# The Influence of Plant and Herbivore Characteristics on the Interaction between Induced Resistance and Herbivore Population Dynamics

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ABSTRACT: Induced plant resistance may contribute to regulating or driving fluctuations in insect herbivore populations. However, experimental demonstrations of induced resistance affecting long-term herbivore population dynamics are lacking, and few models find that induced resistance drives cycles in herbivore populations. Here a simulation model is used to explore the influence of characteristics of the plant-herbivore system on the likelihood that induced resistance can regulate or drive cycles in herbivore populations. Results of this model suggest that induced resistance may cause fluctuations in herbivore populations under more conditions than previously thought. The model incorporates parameters for the timing and strength of induced resistance and for herbivore mobility and host-plant selectivity. Results are presented for two configurations of the model: forest (many herbivore generations per plant generation) and crop (few herbivore generations per plant generation). In simulations of this model, induced resistance in the absence of other density-dependent factors can regulate herbivore populations. Induced resistance can also drive fluctuations in herbivore populations when there is a time lag between damage and the onset of induced resistance. The time lag required to cause fluctuations depends on characteristics such as the strength of induced resistance and the mobility of the herbivore.

*Keywords:* induced resistance, population dynamics, plant-insect interactions, selectivity, timing, mobility.

Determining which factors regulate or drive fluctuations in herbivorous insect populations continues to be a focus of both ecological and agricultural research (e.g., Cappuccino and Price 1995). Because induced resistance in

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the host plant can be a density-dependent function of herbivore damage and, thus, of herbivore population size (e.g., Karban and English-Loeb 1988; Myers 1988a; Kogan and Fischer 1991; Baldwin and Schmelz 1994), it could provide the negative feedback necessary to regulate or drive cycles in herbivore populations (Rhoades 1985; Turchin 1990). However, few experiments have examined whether induced resistance can affect long-term herbivore population dynamics (Karban 1986), and few models have found that induced resistance can drive sustained fluctuations in herbivore populations (Edelstein-Keshet and Rausher 1989; Lewis 1994). In this article, I present a simulation model that explores how characteristics of the plant and herbivore may influence the interaction of induced resistance and herbivore population dynamics. Results of this model suggest that induced resistance may be more likely to contribute to fluctuations in herbivore populations than previously thought and that characteristics of the plant and herbivore can affect the impact of induced resistance on herbivore population dynamics.

Induced resistance can be defined as any change in plant quality that results from herbivore damage and has a negative effect on herbivore preference for or performance on the plant (Karban and Myers 1989; Karban and Baldwin 1997). Many plant characteristics, ranging from secondary chemistry to thorn density, can change in response to herbivore damage (Karban and Baldwin 1997). Induced resistance has been found in a wide variety of plant-herbivore systems (Karban and Myers 1989; Karban and Baldwin 1997) involving annuals and perennials, herbs and woody plants, and sedentary and mobile herbivores. Given the variety of induced responses and types of systems with induced resistance, the effects of induced resistance on herbivore population dynamics may vary across systems. Characteristics of the plant (timing and strength of induced resistance) and herbivore (mobility and selectivity) may be important for determining how the effects of induced resistance differ among systems (Karban and Myers 1989).

Two aspects of the timing of induced resistance should influence the interaction between induced resistance and herbivore dynamics: the time lag from damage to induced resistance and the decay rate of induced resistance in the absence of herbivory. A lag between damage and plant response would delay the density-dependent action of induced resistance. This delay should increase the likelihood of cycles in the herbivore population (Benz 1974; Rhoades 1985; Myers 1988*b*) since delayed density dependence causes cyclic dynamics in both discrete- and continuous-time models of single species populations (May 1973; Berryman et al. 1987). Lags could arise if the mechanism for increased resistance does not work instantaneously (e.g., if induced resistance is expressed only in plant parts produced after damage) or if a damage threshold must be exceeded to provoke induced resistance (e.g., Wallner and Walton 1979; Williams and Myers 1984). Once induced resistance is produced, it may decay in the absence of damage (e.g., Iannone 1989; Underwood 1997). Without such a decay, feedback to herbivore population size should be reduced because plants could respond only to herbivore population increases, not decreases. Previous models (Edelstein-Keshet and Rausher 1989; Lundberg et al. 1994) suggest that the decay rate of induced resistance can affect the likelihood of herbivore population regulation.

The mobility and selectivity of the herbivore may also affect the impact of induced resistance on herbivore dynamics. Many models of induced resistance have assumed that herbivores are mobile and nonselective (but see Lewis 1994; Morris and Dwyer 1997). However, herbivores are known to vary in their mobility and selectivity (ability to detect and respond to variation in plant quality; Bernays and Chapman 1994). The relative speed of induced resistance and herbivore movement may affect the impact of induced resistance on herbivore populations and the degree of heterogeneity in induced resistance among plants. Selective herbivores might be less affected by induced resistance because they can choose less resistant plants, assuming that induced resistance varies among plants. Results of a previous model (Edelstein-Keshet and Rausher 1989) suggest that mobile, nonselective herbivores do not maintain variation in induced resistance in plant populations.

Relatively few theoretical studies have addressed the interaction of induced resistance and herbivore dynamics. Models have addressed the effect of induced resistance on herbivore spatial dynamics (Lewis 1994; Morris and Dwyer 1997), the evolution of induced resistance (Frank 1993; Adler and Karban 1994), and the effect of induced resistance on herbivore population dynamics (Fischlin and Baltensweiler 1979; Edelstein-Keshet 1986; Edelstein-Keshet and Rausher 1989; Frank 1993; Lundberg et al. 1994). Some of these models have found that induced resistance

may have important consequences for herbivore dynamics, such as regulating or driving cycles in herbivore populations under restricted conditions.

However, previous models have not thoroughly explored how characteristics of the plant-herbivore system may influence the interaction of induced resistance and herbivore dynamics. In particular, while time lags may be critical for cycling, previous models have not explicitly manipulated lags (though in some studies, time delays arising from other aspects of the models are related to cycling: Edelstein-Keshet and Rausher 1989; Lundberg et al. 1994). Several models have considered the effects of herbivore selectivity or mobility (Lewis 1994; Morris and Dwyer 1997), but no previous model has addressed both characteristics of the plant and the herbivore. In the model presented here, I explore the influence of individual characteristics of the plant-herbivore system and their interactions on the likelihood that induced resistance can regulate or drive cycles in herbivore populations. As a result of the complexity of explicitly modeling these interactions, I have used computer simulations rather than an analytical model.

## A Simulation Model

This model is based loosely on the analytical framework of Edelstein-Keshet and Rausher (1989) and describes an inducible plant-herbivore system with a quantitative induced response. More qualitative or discrete responses, such as leaf drop or changes in phenology (e.g., Preszler and Price 1993), require a different modeling approach. The model follows each individual in the herbivore and plant populations but ignores stage structure (such as differences between adult and larval insects) within populations. There are three nested loops in the model. The "herbivory" loop consists of herbivore movement among plants, herbivore feeding, and changes in levels of induced resistance in plants. The "herbivore generation" loop includes multiple herbivory loops, followed by herbivore reproduction. The "plant generation" loop consists of multiple herbivore generation loops and plant reproduction.

Two special cases of plant reproduction are considered here. In the first case, the plant reproduction loop is omitted entirely. This case approximates a forest system with a large number of herbivore generations in each plant (tree) generation. The second case approximates an annual agricultural crop, where levels of induced resistance in plants are set to zero each generation by replanting, but plant population size is constant. Because plant population dynamics are ignored in these two cases, the model consists of two basic equations describing the dynamics of induced resistance and the herbivore population. The first equation

describes the level of induced resistance in an individual plant $i$ at time $t + 1$ ($I_{i,\ t+1}$):

$$I_{i,\ t+1} = \frac{\alpha_{i,\ t}H_{i,\ (t-\tau)}}{b + H_{i,\ (t-\tau)}} + I_{i,\ t}(1 - \delta). \qquad (1)$$

The first term on the right-hand side of this equation represents the increase in resistance in a plant in response to herbivore damage in one time step as a saturating function of the number of herbivores on the plant $\tau$ time units (herbivory loops) previously ($H_{i,\ t-\tau}$; fig. 1A). The time lag between damage and induced resistance is thus represented by $\tau$. In this term, induced resistance increases to a maximum $\alpha_{i,\ t}$ at a rate governed by the half-saturation constant (b). Empirical evidence from several systems suggests that induced resistance often increases with increasing damage at a single damage event (e.g., Karban 1987; Kogan and Fischer 1991; Underwood 1997). The second term on the right-hand side of equation (1) represents the decay of previously induced resistance at rate $\delta$.

Two further assumptions about induced resistance are incorporated into the expression determining the value of $\alpha_{i,\ t}$ in equation (1). First, it is assumed that there is a physiological limit ($\beta$) to the level of induced resistance in an individual plant (fig. 1B). Factors that could cause such a limit include resource limitation or autotoxicity if resistance is a result of the 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 ($\alpha_{i,\ t}$) is assumed to be a linear function of the resistance level of plant $i$ at time $t$, ($I_{i,\ t}$; see also fig. 1B): $\alpha_{i,\ t} = (-\frac{\hat{\alpha}}{\beta}I_{i,\ t} + \hat{\alpha})$. The maximum value of $\alpha_{i,\ t}$ is $\hat{\alpha}$, which occurs when $I_{i,\ t} = 0$ (i.e., in an uninduced plant). The closer the plant is to the physiological limit of induced resistance ($\beta$), the more restricted its ability to respond becomes.

The second equation in the model describes the herbivore population size in one generation ($H_{t+g}$) as a function of its size in the previous generation ($H_t$; where one herbivore generation consists of $g$ herbivory loops), and the mean level of induced resistance in plants eaten by herbivores ($\bar{I}$):

$$H_{t+g} = H_t\left[1 + \gamma\left(1 - \frac{\bar{I}}{I_c}\right)\right]. \qquad (2)$$

It is important to note that this equation includes no density-dependent effects other than induced resistance, which according to equation (1) is a function of herbivore density. In equation (2), $\gamma$ is the herbivore population growth rate in the absence of density dependence, $\bar{I}$ (ranging from
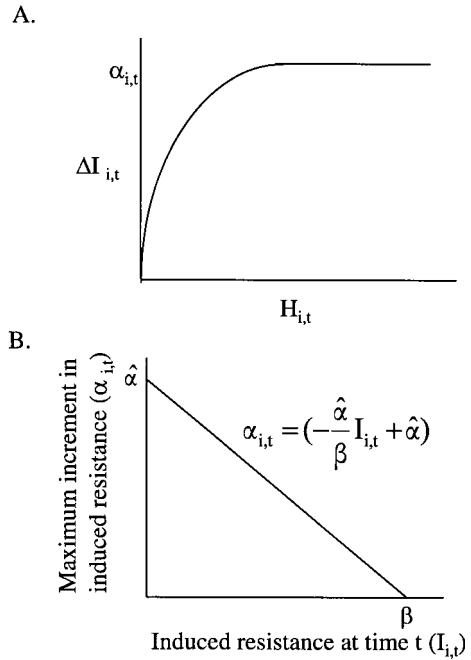


**Figure 1:** Two assumptions of the model about induced resistance. *A,* The amount of new induction in response to any one event ($\Delta I_{i,\ t}$) is a saturating function of the amount of damage ($H_{i,\ t}$) with maximum $\alpha_{i,t}$. The maximum increase in induction in plant $i$ from time $t$ to time $t + 1$ ($\alpha_{i,\ t}$) is a linear function of the level of induced resistance already present in the plant ($I_{i,\ t}$). The maximum increase $\alpha$ cannot exceed $\beta$, the maximum possible level of induced resistance.

0 to $\beta$, the maximum level of induced resistance) is the average level of induced resistance in plants eaten by herbivores over the previous generation, and $I_c$ is the critical level of induced resistance required to reduce herbivore population growth rate to zero. Note that as $I_c$ increases, the impact of a given average level of induced resistance ($\bar{I}$) decreases.

The model incorporates two assumptions concerning the herbivores. The first assumption is that after leaving a plant, an herbivore is equally likely to arrive at any other plant; spatially explicit movement is not included in the model. Although herbivores alight on plants at random, they may leave plants nonrandomly (selective herbivores) or randomly (nonselective herbivores). It is reasonable to assume that selectivity operates primarily when herbivores leave plants, if herbivores distinguish between host plants only through contact with the plant. Although there is evidence for both prealighting and postalighting discrimination among individual plants (Bernays and Chapman 1994), it is not yet clear if one or the other of these mechanisms is more common, and there are systems in which insects do appear to land on plants at random (Rausher 1983). I performed simulations of the model exploring

four alternative herbivore movement rules (table 1). These rules allow the model to mimic herbivores that have high or low mobility and are either selective or nonselective.

To examine the effects of induced resistance alone on herbivore dynamics, the model also assumes that herbivores experience no density-independent mortality. Density-independent mortality is undoubtedly common in the field, but because it does not provide a negative feedback to herbivore densities, it should not cause regulation or cycles, although it might strongly affect average herbivore population size.

## Simulations

I used simulations of the model to determine how characteristics of the plant-herbivore system influence the likelihood that induced resistance will regulate or drive cycles in herbivore populations. To examine the effect of the timing of induced resistance, I manipulated $\tau$ (time lag to induced resistance) and $\delta$ (decay of induced resistance). To examine the strength of induced resistance, I manipulated $I_c$ (level of induced resistance reducing herbivore population growth rate to zero), and to examine the mobility and selectivity of the herbivores, I ran the model with each of the four herbivore movement functions. For the runs reported here, all other parameters were held constant, with $\hat{\alpha}$ and $\beta = 100$, b = 10, and $\gamma = 2$. For $\hat{\alpha}$ and $\beta$, the specific (arbitrarily chosen) values are less important than their relative values, with equal values indicating that the maximum induction at one time equals the physiological maximum over time. The value of b was also chosen arbitrarily. Increasing or decreasing b causes linear increases or decreases in *H*, leading to extinction in some cases where populations are close to zero for other reasons (data not shown). Values of $\gamma$ measured in insect populations range from 1.3 to 75 (Hassell et al. 1976). Increasing $\gamma$ beyond 2 can (depending on values of other parameters) cause stable herbivore populations to move to cycling and then extinction (as a result of cycles intersecting the *Y*-axis; data not shown; also see Hassell et al. 1976). There were 30 herbivory loops per herbivore generation in each run, and all runs were started with 50 plants and 10 herbivores. Decreasing the ratio of plants to herbivores (from 10 through 0.1) decreases the herbivore population (data not shown), leading to extinction in some fluctuating populations.

The results presented here are for two configurations of the model, both of which omit plant population dynamics. The "crop" configuration has three herbivore generations per plant generation, mimicking an annual crop plant–trivoltine insect system. The "forest" configuration has no plant reproduction, only herbivore reproduction. I chose to focus on these configurations because omitting

**Table 1:** Movement rules describing the probability that an herbivore moves from individual plant *i* at time *t* as a function of the level of induced resistance in the plant $(I_{i,\ t})$

| Herbivore selective? | Herbivore mobility | |
|---|---|---|
| | Low | High |
| No | .35 | .85 |
| Yes | $(1/.67\beta)\ I_{i,\ t}$[a] | $(1/.67\beta)\ 1_{i,\ t} + .5$[a] |

Note: Herbivores may have high or low mobility and may or may not be selective (i.e., respond to the level of induced resistance encountered). Values for high and low mobility were chosen arbitrarily. In the nonselective case, approximately 35% (low) and 85% (high) of herbivores move each herbivory loop. In the selective case, the number of herbivores moving depends both on whether they have high (*y*-intercept = .5) or low (*y*-intercept = 0) mobility and on the quality of plants encountered $(I_{i,\ t})$.

[a] Maximum = 1.

plant population dynamics simplifies exploration of the model considerably. In addition, crop and forest configurations are of considerable interest because of the potential use of induced resistance to control pests in agricultural systems (Karban et al. 1997) and because the most striking cycles in insect herbivore populations occur in forest systems.

Simulations of the model were run for either 150 herbivore generations or long enough that the output appeared to converge on the asymptotic dynamics (up to 300 herbivore generations). Runs were not replicated because it was found in initial replicate runs that the only random element in the model (herbivore movement) did not in practice generate appreciable variation among runs. The data recorded from each run included the size of the herbivore population, the average level and coefficient of variation of induced resistance in all plants, and the average level of induced resistance in plants eaten by herbivores in each generation. These values were calculated after the dynamics had reached their final state, using a minimum of 50 herbivore generations worth of data. The system was considered to have reached its final state when its behavior was consistent over at least 50 generations.

I characterized the steady state herbivore population size as the mean number of herbivores in the population over time. I classified the steady state behavior of the herbivore population into one of five (for the forest configuration) or four (for the crop configuration) categories. For both configurations, there were two categories in which herbivore populations were unregulated; herbivore populations less than one were considered extinct, and populations that exceeded 20,000 individuals within 50 generations were considered to have "escaped" regulation. It is possible that some runs that appeared to escape would have eventually leveled off at some very high equilibrium

or crashed to lower densities. For the forest configuration, regulated populations fell into three categories: stable, damped oscillations (taking more than three full oscillations to become stable), and cyclic (periodic, nondamping, oscillations). For the crop configuration, regulated populations fell into two categories: three-point or six-point cycles.

The simulation program was written in ANSI C, and simulations were run on a Sun SparcStationIPC Workstation. Descriptive statistics for each run were calculated using the Means procedure of SAS (SAS Institute 1989). As a check of the accuracy of the simulations, I obtained the steady state solution for the model by making additional assumptions allowing the dynamics of the plants and herbivores to be described by a system of two equations, one describing induced resistance, and one describing herbivore abundance. In all cases, simulation results match the steady state expectations closely.

## Results

In both the crop and forest configurations of the model, induced resistance can regulate herbivore populations, provided that $I_c \leq \beta$ (i.e., induced resistance must be strong enough to reduce herbivore population growth rate to zero). When $I_c > \beta$, simulated populations escape regulation (grow without bound). When $I_c < \beta$, whether or not induced resistance regulates populations depends on the level of $I_c$, and the timing of induced resistance ($\tau$ and $\delta$).

Simulated herbivore populations exhibit a range of dynamical behaviors including stability, damped oscillations, fairly extreme and persistent cycles, and irregular fluctuations. Whether induced resistance generates oscillations in herbivore populations depends on the relative lengths of the lag time ($\tau$) and herbivore generation time, the level of induced resistance necessary to reduce herbivore population growth to zero ($I_c$), and the number of herbivore generations per plant generation (crop vs. forest configuration). The effects of these individual parameters on oscillation of herbivore populations are described below. Oscillations of various periodicities were observed, including 6-, 8-, 10-, and 14-point cycles and irregular fluctuations. The amplitude of fluctuations is in some cases constant and in other cases variable within a run.

### Effects of Characteristics of the Plant and Herbivore on the Interaction of Induced Resistance and Herbivore Population Dynamics
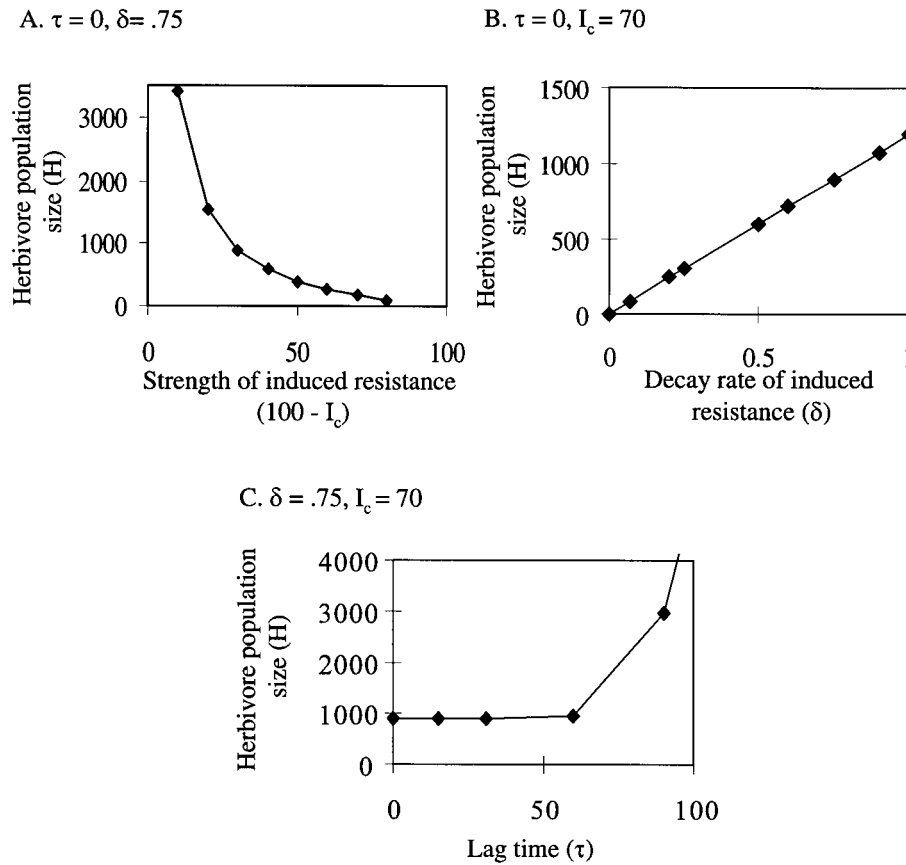
*Number of Herbivore Generations per Plant Generation.* The strongest effect of the number of herbivore generations per plant generation is that crop configurations of the
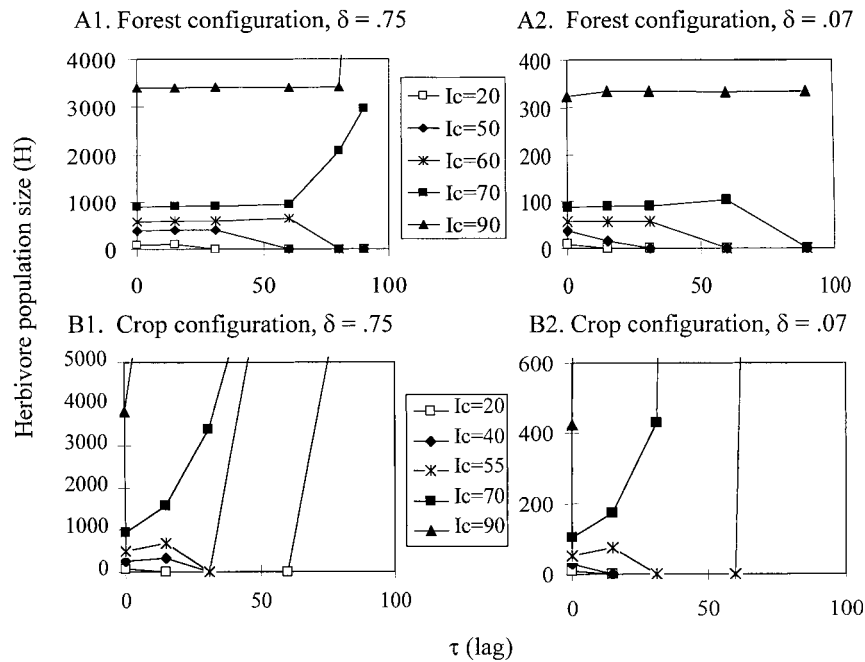
model are always subject to a "yearly" cycle generated by the advent of new, uninduced plants every third herbivore generation. Initially, herbivore populations increase. Over the next two generations, induced resistance causes the herbivore population to decrease, but then a new crop of plants again causes an increase. These cycles are not intrinsic but are driven by the outside intervention of forcing induced resistance to zero every three generations. Nevertheless, cycles such as this may be a common feature of systems with annual crops and multivoltine herbivores. If levels of induced resistance rise in a crop over the season, as in this model, herbivore populations would be expected to first increase and then decrease later in the season as plant quality deteriorates. In fact, censuses of some insect populations on crop plants show a pattern of initial increase, followed by decrease (e.g., Soroka and Mackay 1990; Boyd and Lentz 1994; Riggin-Bucci and Gould 1997). Although this pattern is consistent with the action of induced resistance, other factors, such as temperature changes and plant senescence, surely also contribute to decreases in herbivore populations later in the season.

*Characteristics of Induced Resistance* (*Strength and Timing*). The strength of induced resistance strongly affects average herbivore population size. The steady state size of the herbivore population increases exponentially as higher levels of induced resistance are required to reduce herbivore population growth rates to zero (fig. 2*A*). Weak induced resistance (high $I_c$) can lead to populations growing without bound, while very strong induced resistance (low $I_c$) can drive populations so low that they become extinct. The strength of induced resistance ($I_c$) also interacts with the timing of induced resistance to influence the likelihood of regulation and fluctuations in herbivore populations (see below).

The decay rate of induced resistance ($\delta$) has a relatively straightforward effect on herbivore dynamics in this model. Average herbivore population size increases with decay rate (fig. 2*B*), and the slope of this relationship remains constant over values of $\tau$. As decay becomes rapid, plant resistance levels become lower, and herbivore reproduction increases. The decay rate also interacts with the strength of induced resistance (e.g., fig. 3). Slower rates of decay lead to extinction of herbivore populations (lack of population regulation) at weaker levels of induced resistance (cf. $\delta = .07$ and $\delta = .75$ in fig. 3). There is also a suggestion that slower decay rates reduce the likelihood of persistent cycles, largely because populations that would otherwise exhibit cycles are driven extinct (fig. 3). This is in contrast to one previous model (Lundberg et al. 1994) in which longer decay times promoted damped oscillations of herbivore populations.

Time lags between damage and the production of in-

## A. $\tau = 0$, $\delta = .75$

## B. $\tau = 0$, $I_c = 70$

## C. $\delta = .75$, $I_c = 70$

**Figure 2:** The effect of strength of induced resistance ($100 - I_c$), decay rate of induced resistance ($\delta$), and time lag from damage to induction ($\tau$) on average herbivore population size ($H$). All data are for the forest configuration, and points indicate results of individual runs of the model.

duced resistance can influence the likelihood of regulation of herbivore populations. In general, as time lags increase, the likelihood of regulation (prevention of extinction or escape) decreases (fig. 3). How long a lag is required to prevent regulation depends on the strength of induced resistance and the decay time. Long lag times decrease the strength of induced resistance (increase $I_c$) needed to drive populations to extinction and allow the escape of populations at stronger levels of induced resistance (lower $I_c$). Lags less than a single herbivore generation can cause loss of regulation when induced resistance is very strong (e.g., fig. 3B1, B2). Crop configurations (systems with few herbivore generations per plant generation) are less likely to be regulated than forest configurations; they go extinct or grow without bound over a wider range of values of $\tau$.

Time lags strongly influence the likelihood that induced resistance will drive fluctuations in herbivore populations. In general, long lags drive fluctuations, but the length of lag required to cause fluctuations depends on the strength of induced resistance in the system. For shorter lag times,

persistent fluctuations occur with stronger induced resistance, while for longer lags, weaker induced resistance promotes fluctuations (fig. 4). Persistent fluctuations in crop configurations of the model are observed as six-point cycles rather than the yearly three-point cycle. In the crop configuration of the model, internally persistent cycles are produced at shorter lags and stronger levels of induced resistance than in the forest configuration.

The model suggests that lag time can also affect the mean size of the herbivore population ($H$) through its effect on population fluctuations (fig. 2C). Increasing lag times has no effect on herbivore population size until the lag becomes sufficiently long to provoke cycles. Cycling populations are then considerably larger on average than their stable counterparts.

*Characteristics of the Herbivore* (*Mobility and Selectivity*). In these simulations, populations of highly mobile herbivores exhibit cycles at shorter lag times than populations of relatively immobile herbivores (fig. 5). Herbivore mo-

**Figure 3:** Average herbivore population size (*H*) plotted against $\tau$ (lag time) for various values of $I_c$ (induced resistance reducing herbivore population growth rate to zero) and two values of decay rate of induced resistance ($\delta$). Each point represents a single run of the model. Points at 0 indicate extinct populations, trajectories that are truncated at the top of the graph indicate populations that have escaped (grow without bound). As time lags increase, herbivore populations cease to be regulated, either going extinct or escaping to very high densities.

bility alone does not strongly effect average herbivore population size (fig. 6), but there are effects of mobility on herbivore populations at a very fine scale. More mobile herbivores have very slightly higher population sizes than less mobile herbivores (fig. 7*A*). Mobile herbivores have larger populations because they experience very close to (or exactly) the average level of induced resistance in the plant population, while less mobile herbivores experience plants that are slightly more strongly induced than average (have lower $I_c$; fig. 7*B*). Less mobile herbivores experience more strongly induced plants because, by chance, some plants receive more herbivores than others and less mobile herbivores remain on these plants in spite of increasing levels of resistance. This causes variation among plants in their levels of induced resistance (fig. 7*C*).

The selectivity of herbivores had little effect on overall herbivore population size (fig. 6), except to increase the likelihood of herbivores escaping regulation at longer lag times. Selectivity did not strongly affect the likelihood of fluctuations in highly mobile herbivore populations (fig. 5) but did increase the likelihood of sustained fluctuations at higher strengths of induced resistance (lower $I_c$) in herbivores with low mobility. Selective herbivores, like highly mobile herbivores, experience close to the average level of induced resistance in the plant population, while nonse-

lective herbivores tend to experience slightly more highly induced plants (fig. 7*B*). Again, this occurs because nonselective herbivores tend to remain on induced plants, increasing the variance among plants in induced resistance level (fig. 7*C*).

### Can Herbivores Maintain Variation in Resistance Levels among Plants?

In this model, variation in induced resistance among plants is maintained over broad ranges of parameters. Variation among plants in resistance (coefficient of variation of $I_{i, t}$) is negatively exponentially related to herbivore population size (fig. 8*A*). As herbivore populations increase, variation among plants disappears because all plants become fully induced. However, variance among plants can be maintained with large herbivore populations if the population fluctuates (fig. 8*B*).

### Discussion

Three points stand out from this study. First, in this model, induced resistance can both regulate and drive persistent fluctuations in herbivore populations in the absence of other density-dependent factors. Second, characteristics of
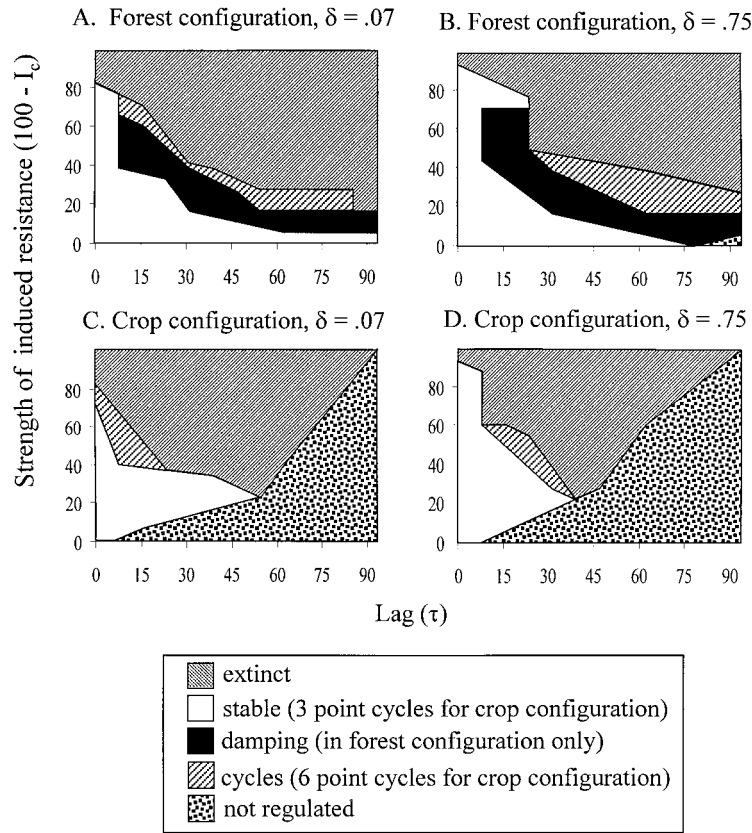
A. Forest configuration, δ = .07

B. Forest configuration, δ = .75

C. Crop configuration, δ = .07

D. Crop configuration, δ = .75

Lag (τ)

Strength of induced resistance (100 − $I_c$)

▨ extinct

☐ stable (3 point cycles for crop configuration)

■ damping (in forest configuration only)

▨ cycles (6 point cycles for crop configuration)

▨ not regulated

**Figure 4:** Dynamic behavior of herbivore populations in forest (*A*) and crop (*B*) configurations of the model under different combinations of the strength of induced resistance (100 − $I_c$) and lag time between damage and production of induced resistance (τ).

the plant and herbivore can affect the impact of induced resistance on herbivore dynamics. For example, both the strength and timing of induced resistance influence the likelihood of regulation or fluctuations and affect the average size of herbivore populations. Likewise, herbivore selectivity and mobility both affect the likelihood of fluctuations in the herbivore population. Importantly, the effects of these characteristics interact with each other, so that the effects of herbivore mobility, for instance, will depend on the length of the lag time in the system. The third important result of this study is that variation among plants in level of induced resistance can be maintained under many conditions in this model.

The question of what regulates insect herbivore populations has long been an issue in ecology (e.g., Turchin 1995). The results of this study, and previous theoretical results, indicate that induced resistance has the potential to regulate herbivore populations. The likelihood of regulation in this model is modified by the timing of induced resistance such that as the decay rate (δ) increases, fewer

populations are regulated as lags (τ) increase. This agrees qualitatively with Edelstein-Keshet and Rausher's (1989) finding that regulation depends on the relationship between decay rate and a composite parameter that can be thought of as the "time to induced resistance" (i.e., the ratio of the maximum rate of induction to the critical level of induced resistance reducing herbivore reproduction to zero). The strength of induced resistance can also affect the likelihood of regulation in the simulation model presented here. Regulation is only possible when induced resistance is strong enough to reduce herbivore population growth rates to zero (when $I_c < \beta$). Studies that have measured the impact of induced resistance on herbivore populations in the field have found that induced resistance is capable of reducing population growth rates (e.g., Hougen-Eitzman and Karban 1995; Karban and Baldwin 1997). Although induced resistance alone may not be strong enough in all systems to regulate herbivore populations, the effectiveness of induced resistance can be increased by combination with other density-dependent
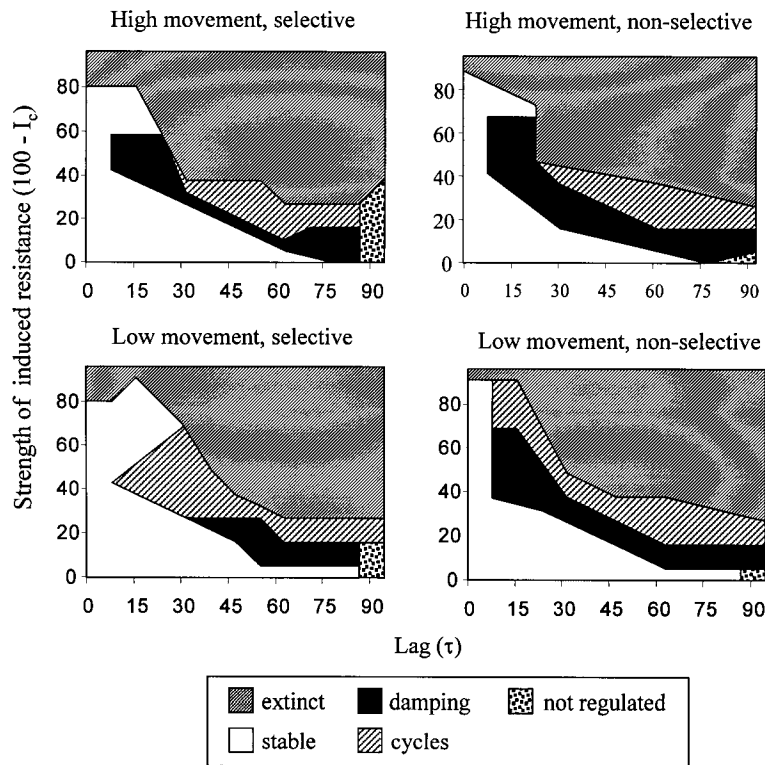
**Figure 5:** Dynamic behavior of four types of herbivore populations as a function of strength of induced resistance $(100 - I_c)$ and lag time between damage and induced resistance $(\tau)$ for the forest configuration of the model. For all graphs, $\delta = .75$.

factors, which would likely be acting on herbivore populations in the field.

Many authors have suggested that induced resistance might cause cycles in herbivore populations (e.g., Benz 1974; Haukioja 1980; Rhoades 1985; Myers 1988a). Although previous models have shown that induced resistance can rarely drive persistent cycles in herbivore populations (Edelstein-Keshet and Rausher 1989; Lundberg et al. 1994), in the model presented here, cycles are more common though still limited to a restricted set of parameter values. The ubiquitous yearly cycles observed in crop configurations of this model are likely to be restricted to annual plant systems where herbivores have more than one generation per season, or perennials whose level of induced resistance is reset to the uninduced state at the beginning of each growing season. Persistent cycles (and persistent irregular fluctuations) in herbivore populations were generated by a number of parameter combinations in this model, more often when induced resistance was relatively weak and time lags were relatively long (fig. 4). Time lags longer than an herbivore generation between damage and induced resistance have been observed in nat-

ural populations (e.g., Karban 1990; Bryant et al. 1991), and induced resistance lasting longer than one herbivore generation (which would also cause delayed-density dependence) is relatively common in woody species (Wallner and Walton 1979; Rhoades 1983; Hunter 1987). The model can produce fluctuations over four orders of magnitude, consistent with observations from the field (Turchin 1990). Because lag times are explicitly manipulated in this model, the results of these simulations provide the strongest theoretical support to date for the intuitively sensible idea that induced resistance might drive fluctuation in herbivore populations.

This model suggests that we might expect cycling or fluctuation to be more common in selective and less mobile versus nonselective and highly mobile herbivore populations, assuming that the herbivore is monophagous. The model also predicts that, for monophagous herbivores, greater selectivity may be linked to higher population sizes. Although perhaps the majority of the world's herbivorous insects are specialists (Bernays and Chapman 1994), there are also many species that are polyphagous. The effects of selectivity on herbivore dynamics might be different for
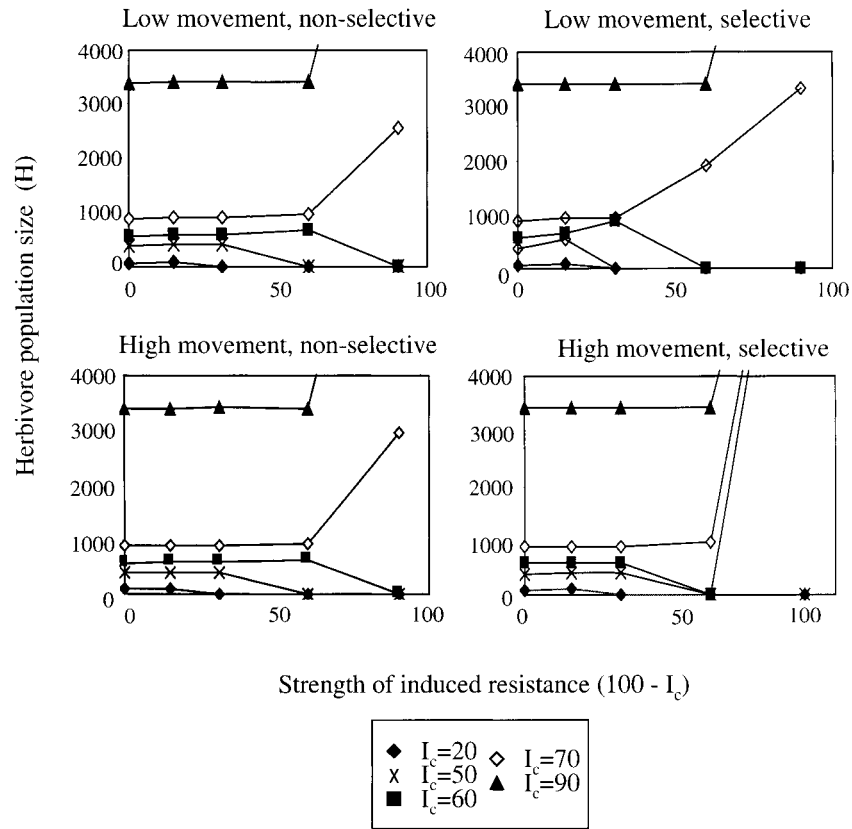
**Figure 6:** Mean herbivore population size for four types of herbivores, as a function of time lag and strength of induced resistance. Points at 0 indicate extinct populations. Trajectories that are truncated at the top of the graph indicate escaped populations. For all graphs, $\delta = .75$.

polyphages, which can choose among species of plants with and without induced resistance, in addition to choosing among individual plants within a species.
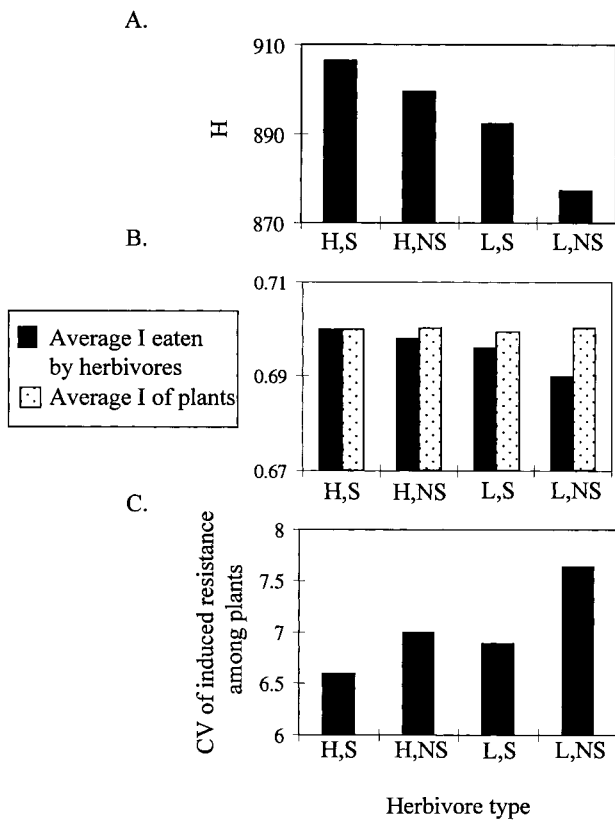
Unlike Edelstein-Keshet and Rausher (1989), the model presented here indicates that variance in levels of induced resistance among plants can be maintained even in the absence of recruitment of new plants into the population. In this model, where herbivores alight on plants at random, variance in induced resistance is maintained when herbivore population sizes are small, even when herbivores are highly mobile and nonselective. With few herbivores in the population, some plants are free of herbivores and return to lower levels of induced resistance by chance. Fluctuating herbivore populations also maintain variance in induced resistance (fig. 8*A*) because fluctuating populations are sometimes small. Variation among plants in induced resistance levels may influence how induced resistance affects herbivores. Variation in quality among plants may cause selective herbivores to move more in search of suitable hosts (Schultz 1983). Such movement could increase the herbivore's risk of predation or involve

costs, such as lost foraging time (factors that are omitted from the model presented here).
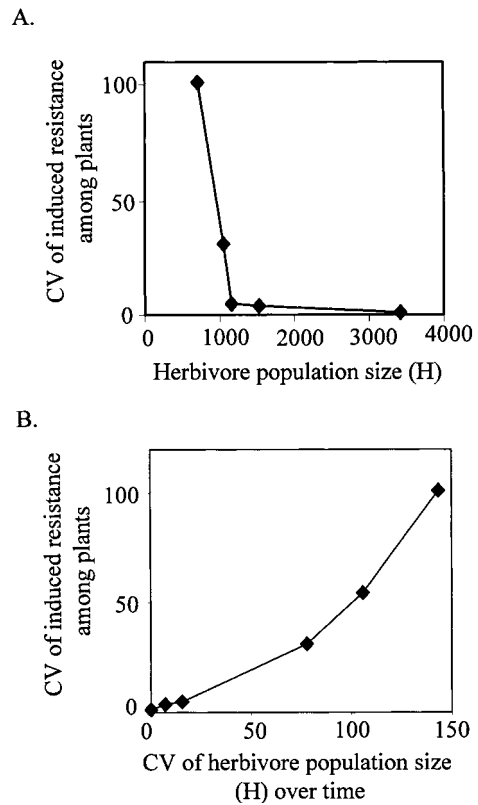
Experimental data on the effects of induced resistance on aspects of long-term population dynamics, such as population regulation and fluctuation, are still rare because these data are difficult to obtain, especially in an experimental setting (but see Harrison and Cappuccino 1995; Underwood 1997). This lack of data makes it difficult to directly compare the predictions of this model with observations from the field. The model presented here suggests that the effect of induced resistance on herbivore population dynamics should not be consistent across systems with different characteristics. Future studies may thus benefit from comparing the effects of induced resistance among systems. For example, the effect of induced resistance on herbivore dynamics could be compared between selective and nonselective herbivores or among genotypes or species of plants with different timings or strengths of induced resistance.

That induced resistance regulates herbivore populations in this model supports the idea that induced resistance

might be useful for controlling pests in agricultural systems (Karban 1991). The potential for very strong induced resistance to cause local herbivore extinction could be an extremely useful asset in a crop plant. The results of this analysis suggest, however, that regulation may be less common in annual crop systems than in natural or agricultural forest systems. In fact, failures of regulation in crop configurations of the model result more often from escapes to very high population densities (an undesirable result) than from extinctions. The exponential relationship between the strength of induced resistance and herbivore population size predicted by the model suggests that for a plant with weak induced resistance, small increases in the efficacy of resistance might produce large reductions of herbivore populations. Although large gains in control of pest populations could result initially from breeding for increased induced resistance, efforts to increase resistance beyond some point may not be as productive. Results of

A.



B.



**Figure 8:** *A,* Coefficient of variation (*CV*) among plants in their levels of induced resistance decreases with herbivore population size (*H*). Each value of *H* along the *X*-axis is associated with a different value of $I_c$ (higher $I_c$ leads to higher *H*). *B, CV* of levels of induced resistance increases with the degree of fluctuation in herbivore population size (*CV* of *H* over time). For both *A* and *B*, points indicate results of individual runs of the model with low mobility, nonselective herbivores, $\tau = 60$ and $\delta = .75$.

the model presented here suggest that knowing the characteristics of individual plants and herbivores in a system may help to determine whether an herbivore population is likely to exhibit cycles. Cycles may be undesirable in agricultural systems for at least two reasons. First, cycling populations may simply be harder to manage. Second, results of the model suggest that persistent population fluctuations may be associated with larger average population sizes. Breeders hoping to use induced resistance to control pest populations thus might want to avoid long lags, because lags may lead to both unstable and larger herbivore populations.

A.

B.



C.

**Figure 7:** Effect of herbivore selectivity and mobility on (*A*) herbivore population size (*H*), (*B*) average induced resistance of plants and plants eaten by herbivores, and (*C*) coefficient of variation of induced resistance among plants. Herbivore type: *H* = high mobility, *L* = low mobility, *S* = selective, *NS* = nonselective. For all graphs lag = 0, $\delta = .75$ and $I_c = 70$.

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