical planting and infestation dates each year. Calendar date has been proposed as a useful method for predicting the timing of beetle emergence in corn fields (Bergman and Turpin 1986), and in many years with similar temperatures during spring and summer, emergence may occur at approximately the same time. In years during which seasonal temperatures differ markedly from those typical for a region, as they did in eastern South Dakota in 1988, calendar date may provide poor prediction of the timing of beetle emergence.

Adult emergence and population development were synchronized with corn plant phenology, although the degree of synchrony differed somewhat among years. Ludwig and Hill (1975) found that beetles feed primarily on corn. Beetles tend to move to another corn field upon leaving a field and do not forage much in other plant communities (Hill and Mayo 1980). Lance et al. (1989) found that adults emigrate from cornfields at an increasing rate as corn plants progress beyond the flowering stage of development. Elliott et al. (1990a) found that survival and oviposition decrease as the corn upon which adults feed progresses beyond flowering to the grain filling stage; oviposition and survival proceed at reduced rates during grain filling, but decrease to very low levels during the grain drying stage.

In the present study, reproductive development and oviposition occurred primarily while corn in the field was flowering, and oviposition was essentially complete 25 days after females began to oviposit. Furthermore, oviposition levels were relatively low. Hein and Tollefson (1985) observed significant oviposition occurring over a longer period, about 45 days, in corn fields in Iowa. The relatively short ovipositional period and low egg densities observed in our fields may be explained as follows. Our study was conducted during two years in which very dry weather prevailed during summer. As a result, corn in our fields progressed rapidly through the grain filling and drying stages each year. Furthermore, beetle populations in most nearby corn fields were typically one-tenth or less as dense as those in our artificially infested fields (N.C.E. personal observation). As a result of the rapid maturation of corn in our fields, mortality and emigration of beetles from our fields would proceed rapidly as corn became less acceptable as food. However, because our study plots were essentially isolated from corn fields with large resident western corn rootworm populations, very few of these beetles would be replaced by immigrants from neighboring corn fields. The net result would be a relatively short ovipositional period that was well synchronized with corn flowering. In regions where beetle populations are generally high, oviposition probably occurs for a

longer time in most fields because of the interaction among beetle populations from different fields. Because of the differential attractiveness of fields to dispersing beetles, the duration of the ovipositional period in a field in such regions may depend on the phenology of the corn plants in the field relative to those in nearby fields (Hill and Mayo 1974, Godfrey and Turpin 1983).

When maintained in the laboratory on a near optimal diet, *D. virgifera* adults can achieve an average life span of 94.8 days (Branson and Johnson 1973). In our study beetles suffered rapidly increasing mortality at relatively young ages suggesting that the deteriorating quality of corn as food plays an important role in the population dynamics of *D. virgifera*.

The nearly two times greater end-of-season egg density in 1988 than in 1989 is inconsistent with the observation that similar numbers of reproductive female beetle-days accumulated each year. With similar seasonal densities of reproductive females we would expect similar oviposition levels. A possible explanation for the discrepancy in egg densities may be that the number of reproductive female beetle-days accumulating while corn in the field was flowering differed markedly among years. In 1988, 112.9 reproductive female beetle-days accumulated per m^2 while corn in the field was flowering, while in 1989 only 49.9 reproductive female beetle-days accumulated during flowering. Beetles of identical age fed flowering corn are much more fecund than beetles fed post-flowering corn, and the difference in fecundity increases as corn upon which they are fed becomes increasingly more mature (Elliott et al. 1990a). Dividing total end-of-season egg densities by the number of reproductive female beetle-days accumulated per m^2 during the flowering period yields an estimate of 11.0 eggs per reproductive female beetle-day in 1988, compared with an estimate of 11.8 in 1989; these estimates are very similar. The observation that approximately 3/4 of eggs had been laid each year by the time corn had completed flowering (Fig. 3) lends support to the contention that most oviposition in our fields occurred by beetles feeding on flowering corn early in their reproductive lifetimes. The results suggest that although emigration, mortality, or both factors occurred at a more rapid rate in 1988 than in 1989, perhaps partially due to the short duration of the grain filling stages that year, the number of reproductive females present while corn was flowering was the primary determinant of total oviposition in both fields. Temporal synchrony of adult populations with flowering corn may play a critical role in the population dynamics of *D. virgifera* through its influence on dispersal, mortality, and oviposition rates.

ACKNOWLEDGMENTS

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