

INDUCED VS. CONSTITUTIVE RESISTANCE AND THE SPATIAL DISTRIBUTION OF INSECT HERBIVORES AMONG PLANTS

NORA UNDERWOOD,¹ KURT ANDERSON,² AND BRIAN D. INOUE

Department of Biological Science, Florida State University, Tallahassee, Florida 32306 USA

Abstract. Because herbivores can move away from plants of low quality, induced resistance should affect the spatial distribution of herbivore damage (or herbivores) within or among plants. We used a spatially explicit simulation model and data from a field experiment to examine the effect of induced resistance on the distribution of herbivores and their damage among plants within a population. The model is appropriate only for rapid (as opposed to delayed) induced resistance, assumes that resistance affects herbivore behavior but not performance, and assumes no interplant communication. It is also appropriate only for induced resistance that decays in the absence of herbivore damage. The simulation tracks herbivores on a linear array of plants or plant parts with reflecting boundaries and allows manipulation of the timing of induced resistance and the initial distribution of herbivores. Our model suggests that increasing lags and thresholds for the production of induced resistance causes increasing aggregation of herbivores and their damage, but in the absence of either a lag or a threshold, induced resistance can lead to an even distribution of herbivores. The formation of even or aggregated distributions of herbivores depends not on initial distributions, but on the characteristics of the induced resistance. In the field experiment, we measured the degree of aggregation of Mexican bean beetle larvae among plants within experimental soybean populations consisting of soybean varieties that had no resistance (low constitutive, low inducible resistance), induced resistance (and low constitutive resistance), or constitutive resistance (and low inducible resistance). In general agreement with qualitative predictions of the model, we found that larvae on soybean varieties with induced resistance remained significantly more aggregated than larvae on varieties with no or high constitutive resistance.

Key words: *distribution of damage; Epilachna varivestis; Glycine max; induced resistance, spatial distribution of herbivores; spatially explicit model.*

INTRODUCTION

Induced resistance (a change in plant resistance to herbivory in response to herbivore damage due either to changes in chemical or physical defenses or change in nutritional quality) has been shown to affect herbivore performance (see review in Karban and Baldwin 1997), temporal population dynamics (e.g., Underwood and Rausher 2002), and both feeding and movement behavior (see, e.g., Bergelson et al. 1986, van Dam et al. 2000). Much is known about the effects of induced resistance on individual herbivore performance, yet few studies have addressed its population level effects and, in particular, whether effects on individual performance and behavior can mediate changes in spatial population dynamics.

Edwards and Wratten (1983) suggested that the effect of induced resistance on herbivore movement should in turn cause distributions of herbivore damage that are more even than random (or “overdispersed”) as her-

bivores move away from areas of previous damage. They speculated further that this effect might provide a fitness benefit to plants both because dispersed damage might be less costly for the plant and because moving herbivores spend less time feeding and more time exposed to predators. The intuitively appealing idea that induced resistance should cause even distributions of herbivore damage has been widely discussed, but few empirical studies have documented patterns of damage or herbivore distribution while manipulating induction (Bergelson et al. 1986, Silkstone 1987), and these studies found both dispersed and aggregated distributions of damage. Two theoretical studies that examined the effect of induced resistance on herbivore spread and spatial pattern (Lewis 1994, Morris and Dwyer 1997) suggest that plant resistance can affect spatial patterns of herbivores, but neither included details of the induced response such as time lags or an induction threshold. Several authors (e.g., Marquis 1992, Mauricio et al. 1993) have found that the distribution of damage does affect plant fitness, and several studies (e.g., Stamp 1980, Denno and Benrey 1997) have shown that the distributions of herbivores can affect the herbivore success. Given that the spatial dynamics of herbivory should affect both the plant and

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¹ E-mail: nunderwood@bio.fsu.edu

² Present address: Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA.

TABLE 1. Definitions of functions and parameters used in the simulation model.

Function or parameter	Definition
Component functions	
$I_{i,t}$	level of induced resistance in plant i at time t
$H_{i,t}$	number of herbivores on plant i at time t
$\alpha_{i,t}(I_{i,t})$	maximum increase in induction in plant i at time t to a single herbivory event
$p_{i,t}(I_{i,t})$	probability that an herbivore will leave plant i at time t
Parameters	
θ	level of herbivory required to initiate induction of resistance
τ	time lag between herbivory and effect of induction on herbivores
b	half-saturation constant of induction response to herbivory
δ	decay rate of inducible resistance
$\hat{\alpha}$	maximum amount of change in induced resistance
β	physiological limit to the amount of induced resistance in a plant

the herbivore, it seems worthwhile to determine the effects of induced resistance on distributions of herbivores and their damage.

To examine the possibility that induced resistance has behaviorally mediated consequences for the spatial distribution of herbivore populations and damage among plants or plant parts, we used a spatially explicit simulation model. This model was designed to explore how some characteristics of induced resistance might influence the interaction between induced resistance and distributions of herbivores and their damage. The model also allows us to compare the spatial consequences of induced resistance with constitutive resistance. Our model is formulated to demonstrate key concepts in a simple context, rather than focusing on a particular plant–herbivore system. We compared the qualitative predictions of our model with data from a field experiment in which we had followed the distribution of herbivores (Mexican bean beetles [MBBs]) in soybean populations that differed in their resistance characteristics.

METHODS

Model

To examine how induced resistance affects herbivore spatial distributions, we explored a spatially explicit model of individual plant resistance and herbivore movement in a linear array of plants or plant parts. The model was based on the nonspatial model of Underwood (1999), but omitted herbivore and plant reproduction. The model, therefore, had two parts: one expression for plant resistance and one for herbivore movement. By focusing on herbivore movement, we implicitly limited our model to considering behavioral, rather than toxic affects of induced resistance on the herbivore.

We considered only “rapid” (as opposed to “delayed”) induced resistance; that is, induced resistance occurring within individual herbivore lifetimes (Haukioja 1990). This model can be thought of as describing either systemic induced resistance and movement of herbivores among plants, or local chemical induced

resistance and movement of herbivores within plants. The model is not appropriate for resistance mechanisms that do not decay in the affected unit in the absence of damage such as hypersensitivity or leaf abscission. For simplicity, we will phrase the rest of the paper in terms of systemic resistance. Thus, we treated resistance as an isolated trait of an individual plant, so interplant communication (Dicke and Bruin 2001) or other aggregate population-level responses do not contribute to induced resistance in this model. We further assumed, for simplicity and ease of interpretation, that resistance, regardless of whether it represents a single factor or a multitude of traits including defensive chemistry or nutritional deterioration, could be quantified by one aggregate measure.

The model allowed for both a threshold level of herbivory (θ), below which induction never occurred (Underwood 2000), and a time lag (τ) between damage and induced resistance. If herbivore damage was above the threshold value, the level of induced resistance in an individual plant i at time $t + 1$ ($I_{i,t+1}$) was a function of herbivore damage and current resistance, and otherwise decayed at a constant rate, δ :

$$I_{i,t+1} = \begin{cases} \frac{\alpha_{i,t} H_{i,t-\tau}}{b + H_{i,t-\tau}} + I_{i,t}(1 - \delta) & H_{i,t-\tau} > \theta \\ I_{i,t}(1 - \delta) & H_{i,t-\tau} \leq \theta. \end{cases} \quad (1)$$

All parameters used in our model are defined in Table 1. For constitutive resistance, $I_{i,t} = I_{i,t+1} = 80$ (changing the level of constitutive resistance did not affect herbivore distributions; results not shown). We defined the amount of damage to a plant at each time step as equal to the number of herbivores present on that plant at that time. If herbivore damage was above the threshold value θ , the level of induced resistance in an individual plant i at time $t + 1$ included an additional dependence on herbivore damage. We assumed that a plant’s increase in resistance (as perceived by the herbivore) in response to herbivore damage in one time step was a saturating function of the number of herbivores on the plant τ time units previously ($H_{i,t-\tau}$). The units for τ

are model time steps. Small values of τ reflect situations in which herbivores experience changes in induction below or near the same time scale of movement, whereas larger values describe longer delays. The limiting case of $\tau = 0$ represents the hypothetical extreme where induction is instantaneous. Lags in real systems range from days (e.g., Orians et al. 2000) to months (e.g., Haukioja 1990). Induced resistance increases to a maximum $\alpha_{i,t}$ at a rate governed by the half-saturation constant b . Induced resistance often increases with increasing damage at a single damage event (e.g., Kogan and Fischer 1991, Underwood 2000). In the present study, the value of b was arbitrarily held constant at 10 (changing the value of b does not qualitatively alter the results, data not shown).

We made two further assumptions when determining the value of $\alpha_{i,t}$ in Eq. 1. First, we assumed that the level of induced resistance in an individual plant has a physiological limit (β , for convenience, $\beta = 100$). Such a limit might reflect resource limitation or autotoxicity due to production of a secondary compound (Baldwin and Callahan 1993). Second, the maximum amount of change in induced resistance in response to a single damage event ($\alpha_{i,t}$) was assumed, for simplicity, to be a linear function of the resistance level of plant i at time t , ($I_{i,t}$):

$$\alpha_{i,t}(I_{i,t}) = \left(-\frac{\hat{\alpha}}{\beta} I_{i,t} + \hat{\alpha} \right). \quad (2)$$

The maximum value of $\alpha_{i,t}(I_{i,t})$ (was $\hat{\alpha}$ (for convenience $\hat{\alpha} = 100$), which occurred when $I_{i,t} = 0$ (i.e., in an uninduced plant). The closer the plant was to the physiological limit of induced resistance (β), the more restricted its ability to respond to further damage became.

The probability, p , that an herbivore will leave plant i at a particular time t is determined by the level of induced resistance of the plant the herbivore is on:

$$p_{i,t}(I_{i,t}) = \left(\frac{100}{0.67 \times \beta} I_{i,t} \right) = \frac{I_{i,t}}{0.67}. \quad (3)$$

After an herbivore emigrates from its current host plant, it moves randomly to one of the two neighboring plants. Our simulated plant array had reflecting boundaries such that herbivores that attempted to move off the edge of the array remained on their original host plant. While it is common for aggregations to occur at reflecting boundaries in models with random movement, such patterns did not occur to a large extent in our model because of the addition of herbivore responses to plant resistance: Since aggregation of herbivores at the edges leads to higher plant resistance, herbivores move away from the edge at high rates. The expression for herbivore selectivity (Eq. 3) implies that herbivores cannot assess plant resistance before they land on a plant and can only exercise host choice by increasing their probability of leaving high-resistance plants. While movement decisions in nature can be quite com-

plex, studies suggest that random searching is a good first approximation for many types of invertebrate herbivores (Bernays and Chapman 1994, Turchin 1998). MBB's as adults do exhibit attraction to conspecifics over large spatial scales, but their short-term movements can be adequately described by a random walk (Turchin 1986). There is no evidence that MBB larvae show complex movement behavior (W. F. Morris, unpublished data).

We described the spatial distribution of herbivores among plants with the index of crowding ($J = \sigma^2/\bar{X}^2 - 1/\bar{X}$), where \bar{X} and σ^2 are the mean and variance of the number of herbivores per plant (Ives 1991). When $J = 0$, herbivores are randomly distributed. When $J < 0$, herbivores are more evenly distributed than random, and when $J > 0$, herbivores are more aggregated than random. We described the distribution of damage among plants or plant parts by the coefficient of variation of cumulative damage ($cv_d = \text{variance in cumulative damage among plants}/\text{mean cumulative damage}$). When $cv_d = 0$, total lifetime damage is completely evenly distributed across plants. As cv_d of damage rises, damage is less evenly distributed.

Simulations were run with 100 plants and 500 herbivores under one of three initial distributions: herbivores distributed evenly, randomly, and extremely aggregated (herbivores all on a single plant in the center of the array). The ratio of herbivores to plants (herbivore density) affected mean J values, but did not change qualitative patterns; lower ratios tended to result in higher J values (data not shown). The rate of decay of induced resistance (δ) did not change the qualitative effect of induction on herbivore aggregation (data not shown) and was arbitrarily held constant at 0.75 for the results reported here. We concentrated on the effects of lag and threshold, varying these parameters independently. Each replicate of the model was run for 5000 iterations, which was long enough to reach stochastic fluctuations around apparent equilibrium values of J (referred to hereafter simply as "equilibrium" values). We used only data from the last 500 iterations to calculate values of J and cv_d that reflect the equilibrium values. We calculated the mean values J and cv_d used in our analyses from seven replicate runs of each set of parameter values. To examine the rate at which the model approached an equilibrium value of J from its initial distribution, we calculated the half-saturation constant (t_H) from the relationship

$$J^* = (100 - \bar{X}_{r=4500-5000}) - \frac{a\Delta t}{t_H + \Delta t} \quad (4)$$

where Δt is one time step. The simulations and calculations of J and cv_d were done with C++ (Microsoft 1998); see the electronic Supplement for code.

Field experiment

To examine the effect of induced resistance on herbivore distributions in the field, we used data from an

experiment using soybeans (*Glycine max*, Fabaceae) and one of their herbivores, Mexican bean beetles (*Epilachna varivestis*, Coccinellidae). This experiment was designed to address questions about the effect of induced resistance on beetle numerical dynamics, but provided sufficient data to examine herbivore distributions as well. Mexican bean beetles (MBBs) lay their eggs on soybean leaves, and adults and larvae feed on the leaves. Larvae older than the first instar are able to walk both within and among plants (see Underwood and Rausher 2002 for more details about the experimental protocol and species). In this experiment, we recorded the distribution of herbivores among (but not within) plants, but did not record the distribution of herbivore damage because of logistical limitations.

In soybeans, induced resistance to MBB damage is systemic, and both constitutive and induced resistance are known to affect MBB feeding preference, mortality, and growth in the laboratory and the field (Kogan and Fischer 1991, Underwood et al. 2000). From previous greenhouse trials, we chose two soybean varieties with "no resistance" (low constitutive and no induced resistance, varieties Bragg and Gasoy), two with "induced resistance" (low constitutive and high induced resistance, varieties Davis and Stonewall), and two with "constitutive resistance" (high constitutive and no induced resistance, varieties Lamar and PI 416937; Underwood et al. 2000). It should be noted that, while varieties within resistance types were chosen to be as unrelated as possible, they might share traits linked to resistance characteristics that might have affected our results. Soybean seed was obtained from T. Carter and J. Burdon (North Carolina State University, Raleigh, North Carolina, USA), from L. Lambert (USDA-ARS-SIML, Stoneville, Mississippi, USA) and from R. Nelson (USDA Soybean Germplasm Collection, Urbana, Illinois, USA).

The experiment was carried out in 1998 at the Duke University Biology Department field station in Durham, North Carolina. Five densities of beetle populations (2, 6, 10, 14, and 20 founding adults with a 1:1 sex ratio on 20 plants per cage) were created on each of the six soybean varieties in three replicate spatial blocks. These densities span a range within that observed in the field in North Carolina (Deitz et al. 1976). This design was carried out twice during the summer of 1998 (i.e., in two temporal blocks) yielding a total of 160 experimental populations. Each population was located in a screen cage $1.5 \times 1.5 \times 2$ m with a door opening to the outside above a 0.5-m sill (which helped to contain walking beetle larvae). Each block of 30 cages was surrounded by a 2 m wide strip of soybean plants designed to attract natural enemies that might use cues from the host plants. Mexican bean beetles did not occur at this site, but soybeans were subject to damage caused by other insects (e.g., grasshoppers and lepidopteran larvae) throughout the experiment.

We allowed the MBB adults to mate and lay eggs for 1 wk before removing them and opening the doors of the cages to the surrounding soybean field to allow predators and competitors access to the cages. We allowed predators access to experimental beetle populations to include both direct and indirect effects of host-plant resistance on larval distributions. Cage doors remained open until larvae began to pupate. Each population was censused weekly for one generation (5–6 wk). Each week we counted the number of larvae in each instar on each plant. We consistently observed larvae walking both within and among plants within cages, but did not quantify these rates. Analyses of beetle performance were reported by Underwood et al. (2002), and analyses of the effect of plant resistance on the temporal population dynamics of the beetle by Underwood and Rausher (2002).

As in the model above, the distribution of larvae among plants each week during the experiment was described by the index of crowding (J). To examine the effect of plant resistance type and beetle density on beetle spatial distributions, we used repeated-measures ANOVA (Proc MIXED; SAS Institute, 2000) with $\ln(J + 1)$ as the response variable and plant resistance type, initial beetle density, temporal block, and spatial block as factors. Each cage (plant and beetle population) was considered a replicate in this analysis. Three-way interactions were not significant and were removed from the models considered here. Variety nested within resistance type was also never significant and so was also removed from the models. First-instar larvae were not included in these calculations because, unlike older instars, first instars are found only on the leaf of the clutch from which they hatch, so plant resistance type had no opportunity to affect their spatial distribution.

RESULTS

Model results

Herbivore distributions among plants.—Inducible resistance caused both even and aggregated distributions of herbivores (Fig. 1), as well as distributions of herbivores indistinguishable from random. Constitutive (i.e., non-inducible) resistance produced a distribution of herbivores that was very close to random (J values ranged from -0.001 to 0.024). When induced resistance had no lag ($\tau = 0$) or a very low threshold, herbivore distributions could be slightly more even than random. Herbivore distributions became aggregated when $\tau > 0$. When the threshold level of damage required for a change in plant resistance was greater than the mean number of herbivores per plant, resistance was rarely induced, and the herbivores converged on a random distribution. If the threshold was less than or equal to the mean number of herbivores per plant, increasing either lag or threshold (to the point where threshold = mean) increased aggregation. The thresh-

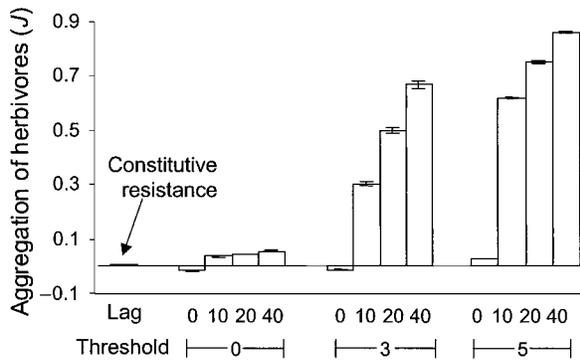


FIG. 1. The effects of lag (τ , the time lag between herbivore damage and the onset on induced resistance) and threshold (amount of herbivore damage necessary to produce an induced response) for induced resistance on the degree of aggregation (J) of herbivores among plants in the model. When $J = 0$, herbivores are randomly distributed; when $J < 0$, herbivores are more evenly distributed than random; and as J rises above zero herbivores become more aggregated. Each bar represents the mean \pm 1 SE of seven replicate runs of the model. For comparison, results for constitutive resistance are indicated by the bar on the far left. As τ increases, resistance becomes slower relative to herbivore movement ($\tau = 0$ indicates instantaneous induction), and as J increases, larger amounts of herbivore damage are required to provoke increased resistance.

old also strongly magnified the effect of lag. When the decay of the induced response was slow (values of δ were low), the results were qualitatively similar, but the degree of aggregation tended to be lower because slow decay increased the similarity among plants over time.

The equilibrium degree of herbivore aggregation formed fairly quickly from the initial herbivore distribution (Fig. 2). From an initially aggregated distribution (e.g., an egg clutch), the rate of decay of aggregation was much lower for plants with inducible resistance than for plants with constitutive resistance (Fig. 2A). The rate of approach to equilibrium levels of aggregation decreased approximately linearly (from Eq. 4 $t_H \approx 1.5 \times \text{lag}$) as the lag between damage and induction of resistance increased ($t_H = 0.6$ for constitutive resistance). For an even initial distribution of herbivores and τ and $\theta > 0$, the distribution of herbivores on plants with constitutive resistance converged to a random distribution, whereas the distribution on plants with inducible resistance quickly became aggregated (Fig. 2B).

The rapidity of spatial pattern formation in real systems will depend on the relative rates of herbivore movement and plant responses to herbivory. Model time steps are assumed to be relatively fast (i.e., hours or days), since the model allows for only herbivore feeding and movement, but not reproduction. For MBBs on soybean plants, data on the movement of larvae between plants suggest that a single model time step is on the order of 1/10th to 1/25th of a day (W. F.

Morris, unpublished data), corresponding to several hundred-time steps during larval growth. No data are available for direct comparison of this system with other model parameters.

Damage to plants.—The herbivore distribution among plants affected the distribution of damage both on individual plants through time and among plants in space. Plants with constitutive resistance had a random number of herbivores in each model time step, and thus, the distribution of the amount of damage in each time step followed a Poisson (random) distribution (Fig. 3A). However, when plants were inducible, they received herbivores in bouts, resulting in an aggregated distribution of the amount of damage among plants at any one time (Fig. 3B). Because the herbivore population size in the model was constant, the mean amount of damage over time was the same for plants with constitutive or inducible resistance, but the latter generally received very little damage at any one time and suffered rare bouts of severe damage.

Inducible resistance could lead to aggregated, random, or even distributions of damage among plants, depending on the details of induced resistance and the time scale considered (Fig. 4). The variation in cumulative damage received by plants with constitutive resistance declined over time from an initial high produced by the initial random distribution of herbivores

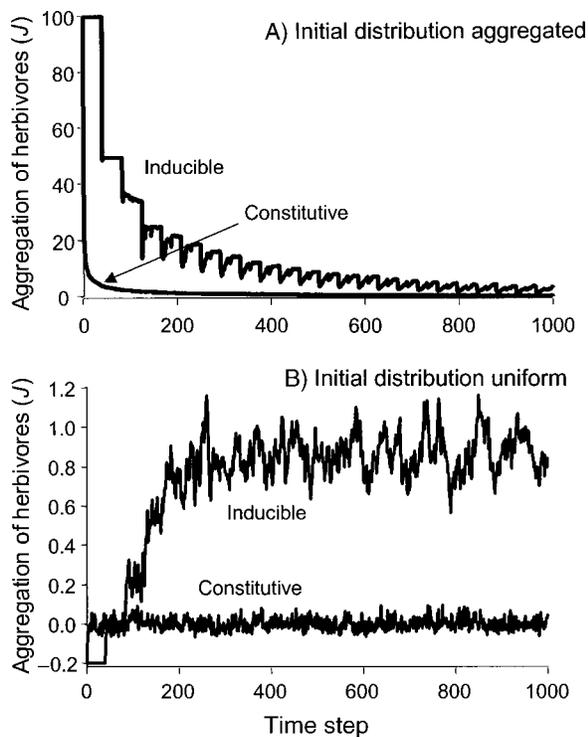


FIG. 2. Approach to equilibrium distributions of herbivores among plants from (A) initially aggregated and (B) initially uniform herbivore distributions. For these runs of the model, lag (τ) = 20, and threshold = 5.

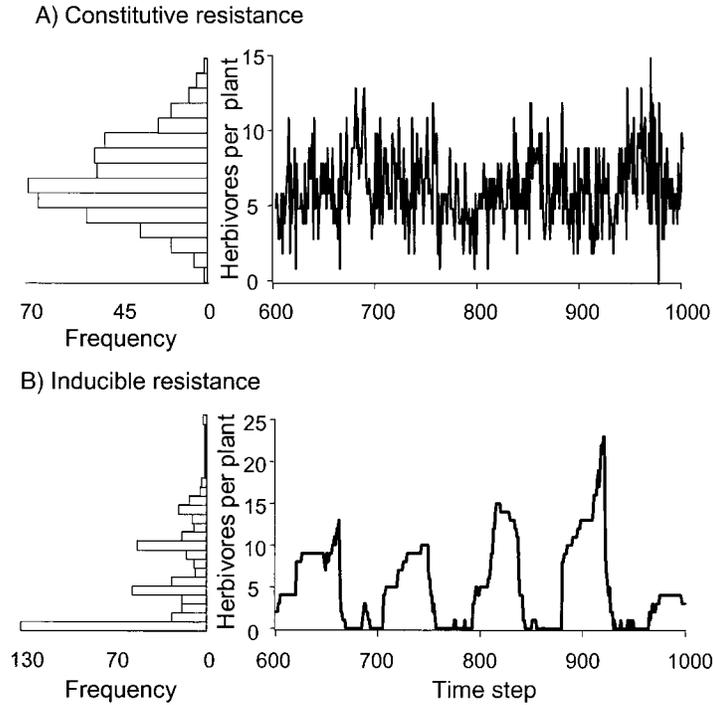


FIG. 3. The effect of (A) constitutive and (B) inducible plant resistance on the pattern of herbivore damage to a single plant over time. The panels on the right show the number of herbivores on an individual plant over one run of the model, and the panels on the left show the frequency distributions of points in the right panels. The frequency distributions show that, with constitutive resistance, damage to the plant is Poisson-distributed over time but that, with inducible resistance, damage is aggregated into periods of high and low damage. For the run with constitutive resistance, plant resistance = 100; for inducible resistance, lag (τ) = 20, and threshold = 5.

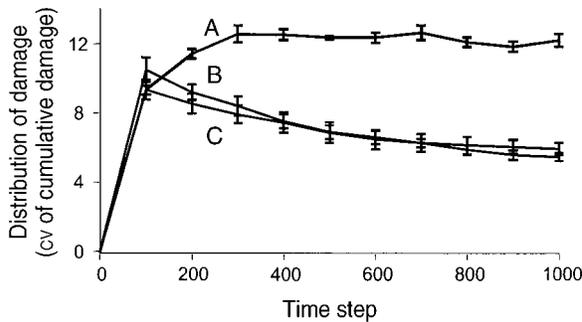


FIG. 4. Over the time scale shown, the distribution of damage among plants over time could be aggregated or random, depending on characteristics of the induced response: (A) inducible resistance, initially aggregated herbivore distribution; (B) constitutive resistance, initially random herbivore distribution; and (C) inducible resistance, initially even herbivore distribution. Inducible resistance with lags or a threshold led to aggregated damage distributions that persisted for thousands of time steps. Instantaneously inducible resistance led to slightly more-even-than-random distributions. Each point represents the mean ± 1 SE of seven replicate runs of the model. For inducible resistance (aggregated), lag (τ) = 20 and threshold = 5. For inducible resistance (even), lag (τ) and threshold = 0.

after the first few bouts of herbivore movement. If induced resistance arose instantaneously ($\tau = 0, \theta = 0$), the distribution of damage was similar to the distribution for plants with constitutive resistance but could eventually lead to an even lower cv of damage than for plants with constitutive resistance. If there was a lag or threshold for induced resistance, then the distribution of damage over the short term was also aggregated, but plants with a lag or threshold eventually (after $\gg 5000$ model iterations) also produced a distribution of damage that was more even than for plants with constitutive resistance (data not shown). For most real plant-herbivore systems, these long-term results ($\gg 5000$ iterations) are probably not relevant. This time scale vastly surpasses our experimental time scale (5000 time steps would be 200 to 500 d, which is much longer than MBB life-spans), and we did not have any opportunity to observe such a pattern.

Field experiment results

All populations started with aggregated distributions because MBB lay their eggs in large clutches and not all plants received egg masses. Beetle adults and larvae were observed to move among plants during the experiment. Overall, second- through fourth-instar beetle larvae tended to be more aggregated on populations of plants with inducible resistance than on plants with

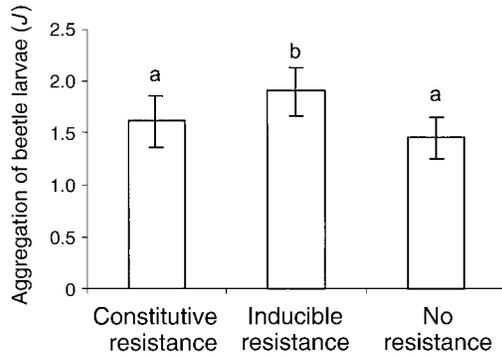


FIG. 5. The effects of genotypes of soybean with three different types of plant resistance on the mean (± 1 SE) dispersion of Mexican bean beetle larvae among experimental plants; N (constitutive resistance) = 188, N (inducible) = 211, and N (no resistance) = 202. Bars labeled with matching letters are not significantly different ($P > 0.05$).

either high or low constitutive resistance, although this trend was not significant at the 0.05 level (main effect of plant resistance type in ANOVA, $F_{2, 128} = 2.57$, $P = 0.08$; Fig. 5). Post hoc contrasts between resistance types indicate that high and low constitutive resistance did not differ in the beetle aggregation that they caused ($F_{1, 128} = 0.01$, $P = 0.93$), but beetles were significantly more aggregated on plants with induced resistance than on either of the other resistance types (induced vs. low constitutive, $F_{1, 128} = 3.91$, $P = 0.05$; induced vs. high constitutive, $F_{1, 128} = 3.85$, $P = 0.05$; Fig. 5). Resistance and time interacted significantly ($F_{10, 410} = 2.31$, $P = 0.01$; Fig. 6). Inducible resistance also seemed to produce slower decay of aggregation than did high and low constitutive resistance. Larvae on plants with constitutive resistance lost aggregation quickly and finished with random distributions. Larvae on plants with inducible resistance lost aggregation more slowly and finished with significantly aggregated distributions. Initial beetle density and census date also interacted significantly, suggesting an effect of density on aggregation, but the pattern was not easily interpretable.

DISCUSSION

Results of our model suggest that induced and constitutive resistance can affect the spatial distribution of herbivore damage differently. The effect of induced resistance depended on characteristics of the induced response, such as the lag between damage and induction and the threshold amount of damage required to provoke an induced response. Over the very long term, induced resistance of the kinds considered in our model all led to more even distributions of damage among plants or plant parts than did constitutive resistance. This result is in agreement with the qualitative predictions of Edwards and Wratten (1983). However, over the shorter time scales that are the focus of our modeling efforts, induced resistance with any lag or thresh-

old led to more aggregated distributions of damage than did constitutive resistance.

Our model also makes predictions about the distribution of damage over time. With constitutive resistance or instantaneously inducible resistance, plants received a random amount of damage every time step, but where inducible resistance was lagged, plants received damage in bouts. If plants grow exponentially (see, e.g., Weiner et al. 1990), then damage that occurs in bouts will, on average, reduce plant growth (and average biomass; Nisbet et al. 1997) more than damage that is less variably applied. To our knowledge, tests of the effects of evenness of damage in space have not considered the impacts of the distribution of damage over time.

Our model suggests that some kinds of induced resistance can affect not just the distribution of herbivore damage, but also the spatial distribution of herbivores. When induced resistance was instantaneous (has no lag and no threshold) but still responsive to herbivore density, herbivore distributions with induced resistance could be slightly more even than distributions with constitutive resistance, but otherwise, herbivore distributions were more aggregated than distributions with constitutive resistance. Both of these characteristics of induced resistance have been observed (e.g., from lags in trees of up to a year [Haukioja 1990] to lags on the order of hours in some herbaceous plants [e.g., Edwards et al. 1985] and thresholds in soybeans [Underwood 2000]), but relatively few published data address details of the timing of induced responses to herbivores.

The results from our field experiment were consistent with the qualitative predictions of the model that inducible resistance would often lead to aggregated distributions of herbivores in space. Although lag times have not been measured with these species in the field,

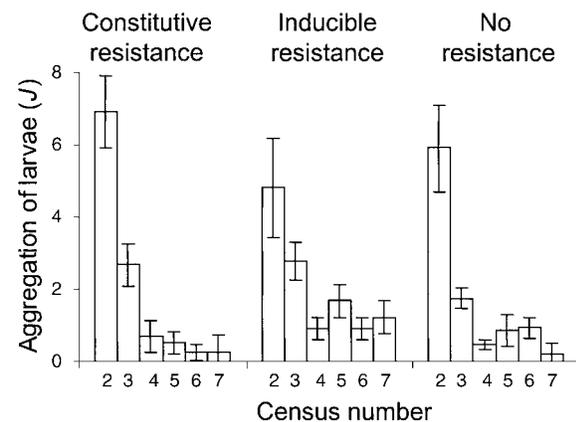


FIG. 6. The effect of soybean resistance type on the distribution (mean ± 1 SE) of beetle larvae among experimental soybean plants over time. Inducible resistance appears to slow the spread of larvae from their initial egg masses, as well as leading to a higher level of aggregation, on average (significant interaction of time and plant resistance type). Values of N for each bar range from 12 to 52.

we do have evidence of thresholds for the production of induced resistance in soybeans (Underwood 2000). Beetle larvae on soybean genotypes with inducible resistance were significantly more aggregated overall than those on plants with high or low constitutive resistance. Likewise, just as in the model, larvae on plants with inducible resistance lost their initial aggregation more slowly than larvae on plants with constitutive resistance and remained more aggregated, although not because they remained on the same plants throughout their lives (larvae were observed to move during the experiment). Data on MBB larval movement from a separate experiment (W. F. Morris, *unpublished data*) suggest that results from the field experiment (Fig. 6) correspond to several hundred time steps of the model (cf Fig. 2A).

Resource-mediated aggregation of consumers is a well-studied phenomenon (see Parrish and Edelstein-Keshet 1999). However, most previous models have investigated the spatial dynamics of consumer–resource interactions when consumers were able to evaluate and move in response to resource and conspecific densities (e.g., Gueron and Liron 1989, Lewis 1994) or over long time scales with resource or herbivore replenishment (e.g., Lewis 1994, Nisbet et al. 1997, Wilson and Richards 2000). Our model demonstrates that consumers can aggregate in areas of higher resource quality over short time scales (i.e., <1 plant or herbivore generation) and with minimal complexity in foraging behavior (i.e., herbivores respond to local assessments of plant resistance by means of random dispersal). Because animal aggregations have been implicated as a mechanism in maintaining the coexistence of competitors (e.g., Inouye 1999, Richards et al. 2000), stabilizing host-parasitoid population dynamics (e.g., Hassell and Wilson 1997), and influencing social- and mating-system evolution (Krebs and Davies 1993), it is important to note the ease with which aggregations occur in our model in the complete absence of complex foraging processes or external forcing (see also Wilson and Richards 2000).

The model we have presented relies on a number of assumptions and simplifications that do not match the complexity of real plant–herbivore interactions. Our goal was to examine whether inducible resistance could generate sufficient variability in plant resistance to generate aggregated herbivore distributions. The predictions of our model, which are qualitatively consistent with our field data, show what is possible given very simple assumptions. Many of our assumptions relate to the way in which we describe the induction mechanism; for example, we treat induction simply as an overall change in plant resistance, and assume no interplant communication. However, we have shown that certain aspects of the induction response can have potentially large effects on herbivore distributions, which highlights the need for more data quantifying the dynamics of inducible resistance in different systems.

Furthermore, adding sophistication to herbivore behavior could have large impacts on predicted herbivore distributions. Taxis of insect herbivores towards conspecifics or of predators towards herbivore aggregations have been shown in other contexts to be capable of generating unexpected spatial patterns; incorporating these mechanisms into simple models of inducible resistance such as ours would be a logical next step. Predictions for particular systems will obviously depend on the details of those systems.

Results from our modeling and empirical studies suggest that some types of induced resistance can influence herbivore distributions. Contrary to previous suggestions, induced resistance was most likely to provoke aggregated distributions of herbivores and their damage over short to moderate time scales. Previous studies have shown that damage distribution can affect plant fitness (Marquis 1992, Mauricio et al. 1993) and herbivore distribution can influence herbivore performance (Stamp 1980, Denno and Benrey 1997). The results of our study thus suggest that to understand population-level interactions of induced resistance and herbivores, we must consider these interactions in a spatial context.

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SUPPLEMENT

Source code for simulations described in this paper is available in ESA's Electronic Data Archive: *Ecological Archives* E086-032-S1.