

Reprinted from pages 211-230 in A. A. Agrawal, S. Tuzun, and E. Bent, editors. 1999. **Inducible plant defenses against pathogens and herbivores: Biochemistry, ecology, and agriculture.** American Phytopathological Society Press, St. Paul, MN (USA).

The Influence of Induced Plant Resistance on Herbivore Population Dynamics

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Abstract

Verbal and mathematical theory suggest that induced resistance in plants may affect the long-term population dynamics of herbivores. However, there is little direct empirical evidence that induced resistance affects herbivore dynamics in the field. This chapter reviews both theoretical and empirical evidence that induced resistance may affect herbivore population dynamics. Methods for gathering new evidence, including the use of chemical elicitors, natural damage and genotypic variation to manipulate induced resistance, are also discussed. Finally, a simulation model of the interaction of induced resistance and herbivore population dynamics that includes plant population dynamics is presented. This model suggests that the relative number of herbivore to plant generations in a system should strongly affect the influence of induced resistance on herbivore population dynamics.

Introduction

Induced plant resistance to damage has clearly been shown to affect both the behavior and performance of individual herbivores. Induced resistance may also contribute to aspects of herbivore population dynamics such as outbreaks, cycles, and population regulation that have long fascinated ecologists (Cappuccino 1995). From the perspective of understanding herbivore population dynamics, induced resistance can be defined as any change in a plant resulting from damage and having a negative effect on herbivores (Karban and Baldwin 1997). Induced resistance is likely to be important for long-term herbivore dynamics because in at least some systems, the strength of induced resistance is a density dependent function of the amount of damage the plant receives (see below). This density dependence makes induced resistance a potential source of the negative feedback necessary to regulate herbivore populations (Rhoades

1985, Turchin 1990). Induced resistance that is delayed relative to the time of damage might also increase the likelihood of fluctuations in herbivore populations, because delayed density dependence has been shown to drive cycles in population dynamics models (May 1973, Berryman et al. 1987). Although it has frequently been suggested that induced resistance could be responsible for regulating or driving cycles in herbivore populations (Benz 1974, Haukioja 1980, Rhoades 1985, Myers 1988), very few empirical or theoretical studies have directly addressed the effects of induced resistance on long-term herbivore population dynamics.

Empirical Evidence that Induced Resistance Affects Herbivore Population Dynamics

Several kinds of indirect evidence can help us understand how induced resistance may affect the population dynamics of herbivores. For example, we can determine whether induced resistance affects herbivore characters such as population growth rate or mortality, which influence population dynamics. We can also ask whether the effects of induced resistance on herbivores are of the type that might regulate herbivore populations (density dependent effects) or produce cycles in those populations (delayed density dependence). However, even if indirect evidence indicates that induced resistance has the potential to influence herbivore populations, direct evidence is still required to demonstrate that induced resistance alters long-term patterns of herbivore population dynamics. In this section, direct and indirect empirical evidence for effects of induced resistance on herbivore population dynamics are briefly reviewed (see Karban and Baldwin 1997 for a recent review), and the pros and cons of methods available for gathering further evidence are discussed.

Studies in both the lab and the field have demonstrated that induced resistance affects herbivore performance characters (such as feeding preference, growth rate, fecundity, and survival) that should influence herbivore population size (Karbon and Myers 1989, Karban and Baldwin 1997). This evidence suggests that induced resistance has the potential to influence herbivore population dynamics. Studies of herbivore populations over a few generations have also demonstrated negative effects of induced resistance on aspects of short-term dynamics such as population size or population growth rate (Karbon and Baldwin 1997).

There is also evidence that induced resistance is density dependent in many systems (e.g., Karban and English-Loeb 1988, Baldwin and Schmelz 1994), and thus has the potential to regulate herbivore populations. For induced resistance *alone* to regulate herbivore populations, it should be able to reduce herbivore population growth rates to zero (Underwood 1999). How often induced resistance is this strong is not yet clear, though in most studies effects on herbivore performance are not very large (Karbon and Baldwin 1997). However, induced resistance could work in conjunction with other density dependent influences, such as predation, to regulate herbivore populations

(Underwood 1999). There have as yet been no experimental demonstrations that induced resistance regulates, or contributes significantly to regulating, any population. While the influence of density dependence has been demonstrated in herbivorous insect populations (e.g., Woiwood and Hanski 1992), this density dependence has not been linked to induced resistance.

Theory suggests that for induced resistance to drive cycles in herbivore populations, the effect of induced resistance on herbivores must be delayed relative to herbivore generation time so that damage by herbivores in one generation influences the performance of later generations (e.g., Edelstein-Keshet and Rausher 1989, Underwood 1999). Induced resistance can be delayed either by a lag between damage and the induction of resistance or by slow decay of induced resistance in the absence of further herbivory. Existing data on the timing of induced resistance support the idea that induced resistance could contribute to cycles in some herbivore populations (Karban and Baldwin 1997). Studies of induced resistance in annual plants (e.g., Edwards et al. 1985, Baldwin 1988a, Malcolm and Zalucki 1996, Underwood 1998) indicate that lag and decay times are generally fairly short relative to herbivore generation times, although even short lags might contribute to cycles in herbivores with very short generation times (e.g., aphids or mites). Studies in several cycling forest systems indicate that the decay of induced resistance can be substantially longer than herbivore generation times (decays taking several years) (Baltensweiler 1985, Haukioja and Neuvonen 1987). This indirect evidence suggests that induced resistance may contribute to cycles in herbivore populations.

Although indirect evidence thus suggests that induced resistance might affect long-term herbivore dynamics in at least some systems, there are very few direct observations of effects on population dynamics in either the lab or the field. This lack of data is understandable given the difficulty of studying population dynamics directly (especially in the forest systems that may be strongly influenced by induced resistance). The demonstrated effects on short-term population size do indicate that induced resistance may be useful in controlling pests on crops within a season (Karban 1991), and that induced resistance has the potential to influence long-term dynamics in agricultural and natural communities. However, these data cannot tell us whether induced resistance actually affects the aspects of long-term population dynamics that have excited the most interest in this field (regulation and cyclic fluctuation).

Techniques for Gathering Further Evidence

The ideal approach to evaluating the relative importance of induced resistance and other factors in influencing the population dynamics of herbivorous insects would be to conduct controlled experiments at the scale of whole populations, in which induced resistance is manipulated and effects on long-term population dynamics are observed. Unfortunately, experiments of this sort would be prohibitively difficult in most systems. There are however, more feasible approaches that can provide useful information about the effect of

induced resistance on long-term dynamics, including correlational studies, direct observation of rapid-cycling herbivores, and density manipulation experiments.

Most studies that have explicitly addressed induced resistance and long-term herbivore dynamics in the field have been carried out in forest systems using techniques such as correlating herbivore dynamics with changes in plant-quality (e.g., Benz 1974), and transplanting herbivores between outbreaking and non-outbreaking populations (e.g., Myers 1981). These techniques allow a high level of realism by examining herbivore dynamics at very large scales, and comparing current conditions with existing long-term census data. However, because induced resistance cannot be manipulated, the precision with which the effects of induced resistance can be isolated from other factors is limited in these studies.

Studying herbivores with very short generation times (such as aphids, mites, whiteflies and thrips) might be one practical way to combine direct observations of long-term dynamics with manipulation of induced resistance. Several studies of induced resistance in systems with rapidly cycling herbivores do contain data over what must be many herbivore generations (e.g., Karban 1986, Shanks and Doss 1989). However, these studies sample population size only a few times - making it difficult to use these data to examine long-term population dynamics. Many census data points are required to adequately describe patterns of population dynamics, and particularly to assess effects on regulation (Turchin 1997). More frequent sampling might allow for characterization of within-season dynamics in these populations. However, since populations of these insects are also strongly affected by seasonal patterns, census data over many years may still be necessary to provide a true picture of their dynamics (Harrison and Cappuccino 1995). Once long-term census data are gathered, regardless of the generation time of the herbivore, several kinds of information can be extracted. A number of methods can be used to detect the regulating action of density dependence in census data, though this field has been very contentious (Turchin 1997). The presence and periodicity of cycles can be assessed from the autocorrelation function for the data (Berryman and Turchin 1997). Finally, a population dynamic model can be fit to the data and used to analyze the stability of the population dynamics (Edelstein-Keshet 1988).

In cases where direct observation of population dynamics is not possible, density manipulation experiments allow estimation of long-term dynamics from short-term (as little as one generation) population data. In this type of design, populations with a range of initial densities are followed for one or more generations, and data on initial density and density in the next generation are used to construct a recruitment curve. This curve can be fit with a discrete population dynamics model (such as the Ricker (Edelstein-Keshet 1988) or Hassell (Hassell 1975) models), and the model can be analyzed to determine the equilibrium population size, the stability of the equilibrium and tendency of the population to cycle. For organisms with overlapping or continuous generations, a similar approach could be used by fitting continuous population

dynamic models to census data, with the power of the method being improved by combining data from populations initiated at several initial densities (Pascual and Kareiva 1996).

Combination of density-manipulation with manipulation of induced resistance would allow examination of the effect of induced resistance (or even different levels or types of induced resistance) on the estimated long-term dynamics of herbivore populations. Depending on the choice of system, this design could incorporate effects at the scale of the whole population, or at much smaller scales. Density manipulation approaches are only beginning to be used in ecological experiments (Belovsky and Joern 1995, Underwood 1997), though related techniques are standard in the management of fisheries (Roughgarden 1998). Harrison and Cappuccino (1995) discuss guidelines for this type of experiment, and suggest that this technique should be more widely used to search for population regulation.

Estimating long-term dynamics using density manipulation and model fitting also has several drawbacks, one of which is that the experiments can be very labor intensive. A more serious drawback is that using models fit to field data in one generation to estimate dynamics over long periods of time assumes that the parameters of the model will not change over time. This assumption may be more valid for some systems than for others. For instance, the characteristics of crop plants are likely to remain fairly constant from year to year, as opposed to natural perennial plants whose characteristics may change with age between years. Estimation of long-term dynamics is thus not suitable for precise prediction of the size of particular populations over time, but should allow examination of qualitative differences among populations subject to different conditions.

Manipulating Induced Resistance

Whether population dynamics are directly observed or estimated, the most rigorous experimental examination of the effects of induced resistance requires the experimenter to manipulate induced resistance and create appropriate controls. A new and appealing method of manipulation is the application of chemical elicitors that cause the plant to produce induced resistance. Because elicitors can be easily applied to the plant, and because their effects are dose-dependent (Farmer and Ryan 1990, Baldwin et al. 1998), elicitors have clear advantages in precision and ease of manipulation. However, there are several drawbacks that might outweigh these advantages for studies of the ecological effects of induced resistance. Some elicitors, jasmonic acid for instance, have widespread effects on plant physiology (Creelman and Mullet 1997), so that the effects of elicitor-induced resistance could be confounded with other physiological changes in the plant that are not normally caused by herbivore feeding. Another potential drawback is that while elicitors can turn plants “on” and keep them on via repeated application (Thaler et al. 1996), there is nothing to prevent untreated plants from also being turned on by herbivores.

So while elicitors can create initially different conditions, any experiment that runs long enough to allow “natural” induction might run into the problem of elicitor and non-elicitor treatments converging in induction over time. This problem may not materialize if elicitors produce larger responses than herbivores do (Thaler et al. 1996), although if the induced resistance caused by elicitors is outside the natural range of responses, results of experiments using elicitors may not accurately reflect natural conditions.

It might be possible to correct the problem of induced and non-induced treatments converging during an experiment by combining elicitors with methods of inhibiting induced resistance. These methods include pot-binding, which has been shown in at least one case to block induced resistance (Baldwin 1988b), and chemical inhibitors of induced resistance (Hartley 1988, Baldwin et al. 1990, Stout et al. 1998). Pot-binding has the advantage of potentially remaining effective throughout the experiment, thus maintaining differences between treatment and control plants. Disadvantages of pot-binding are that it has only been shown to work in one system, and it may affect aspects of the plant’s physiology that influence herbivores in addition to induced resistance. Like chemical elicitors of induced resistance, chemical inhibitors have the potential drawback of affecting aspects of the plant’s physiology not normally associated with induced resistance.

Another method of manipulating induced resistance levels is pre-damaging plants using either artificial damage (e.g., Edwards et al. 1985, Hanhimaki 1989) or application of herbivores (e.g., Hanhimaki 1989, Shanks and Doss 1989, Karban 1993, Agrawal 1998). The dynamics of herbivore populations on pre-induced plants could then be compared with those on plants that start out with no damage, and thus no induced resistance. Artificial damage is relatively precise and easy to produce. However, a number of studies indicate that in some systems artificial damage does not produce the same type or strength of induced resistance as natural damage (Baldwin 1988a, Hanhimaki 1989). Using herbivores to produce the initial damage is logistically more difficult, but has the virtue of being more likely to provoke the appropriate induced response. Both methods of pre-damaging plants are subject to the problem of convergence between induced and non-induced treatments during the experiment.

An alternative approach for creating induced and non-induced treatments is using genotypes of plants that inherently differ in their levels of induced resistance. This technique is currently being used to examine the effects of induced and constitutive resistance on herbivore population dynamics in time (N. Underwood, unpublished data) and in space (W. Morris, unpublished data), and has been used to look for relationships between induced and constitutive resistance (Zangerl and Berenbaum 1991, Brody and Karban 1992, English-Loeb et al. 1998, N. Underwood, unpublished data). Among plant differences in characters other than induced resistance could complicate the interpretation of differences in herbivore dynamics among genotypes differing in induced resistance. In theory, it should be possible through screening of genotypes,

breeding or transgenics, to obtain lines that are isogenic except for genes controlling the production of induced resistance. Significant genetic variation for induced resistance has been documented in several systems (e.g., Zangerl and Berenbaum 1991, Brody and Karban 1992, English-Loeb et al. 1998, Agrawal, this volume, N. Underwood, unpublished data). Agricultural systems, where resistance and other characters have already been documented for a variety of genotypes, may provide particularly convenient places to search for appropriate genotypes. Once appropriate genotypes are located, using genotypic variation to create treatments with high and low induced resistance is convenient, and differences among treatments should be maintained throughout experiments. A further advantage of this approach is that it allows consideration of evolutionary as well as population dynamic questions.

Evidence from Mathematical and Simulation Models

Over the past three decades, many authors have presented verbal theory concluding that induced resistance might regulate and drive cycles in herbivore populations (Karbon and Baldwin 1997). More recently, both analytical and computer simulation modeling have been used to more rigorously explore the interaction between induced resistance and herbivore populations. Some of these models explicitly focus on effects of induced resistance on long-term population dynamics (Fischlin and Baltensweiler 1979, Edelstein-Keshet and Rausher 1989, Lundberg et al. 1994, Underwood 1999). Other models focusing on issues such as the evolution of induced resistance (Frank 1993, Adler and Karban 1994), and effects of induced resistance on the spatial dynamics of herbivores (Lewis 1994, Morris and Dwyer 1997), also make predictions about temporal dynamics. The predictions of these models vary with the type of plant-herbivore system they model, suggesting that characteristics of the plant-herbivore system, such as the strength and timing of induced resistance, mobility and selectivity of the herbivore, and relative lengths of plant and herbivore generation times, will affect the influence of induced resistance on herbivore population dynamics.

Results of existing models suggest that induced resistance has the potential to regulate herbivore populations (i.e., prevent extinction and growth without bound). Regulation is only possible when induced resistance can reduce herbivore population growth rates to zero, and the probability of regulation tends to increase with the strength of induced resistance, though regulation can also depend on the timing of induced resistance, and the relative lengths of plant and herbivore generations (Edelstein-Keshet and Rausher 1989, Underwood 1999).

The likelihood that induced resistance can produce cycles in herbivore populations varies among models. Some models have found that induced resistance by itself cannot produce persistent cycles, though it may produce cycles that damp over time (Frank 1993, Adler and Karban 1994, Lundberg et al. 1994, Morris and Dwyer 1997). Other models have found that induced resistance drives persistent cycles in herbivore populations under certain conditions (Fischlin and Baltensweiler 1979, Edelstein-Keshet and Rausher

1989, Lewis 1994, Underwood 1999). Both damping and persistent cycles are associated with delays in the timing of induced resistance. The longer the delays relative to herbivore generation time, the more likely cycles are, and the less likely regulation becomes.

Induced resistance has been found in a very wide variety of plant-insect systems, involving annual and perennial plants, and both uni- and multivoltine insects. This raises the question of how the relative lengths of the generation times of the plant and herbivore affect the impact of induced resistance on herbivore dynamics. To examine this question, models need to include plant population dynamics as well as herbivore dynamics. Adding plant dynamics to models might increase the likelihood of cycling simply due to the interaction between equations for the two populations, as occurs in some predator-prey models (Edelstein-Keshet 1988). Several continuous time analytical models have included plant population dynamics, with plant and herbivore generation times equal in all cases (Frank 1993, Adler and Karban 1994, Lundberg et al. 1994). All three of these models have some tendency towards oscillation in plant and herbivore populations, although plant dynamics are not discussed at length for these models.

A Model Including Both Plant and Herbivore Population Dynamics

The simulation model of Underwood (1999) can be modified to examine how variable plant population size and the relative lengths of plant and herbivore generations affect the influence of induced resistance on herbivore population dynamics. The model described in Underwood (1999) follows individual plants and herbivores, and consists of three nested loops: a herbivory loop (describing herbivore movement and feeding, and changes in induced resistance in plants), a herbivore generation loop consisting of 30 herbivory loops, and a plant reproduction loop consisting of variable numbers of herbivore generations. There are two equations in the model. The first describes the level of induced resistance in individual plant i at time $t+1$ ($I_{i,t+1}$) as a function of damage to the plant, which is equal to the herbivore load on that plant ($h_{i,(t-\tau)}$):

$$I_{i,t+1} = \frac{\left(-\frac{\hat{\alpha}}{\beta} I_{i,t} + \hat{\alpha}\right) h_{i,(t-\tau)}}{b + h_{i,(t-\tau)}} + I_{i,t} (1 - \delta) \quad (1)$$

In this equation, β represents a physiological maximum induced resistance in an individual plant, $\hat{\alpha}$ is the maximum increase in induced resistance at one time, b is the half-saturation constant, δ is the decay rate of induced resistance and τ is the lag time between damage and induced resistance. In this model it is assumed that $\hat{\alpha} = \beta$. The second equation describes 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), the level of induced

resistance herbivores have encountered (\bar{I}), and the strength of induced resistance (critical level of induced resistance reducing herbivore reproduction to zero, I_c):

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

where γ is the population rate of increase for herbivores.

To incorporate plant population dynamics, a third equation can be added to the model. This equation describes the size of the plant population in one generation (P_{t+n^*g}) as a function of its size in the previous generation (P_t) (where one plant generation consists of n^*g herbivory loops), the average damage incurred by plants (\bar{D}), and the critical damage level reducing plant reproduction to zero (D_c):

$$P_{t+n^*g} = P_t \left(1 + \lambda \left(1 - \frac{\bar{D}}{D_c} - \frac{P}{K}\right)\right) \quad (3)$$

This formulation of plant reproduction assumes that there is no cost of induced resistance to the plant. In this equation λ is the plant population growth rate and K is a carrying capacity for the plant population set by factors other than herbivore damage. \bar{D} is calculated as the average damage to individual plants in the population at one time (h_i), averaged over all time steps in a plant generation (n^*g):

$$\bar{D} = \frac{\sum_{t=1}^{n^*g} \sum_{i=1}^P h_i}{n^*g}$$

Because in this model all herbivores occupy a plant at all times, $\sum_{i=1}^P h_i = H$. If

it is assumed that $\tau = 0$, an equilibrium solution for this model can be found. At

equilibrium, $I_t = \bar{I} = I^*$, $H = H^*$ and $h_i = \frac{H^*}{P^*} = \bar{D}$. Substituting these into

equations 1 and 2 and combining the two it can be shown that the equilibrium conditions for H are $\gamma = 0$ and:

$$\frac{H^*}{P^*} = \frac{bI_c \delta}{\hat{a} - I_c} \quad (4).$$

Equation 4 implies that the ratio of herbivores to plants at equilibrium is a constant (θ) determined by the properties of induced resistance. See Underwood (1999) for a more detailed explanation of this model and its results, and Underwood (1997) for derivation of the equilibrium condition. The equilibrium

conditions for the plant population are $\lambda = 0$ and:

$$P^* = K \left(1 - \frac{H^*}{D_c} \right). \quad (5).$$

Equation 5 implies that the equilibrium number of plants is determined by the plant carrying capacity and the influence of herbivores on plants through damage. Note that without an independent carrying capacity for plants (that is, if the plant population is influenced only by herbivores), the model is unstable at all points except $D_c = \theta$.

The effect of induced resistance on herbivore and plant population dynamics was explored by running simulations of the model. All runs had 30 herbivory loops per herbivore generation, and runs were started with initial plant and herbivore populations of 100 individuals. Starting with different initial population sizes did not change the behavior of the model. The effects of the strength of induced resistance (I_c) and the critical damage level for plants (D_c) on plant and herbivore populations were explored over a range of relative numbers of herbivore to plant generations including 1:1, 10:1 and no plant reproduction. The effects of lags in induced resistance (τ) were also considered. For the runs reported here, all other parameters were held constant, with α and $\beta = 100$, $b = 10$, $\gamma = 2$, $\lambda = 1$, $\delta = .07$, and $K = 100$. These parameter values were chosen largely arbitrarily (see Underwood 1999 for discussion of the consequences of changing them).

All simulations were run for at least 150 herbivore generations, or long enough for the output to converge on the asymptotic dynamics. Runs were not replicated because initial exploration of the model indicated that there was not appreciable variation among runs with the same parameter values. Data on average plant and herbivore population sizes were calculated after the dynamics reached their final state (when the behavior of plant and herbivore populations was consistent over at least 50 generations). The behavior of the plant and herbivore populations was divided into the following 5 categories: herbivore extinction, stable herbivore and plant populations, damping cycles in the herbivore population (with stable plants), cycles or fluctuations in the herbivore population (with stable plants), both plants and herbivores cycling, and plant extinction (caused by the uncontrolled increase of herbivores).

Results

Increasing the strength of induced resistance (decreasing I_c) decreases herbivore population size in this model. Smaller herbivore populations allow the plant population to grow, so that plant population size increases with increasing strength of induced resistance (up to the plant carrying capacity K) (Fig. 1). The effect of the strength of induced resistance (I_c) on herbivore and plant populations is modified by the sensitivity of plant reproduction to herbivore

damage (D_c). As plants become more sensitive (D_c decreases), plant populations

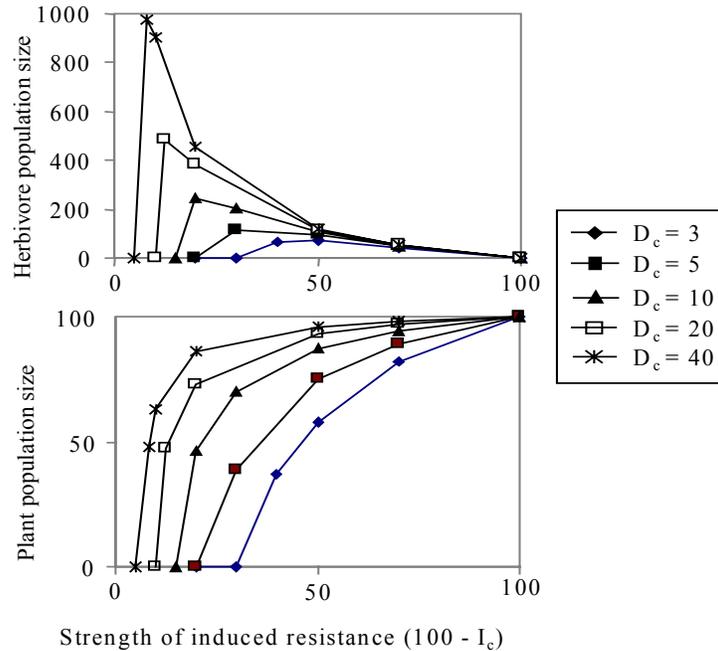


Figure 1: Herbivore and plant population size as a function of the strength of induced resistance. D_c (plant sensitivity to herbivore damage) is the critical damage level reducing plant reproduction to zero. Each point results from a single simulation of the model with one herbivores generation per plant generation and no lag in induced resistance. For these results, plant carrying capacity (K) = 100.

decrease. Small plant populations lead to more herbivores per plant, which causes induced resistance levels in the plants to rise and herbivore populations to fall. The likelihood that herbivore populations are regulated (not extinct or growing without bound) decreases as the number of herbivore generations per plant generation decreases (Fig. 2). Induced resistance is least able to control herbivore populations when herbivore and plant generation times are equal (Fig. 2C). When plants do not reproduce, lags in induced resistance decrease the likelihood that the herbivore population is regulated, and increase the likelihood of persistent cycles in the herbivore population at weaker levels of induced resistance (Fig. 2A). When plants do reproduce, lags still have a destabilizing effect on the herbivore population. As the lag time to induced resistance increases, the likelihood that the herbivore population is unregulated (thus driving plants extinct) or goes extinct (due to induced resistance) increases (Fig. 2B and C).

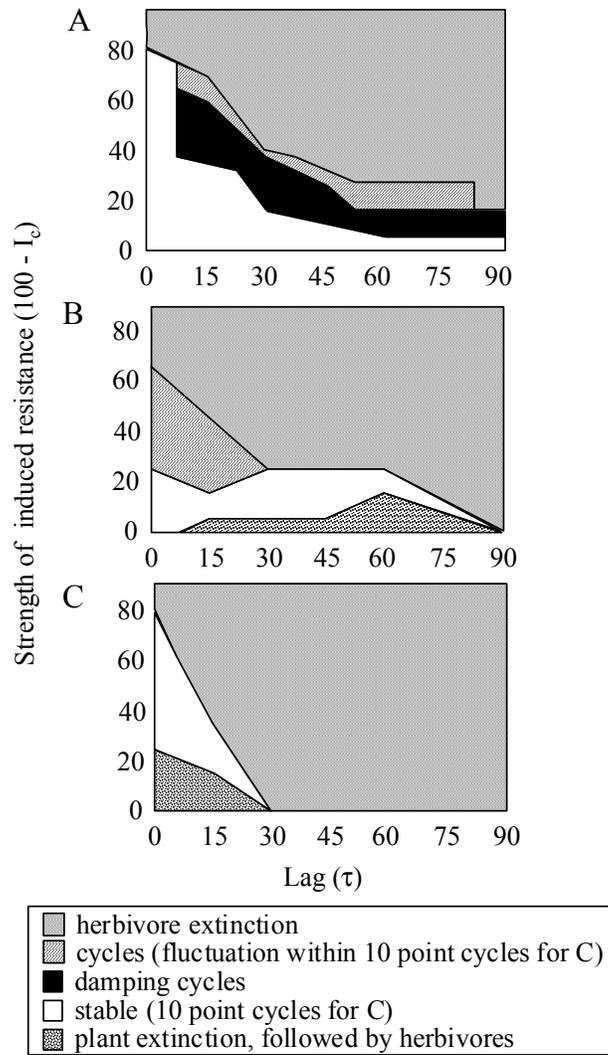


Figure 2: Long-term dynamic behavior of herbivore populations in simulations with A: no plant reproduction, B: ten herbivore generations per plant generation, or C: one herbivore generation per plant generation.

The large majority of the fluctuations exhibited by the model with plant reproduction occur only in the herbivore population, and are forced by the resetting of induced resistance to zero at the beginning of each plant generation. These cycles only occur when herbivores have more than one generation per plant generation (for example, 10 point cycles with 10 herbivore generations per plant generation, Fig. 3A). The reason that cycles driven by lags in induced

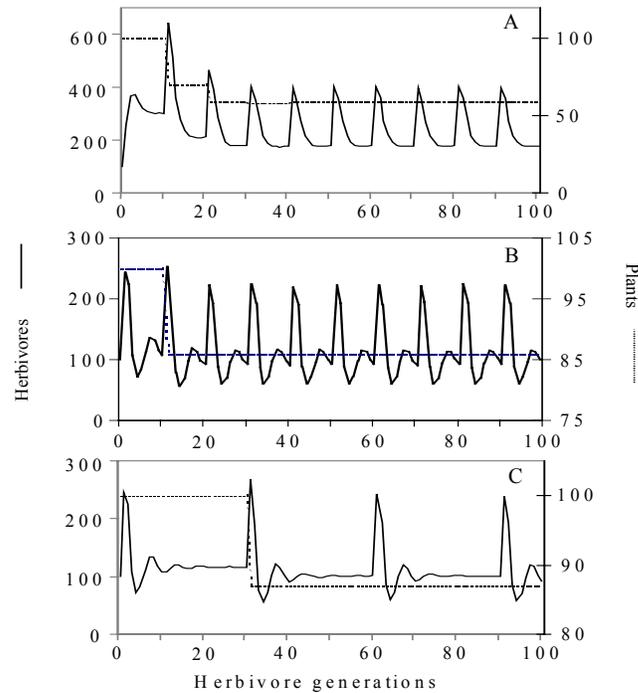


Figure 3: Cycles in the herbivore population forced by plant reproduction, and fluctuations within those cycles, in individual runs of the model. A) and B) 10 herbivore generations per plant generation, c) 30 herbivore generations per plant generation. A) $I_c = 80$, B) $I_c = 60$, C) $I_c = 60$, $\tau = 15$ for all three runs.

resistance rarely occur with plant population dynamics included in the model is that the effect of lags is complicated by the effect of the number of herbivore generations per plant generation. As the number of herbivore generations per plant generation increases, the likelihood of herbivore extinction decreases, and fluctuations within the cycles forced by plant reproduction appear when induced resistance is relatively strong (I_c is relatively low) (Fig. 3B). For example, with 10 herbivore generations per plant generation, there is a region in which the smooth 10-point cycles forced by plant reproduction with relatively weak induced resistance ($I_c = 80$) (Fig. 3A) are replaced by oscillations with two peaks, one larger and one smaller (Fig. 3B). This second peak is due to a damping oscillation in the herbivore population that is interrupted every 10 generations. These damping oscillations are more apparent if the number of herbivore generations per plant generation is increased (Fig. 3C). These fluctuations within the cycles forced by plant reproduction occur at weaker levels of induced resistance as the lag time gets longer, just as stable and longer damping cycles occur at weaker levels of induced resistance as the lag time gets longer without plant population dynamics.

Initial explorations of this model indicate that it is very rare for the interaction between herbivores and plants in this model to produce joint fluctuations in the plant and herbivore populations. Plant populations remain stable in most configurations of the model because the effect of herbivores on plants is generally either very small, or so large that it drives the plants extinct (Fig. 4A). The effect of herbivores on plants in this model is represented by \bar{D} , the amount of damage each plant receives. As shown above, at equilibrium, $\bar{D} = H^*/P^* = \theta$ (the constant describing the characteristics of induced resistance). The relationship between \bar{D} and I_c (the strength of induced resistance) is exponential (Fig. 4A). This means that at most levels of I_c herbivores have relatively little effect on plants, but as I_c increases the effect of herbivores on plants suddenly becomes very large, generally driving the plant population extinct. Persistent cycles occur only in the region between little effect and extinction, and because of the steeply accelerating curve, that region is very small. For example, in Fig. 4B, joint fluctuations of plants and herbivores are found only along a single line dividing stable herbivore and plant populations from plant extinction.

In summary, the following results arise from this model of induced resistance and plant and herbivore population dynamics. First, the interaction between plant and herbivore populations very rarely results in cycling in both populations. Second, the most frequent cycles produced in this model are herbivore population cycles forced by plant reproduction. This result suggests that herbivores with rapid generation times relative to their host plants might be expected to exhibit cyclic dynamics more frequently than herbivores whose generation time is close to the generation time of their host. These forced cycles would, however, only be expected in cases where plant recruitment is relatively synchronous, such as in annual plants, or in perennials whose level of induced resistance is returned to zero when the plant dies back (due to winter or a dry season) and then re-grows. In the field, these cycles would happen within a season, and would be most likely to occur in rapid cycling insects or mites. Such patterns are observed, but are difficult to distinguish from patterns driven by environmental factors such as temperature (see Underwood 1999).

Lags in this model reduce the stability of plant and herbivore populations. However, other than cycles forced by plant reproduction, induced resistance rarely drives cycles in the herbivore or plant populations regardless of lag time, although at intermediate strengths of induced resistance the forced cycles can be complicated by internal fluctuations, giving the appearance of complex behavior.

A clear, though not very surprising, outcome of this model is that the relative number of herbivore to plant generations strongly affects the influence of induced resistance on herbivore population dynamics. A higher number of herbivore generations per plant generation generally increases stability, and also increases the likelihood of stable cycles (both forced and otherwise). This observation suggests that systems with many herbivore generations per plant

generation should be more likely to show stable cycles than systems with very

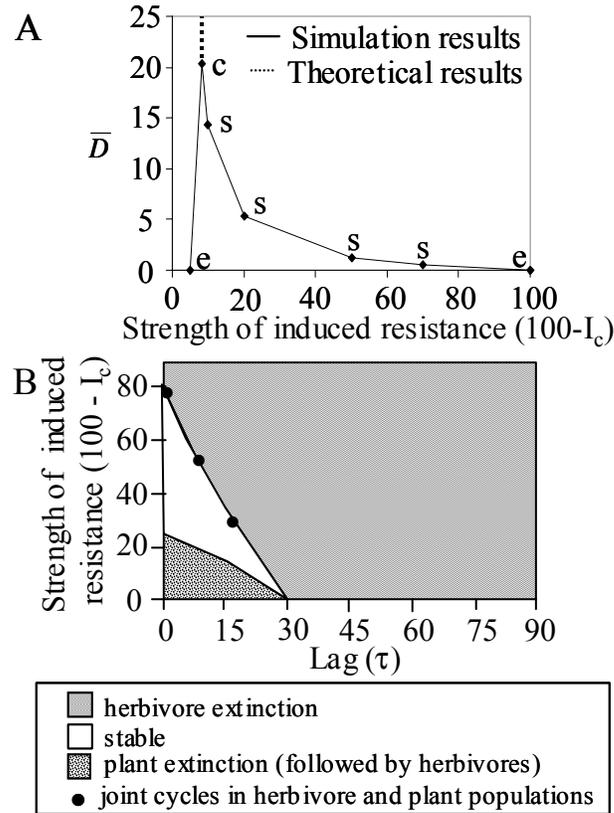


Figure 4: A. Relationship between the strength of induced resistance (I_c) and the influence of herbivores on plants (\bar{D}). Points on the line indicate equilibrium value of \bar{D} for single runs of the model. Letters above points indicate dynamic behavior of herbivore and plant populations at each point (s = stable, c = cycles, e = extinct), and the dotted line indicates the relationship predicted by the equations in the model. B. Dynamic behavior of herbivore and plant populations over a range of strengths of induced resistance and lag times, with one herbivore generation to each plant generation. Boxes indicate joint cycles in the plant and herbivore population for lags of 0, 8, and 15 herbivory loops.

few herbivore generations per plant generation. In fact, all observations of long-term cycles in insect herbivore populations that have been attributed (tentatively) to induced resistance occur in systems with long-lived trees and short-lived herbivores (Karban and Baldwin 1997). It is important to emphasize that it is the relative number of herbivore and plant generations that should be considered in predicting the effects of induced resistance on population

dynamics, rather than whether the herbivore is univoltine versus multivoltine, or the plant is annual versus perennial.

Synthesis

The ecological literature includes many discussions, both theoretical and empirical, of how induced resistance should affect short and long-term herbivore population dynamics. There is, however, very little direct evidence that induced resistance can either regulate or drive cycles in herbivore populations. Although the current lack of data arises largely from the difficulty of approaching this issue experimentally, there is a range of techniques, some of which have only recently been developed, that should allow researchers to empirically address the effects of induced resistance on herbivore population dynamics. Future empirical studies could be guided by existing theoretical explorations of induced resistance and herbivore dynamics, which make some broad predictions for when induced resistance might regulate or drive cycles in herbivore populations. For example, theory predicts that cycles should be more frequent with delays in either the onset or decay of induced resistance. Measuring the timing of induced resistance in the field will be difficult with long-lived plants, but is conceptually straightforward (Underwood 1998), so that the dynamics of herbivore populations in systems with longer versus shorter lag or decay times could be compared. The model presented here provides further predictions of how relative generation times might affect the likelihood of cycles. These predictions remain to be tested. In general, the study of induced resistance and herbivore population dynamics would benefit from a wider use of controlled experiments and model fitting.

Future Directions

Just as induced resistance may affect the population dynamics of herbivores, it may have important effects on the population dynamics of plant pathogens. Because plant pathogens are so much smaller and faster reproducing than their hosts, induced resistance likely affects pathogen population dynamics at two scales: within- and among-hosts. However, most models and studies of plant disease dynamics address only among host dynamics, leaving the dynamics of the disease within the host, as well as plant population dynamics, unknown (Thrall et al. 1997). Results from metapopulation theory suggest that taking into account local (within host) dynamics might change predictions for among host dynamics (e.g., Hastings and Wolin 1989). Because herbivores and pathogens are nearly always both present in plant populations, it would also be valuable to determine how pathogens and herbivores affect each other's population dynamics. The importance of this interaction should depend in part on the specificity of the plant's induced responses (Stout and Bostock, this

volume).

The effect of induced resistance on herbivore spatial dynamics also deserves further attention. The few spatially explicit models of induced resistance and herbivore dynamics (Lewis 1994, Morris and Dwyer 1997) suggest that induced resistance may affect herbivore spread differently from constitutive resistance. Few empirical studies have addressed the effect of induced resistance on herbivore movement (e.g., Harrison and Karban 1986, W. Morris, unpublished data) and these have considered relatively small scales. Studies that examine how induced resistance and herbivore characters such as mobility and selectivity interact to determine herbivore spatial distributions could shed light on pest movement as well as the dispersion of native herbivores in natural systems.

Finally, although there is evidence for genetic variation in induced responses from several systems, most discussions of induced resistance and herbivore population dynamics have not explicitly considered variation in induced responses among plants. It would be interesting to determine how variation among plants affects the influence of induced resistance on herbivore population dynamics, especially for systems with selective herbivores. Understanding the effects of population genetic variation for resistance characters such as induced resistance may help evaluate the application of mixed cropping systems in agriculture, as well as improving our understanding of natural systems. Considering variation in induced resistance may also provide an opportunity to link population dynamics and evolution in plant-herbivore systems.

Acknowledgements

I thank A. Agrawal, B. Inouye, R. Karban, M. Rausher, M. Sabelis, P. Tiffin and J. Thaler for thoughtful discussions and helpful editing. This work was supported by NSF DEB grant #9615227 to M. Rausher and by NRI Competitive Grants Program/USDA award #98-35302-6984 to N. Underwood.

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