The Effects of Host-Plant Genotype on Herbivore Population Dynamics

Nora Underwood; Mark D. Rausher

Ecology, Vol. 81, No. 6. (Jun., 2000), pp. 1565-1576.

Stable URL:
http://links.jstor.org/sici?sici=0012-9658%28200006%2981%3A6%3C1565%3ATEOHGO%3E2.0.CO%3B2-U

Ecology is currently published by The Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/esa.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org
Tue Apr 10 14:18:43 2007

Ecology, 81(6), 2000, pp. 1565–1576
© 2000 by the Ecological Society of America

THE EFFECTS OF HOST-PLANT GENOTYPE ON HERBIVORE POPULATION DYNAMICS

NORA UNDERWOOD[1] AND MARK D. RAUSHER

Department of Zoology, Duke University, Durham, North Carolina 27708-0325 USA

Abstract. To determine whether plant genotype can affect long-term herbivore population dynamics, we used a density manipulation experiment to compare the dynamics of Mexican bean beetle populations living on four genotypes of soybeans. Five densities of beetle populations were created on each plant genotype. Each combination of density and genotype was replicated four times, yielding 80 experimental beetle populations. Populations were initiated by releasing adult beetles into 2.25 m^2 cages filled with soybeans and located in a small soybean field. Beetle populations were censused weekly for one generation. Recruitment curves for beetle populations on each soybean genotype were plotted by fitting a Ricker model to the data using likelihood methods. The recruitment curves for all genotypes were significantly different from the curves for all other genotypes. The equilibrium beetle density predicted from the curves varied among genotypes by nearly twofold, and the predicted dynamics were fluctuating for all genotypes, with the period of fluctuations differing among genotypes. Performance of beetles also differed among genotypes, suggesting that these genotypes vary in some aspect of their quality as hosts for the beetles. These results indicate that differences in quality among genotypes have the potential to affect long-term herbivore dynamics.

Key words: Epilachna varivestis; Glycine max; *Mexican bean beetle; plant–insect interactions; population dynamics; recruitment curve; soybean.*

INTRODUCTION

Population ecologists have long been concerned with understanding the factors that govern population regulation, cyclic fluctuations, and outbreaks in herbivorous insect populations (e.g., Andrewartha and Birch 1954, Hairston et al. 1960, Rhoades 1983, Hassell 1985, Cappuccino and Price 1997). It is still not clear, however, what factors are most important for shaping these long-term patterns in insect population dynamics. Although many studies have focused on predators or parasites (top-down factors) as likely determinants of herbivore population dynamics, it is becoming clear that the host plant (a bottom-up factor) may also have important effects on herbivore populations (Hunter and Price 1992). Plant characters such as architecture, trichome density, leaf toughness, and nutrient and secondary chemical content, have been shown to affect insect feeding preference, performance characters such as growth, survival, and fecundity (e.g., Levin 1973, Rausher 1981, Rossiter et al. 1988, Zangerl 1990), and vulnerability to predators and parasites (e.g., Fritz 1995). These results indicate that plant traits can strongly affect not only the success of individual insects, but also characters that may influence population growth rates, and thus long-term population dynamics.

A number of factors can influence the overall quality of a plant as a host for insects, and have been cited as possible causes of variation in herbivore population dynamics (e.g., Haukioja 1980, White 1984, Brodbeck and Strong 1987, Myers 1988, Edelstein-Keshet and Rausher 1989). Plant quality is defined here by the performance of herbivores on the plant, with herbivores having higher fitness on higher quality plants. Overall plant quality for a particular herbivore is likely to be affected by many specific plant-quality characters, such as alkaloid content or trichome density. It has been suggested that stress imposed by the abiotic environment can change plant quality (White 1984, Louda and Collinge 1992), and perhaps lead to outbreaks of herbivores such as forest insects and mites (English-Loeb 1990, Reeve et al. 1995). Herbivore and pathogen damage can also affect plant quality by provoking induced resistance or susceptibility in the plant (Karban and Myers 1989), and it has been suggested that herbivore-induced changes in plant resistance might drive fluctuations in insect populations (Haukioja 1980, Rhoades 1985, Edelstein-Keshet and Rausher 1989). Finally, it is well known from work in both agricultural (see Gould 1983 for review) and natural systems (Maddox and Root 1987, McCrea and Abrahamson 1987, Karban 1992, Hwang and Lindroth 1997) that plant quality can vary among host-plant species and genotypes. Differences among genotypes are of particular interest for understanding plant–insect interactions because they raise the possibility of linking population dynamics and evolution in these systems. If genetic differences among plants give rise to different dynamics in the

---

Manuscript received 14 September 1998; revised 3 May 1999; accepted 4 May 1999.

[1] Current address: Center for Population Biology, University of California, Davis, California 95616 USA.

populations of insects that feed on them, then evolutionary changes in plant characters affecting herbivores (such as resistance characters) might lead to changes in long-term herbivore dynamics (Rhoades 1983).

There is a great deal of verbal and mathematical theory addressing how host plants might influence the long-term population dynamics of herbivores (e.g., White 1984, Rhoades 1985, Edelstein-Keshet and Rausher 1989, Hunter and Price 1992, Morris and Dwyer 1997). There is as yet, however, little direct evidence that plant characters, or differences in characters among genotypes, can affect long-term herbivore dynamics (but see Karban 1986, English-Loeb 1990). For logistical reasons, the large majority of experiments document host-plant effects within a single herbivore lifetime, or over only a few generations (e.g., Webb and Moran 1978, Reeve et al. 1995, Riggin-Bucci and Gould 1997). While results of these studies generally support the idea that the host plant can affect short-term dynamics (e.g., population growth rate), they do not provide information about the aspects of long-term dynamics that have inspired theoretical studies (e.g., population fluctuations). More direct evidence comes from studies that correlate plant traits or amounts of damage with herbivore dynamics in long-term census data (e.g., Haukioja 1980, Myers 1988), or compare the behavior of perturbed and unperturbed populations (e.g., Myers 1990). However, the ideal type of data would come from experimental manipulation of aspects of the plant population, followed by direct observation of herbivore populations over a large number of generations. Unfortunately, this type of experiment is prohibitively time consuming in most cases. Density-manipulation experiments are an alternative method allowing estimation of aspects of the long-term dynamics of a population from data gathered over the short term (Harrison and Cappuccino 1996, Belovsky and Joern 1997).

Here we use a density-manipulation experiment to examine whether the long-term dynamics of herbivore populations can differ among genotypes of host plant, using soybeans (*Glycine max,* Fabaceae) and Mexican bean beetles (*Epilachna varivestis,* Coccinellidae). The aim of this study is not to elucidate the exact quantitative dynamics of this plant–herbivore system, but to determine whether it is possible, in any system, for plant genotype to qualitatively influence long-term herbivore population dynamics. Although this study does not reveal the specific plant-quality traits that are responsible for differences among genotypes, our results show that beetle performance differs among genotypes of soybeans, suggesting that genotypes differ in their quality as hosts. Finally, we briefly consider the implications of our results for understanding interactions between herbivore population dynamics and the evolution of plant resistance.

Methods

System

Soybeans are grown extensively in North Carolina, where this research was conducted, from early May until early October. Genotypes of soybeans are known to vary in their constitutive resistance to disease, fungi, nematodes, and insect herbivores. The strength and form of induced responses to Mexican bean beetle damage also varies among genotypes, and these induced responses affect beetle feeding preference, mortality, and growth in the lab (Kogan and Fischer 1991, Underwood 1997). Soybean genotypes, therefore, vary in two plant characters—constitutive and induced resistance—that affect herbivore performance, and thus might be expected to affect herbivore dynamics in the field. Genotype differences in induced resistance are particularly interesting because many authors have suggested that induced resistance might be capable of regulating herbivore populations, and could drive fluctuations in population size (Haukioja 1980, Rhoades 1985, Edelstein-Keshet and Rausher 1989). Soybean seed for this experiment was supplied by North Carolina State University, Raleigh, North Carolina, USA, and the National Soybean Germplasm Collection, Urbana, Illinois, USA.

Mexican bean beetles are specialists on legumes and economic pests of soybeans in the midwestern United States. In North Carolina, they are normally found at low densities in soybean fields, but their abundance fluctuates, occasionally resulting in economically important damage. Densities in soybean fields in North Carolina range from ~32 beetles/m^2 to only one beetle in 13 m^2, averaging ~1.5 beetles/m^2 (Deitz et al. 1976). Both adult and larval beetles feed on the leaves of the plant, and eggs are laid on the undersides of the leaves. Adults overwinter under leaf litter. In North Carolina, Mexican bean beetles can complete three generations each year. Beetles for this experiment were obtained from a New Jersey Department of Agriculture laboratory colony (West Trenton, New Jersey, USA).

Experimental approach

To determine whether soybean genotype (cultivar) can affect Mexican bean beetle population dynamics, we compared the dynamics of caged beetle populations in the field on four genotypes of soybeans. To improve the chance of detecting an effect of genotype on herbivore dynamics, we used genotypes that varied in their levels of induced resistance, a character that may be likely to influence dynamics. It is important to emphasize, however, that these genotypes also varied in other characters that might affect herbivore dynamics (e.g., rate of maturation). Therefore, this experiment could detect an overall effect of plant genotype on herbivore dynamics, but could not unambiguously isolate the effect of any particular quality character (such as induced resistance). Because it has been shown that genetic

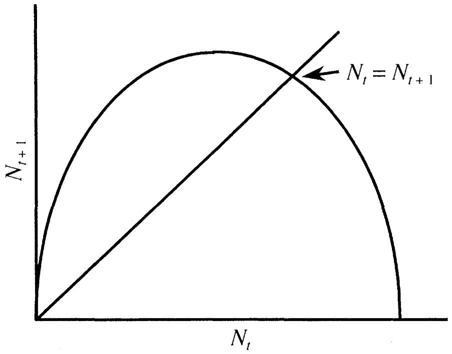

FIG. 1. A hypothetical recruitment curve. N_t indicates the number of individuals in the population at time t, N_{t+1} indicates the number of individuals in the population in the next generation. The expected equilibrium population size is found where $N_t = N_{t+1}$.

variation among host plants can affect the impact of predators on herbivores (Fritz 1995), we allowed predators access to experimental beetle populations. This means that both direct and indirect effects of the host plant are included in our estimates of the effect of soybean genotype on beetle population dynamics.

Rather than following beetle populations over many generations, we characterized beetle dynamics by estimating recruitment curves for beetle populations on each genotype of soybeans. Belovsky and Joern (1997), and production functions used in fisheries management (Roughgarden 1998) are examples of related uses of recruitment curves. We did this by creating five initial densities of beetle populations on each of the four genotypes of soybeans in the field, following each of these populations for one generation, and then using these data to estimate a recruitment curve for beetle populations on each host plant genotype.

The recruitment curve (Fig. 1) allows the extrapolation of two important features of long-term dynamics—the pattern of dynamics over time and the equilibrium population size—from the size of the population in two consecutive generations. The curve allows prediction of the pattern of dynamics because for any given population size in one generation it gives the population size in the next generation. The equilibrium population size can be found where the number in one generation (N_t) equals the number in the next generation (N_{t+1}). The stability of this equilibrium can be determined from the slope of the recruitment curve at the equilibrium point (Edelstein-Keshet 1988). Specifically, if the absolute value of the slope of the curve at equilibrium is greater than one, the equilibrium will be unstable, and small deviations from the equilibrium will tend to grow over time.

Using recruitment curves to predict long-term effects on population dynamics, rather than directly observing dynamics over time, requires the assumption that the shape of the recruitment curve will not change over the time of the prediction, and that the curve reflects all important influences on dynamics. The shape of the curve might be expected to change over time due to changes in the environment or aging of the plant or herbivore; though, to our knowledge, no data are available on how these curves change over time in the field. Changes of this kind may not be very important in this system because field populations of Mexican bean beetles can encounter newly planted soybeans almost every generation, particularly in late-planted crops. The assumption that the curve estimated from one generation's data accurately represents the shape of the curve that would be observed over longer periods of time is thus more valid for this system than it might be in a system with many generations of herbivores for each generation of plants (such as forest lepidopterans). The recruitment curves estimated in this experiment did not, however, include the influence of any delayed density-dependent factors (such as maternal effects). Delayed density-dependent factors have been shown in other systems to have a potentially important influence on population dynamics (Prout and McChesney 1985, Turchin 1990, Rossiter 1991).

The aim of this experiment was to determine whether it is possible for differences in host plants among genotypes to influence long-term herbivore dynamics, under conditions incorporating as many aspects of the unmanipulated system as possible. It is important to emphasize, however, that this experiment is not meant to predict the exact dynamics of any particular population under natural conditions, but only to demonstrate the qualitative types of host-plant effects that are possible.

Experimental design

This experiment was carried out at the Duke University Zoology Department field station in Durham County, North Carolina. We used four genotypes of soybeans (Bragg, Centennial, Clark 63, and Williams 82) that differ in induced, but not constitutive, levels of resistance to Mexican bean beetles (USDA/ARS Germplasm Resources Information Network;[2] Underwood 1997). Five densities of beetle populations (2, 6, 10, 14, and 18 per cage) were created on each of the four soybean genotypes in four replicate spatial blocks, yielding a total of 80 experimental populations. Each of these populations was located in a 2.25 m^2 screen cage. Cages were grouped into four replicate blocks of 20 cages each. Each cage was 2 m tall and had a door opening to the outside of the block. The bottom sill of each door was ~0.5 m above the ground. Each block was surrounded by a 2-m-wide strip of soybean plants which served to attract beetle predators or parasites that might be attracted by the host plant. Generalist predators were in fact observed in the cages throughout the experiment. There is no natural population of Mexican bean beetles at this site, and the nearest agricul-

---

[2] URL: ⟨http://www.ars-grin.gov/npgs/⟩

tural fields that might have such populations are >10 km away.

Each cage was filled with 20 potted plants of one of four genotypes of soybeans. Soybeans were planted in 15 cm pots in a mixture of field soil and perlite (3 soil : 1 perlite with lime added to correct for slightly acid soil). Each plant had approximately five fully expanded trifoliate leaves at the beginning of the experiment. All soybeans were fertilized with Osmocote (The Scotts Company, Columbus, Ohio, USA) time release fertilizer when they had two fully expanded trifoliates. Soybeans were subject to natural damage by insects other than Mexican bean beetles (primarily grasshoppers and lepidopteran larvae) throughout the experiment.

Prior to the experiment, Mexican bean beetles were reared in the laboratory on snap bean plants to avoid physiological adaptation to any particular soybean genotype. We initiated beetle populations by releasing equal numbers of male and female adult beetles into the cages. Adult beetles were marked with one or two spots of enamel paint on their elytra identifying the cages in which they belonged. We allowed the adults to mate and lay eggs for 2 wk before removing them and opening the cages to the surrounding soybean field to allow predators access to the cages. Cage doors remained open until larvae began to pupate. Soybean plants surrounding the cages were examined periodically to determine if any larvae left the cages during this time. Each experimental population was censused weekly for one generation. The number of clutches of eggs, larvae in each instar, pupae, and new adults emerging in the next generation were recorded. Egg masses and new adults were individually marked, so counts of these stages were likely very accurate, while counts of larvae in each instar were more approximate.

Analysis

We used the data from the field experiment to estimate recruitment curves for beetle populations on each genotype. We fit both a Hassell ($N_{t+1} = N_t\lambda(1 + aN_t)^{-b}$) (Hassell 1975) and a Ricker ($N_{t+1} = N_t re^{-bN_t}$) (Edelstein-Keshet 1988) population model to the data set for each genotype using likelihood techniques (Edwards 1992). In these models, N represents beetle population size, λ and r represent per capita population growth rate, and b represents the form of density dependence in the system. A maximization routine, the Simplex algorithm (Press et al. 1986), was used to find parameters that maximize the log likelihood of the data given the model, assuming Poisson-distributed errors. Because the fit for the Hassell model was always inferior to the Ricker model, despite the fact that the Hassell model contains an additional parameter, the Ricker model was used for all subsequent analyses. An approximate measure of the lack of fit of the best-fit Ricker model to the data for each genotype was obtained using the procedure outlined by Draper and Smith (1966), which tests the ratio of the mean squared deviations to the mean square due to pure error against an F distribution. This method gives only an approximate test of lack of fit for these data because the Ricker model is nonlinear, and therefore the distribution of the ratio is not known. Nevertheless, ratios approximately ≤ 1 can be taken to indicate no lack of fit to the data.

We compared the fitted recruitment curve for each genotype to the curves for each of the other genotypes using likelihood ratio tests (Edwards 1992) with 2 df and Bonferroni correction for multiple comparisons. We also generated 95% confidence contours for the best-fit parameters for each genotype (Mallet and Barton 1989). The 95% contour contains all the combinations of the two parameters of the Ricker model that are not significantly different from the best-fit parameters. The highest and lowest values of each parameter on the contour then constitute the 95% CI for each parameter estimate.

To examine the predicted long-term beetle dynamics, we used computer simulation to iterate the best-fit Ricker models for each genotype over 50 beetle generations. We used integer numbers of beetles for these iterations. Results using continuous numbers are qualitatively similar. We determined the predicted equilibrium size of beetle populations on each genotype of soybeans (N^*) by setting $N_t = N_{t+1} = N^*$ and solving the best-fit Ricker equation for each genotype for N^*. The stability of these predicted equilibria was determined by differentiating the best-fit Ricker model evaluated at N^*. Estimates of the 95% CI around each predicted equilibrium were obtained by finding the highest and lowest equilibrium population sizes for combinations of parameters on the 95% confidence contour.

Although the focus of the experiment was to measure changes in beetle population density over a full generation, we also examined how host-plant genotype affected several rough measures of beetle performance. The measures of performance obtained from this experiment are only approximate, because it was logistically impossible to follow individual beetles from census to census, or to count the number of eggs in each egg mass. Data from weekly censuses allowed estimation of approximate growth rate (mean time from first observation of clutches to emergence of first adults in each cage), fecundity (mean number of egg masses laid per adult in each cage), and survival from each of the four larval instars to the next instar and pupal stage (total number of beetles in each instar over the entire experiment divided by total number of beetles in the previous instar). Measures of survival sometimes exceeded one, probably because later instars last longer and are easier to locate. This bias in estimating survival is not problematic because relative, rather than absolute, rates of survival are of interest, and there is no reason to suspect that any bias in survival estimates would differ among genotypes. Analysis of variance and multivariate analysis of variance were used to assess the effects of spatial block, initial beetle popula-

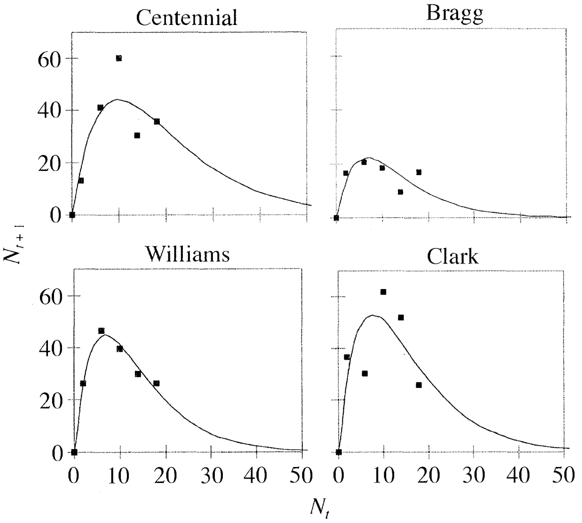

FIG. 2. Recruitment curves estimated in the field for populations of beetles on four genotypes of soybeans. N_t = number of adults in the first generation; N_{t+1} = number of adults in next generation. Points indicate data (N for each point = 4), and curves indicate the best-fit Ricker model for each genotype.

tion density, and host-plant genotype on each of the beetle performance characters (SAS 1989:GLM procedure). Data for survival and fecundity were square root transformed to normalize their distributions.

RESULTS

In all populations, adult beetles mated and laid eggs within the first week after they were released into the experimental cages. Instances of generalist predation on adult beetles (by spiders), and on larvae and pupae (by spiders, Reduviids and other Hemipteran larvae, Neuropteran, and predacious Coleopteran larvae) were observed before (some predators entered the cages before the experiment began), during, and after the cages were opened to the field. Very few Mexican bean beetle larvae were observed on the soybean plants surrounding the experimental cages, indicating that there was little to no migration of larvae out of cages. Because the experimental site has no resident population of Mexican bean beetles, immigration into the cages by adults or larvae was highly unlikely. Soybean plants flowered and set seed in all cages by the end of the experiment.

Effects of plant genotype on insect population dynamics

The observed and best-fit recruitment curves for beetle populations on each genotype of soybeans are shown in Fig. 2, and the parameters of the best-fit Ricker models are shown in Table 1. There was no evidence of lack of fit of the Ricker model to the data for any of the four genotypes (Bragg: $F_{17,15} = 0.89$, Centennial: $F_{17,15} = 1.02$, Clark: $F_{17,15} = 1.14$, Williams: $F_{17,15} = 0.89$; nominal P values all >0.5). More importantly, all ratios were very close to one, suggesting that the error around the fit curves was not greater than the estimate of pure error. Thus, it appears that the Ricker model is an appropriate description of the data from this experiment.

The shapes of the recruitment curves differed among soybean genotypes in both the height of the peak and steepness of the curve at the equilibrium. While statistical comparison of specific characteristics of the recruitment curve (such as height) is problematic, pairwise comparisons of all possible combinations of the four genotypes revealed that, in all cases, the parameters of the estimated Ricker curves differed significantly among soybean genotypes (likelihood ratio test, df = 1; $P < 0.001$ for all comparisons). The 95% confidence contours around the best-fit parameters for each genotype do not overlap (Fig. 3), reinforcing the conclusion that plant genotypes differed significantly in the estimated parameters of the Ricker model.

The equilibrium population values predicted from the fitted Ricker curves for the four genotypes ranged from 15 to 25 beetles/1.5 m^2, a difference of up to 40%. With one exception (a small overlap between Clark and Williams), 95% CI around the equilibria did not overlap among genotypes. All four equilibria were predicted to be unstable, indicating that in all cases the populations are expected to exhibit fluctuations around the equilib-

TABLE 1. Maximum likelihood estimates of the parameters (r and b) of the Ricker model, and results of stability analysis of the fitted Ricker curves for populations of beetles on four genotypes of soybeans.

Estimate	Bragg	Centennial	Clark	Williams
r (95% CL)	8.86 (7.02, 11.09)	11.95 (10.07, 14.14)	18.51 (15.92, 21.46)	17.43 (14.81, 20.43)
b (95% CL)	0.148 (0.127, 0.169)	0.100 (0.086, 0.114)	0.129 (0.116, 0.142)	0.144 (0.130, 0.158)
N^* (95% CL)	14.74 (14.2, 15.3)	24.80 (22.4, 27.2)	22.63 (21.4, 24.2)	19.85 (18.7, 21.2)
$\frac{d}{dN}(N_t re^{-bN_t})\|_N$	$\|1.17\|$	$\|1.47\|$	$\|1.87\|$	$\|1.84\|$
Projected dynamics	2-point cycles	4-point cycles	5-point cycles	5-point cycles

Note: Estimates of the parameters and equilibrium population size (N^*) are followed by their 95% confidence limits. Confidence limits for N^* were obtained from 95% confidence contours for the maximum likelihood estimates of the parameters (Fig. 3). The derivative of the function evaluated at the equilibrium population density gives the stability properties of the equilibrium. Values less than 1 indicate stable (nonfluctuating) dynamics. Values greater than 1 indicate unstable dynamics.

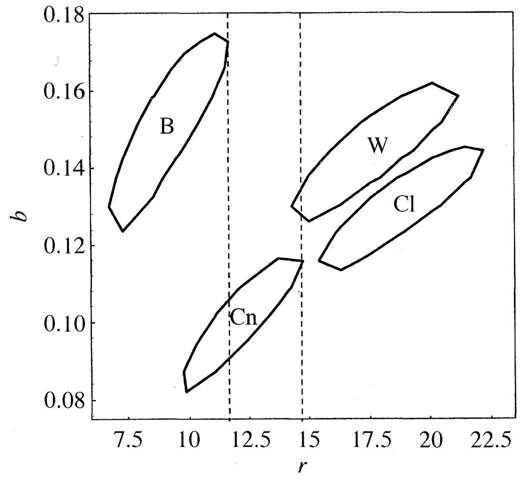

FIG. 3. Confidence contours (95%) for maximum likelihood estimates of parameters (r and b) of the Ricker model for beetle populations on four genotypes of soybeans (B = Bragg, W = Williams, Cl = Clark, Cn = Centennial). The contours contain all the combinations of parameters that are not significantly different from the maximum likelihood estimates according to a likelihood ratio test ($\alpha = 0.05$, 2 df). The lack of overlap among contours indicates that parameter estimates differ among genotypes. The vertical lines divide the parameter space into regions where the Ricker model exhibits 2-point cycles (below $r = 11.5$), 4-point cycles (between $r = 11.5$ and 14.6), and higher period fluctuations (above $r = 14.6$).

rium (Table 1). The differences in equilibrium population size thus reflect different average population sizes over time, rather than a single stable equilibrium size. Computer simulation of the fitted Ricker models verified that fluctuating dynamics were predicted for all genotypes, with the genotypes varying in both the magnitude and period of the projected fluctuations (Fig. 4). Beetle populations on Bragg were predicted to fluctuate with a 2-point cycle, Centennial with a 4-point cycle, and Clark and Williams with 5-point cycles. The confidence contour for Centennial straddles the line (Fig. 3) dividing the parameter space into regions characterized by 2- or 4-point cycles (Renshaw 1991). The best estimates of the parameters of the Ricker model for each genotype thus yield both qualitatively and quantitatively different dynamics.

The shape of the recruitment curves for all genotypes confirm that density dependence was acting on the beetle populations in this experiment. The per capita growth rate of beetle populations on all genotypes of soybeans was significantly affected by the initial density of the population (ANOVA, $F = 28.15_{1,72}$; $P < 0.0001$), with per capita growth rate declining with initial density (Fig. 5). The fact that the predicted population dynamics on different host-plant genotypes differ suggests that there should be some difference among genotypes in the impact of density dependence. Analysis of variance indicates that there was a nearly significant effect of host-plant genotype on per capita population growth rate ($F_{3,72} = 2.51$; $P = 0.065$). There was not, however, any significant interaction between initial population density and host plant genotype, suggesting that the genotypes do not differ in their magnitude of density dependence (the slope of the relationship), but that the relationships for different genotypes have significantly different y-intercepts.

Effects of density and plant genotype on insect performance

All measures of beetle performance were significantly affected by initial population density, indicating that these aspects of performance are density dependent. Survival from one instar to the next tended to decrease with initial population density, especially in the later instars (MANOVA, Wilk's lambda, $F = 15.88$; $P < 0.0002$) (Fig. 6). Fecundity (per capita egg mass production) (ANOVA, $F_{1,251} = 3.40$; $P = 0.01$), and development time from first eggs laid to first adults emerging (ANOVA, $F_{1,68} = 7.86$; $P = 0.007$), both increased with density (Fig. 7). Several aspects of beetle performance also varied among plant genotypes, including fecundity (Fig. 7) (ANOVA, $F_{3,230} = 2.98$; $P = 0.032$), development time (Fig. 7) (marginally significant, ANOVA, $F_{3,68} = 2.52$; $P = 0.065$), and survival (MANOVA, Wilk's lambda, $F = 1.85$; $P < 0.05$). The interaction of plant genotype with initial density was not significant for either fecundity or development time, but was marginally significant for survival (Fig. 6) (MANOVA, Wilk's lambda, $F = 1.79$; $P = 0.054$), indicating that the form of density dependence in survival varied among genotypes.

DISCUSSION

Plant genotype and herbivore dynamics

The results of this study provide experimental evidence that differences among host-plant genotypes

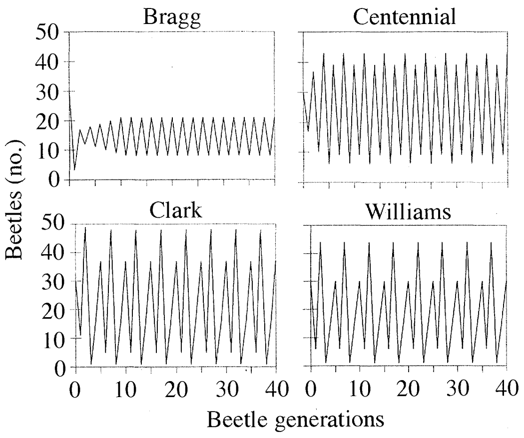

FIG. 4. Predicted long-term dynamics of beetle populations on four genotypes of soybeans. Predictions result from computer simulation of the Ricker models fitted to recruitment curves estimated in the field.

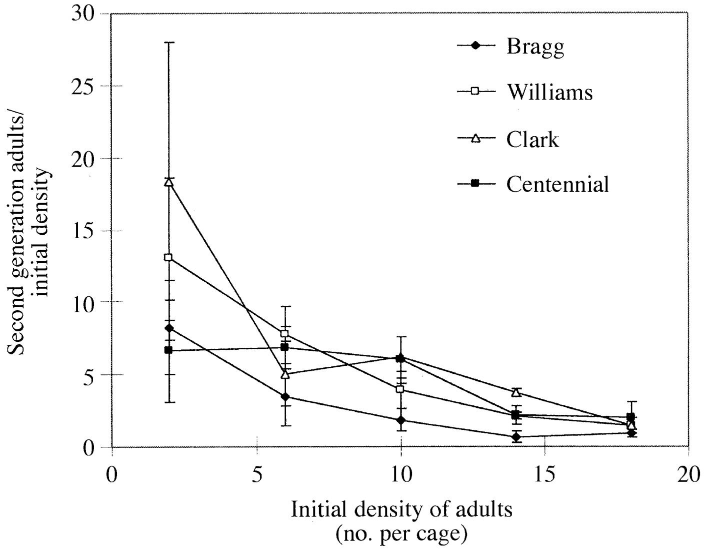

FIG. 5. The per capita growth rate of beetle populations declined with initial population density on all four host-plant genotypes. Error bars indicate ± 1 SE. $N = 4$ for each point.

have the capacity to contribute to differences in long-term insect–herbivore population dynamics. Beetle populations on different plant genotypes exhibited significantly different recruitment curves, and those curves predict substantial differences in equilibrium beetle population sizes, as well as differences in the magnitude and period of population fluctuations (Figs. 2 and 4, Table 1).

Variation among host genotypes in predicted beetle population dynamics arose from differences in the maximum likelihood estimates of both parameters of the Ricker model (r representing the intrinsic rate of in-

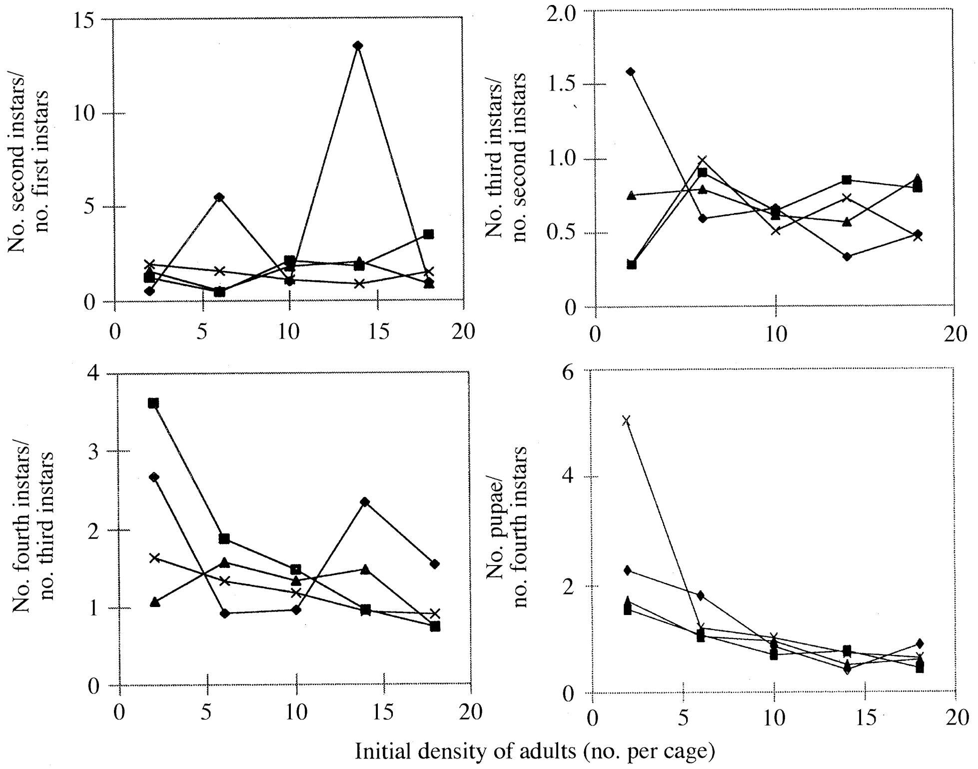

FIG. 6. Proportion of beetle larvae surviving from one instar to the next instar for populations on four genotypes of soybeans (◆ = Bragg, ■ = Centennial, ▲ = Clark, × = Williams). MANOVA indicates that survival decreased with initial density ($P < 0.0002$) and varied among genotypes ($P < 0.04$).

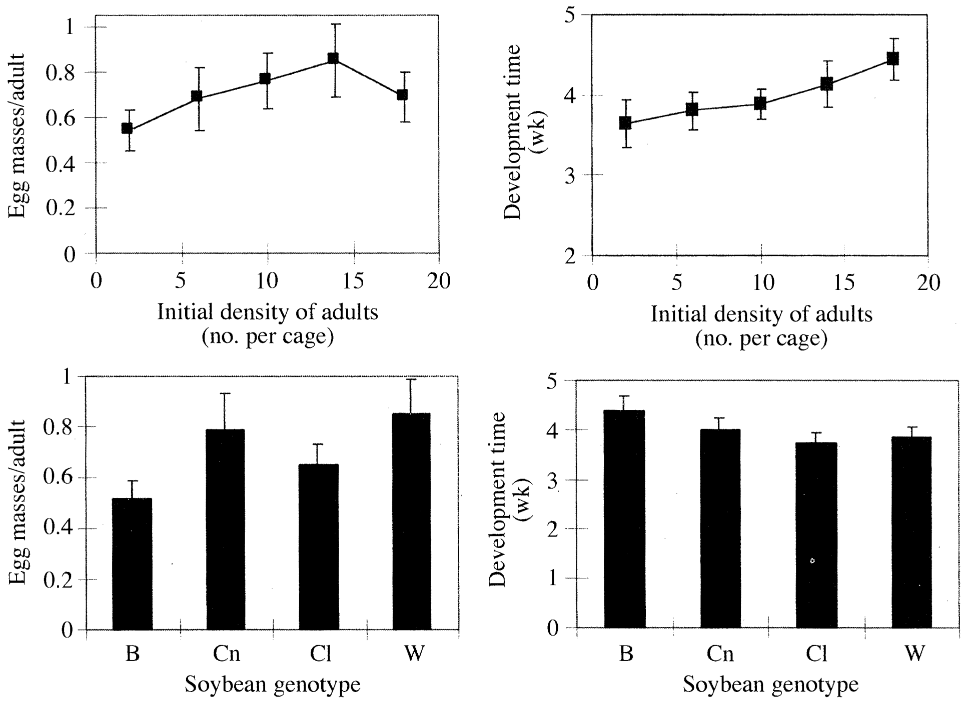

FIG. 7. Beetle fecundity (egg masses/adult) and development time (days from first egg masses to first adults) both increased with initial population density (N for each point = 16). Analysis of variance also indicates a significant effect of host-plant genotype (B = Bragg, Cn = Centennial, Cl = Clark, W = Williams) on fecundity ($P < 0.03$), and a weak effect of genotype on development time ($P < 0.06$) ($N = 20$ for each bar). Error bars indicate standard errors.

crease, and b representing the form of density dependence). However, there was a greater range of variation in r than in b, with r varying over a twofold range among cultivars, while b varied by only a factor of 0.6 (Fig. 3). In the Ricker model, the parameter r controls the period of fluctuations in population size (Renshaw 1991). For example, in Fig. 3, the vertical lines indicate the transition between values of r that lead to 2-point cycles and 4-point cycles, and the transition between 4-point cycles and fluctuations with a higher period. In this experiment, the range of differences in r among genotypes was great enough to produce differences in the predicted period of fluctuations of beetle populations. The fact that the confidence contour for the best estimate of the Ricker parameters for Centennial straddles the line between the 2-point and 4-point regions of parameter space suggests that beetle populations on this genotype of host could exhibit either 2- or 4-point cycles, depending on how environmental conditions affect the value of r in a particular population.

It is not yet clear what particular plant traits account for the observed differences in herbivore population dynamics among plant genotypes in this experiment. The most likely explanation for these differences is variation in the intrinsic quality of host foliage (as opposed to variation in predation rates), since host genotypes differed not just in beetle survival, but also in fecundity, and, to some extent, in growth rate. Leaf nutrient content and secondary chemistry are two foliage characters that seem likely to be important, but data on these characters are not available in a form that allows comparison among all four genotypes. Trichome density seems unlikely to be influencing the observed differences in dynamics since all four cultivars have similar ("normal") trichome densities (USDA/ARS Germplasm Resources Information Network). Plant maturation rate can also influence beetle performance (McPherson et al. 1996). In this experiment, the two genotypes with 5-point cycles (Williams and Clark) are both faster maturing (maturity group 3 and 4, respectively) than the genotypes with lower-period cycles (Centennial and Bragg, maturity groups 6 and 7, respectively). However, equilibrium population size does not correlate well with maturation rate. It is also possible that plant traits had indirect effects on the beetles, mediated through predators or competing herbivores. However, since we made no direct measures of predation or competition, we cannot distinguish direct from indirect effects.

The soybean genotypes used in this study vary in their levels of induced resistance to Mexican bean beetles (Underwood 1998; N. Underwood, *unpublished data*), and so it is possible that differences in induced resistance contributed to the differences in population dynamics. In fact, the rank order of estimates of the stability (slope of the recruitment curve at equilibrium) of beetle populations on these four genotypes is the same as the rank order of the strength of induced resistance in each genotype, measured in the greenhouse (Clark > Williams > Centennial > Bragg) (N. Underwood, *unpublished data*). While this relationship suggests that induced resistance may influence beetle dynamics in this system, the predicted equilibrium population sizes do not correlate particularly well with the strength of the induced response. We also cannot rule out the possibility that variation in maturation rate or other non-inducible resistance characters could be responsible for the observed differences in herbivore dynamics. Further research will be required to determine what specific characters account for differences in beetle population dynamics among these genotypes, and what role induced resistance may play in this system.

The goal of this experiment was to determine whether host-plant genotype has the capacity to affect long-term herbivore population dynamics. Our finding of qualitative differences among genotypes in the predicted population dynamics of herbivores is likely to be robust for several reasons. First, the effects observed in this experiment were relatively strong, despite the fact that many sources of potentially confounding or conflicting natural variation were included. For example, the experiment included effects of predators and competitors, natural photoperiod and climatic regimes, and the cages were large enough to allow beetles to move among many plants, thus incorporating at least small scale spatial effects of different genotypes on population dynamics. This experiment thus provides more realistic estimates of the relative effects of these genotypes on herbivore dynamics than laboratory or more controlled field experiments could. Second, even if there is year to year variation in the parameters of the Ricker model for each population (the likely situation), as long as the differences among genotypes are on average similar to those observed in this experiment, qualitative differences in long-term dynamics among plant genotypes would remain.

Caveats

Although our goal was not to precisely predict the dynamics of particular populations, the Ricker model's fit to our data does make specific predictions. Several considerations limit the accuracy of these predictions. Because we followed beetle populations for only a single generation, we were not able to measure any delayed density-dependent effects (such as maternal effects) in this system. We also did not include the effects of mortality incurred during beetle overwintering. Omitting these factors from the experiment most likely makes the prediction of differences in population dynamics among genotypes conservative, since adding more sources of variation should increase the potential for differences among genotypes. The foliage quality of the plants may also be different when grown in pots (as in this experiment) than when grown in the field, although data suggest that induced resistance, at least, is not hindered by pot-binding in this system (N. Underwood, *unpublished data*). It is also likely that the values of the parameters of the Ricker models for each plant genotype would vary among years. The sensitivity of population dynamics to changes in the parameters of the model (due to factors discussed in this paragraph, or to natural environmental variation) will depend on the initial value of the parameter. For example, the dynamics will be most sensitive to changes in r near transitions between periodicities. This means that the prediction of Bragg having 2-point cycles is more robust than the prediction of Centennial having 4-point cycles, and that beetle populations on Centennial will be more sensitive to small changes in the shape of the recruitment curve than will populations on Bragg. The behavior of beetle populations on a particular genotype in the field may thus deviate from our specific prediction, but it seems unlikely that the influence of these factors would change the qualitative prediction of differences in beetle dynamics among plant genotypes.

Despite the fact that soybean is a crop plant with a long history of artificial selection, differences in plant-quality characters among the genotypes used in this experiment are likely to be within the range of differences found in natural systems. All four genotypes are considered susceptible to Mexican bean beetles, so none of these genotypes has been bred for very strong constitutive resistance (USDA/ARS Germplasm Resources Information Network), and although the genotypes varied in induced resistance, induced resistance has not been artificially selected in this system. In this experiment, each beetle population was exposed to only a single genotype of soybean. This accurately reflects the situation in agricultural fields, but differs from the usually genetically variable nature of natural plant populations. Although some research suggests that genetic diversity in the plant population can contribute to differences in herbivore population dynamics (Power 1991, Riggin-Bucci and Gould 1997), little is known about how the effects of different genotypes (or plants with different quality characters) might combine to affect herbivore dynamics. Rates of movement among genotypes will likely be important for understanding how effects of variable hosts combine.

Herbivore dynamics, plant genetics, and evolution

Previous studies have provided evidence that plant quality (independent of genotype) may affect herbivore population dynamics (Karban 1992), and that herbivores can impose selection on plant-quality characters (Marquis 1992) that differ among plant genotypes. The results of this study link these two previous observations by showing that plant genotype can influence herbivore dynamics. This observation suggests several ways in which herbivore population dynamics, plant genetics, and evolution may be interconnected.

If plant genotype influences herbivore dynamics, variation in the relative abundance of plant genotypes could generate variation in local herbivore dynamics. Shifts in plant genotype frequencies through time, due to the evolution of plant-quality characters or of characters genetically correlated with plant quality, could generate temporal changes in herbivore dynamics (Pimentel 1961). The relative abundance of plant genotypes can also vary across space, due in part to variation in environmental factors such as water availability or soil characteristics (McGraw and Antonovics 1983, Hedrick 1986, Jordan 1991), and thus might contribute to differences in herbivore population dynamics among plants growing in different environments (Denno and McClure 1983, Louda et al. 1987).

If shifts in plant genotype can influence herbivore dynamics, this raises the question of whether, or how, herbivore dynamics may feed back to selection on plant genotypes. There is mounting evidence that herbivores can act as a selective force on plant resistance characters (Berenbaum et al. 1986, Rausher and Simms 1989, Mauricio and Rausher 1997). Resistance characters can strongly affect insect–herbivore performance (e.g., Berenbaum 1978, Rhoades 1979), and thus might be expected to contribute to host-plant effects on herbivore dynamics. As plant resistance evolves, shifts in the frequency of genotypes in a plant population could alter the dynamics of the herbivore population exerting selection on those characters. In turn, these changes in herbivore population dynamics might result in changes in selection on the plants.

The results of our experiment indicate that host-plant genotype can affect both the equilibrium number of herbivores in the population (equilibrium population size), and the period and magnitude of fluctuations in population size (Table 1). The equilibrium number of herbivores would likely affect the strength of selection on resistance characters, perhaps altering the relative fitness of resistance alleles. Fluctuation of herbivore populations may lead to fluctuation in the strength of selection on plant characters. Gillespie (1973) showed that the fitness of an allele under temporally fluctuating selection is the geometric mean of its fitness over time. As the magnitude of fluctuation increases, the geometric mean becomes smaller relative to the arithmetic mean, so that fitnesses decrease with increasing magnitude of fluctuations (Doebeli and Koella 1994). Therefore, it might be expected that, all else being equal, plant genotypes that produce fluctuating populations of herbivores will have lower long-term fitness than genotypes that maintain stable herbivore populations.

Conclusion

This study provides experimental evidence that in at least one system, genetic differences among host plants have the potential to affect herbivore population dynamics. It remains to be determined whether this holds true at larger scales, over longer periods of time, and in other plant–herbivore systems. Differences in dynamics among plant genotypes are likely to be most important for systems where large numbers of insects are exposed to a single plant genotype (for example insects living on clonal plants such as goldenrod or aspen, or agricultural systems where large areas are planted with crops of a single genotype). There is also a need for theoretical exploration of potential feedback between herbivore dynamics and selection on plants, and its consequences for plant and herbivore populations. Existing theoretical studies of the interactions between disease organisms and their hosts (May and Anderson 1983, Antonovics 1994), and on fluctuating selection, may provide good starting places for this work. Finally, breeders of agricultural plants may want to consider effects of resistance characters on pest insect population dynamics as well as on mean population sizes, since some patterns of herbivore fluctuation might affect yields more negatively than others.

ACKNOWLEDGMENTS

We thank A. Agrawal, M. Hunter, B. Inouye, E. Lacey, W. Morris, F. Nijhout, S. Nowicki, two anonymous reviewers, and the members of the Rausher lab group for many helpful comments on this paper. We are grateful to A. Culp, P. Johnson, and A. Small for field assistance, and to C. King for building cages. Thanks to T. Carter and J. Burton (North Carolina State University), and R. Nelson (USDA Soybean Germplasm Collection) for providing soybean seed, and to T. Dorsey (New Jersey Department of Agriculture) for providing beetles and advice on their care. Financial support for this work came from NRI Competitive Grants Program/USDA grant #94–37302-0348 and NSF grant DEB-9615227 to Mark Rausher, an NSF Predoctoral Fellowship and a Sigma Xi Grant-in-Aid of Research to Nora Underwood, and the Graduate School and Zoology Department of Duke University.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

Antonovics, J. 1994. The interplay of numerical and gene-frequency dynamics in host–pathogen systems. Pages 129–145 *in* L. A. Real, editor Ecological genetics. Princeton University Press, Princeton, New Jersey, USA.

Belovsky, G. E., and A. Joern. 1997. The dominance of different regulating factors for rangeland grasshoppers. Pages 359–386 *in* N. Cappuccino and P. W. Price, editors Population dynamics: new approaches and synthesis. Academic Press, New York, New York, USA.

Berenbaum, M. 1978. Toxicity of a furanocoumarin to armyworms: a case of biosynthetic escape from insect herbivores. Science **201**:532–534.

Berenbaum, M. R., A. R. Zangerl, and J. K. Nitao. 1986. Constraints on chemical coevolution: wild parsnips and the parsnip webworm. Evolution **40**:1215–1228.

Brodbeck, B., and D. Strong. 1987. Amino acid nutrition of herbivorous insects and stress to host plants. Pages 347–364 *in* P. Barbosa and J. C. Schultz, editors Insect outbreaks. Academic Press, San Diego.

Cappuccino, N., and P. W. Price. 1997. Population dynamics: new approaches and synthesis. Academic Press, New York, New York, USA.

Deitz, L. L., R. L. Rabb, J. W. VanDuyn, W. M. Brooks, J. R. J. Bradley, and R. E. Stinner. 1976. A guide to the identification and biology of soybean arthropods in North

Carolina. NC Agricultural Experiment Station Technical Bulletin 238.

Denno, R. F., and M. S. McClure, editors. 1983. Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA.

Doebeli, M., and J. C. Koella. 1994. Sex and population dynamics. Proceedings of the Royal Society of London B. **257**:17–23.

Draper, N. R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, New York, New York, USA.

Edelstein-Keshet, L. 1988. Mathematical models in biology. Random House, New York, New York, USA.

Edelstein-Keshet, L., and M. D. Rausher. 1989. The effects of inducible plant defenses on herbivore populations. 1. mobile herbivores in continuous time. American Naturalist **133**:787–810.

Edwards, A. W. F. 1992. Likelihood. Johns Hopkins University Press, Baltimore.

English-Loeb, G. M. 1990. Plant drought stress and outbreaks of spider mites: a field test. Ecology **71**:1401–1411.

Fritz, R. S. 1995. Direct and indirect effects of plant genetic variation on enemy impact. Ecological Entomology **20**: 18–26.

Gillespie, J. H. 1973. Natural selection with varying selection coefficients—a haploid model. Genetical Research **21**:115–120.

Gould, F. 1983. Genetics of plant–herbivore systems: interactions between applied and basic study. Pages 599–653 *in* R. F. Denno and M. S. McClure, editors Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **95**:421–425.

Harrison, S., and N. Cappuccino. 1996. Using density-manipulation experiments to study population regulation. *in* N. Cappuccino and P. W. Price, editors Population dynamics: new approaches and synthesis. Academic Press, New York, New York, USA.

Hassell, M. P. 1975. Density-dependence in single-species populations. Journal of Animal Ecology **44**:283–295.

Hassell, M. P. 1985. Insect natural enemies as regulating factors. Journal of Animal Ecology **54**:323–334.

Haukioja, E. 1980. On the role of plant defenses in the fluctuation of herbivore populations. Oikos **35**:202–213.

Hedrick, P. W. 1986. Genetic polymorphism in heterogeneous environments: a decade later. Annual Review of Ecology and Systematics **17**:535–566.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**: 724–732.

Hwang, S., and R. L. Lindroth. 1997. Clonal variation in foliar chemistry of aspen: effects on gypsy moths and forest tent caterpillars. Oecologia **111**:99–108.

Jordan, N. 1991. Multivariate analysis of selection in experimental populations derived from hybridization of two ecotypes of the annual plant *Diodia teres* W. (Rubiaceae). Evolution **45**:1760–1772.

Karban, R. 1986. Induced resistance against spider mites in cotton: field verification. Entomologia Experimentalis Et Applicata **42**:239–242.

Karban, R. 1992. Plant variation: its effects on populations of herbivorous insects. Pages 195–215 *in* R. S. Fritz and E. L. Simms, editors Plant resistance to herbivores and pathogens: ecology, evolution, and genetics. University of Chicago Press, Chicago.

Karban, R., and J. H. Myers. 1989. Induced plant responses to herbivory. Annual Review of Ecology and Systematics **20**:331–348.

Kogan, M., and D. C. Fischer. 1991. Inducible defenses in soybean against herbivorous insects. Pages 347–378 *in* D. W. Tallamy and M. J. Raupp, editors Phytochemical induction by herbivores. Wiley and Sons, New York, New York, USA.

Levin, D. A. 1973. The role of trichomes in plant defense. Quarterly Review of Biology **48**:3–15.

Louda, S. M., and S. K. Collinge. 1992. Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. Ecology **73**:153–169.

Louda, S. M., M. A. Farris, and M. L. Blua. 1987. Variation in methylglucosinolate and insect damage to *Cleome serrulata* (Capparaceae) along a natural soil moisture gradient. Journal of Chemical Ecology **13**:569–581.

Maddox, G. D., and R. B. Root. 1987. Resistance to 16 diverse species of herbivorous insects within a population of goldenrod, *Solidago altissima*: genetic variation and heritability. Oecologia **72**:8–14.

Mallet, J., and N. H. Barton. 1989. Strong natural selection in a warning-color hybrid zone. Evolution **43**:421–431.

Marquis, R. J. 1992. Selective impact of herbivores. Pages 301–325 *in* R. S. Fritz and E. L. Simms, editors Plant resistance to herbivores and pathogens: ecology, evolution, and genetics. University of Chicago Press, Chicago.

Mauricio, R., and M. D. Rausher. 1997. Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. Evolution **51**:1435–1444.

May, R. M., and R. M. Anderson. 1983. Epidemiology and genetics in the coevolution of parasites and hosts. Proceedings of the Royal Society of London B **219**:281–313.

McCrea, K. D., and W. G. Abrahamson. 1987. Variation in herbivore infestation: historical vs. genetic factors. Ecology **68**:822–827.

McGraw, J. B., and J. Antonovics. 1983. Experimental ecology of *Dryas octopetala* ecotypes. I. ecotypic differentiation and life-cycle stages of selection. Journal of Ecology **71**:879–897.

McPherson, R. M., J. R. Ruberson, R. D. Hudson, and D. C. Jones. 1996. Soybean maturity group and incidence of velvetbean caterpillars (Lepidoptera: Noctuidae) and Mexican bean beetles (Coleoptera: Coccinellidae). Journal of Economic Entomology **89**:1601–1607.

Morris, W. F., and G. Dwyer. 1997. Population consequences of constitutive and inducible plant resistance: herbivore spatial spread. American Naturalist **149**:1071–1090.

Myers, J. H. 1988. Can a general hypothesis explain population cycles of forest lepidoptera? Advances in Ecological Research **18**:179–242.

Myers, J. H. 1990. Population cycles of western tent caterpillars: experimental introductions and synchrony of fluctuations. Ecology **71**:986–995.

Pimentel, D. 1961. Animal population regulation by the genetic feed-back mechanism. American Naturalist **95**:65–79.

Power, A. G. 1991. Virus spread and vector dynamics in genetically diverse plant populations. Ecology **72**:232–241.

Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1986. Numerical recipes in Pascal: the art of scientific computing. Cambridge University Press, Cambridge.

Prout, T., and F. McChesney. 1985. Competition among immatures affects their adult fertility: population dynamics. American Naturalist **126**:521–558.

Rausher, M. D. 1981. Host plant selection by *Battus philenor* butterflies: the roles of predation, nutrition, and plant chemistry. Ecological Monographs **51**:1–20.

Rausher, M. D., and E. L. Simms. 1989. The evolution of resistance to herbivory in *Ipomoea purpurea.* I. attempts to detect selection. Evolution **43**:563–572.

Reeve, J. D., M. P. Ayres, and P. L. J. Lorio. 1995. Host suitability, predation, and bark beetle population dynamics. Pages 339–357 *in* N. Cappuccino and P. W. Price, editors Population dynamics: new approaches and synthesis. Academic Press, San Diego, California, USA.

Renshaw, E. 1991. Modeling biological populations in space and time. Cambridge University Press, Cambridge, UK.

Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. Pages 3–54 *in* G. A. Rosenthal and D. H. Janzen, editors Herbivores: their interaction with secondary plant metabolites. Academic Press, New York, New York, USA.

Rhoades, D. F. 1983. Herbivore population dynamics and plant chemistry. Pages 155–220 *in* R. F. Denno and M. S. McClure, editors Variable plants and herbivores in natural and managed ecosystems. Academic Press, San Diego.

Rhoades, D. F. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. American Naturalist **125**:205–238.

Riggin-Bucci, T. M., and F. Gould. 1997. Impact of intraplot mixtures of toxic and nontoxic plants on population dynamics of diamondback moth (Lepidoptera: Plutellidae) and its natural enemies. Journal of Economic Entomology **90**:241–251.

Rossiter, M., J. C. Schultz, and I. T. Baldwin. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. Ecology **69**:267–277.

Rossiter, M. C. 1991. Environmentally-based maternal effects: a hidden force in insect population dynamics? Oecologia **87**:288–294.

Roughgarden, J. 1998. How to manage fisheries. Ecological Applications **8**:s160–s164.

SAS 1989. SAS/STAT user's guide. SAS Institute, Cary, North Carolina, USA.

Turchin, P. 1990. Rarity of density dependence or population regulation with lags? Nature **344**:660–663.

Underwood, N. 1997. The interaction of plant quality and herbivore population dynamics. Dissertation. Duke University, Durham North Carolina, USA.

Underwood, N. C. 1998. The timing of induced resistance and induced susceptibility in the soybean–Mexican bean beetle system. Oecologia **114**:376–381.

Webb, J. W., and V. C. Moran. 1978. The influence of the host plant (*Acacia karroo*) on the population dynamics of *Acizzia russellae* (Homoptera: Psyllidae). Ecological Entomology **3**:313–321.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia **63**:90–105.

Zangerl, A. R. 1990. Furanocoumarin induction in wild parsnip: evidence for an induced defense against herbivores. Ecology **71**:1926–1932.