



Modeling evolution of behavioral resistance by an insect to crop rotation

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Accepted: March 29, 2001

Key words: *Diabrotica virgifera virgifera* LeConte, crop rotation, western corn rootworm, population genetics

Abstract

Crop rotation has traditionally been a valuable method for managing pests, but now a serious insect pest of maize (*Diabrotica virgifera virgifera* LeConte [Coleoptera: Chrysomelidae]) has developed behavioral resistance to rotation. A simple model of adult behavior and population genetics can explain how this resistance may have developed. This general model indicates that evolution may be caused by selection on a single gene for adult movement and that behavioral resistance only develops at high levels of rotation (>80% of plant landscape). In less diverse landscapes, crop rotation selects for the expansion of host preferences (polyphagy) by adults. More diverse landscapes may delay the evolution of resistance to crop rotation depending on the fitness costs and the nature of the genetic system.

Introduction

The practice of rotating host and nonhost crops in alternate years is a traditional method of managing pest damage in agriculture (Metcalf & Flint, 1967). It should not be surprising that this rotation schedule places tremendous selection pressure on a pest species. Insects can evolve resistance to alternate year rotations in at least three ways. Development of immature stages can be delayed, such as in prolonged, multiple-year diapause (Levine et al., 1992; Krafur, 1995), larvae can physiologically adapt to the previous nonhost, alternate crop (Gould, 1984; Castillo-Chavez et al., 1988), or adult behavior may select for placement of the immatures where they can find an adequate host plant upon hatching. Crop rotation exploits an insect's preference for a given host and the inability of relatively immobile feeding stages to use the alternate crop, but as several studies have shown, host preference is not always correlated with host suitability (Jaenike, 1990; Tabashnik, 1986; Thompson, 1988; Via, 1990; Wasserman & Futuyma, 1981; Hawthorne, 1999). We developed a model of host preference in a

landscape dominated by alternate year crop rotation and related this model to the first reported case of insect behavioral resistance to crop rotation.

The adults of *D. virgifera virgifera* LeConte are present in maize fields from July through frost. From late July through September, egg-laying occurs primarily in maize (*Zea mays* L.) fields; few eggs are normally laid in other crops. The eggs of this univoltine insect overwinter in the soil and hatch beginning in late May and early June. The larvae can survive only on the roots of maize and a limited number of grasses (Levine & Oloumi-Sadeghi, 1991) making crop rotation to a nonhost crop in alternate years an effective pest management strategy.

In east-central Illinois and northwest Indiana, 98% or more of soybean fields are rotated to maize the following year (USDA-ERS, 1996); consequently, larvae emerging from eggs deposited in soybean fields will likely emerge in maize fields the following spring and survive. For many years, growers in the United States have controlled the beetle, *D. virgifera virgifera* with an alternate year rotation strategy of maize followed by soybean (*Glycine max* L.) or another nonhost crop.

This univoltine beetle, the western corn rootworm, is the most serious insect pest of maize grown after maize in the United States (Levine & Oloumi-Sadeghi, 1991) and it has now invaded southeastern Europe (Edwards et al., 1998). As recently as eight years ago, many experts believed that this insect was poorly adapted to crop rotation, because adults tended to remain within maize (Krysan, 1993). Since then, reports of serious larval injury to first-year maize in Illinois and Indiana have increased and growers who had successfully used crop rotation for control have suffered serious crop losses. Studies ruled out a prolonged egg diapause as the cause (Levine & Oloumi-Sadeghi, 1996). We now suspect that the maize-soybean rotation has selected for an insect strain that circumvents crop rotation by laying eggs outside of maize fields.

We hypothesize that the newly-observed tendency of adults to inhabit nonmaize areas is the behavioral change that allows the insect to overcome management by crop rotation. This perspective and our simple hypothetical genetic system are comparable to several natural systems. Once a landscape changes, selection for phenotypes that are apt to try new hosts or habitats may lead to change in the host preference of the insect population. Genetic variability was observed both in the oviposition behavior of *Drosophila mojavensis* (Lofdahl, 1986), as well as in a population of *Euphydryas editha* that involved both directed and nondiscriminating oviposition preference for host plants in a heterogeneous population of *Pedicularis semibarbata* (Ng, 1988). Although host preference by insects may involve more than one locus (Jaenike, 1986), it can be controlled by a single locus as in tephritid flies (Huettel & Bush, 1972; de Belle & Sokolowski, 1987).

Model and methods

We propose a simple population-genetics model of *D. virgifera virgifera* in a landscape of maize and nonmaize plants to explain how the resistance to crop rotation may have evolved. The model consists of a vegetative landscape of four plant patches, two of maize and two of nonmaize. Maize grown every year, continuous maize, is represented by M_c and maize that follows a nonmaize patch in a rotation, first-year maize, is represented by M_r . Soybean, S, precedes and follows maize in a rotation while E represents all other vegetation as a patch that is not maize, not rotated to maize and not an alternative host for *D. virgifera vir-*

gifera. Adults are able to disperse amongst all patches, which exist in a larger region consisting of the same patches.

We assume this is an autosomal, single-locus, 2–3 allele, diploid, genetic system. We define an X allele for no movement out of maize, a Y allele for the tendency to move to all patches, and a Z allele for the tendency to move only to the crop most commonly rotated with maize. In the following section we describe the structure of the model, our assumptions and sources of information, and our analytical approach.

Mating. For simplicity and because of a lack of information, we assume that all adults have an equal opportunity to mate. Mating in each patch is random and occurs before movement out of the natal patch. Quiring & Timmins (1990) observed that, under typical field conditions, up to 70% of *D. virgifera virgifera* females were mated during the 24 h following emergence. Females rarely mate more than once (Branson et al., 1977; Hill, 1975).

Movement. Our unpublished data suggest that adult feeding in nonmaize is associated with oviposition outside of maize so, although the model defines the different phenotypes by movement with respect to maize and nonmaize patches, the terminology for adult feeding provides a convenient way to describe the different phenotypes. The terms monophagy (X-phenotype) and polyphagy (Y-phenotype) are useful to understand the locations where adult insects are present. Normal, monophagous, individuals move from the natal maize patch and distribute themselves (and their eggs) uniformly across the two patches of maize. Each patch of maize receives the proportion of total oviposition equal to the area of that patch divided by the total area of maize (Table 1). Polyphagous individuals move into all patches according to their proportional representation in the region. The soybean specialists (Z-phenotype) move only to the soybean patch, and thus, would never find a habitat for egg deposition when the landscape consists only of maize patches. If allele expression is co-dominant or additive the heterozygotes are oligophagous (XZ) with movement to two plant species (maize and soybean) or polyphagous (XY and YZ) and have behaviors of both homozygous phenotypes.

Most movement is short range (97% of flights last less than seven min) or field to field (Coats et al., 1986). In 1978–1979 over a 3.2 km² area, Godfrey & Turpin (1983) observed higher numbers of beetles

Table 1. Parameter values for the six genotypes where the proportion of the landscape in continuous maize, rotated maize, soybean, and extra nonmaize are M_c , M_r , S , and E , respectively, $M_c + M_r + S + E = 1$, and $M_r = S$

Genotype	Allele expression	F , relative fecundity	P , probability of moving to M_c	P , probability of moving to S
XX		1	$M_c/(M_c + M_r)$	0
YY		$1 - (S + E)$	M_c	S
ZZ		0.03	0	1
XY	X dominant	1	$M_c/(M_c + M_r)$	0
	Y dominant	$1 - (S + E)$	M_c	S
	additive	$1 - 0.5(S + E)$	$0.5M_c/(M_c + M_r) + 0.5M_c$	$0.5S$
XZ	X dominant	1	$M_c/(M_c + M_r)$	0
	Z dominant	0.03	0	1
	additive	0.5	$0.5M_c/(M_c + M_r)$	0.5
YZ	Y dominant	$1 - (S + E)$	M_c	S
	Z dominant	0.03	0	1
	additive	$0.5 - 0.5(S + E)$	$0.5M_c$	$0.5 + 0.5S$

in continuous maize during the first four weeks after emergence but equal numbers during the subsequent weeks in rotated and continuous maize fields. They found no significant difference in density of offspring in subsequent years between the two kinds of maize fields indicating that our representation of the normal monophagous phenotypes is probably correct.

Fitness, fecundity, and survival. The fitness of a phenotype is the product of the adult fecundity and the proportion of their offspring hatching in maize. No genetic variation for partial survival on nonmaize roots is included in the model. All larvae hatching in nonmaize patches die. We ignore gender and set the maximum fecundity per individual to 1 for monophagous adults which feed and oviposit only in maize (Table 1). The fecundity of other phenotypes is measured relative to the monophagous phenotype. With a fecundity of 1, the fitness of the monophagous phenotype equals the proportion of maize that is continuous.

For polyphagous adults, unpublished data indicate that females feeding on nonmaize have reduced vigor causing them to have shorter lives and lay fewer eggs. Therefore, we reduce the fecundity of polyphagous individuals by the proportion of nonmaize in the landscape. The offspring are distributed across all four patches in proportion to the area of each patch and only the offspring hatching in maize survive. This is a simplistic approach to including a fitness cost for the change in behavior, but other approaches are difficult to justify without more information.

For soybean specialist adults we assume that feeding occurs for one day in maize while the teneral females are mating and waiting to fly. Given a 33-day lifespan and oviposition period (Hein & Tollefson, 1985), we further assume that one day of feeding provides enough (and the only) nutrition to support a relative fecundity of 0.03 (1/33) per individual in the model.

Most continuous maize (circa 90%) and some first-year maize (circa 10%) is treated with a chemical insecticide (Pike et al., 1991) applied to the soil at planting time. Insecticide use seems to protect yield but does not appear to suppress populations of *D. virgifera virgifera* (Gray et al., 1992). Therefore, we do not include any other density-independent (or density-dependent) mortality factors in the model.

Model equations. The number of eggs $L_{i,j}(t + 1)$ of genotype i in patch j for year $t + 1$ is

$$L_{i,j}(t + 1) = \sum_{k=1}^b P_{k,j} F_k \left[N_{k,c}(t) \sum_{m=1}^b W_{m,k,i} Q_{m,c}(t) + N_{k,r}(t) \sum_{m=1}^b W_{m,k,i} Q_{m,r}(t) \right], \quad (1)$$

where $b = 3$ for 2-allele and $b = 6$ for 3-allele systems. P is the probability of genotype k moving to patch j , and F is the relative fecundity of adults in genotype k (Table 1). Mated beetles produce offspring in an expected genotypic frequency dependent

upon the frequencies of the adult genotypes emerging each year in a patch. Therefore, Q is the frequency of genotype m in patch c or r (continuous or rotated maize, respectively) which is mated to N , the number of adults, of genotype k . Each weight, W , equals the Mendelian proportion of all offspring from the mating of genotypes m and k that result in genotype i .

The number of adult offspring emerging the next year is

$$N_{i,c}(t) = V_c L_{i,c}(t) \text{ in continuous maize,}$$

$$N_{i,r}(t) = V_r L_{i,s}(t) \text{ in maize rotated from soybean,}$$

and

$$N_{i,s}(t) = N_{i,e}(t) = 0 \text{ in other parts of the landscape.}$$

V_n is the survival of offspring hatching in patch n , where $V_c = V_r = 1$ and $V_s = V_e = 0$. All larvae hatching in nonmaize patches die and all those hatching in maize survive.

Initial conditions and analysis. Initial allele frequencies for Y and Z are 10^{-4} . Beetles initially emerge from continuous maize at Hardy–Weinberg equilibrium and respond to the landscape according to their phenotypic behavior. All simulations have $E = 0.05$ with $S > 0.20$ unless noted otherwise. Mutations do not occur during the 200-year simulations.

Our primary interest is to identify the cropping practices that support evolution, a shift in the frequency of alleles and phenotypes in the population. To accomplish this, the model was run using different levels of rotation to identify the threshold at which allele frequencies do not change. The total level of rotation $R = S + M_r$. We then report a level of rotation above and below that threshold at which rapid changes in allele frequency occur. Three combinations of alleles are considered, X - Y , X - Z , and the 3-allele system X , Y , and Z . We also explore how different values of E , the patch that is not maize and not rotated to maize, influence the shift in allele frequencies. Finally, we compare the simulated times for resistance to develop to the real world situation where damage to first year corn was initially observed. We do not consider population densities in this study.

Results and discussion

For the X - Y system, the Y -allele frequency only increases at very high levels of rotation. Significant increases in the Y -allele frequency do not occur by

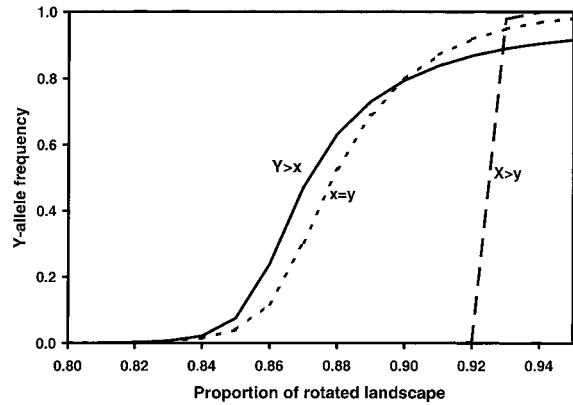


Figure 1. The Y -allele frequency in year 25 as a function of the level of rotation with X dominant ($X > y$), X and Y additive ($x = y$), or Y dominant ($Y > x$).

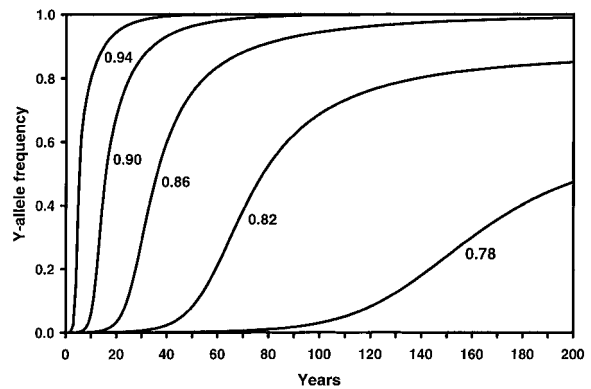


Figure 2. The Y -allele frequencies produced by the additive X - Y system over time for five levels of rotation.

year 25 unless $R > 0.84$ (Figure 1). When X or Y is dominant, $R = 0.77$ is the threshold that determines whether Y disappears or eventually becomes fixed at 1. For the additive scenario, where the XY -phenotype is expressed, the Y allele disappears below $R = 0.726$ and it becomes fixed above $R = 0.844$. Between these values of R , stable polymorphisms exist with the most prevalent genotype switching from XX to XY to YY as R increases. Figure 2 shows how the Y -allele frequency increases over time for the additive X - Y system. The greater the value of R , the faster the Y -allele frequency increases.

In the X - Z system with $R \leq 0.93$, the frequency of Z does not increase when Z is recessive and disappears when Z is dominant. Only the additive case permits the Z -allele frequency to increase in the population. When Z and X are additive, Z disappears for $R < 0.79$. For $R > 0.79$, stable polymorphisms occur, and the Z -allele frequency increases at a faster rate as R in-

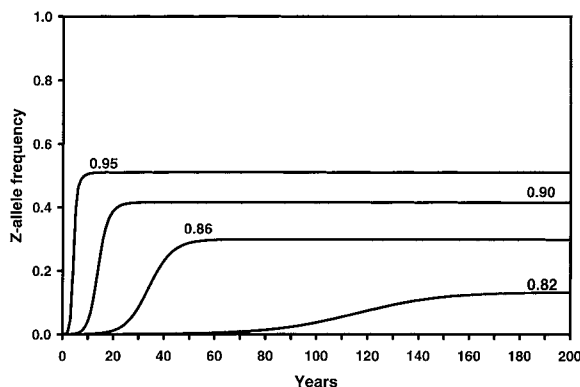


Figure 3. The Z-allele frequencies produced by the additive X - Z system over time for four levels of rotation.

creases (Figure 3). The maximum Z-allele frequency is 53% when there is no continuous maize, $R = 0.95$. As R increases, the fitness of XX and XZ genotypes declines, while the fitness of ZZ does not change. At $R = 0.86$, the Z-allele frequency stabilizes at 30% after 60 years and the normal monophagous phenotype (XX) is the most prevalent. At $R = 0.90$, the Z-allele frequency stabilizes at 42% after 25 years and the intermediate oligophagous phenotype (XZ) is the most prevalent.

Given that Z increases only when X and Z are additive, we evaluated only three scenarios for the 3-allele system. Alleles X and Z are additive with Y recessive, Y additive with the other two, or Y dominant. When Y is recessive to both X and Z, the results are the same as those described above for the additive X-Z system. When all are additive, Z disappears from the system, and the later simulated years mimic the results of the 2-allele, additive X-Y system described above, indicating that Y is superior to Z. When Y is dominant to the other alleles and $R \geq 0.80$, the Y-allele frequency is greater than 65% and the polyphagous phenotypes are most prevalent. As R increases, the final simulated frequencies of X and Z both decline to just over 1%. For $R < 0.75$, both Y and Z disappear.

It is reasonable to assume that landscape diversity increases with E , the area of nonmaize that is not rotated. The diversity of the landscape does not influence the X-Z system (with M_c/R constant), but it has a significant affect on the evolution of polyphagy in the X-Y system. The Y-allele frequency is higher in year 25 at lower values of either E or M_c (continuous maize) (Figure 4). For example, with $M_c = 0.05$ and Y dominant, the allele frequency is higher with $E = 0.05$ (dashed line, Figure 4) than with $E = 0.20$

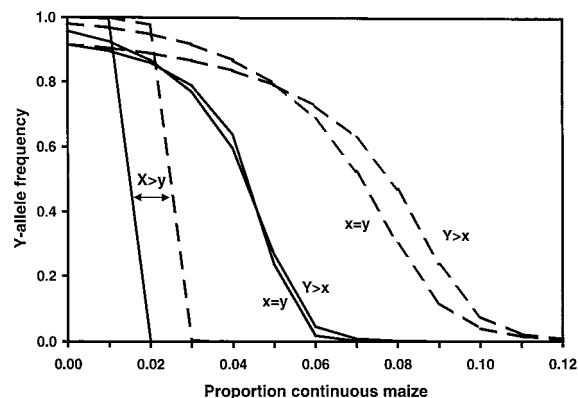


Figure 4. The Y-allele frequency in year 25 as a function of the proportion of continuous maize in the system with X dominant ($X > y$), X and Y additive ($x = y$), or Y dominant ($Y > x$) when extra nonmaize area $E = 0.05$ (dashed lines) or 0.20 (solid lines).

(solid line). At higher values of E , the fecundity of the polyphagous phenotypes decreases. Damage is assumed to be detectable in first year corn when the resistance allele frequency reaches 3%. With $E = 0.20$ and $M_c = 0.05$, the Y-allele frequency reaches 3% after 18 and 17 years for the Y dominant and additive scenarios, respectively, but it never reaches 3% when Y is recessive. These periods are much longer than those produced with $E = 0.05$. For the Y dominant, additive, and recessive scenarios, the Y-allele frequency reaches 3% after 8, 9, and 71 years, respectively, when $R = 0.90$, $M_c = 0.05$, and $E = 0.05$.

As the level of rotation increases and the evolution of behavioral resistance to crop rotation occurs, the winners in these simulations are often polyphagous adults. These results match our field observations that *D. virgifera virgifera* adults move into a variety of crops (not just soybean) in the areas where resistance to maize-soybean rotation has been reported. This may mean that the new strains behave most like our YY or XY genotypes. The oligophagous XZ -phenotypes may be prevalent in reality, but our field observations and the model results for the 3-allele system suggest the superiority of the polyphagous insects to the oligophagous or soybean specialist phenotypes. We have no reason to expect a Z-allele exists in the real population.

Resistance to crop rotation probably started in Ford County, Illinois, during the 1980's (Levine & Oloumi-Sadeghi, 1996; Onstad et al., 1999). How does the landscape in this region compare to those represented in our model? In 1997, both Ford County and the adjacent Champaign County had $R = 0.96$, $M_c = 0.02$,

and $E = 0.02$ (Kepley & Kestle, 1998). Since the late 1960s the value of M_c has varied from 0.02–0.09 in this area. Thus according to our model, the landscapes could have promoted the development of resistance. Even the X -dominant scenario in the X - Y system would have developed resistance with $E < 0.05$ and M_c approximately 0.05 or less.

Diabrotica virgifera virgifera invaded east central Illinois between 1968 and 1970 (Metcalf, 1983), about 16 years before the first observation of resistance to crop rotation (Levine & Oloumi-Sadeghi, 1996; Onstad et al., 1999). Which combination of resistance allele and inheritance or expression allowed detection (3% allele frequency) in less than 16 years? With $R = 0.90$, the additive X - Z system allowed the Z -allele frequency to reach 3% by year 10, whereas the Y -allele frequency reached 3% after eight and nine years for the Y -dominant and additive X - Y systems, respectively. All three genetic systems permit realistic rates of resistance development.

This model can be generalized to consider other situations of potential evolution of an insect in a plant community. The model represents a scenario in which the mobile adults and immobile larvae occur sequentially in time and do not perceive or require the same resource. The resources are different because of location (roots vs. canopy), phenological changes in the same plant, or other factors. Biennial plant populations may provide this type of alternating environment. In our model, adult preference for habitat influences fertility because of the nutritional quality of habitats. A modified version could either consider this to be a general fitness cost as a result of searching or could omit this fecundity-effect since many insect species do not require much, if any, nourishment as adults. The latter change would likely promote the development of resistance compared to scenarios we have modeled. Another assumption in our model is that random mating only occurs within a patch/habitat and not at a landscape or regional level. To study other insects, this assumption may need to be relaxed allowing some or all mating outside the natal patch.

Acknowledgements

We thank David Andow, David Hawthorne, and Anthony Ives for reading an early draft. This work was supported by the Illinois Council for Food and Agricultural Research SRI-IT.

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