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THE EFFECTS OF INDUCIBLE PLANT DEFENSES ON HERBIVORE POPULATIONS.

1. MOBILE HERBIVORES IN CONTINUOUS TIME

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In many plants, damage by herbivores causes changes in the chemical, physical, and/or nutritional composition of the foliage (Fowler and Lawton 1985). Such inducible changes in plant quality, often termed *inducible defenses*, have been shown to affect growth or reproduction in individual herbivores adversely (see, e.g., Bryant 1981; Schultz and Baldwin 1982; Karban 1983; Rhoades 1983*a*; Karban and Carey 1984; Haukioja and Neuvonen 1985; Tallamy 1985; Faeth 1986; Rossiter et al. 1988). These observations have led several workers to suggest that inducible defenses may often greatly influence the dynamics of herbivore populations (but see Fowler and Lawton 1985). In particular, it has been argued that inducible defenses cause crashes in some herbivore populations (Bryant 1981; Rhoades 1985; Smith 1985) and cyclic fluctuations in others (Benz 1974; Fischlin and Baltensweiler 1979; Fox and Bryant 1984).

Many of these arguments are based on models describing predator-prey interactions in which it is assumed that changes in vegetation (prey) abundance are responsible for changes in herbivore (predator) abundance (Rosenzweig and MacArthur 1963; Hassell and May 1973; May 1973, 1974; Noy-Meir 1975; Caughley 1976; see also Crawley 1983). These models are not strictly appropriate, however, since arguments about the role of inducible defenses in herbivore population dynamics postulate that changes in plant *quality*, rather than in plant *abundance*, are responsible for herbivore population fluctuations. Nevertheless, this reliance on inappropriate models is understandable, since there has been little quantitative examination of how, and under what circumstances, inducible changes in plant quality influence the long-term dynamics of herbivore populations (but see Fischlin and Baltensweiler 1979).

A general mathematical framework helps us understand how changes in plant quality influence herbivore population dynamics (Edelstein-Keshet 1986). In this paper we specifically focus on inducible plant defenses and address the following questions. (1) Under what circumstances can inducible defenses by themselves

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regulate populations of herbivores? (2) How do inducible defenses interact with other density-dependent agents to affect herbivore populations? (3) Can inducible defenses by themselves cause populations of herbivores to fluctuate or cycle? If so, under what conditions? (4) What influence can herbivores have on heterogeneity in the levels of inducible defenses within plant populations?

Two characteristics of an herbivore are of prime importance in determining the type of model that is appropriate for a given system: mobility and selectivity. Mobility determines the degree to which an individual herbivore can feed on foliage from a large number of plants. Selectivity governs the degree to which an herbivore preferentially feeds on plants of high quality. Mobility affects the way in which herbivores perceive the vegetation (as a collection of plants with individual traits or as a single population with average or aggregate attributes). Selectivity influences the impact of herbivores on plants. (Low selectivity produces a uniform impact on all plants, regardless of their quality, whereas high selectivity implies that undefended plants suffer disproportionately from herbivory.) Although mobility and selectivity are continuous, graded attributes, it is useful conceptually to consider four extreme herbivore types: mobile and nonselective, mobile and selective, non-mobile and nonselective, and non-mobile and selective.

Here we limit our analysis to herbivores that are mobile and nonselective. Various herbivores are mobile in this sense, including snowshoe hares (Reichardt et al. 1984), ungulates of the African savannas (Pennycuick 1975), various Orthoptera (Gangwere 1961; Otte 1975; Otte and Joern 1977), beetles (Kareiva 1982; Turchin 1986), and even larvae of some Lepidoptera (Rausher 1979, 1980). Moreover, many herbivores are known to be nonselective with respect to plant quality (Blais 1952; Perron et al. 1960; Perron and Jasmin 1963; Stark 1965; Gould 1978; Faeth et al. 1981; Morrill 1982; Prestidge and McNeill 1983; Raupp and Denno 1984). We concentrate here on mobile nonselective herbivores because it is for this group of organisms that a simplification of a previously described general mathematical framework (outlined in Edelstein-Keshet 1986) is possible. This simplification allows a purely analytic treatment and provides a standard against which the other types of herbivores can be compared. (Examination of these cases requires more-detailed assumptions and a greater reliance on numerical analysis.)

FORMULATION OF A MODEL

The model described in this section pertains to plant populations that may consist of many discrete heterogeneous units. These units, which could be individual plants, branches within plants, individual leaves, or other plant components, may differ in their amounts of inducible factor. The variables of the model are q, the level of inducible factor in a single unit of vegetation; t, time; $p(q,t)$, the amount or biomass of vegetation whose level of inducible factor is q at time t; $\bar{Q}$, the average value of q in the vegetation; $\bar{V}$, the variance of q; $h(t)$, the density of herbivores per unit of vegetation at time t; $H(t)$, the total herbivore population at time t; and $P(t)$, the total mass or amount of vegetation at time t.

Because the inducible factor and the herbivore density influence one another, a

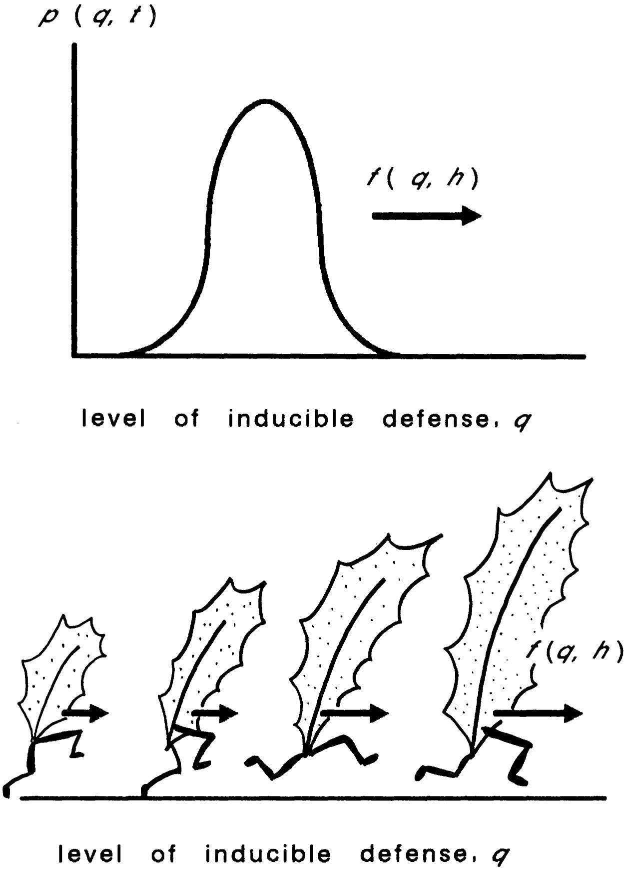


FIG. 1.—*Top*, An example of a hypothetical distribution of plant defenses, $p(q,t)$ at some time t. *Bottom*, The plant response function $f(q,h)$ (defined by eq. 1a) plays the role of a rate of motion of individuals along the q-axis. This function thus enters into the equation that governs changes in the distribution (eq. 2).

single unit of vegetation can be described by two equations (see fig. 1):

$$dq/dt = f(q,h)\,; \tag{1a}$$

$$dh/dt = g(q,h)\,. \tag{1b}$$

The first equation describes the change in the level of defenses of a unit of vegetation whose current defense level is q and that currently harbors herbivores at density h. The second equation describes the change in the numbers of herbivores on that unit.

Equation (1a) implies that, for the entire plant population,

$$\partial p/\partial t = -\partial(fp)/\partial q - \sigma p \tag{2}$$

(Edelstein-Keshet 1986). This equation describes the change in the distribution of inducible defenses in the vegetation over time. The first term in this equation reflects shifts in the units of vegetation along a q-axis, as governed by equation (1a), and the second term reflects a loss of vegetation due to removal. Here, $\sigma = \sigma(q,h,P)$ is the removal rate per unit of the vegetation (i.e., from herbivory or other causes); σ can depend on herbivore density, plant defenses, and total plant density. In the absence of herbivores, σ can be nonzero to account for density-dependent plant growth.

By definition, mobile nonselective herbivores consume foliage randomly with respect to the vegetation state q. Consequently, it is expected that herbivore growth rates, survival, and fecundity are determined by the average quality of the vegetation. Moreover, mobility and nonselectivity of the herbivores implies that at any given time, the density of herbivores should be roughly the same on all units of the vegetation; that is, $H(t) = P(t)h(t)$. Equation (1b) may thus be rewritten as

$$d(H/P)/dt = dh/dt = g(\bar{Q},h) = hR(\bar{Q},h)\,, \tag{3}$$

where $\bar{Q}$ is the average value of q in the vegetation and R is the per capita herbivore rate of increase.

The coupled equations (2) and (3) constitute a detailed model for the dynamics of mobile herbivores interacting nonselectively with a heterogeneous vegetation. The exact forms of the functions f and g depend on the details of particular plant-herbivore systems. Even when these forms are given, however, numerical analysis is usually needed in order to determine the behavior of this coupled system of equations for the arbitrary functions σ, f, and g. However, with the addition of four biologically realistic assumptions, a further simplification of the equations allows analytic solutions.

A. The rate of removal of plants is independent of q; that is,

$$\sigma = \sigma(h,P)\,. \tag{4}$$

Herbivores exhibit no preferences for undefended plants over defended plants. Since we are considering here only nonselective herbivores, this assumption is valid.

B. Herbivory induces the production of plant defenses, which decay spontaneously when herbivory diminishes. This assumption is based on Rhoades' (1983*b*) argument that inducible defenses are costly to a plant and are therefore not likely to be maintained unless a need for them exists. It implies that the plant response function $f(q,h)$ has the general form

$$f(q,h) = S(h) - aq\,, \tag{5}$$

where S is the induction rate, which depends on herbivore density, and a is the decay rate. (This expression is linear in the variable q. See the discussion of a more general linear case, $f(h,q) = f_1(h) + f_2(h)q$, in Appendix A.)

C. New plant units are undefended and enter the population at a rate proportional to the total plant biomass. This assumption implies that

$$\text{birthrate of units} = f(0,h)p(0,t) = \bar{B}P\,, \tag{6}$$

where $\bar{B}$ is the average per capita rate of production of new units of vegetation (fecundity). (This boundary condition is discussed in greater detail in Edelstein-

Keshet 1987.) Note that $\bar{B}$ need not be constant and that it can depend on plant density, on the distribution of defenses, or on herbivore density.

D. The level of inducible factor cannot exceed some maximum, $q_{\max}$.

In Appendix A we show that, subject to these conditions, equations (2)–(6) lead to the following ordinary differential equations for P, $\bar{Q}$, and h:

$$dP/dt = P(\bar{B} - \sigma), \tag{7a}$$

$$d\bar{Q}/dt = S(h) - \bar{Q}(a + \bar{B}), \tag{7b}$$

$$dh/dt = hR(\bar{Q}, h). \tag{7c}$$

These equations describe, respectively, the dynamics of the total amount of vegetation (or mass), the average level of inducible factor, and the density of herbivores per unit of vegetation. Equation (7a) should not be misinterpreted as exponential growth in plants, since the mortality (σ) and the fecundity ($\bar{B}$) may in general be functions of P as well as h. Moreover, since herbivore growth rate (R) is independent of P (plant biomass is not a limiting factor to herbivores), equations (7b) and (7c) can be solved independently of (7a).

It is also possible to determine how the variance of the level of defenses changes over time. In Appendix A we demonstrate that this change is governed by the equation

$$d\bar{V}/dt = -\bar{V}(2a + \bar{B}) + \bar{B}\bar{Q}^2, \tag{8}$$

where a and $\bar{B}$, as defined in equations (5) and (6), are the rate of decay of plant defenses and the average fecundity, respectively.

From equation (8) it follows that a steady-state variance is given by

$$\bar{V}_{ss} = \bar{B}\bar{Q}^2_{ss}/(\bar{B} + 2a). \tag{9}$$

One implication of this result is that, if over a period of time there is no recruitment into the plant population ($\bar{B} = 0$), the variance of the level of inducible defenses decreases to zero; that is, all units in the vegetation eventually have identical levels of expressed defense.

ANALYSIS OF THE MODEL

In this section we apply the general framework described by equations (7) to specific cases in which plants have inducible defenses that affect the net herbivore growth rate. In case 1, inducible plant defenses decrease the herbivore rate of increase; no other density-dependent factors regulate the herbivore population. In case 2, inducible defenses complement the effects of other density-dependent factors. Finally, in case 3, the herbivore growth rate exhibits an Allee effect that is modified by plant defenses. In all three cases we assume that total plant biomass never becomes limiting to the herbivores (R is independent of P as in eq. 7c or P is held fixed). We make this assumption because we are interested primarily in how plant-herbivore interactions are mediated by the state rather than the amount of the vegetation.

To use the model described by equations (7), particular forms must be specified for the functions S and R. The general form of R is dictated by the particular case

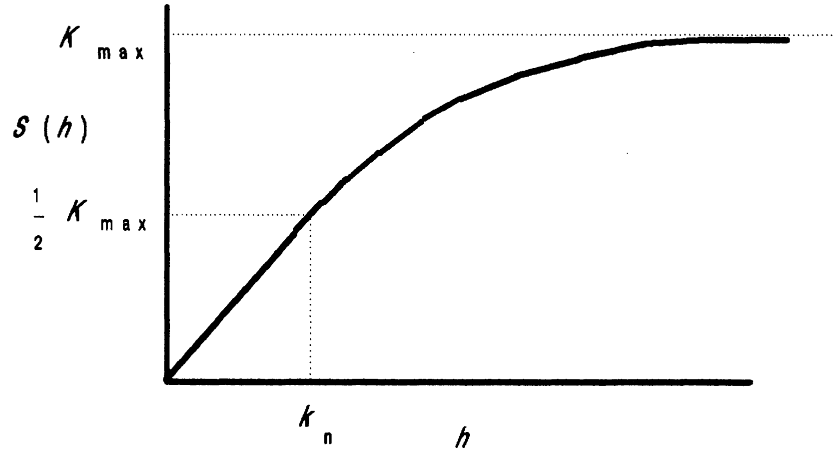


FIG. 2.—The rate of induction of plant defenses, $S(h)$, is taken to be a saturating function of herbivore density (see eq. 12). K_{max} is the maximal rate of induction, and k_n is the level of herbivory (i.e., density of herbivores) that leads to one-half of the maximal induction rate.

under consideration. The function S is determined by the biological properties of the inducible defense. We make three minimal assumptions about these properties: first, defenses are not induced in the absence of herbivory; second, the rate of induction of defenses increases initially as the intensity of herbivory increases; and third, there is a maximal rate of induction. Some empirical support for the second assumption (S increases with R) is provided by studies showing that the level of defenses measured soon after experimental defoliation is proportional to the amount of defoliation (Rossiter et al. 1988). Together, these three assumptions imply that $S(h)$ is an increasing function of h, which levels off to a constant value for large h:

$$S(0) = 0, \qquad dS/dh > 0, \tag{10}$$

$$\lim_{h \to \infty} S(h) = \text{constant}. \tag{11}$$

For the purposes of illustration we adopt for $S(h)$ the form

$$S(h) = K_{\max}h/(k_n + h), \tag{12}$$

which has the properties given in equations (10) and (11) (see fig. 2). Here K_{max} is the maximal rate of induction and k_n is the level of herbivory that stimulates induction at one-half the maximal rate. The results of the model depend only on the properties of S summarized by equations (10) and (11), not on its detailed functional form (Edelstein-Keshet 1987). For example, a sigmoidal induction response for $S(h)$ satisfies the same conditions and leads to essentially identical results.

Case 1: Inducible Defenses Alone

Under what conditions can inducible plant defenses by themselves regulate an herbivore population, and do persistent cyclic population fluctuations accompany such regulation? Consider a situation in which the herbivore population growth rate is influenced only by the average level of plant defenses and not by any other factor (R depends only on $\bar{Q}$). This situation may be modeled using the following equation for the per capita herbivore growth rate:

$$R(\bar{Q}) = r_0(1 - \bar{Q}/q_c), \tag{13}$$

where r_0 is the intrinsic rate of increase for the herbivore in the absence of induced defenses and q_c is the critical level of plant defenses that reduces the herbivore growth rate to zero.

Substituting equations (12) and (13) into equations (7b) and (7c) yields

$$d\bar{Q}/dt = K_{\max}h/(k_n + h) - a\bar{Q}, \tag{14a}$$

$$dh/dt = hr_0(1 - \bar{Q}/q_c). \tag{14b}$$

As will be described below, the behavior of this coupled system of equations depends on the values of certain dimensionless parameters: $\alpha = aq_c/K_{\max}$, which is the ratio of the induction time ($q_c/K_{\max}$) to the half-life of the defenses ($1/a$); and $r = r_0q_c/K_{\max}$, which is the ratio of the induction time to the maximal herbivore doubling time ($1/r_0$) (see Appendix B for a complete dimensional analysis of the equations). Equations (14) can have one or two steady states; (0,0) is always a steady state. A second, nontrivial steady state satisfies

$$h_{ss} = a\bar{Q}_{ss}k_n/(K_{\max} - a\bar{Q}_{ss}), \tag{15}$$

which, together with $dh/dt = 0$, can be solved to obtain the corresponding value

$$\bar{Q}_{ss} = q_c. \tag{16}$$

Figure 3 summarizes the properties of these equations on a $\bar{Q}h$ plane. Axes on this graph are labeled in units of $\bar{Q}/q_c$ and h/k_n. The $\bar{Q}$ axis and the thin-line curve represent loci for which $d\bar{Q}/dt = 0$ (the $\bar{Q}$ null clines); the horizontal line at $\bar{Q}/q_c = 1$ represents the locus for which $dh/dt = 0$ (the h null cline).

Steady states are located at intersections of the h null cline with one of the $\bar{Q}$ null clines. There is always an intersection at (0,0). The second, nontrivial steady state exists if $\alpha < 1$ or, in terms of original parameters, if $1/a > q_c/K_{\max}$. This result implies that a steady state can exist only if the half-life of the defenses is longer than the induction time.

A linear stability analysis (see Appendix C and Roughgarden 1979 for methods) indicates that this steady state is always stable when it exists, regardless of the value of the parameters. Increasing the maximum rate of induction ($K_{\max}$), decreasing the critical defense level (q_c), or decreasing the rate of decay of the defenses (a) each makes it more likely that the steady state will exist and thus increases the likelihood that an induced defense will regulate the herbivore population. Making k_n large, or the difference in the denominator of equation (15) small, tends to increase the absolute magnitude of the steady-state herbivore density. If a is sufficiently small or, equivalently, if both r_0 and $K_{\max}$ are large, the populations may be seen to undergo transient (decaying) oscillations as they approach a steady state. (See Appendix C for details.) However, there is no

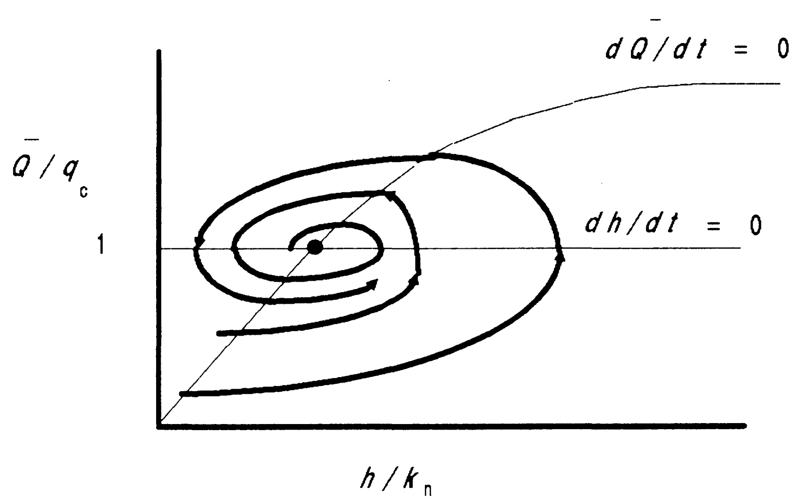


FIG. 3.—Null clines, directions of motion, and typical solution curves are shown in the h/k_n-$\bar{Q}/q_c$ plane for case 1, in which the herbivores are regulated only by inducible defenses in the vegetation (described by the dimensionless eqs. B1). There is a single steady state, which is always stable if the null clines intersect in the positive quadrant. Note that for all (nontrivial) initial starting values of h/k_n and $\bar{Q}/q_c$, the system approaches the steady state in which plant defenses exert a regulating influence on the herbivore population. The approach to steady state may be accompanied by oscillations of decreasing amplitude.

tendency toward persistent stable cycling given the above assumptions. The approximate behavior of the solution curves are the thick-line spirals in figure 3.

The general conclusions about existence and stability of the steady state of this system do not depend on the specific form of R assumed in equation (13). They apply so long as the per capita herbivore growth rate, $R(\bar{Q})$, does not depend on herbivore density and so long as the equation $R(\bar{Q}) = 0$ can be solved to obtain a single explicit equation for the h null cline with $\bar{Q}$ constant (see Edelstein-Keshet 1987).

Case 2: Inducible Defenses Augmenting Other Density-Dependent Factors

The preceding analysis indicates that although inducible defenses can by themselves regulate herbivore populations, they do not necessarily cause the regulated population to fluctuate or cycle. In this section we address a different question: can inducible defenses lead to persistent population cycles when the herbivore population is regulated by some other agent? We also ask whether inducible defenses acting in conjunction with the regulating agent lead to a significantly lower equilibrium herbivore density than occurs when the regulatory agent acts alone.

To address these questions, we consider the case of an herbivore population that exhibits logistic density-dependent growth in the absence of induced defenses. We assume that the carrying capacity of the habitat is negatively related to the level of defenses of the host plant. This type of relationship might occur, for example, if carrying capacity is determined by the abundance of predators,

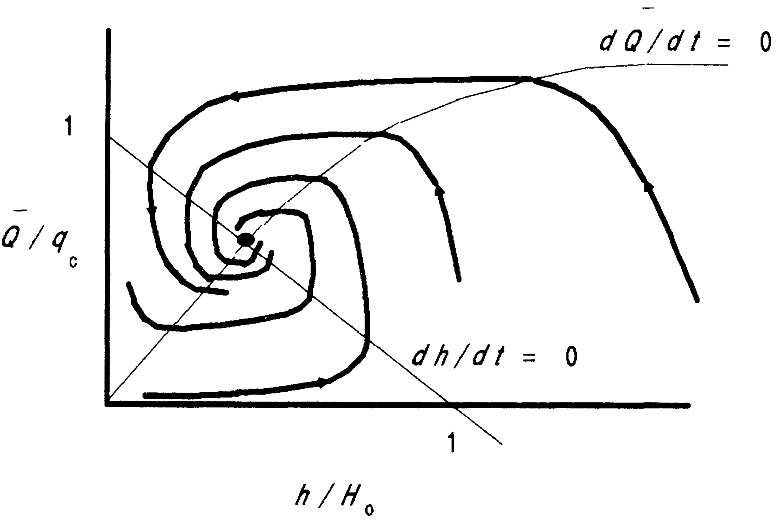


FIG. 4.—Null clines, directions of motion, and typical solution curves in the model for logistic herbivores on vegetation with inducible defenses (case 2), given by the (dimensionless) equations (B2). There is always a single stable steady state that the system approaches. Here, the herbivore population coexists with plants in which a steady level of defenses is expressed. The herbivore density at this equilibrium is given by $h_{ss} = [-A \pm (A^2 + 4\kappa)^{1/2}]/2$, where $A = \kappa - 1 + 1/\alpha$.

parasitoids, and/or pathogens whose effectiveness increases as the plant quality declines (Price et al. 1980; West 1985). This assumption means that in our model, carrying capacity declines as the average value of q increases. For the equations of the model, we now use

$$d\bar{Q}/dt = K_{\max}h/(k_n + h) - a\bar{Q}, \tag{17a}$$

$$dh/dt = hR(\bar{Q},h) = hr_0[(1 - \bar{Q}/q_c) - h/H_0], \tag{17b}$$

where H_0 is the maximal herbivore carrying capacity (in the absence of plant defenses, i.e., when $\bar{Q} = 0$), q_c is the critical level of plant defenses that reduces the herbivore carrying capacity to zero, and all other parameters have their previous meanings. A new dimensionless parameter associated with these equations is $\kappa = k_n/H_0$, which is the ratio of the herbivore density that leads to half the maximal induction rate to the herbivore carrying capacity.

Figure 4 summarizes the nature of equations (17) on a $\bar{Q}h$ plane. Axes are scaled in units of $\bar{Q}/q_c$ and h/H_0, and null clines are drawn with thin lines. Again, the point (0,0) is a steady state of the equations. Note, however, that one of the h null clines is now a straight line that passes through (0,1) and (1,0). This line always intersects the $\bar{Q}$ null cline at a nontrivial steady state $(\bar{Q}_{ss},h_{ss})$. This steady state again satisfies equation (15) together with $dh/dt = 0$. The explicit value of h_{ss} is given by a cumbersome quadratic formula (see fig. 4), but the key feature, which can be seen graphically, is that h_{ss} is to the left of the value $h/H_0 = 1$. This means that the equilibrium herbivore density in the presence of plant defenses is lower than in their absence.

Linear stability analysis indicates that this steady state is always stable, regardless of the parameters that appear in equations (17). Consequently, regardless of the rate of induction or the herbivore growth rate, the system always approaches a constant state, in which plant defenses are maintained at some elevated level $\bar{Q}_{ss}$ and a residual herbivore population h_{ss} coexists with the induced vegetation. The level h_{ss} can be increased (i.e., made closer to its equilibrium value $h = H_0$ in the absence of defenses) by making κ or α large (i.e., increasing k_n, a, or q_c or decreasing K_{max}).

The behavior of solutions to equations (17) is shown by the thick-lined spirals in figure 4. The approach to a steady state may again be accompanied by decaying transient fluctuations. Such fluctuations would be most likely if r is large. (See Appendix D for details.) However, no parameter settings can bring about stable cycles in this system.

As before, conclusions do not depend on the specific form of R. To obtain similar results, it is only necessary to assume that the herbivore growth-rate function $R(\bar{Q},h)$ satisfies two realistic conditions, $\partial R/\partial h < 0$ and $\partial R/\partial \bar{Q} < 0$, and to assume that the equation $R(\bar{Q},h) = 0$ can be solved to obtain $\bar{Q}$ as a continuous function of h, that is, $\bar{Q} = \hat{r}(h)$.

Case 3: Inducible Defenses and the Allee Effect

The preceding analyses might be taken to indicate that inducible defenses cannot under any circumstance cause persistent (stable) oscillations in continuous herbivore populations. Such a conclusion would be erroneous, however. Oscillations driven by the dynamics of inducible defenses can occur when the herbivore population exhibits an Allee effect. Although such an effect may not be common among herbivorous insects, cases have been reported. The classic example is bark beetles, which often undergo large and sometimes cyclic population fluctuations. In many species of bark beetles, populations must be above a critical density to reproduce successfully in healthy host trees (Berryman 1976; Wood 1980). Other examples have been described by Crawley (1983).

To represent an Allee effect, we assume that R increases to a maximal value r_0 at an optimal herbivore density H_0 and thereafter decreases for further increments of h. As before, we assume that R decreases as the levels of expressed chemical defenses increase in the plants. In mathematical form, these assumptions are expressed as $\partial R/\partial h = 0$ for $h = H_0$, $\partial^2 R/\partial h^2 < 0$ for $h = H_0$, and $\partial R/\partial \bar{Q} < 0$ for all h. For technical reasons it is necessary to add the condition that the equation $R(\bar{Q},h) = 0$ can be solved to obtain $\bar{Q}$ as a continuous function of h, that is, $\bar{Q} = \hat{r}(h)$. The above conditions guarantee that the set of points $R(\bar{Q},h) = 0$ (which is the h null cline of the system) has the qualitative properties shown in the humped curves in figure 5. A representative example of equations in which the herbivore growth rate satisfies these conditions is

$$d\bar{Q}/dt = K_{max}h/(k_n + h) - a\bar{Q}, \tag{18a}$$

$$dh/dt = hR(\bar{Q},h) = hr_0[(1 - \bar{Q}/q_c) - \mu(1 - h/H_0)^2]. \tag{18b}$$

In these equations μ is a dimensionless Allee parameter; q_c is the critical level of plant defenses, at which the maximal herbivore reproductive rate is zero; and the other parameters have the same meanings as in cases 1 and 2.

Equations (18) always have a steady state at $\bar{Q}/q_c = 0$ and $h/H_0 = 0$. The "hump" in each herbivore null cline (fig. 5) means that it may intersect the plant-quality null cline at up to two points. (See Rosenzweig 1969 for a discussion of a similar result with an Allee effect in prey populations.) These intersections correspond to additional steady states. It can be shown that all possible configurations of the null clines fall into one of four subcases. These subcases, which are characterized by the number and stability of their steady states, are determined by the relative sizes of the dimensionless parameters as follows (see Appendix E for stability analyses).

Subcase a. $\alpha < 1/(\kappa + 1)$, $\mu < 1$. One intersection occurs to the left of the peak in the herbivore null cline. This equilibrium is unstable (as is the equilibrium at (0, 0)). Poincaré-Bendixson global-stability theory predicts that a stable limit cycle surrounds this equilibrium provided that the q null cline is steeper than the h null cline at their intersection point. Herbivore population size and plant quality thus undergo stable oscillations.

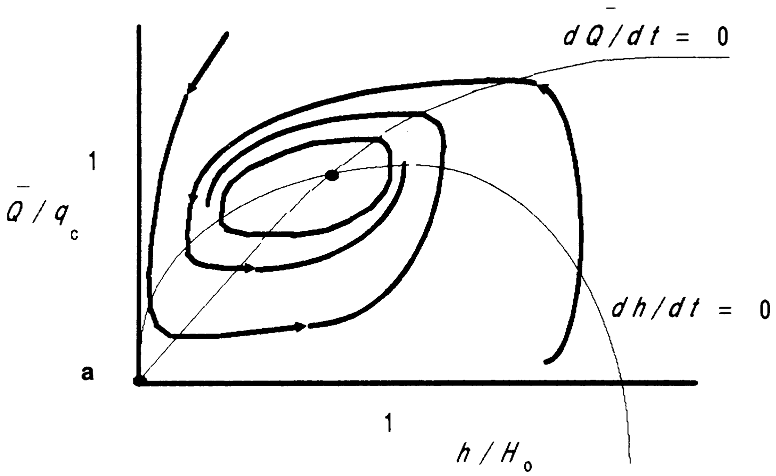
Subcase b. $\alpha > 1/(\kappa + 1)$, $\mu < 1$. One intersection occurs to the right of the peak in the herbivore null cline. This equilibrium is always stable, whereas the (0, 0) equilibrium is unstable. The system thus approaches a steady state characterized by a constant and uniform herbivore density and plant quality.

Subcase c. $\alpha > 1/(\kappa + 1)$, $\mu > 1$. Two intersections occur on opposite sides of the peak. The equilibrium corresponding to the intersection to the left of the peak is unstable; the right intersection is stable. Thus, depending on the initial state of the system, either the herbivore population will crash (and the level of inducible defenses will go to zero), or the system will approach a steady state characterized by constant herbivore density and plant quality.

Subcase d. $\alpha < 1/(\kappa + 1)$, $\mu > 1$. The null clines fail to intersect. In this case, the only equilibrium of the system (at (0,0)) is stable. Herbivores are eliminated, and defenses decay to uninduced levels.

This analysis indicates that the existence of an Allee effect coupled with inducible defenses can produce sustained population cycles in an herbivore, although it does not necessarily do so. Whether persistent fluctuations occur depends on the relative magnitudes of various parameters that characterize the plant-herbivore interaction (i.e., on the herbivore intrinsic rate of increase [r_0], the optimal herbivore density [H_0], the maximal induction rate [K_{max}], and the level of herbivory [k_n] that produces a half-maximal induction rate) and hence on the environmental factors that determine these characteristics.

For this case we have also carried out numerical simulations of the full detailed model using equations (2) and (3) with $\sigma = 0$, $\bar{B} = 0$, and the functions f and R as given by the right-hand side of equations (18). These simulations allow us to follow changes in the distribution of inducible defenses in the vegetation. For parameter choices that lead to a stable limit cycle in the averaged model (subcase a), we found the behavior shown in the plot of p versus q in figure 6. It is evident from these numerical results that the mean of the distribution fluctuates cyclically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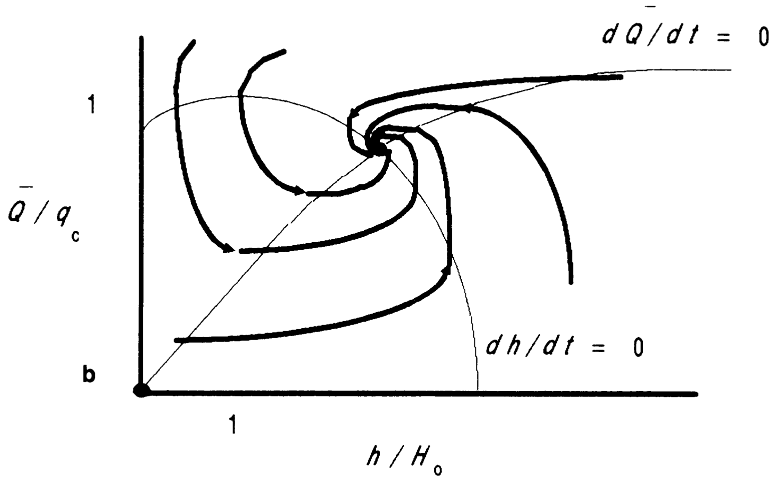
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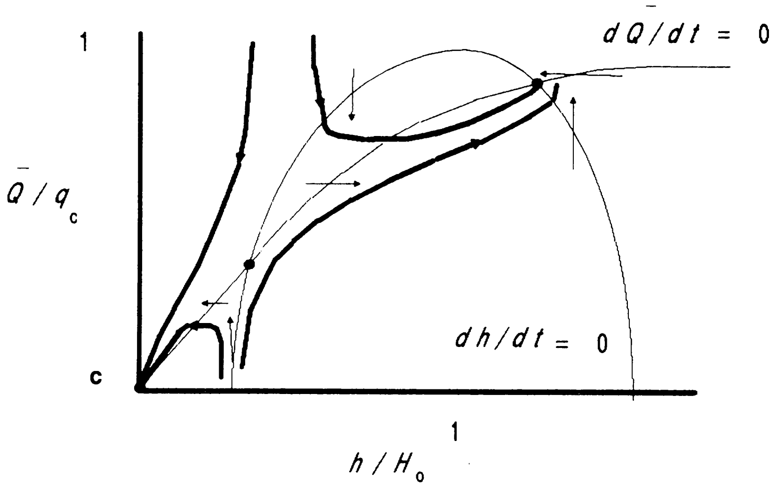
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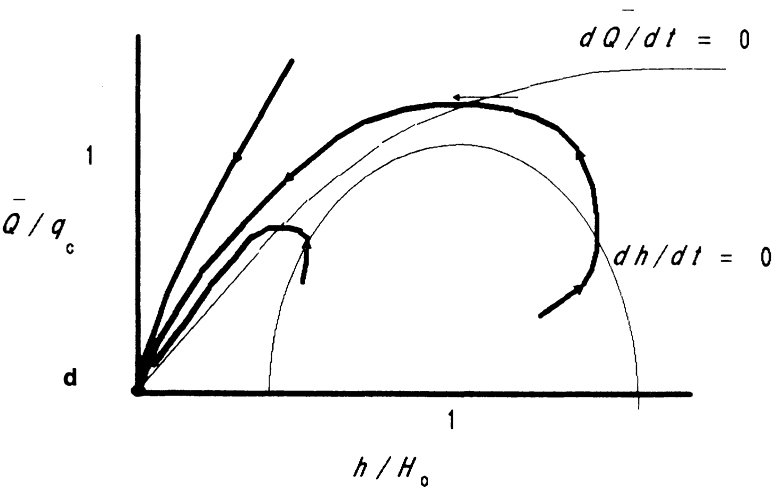

FIG. 5 (*facing page and above*).—Null clines and typical solution curves in the phase-plane diagram of equations (B3). An Allee effect in the herbivore reproduction rate, shown here by the parabolic curves, allows for a variety of null-cline configurations in the h/H_0-$\bar{Q}/q_c$ plane. See the text for an explanation of the cases.

(approaching a stable limit cycle) while the variance decreases, as predicted by equation (8).

DISCUSSION

To examine the dynamics of mobile nonselective herbivores, we have adopted a general model described in detail elsewhere (Edelstein-Keshet 1986). This model describes changes in herbivore abundance and in plant quality using a set of differential equations. Although many temperate-zone herbivores and the plants on which they feed are seasonal and hence are best modeled using difference equations, others, as well as many subtropical and tropical species, grow and reproduce throughout the entire year (Kirkpatrick 1957; Owen and Chanter 1972; Ehrlich and Gilbert 1973; Wolda 1978, 1980; Karban 1986, 1987). These species, which often fluctuate markedly in abundance (Kalshoven 1953; Brereton 1957; Anderson 1961; Gray 1972; Wolda 1978, 1980), may be fairly well described as populations continuous over time and are hence appropriate for a differential-equation model.

The analyses presented above lead to several conclusions. While considering the implications of our models, it should be kept in mind that they apply to situations in which the herbivores are mobile and nonselective and in which changes in both the herbivore population and the level of inducible defenses are reasonably continuous in time.

1. Under a wide range of conditions, inducible defenses by themselves can regulate herbivore populations. In particular, whenever the half-life of the inducible factor is greater than the induction time, inducible defenses can generate

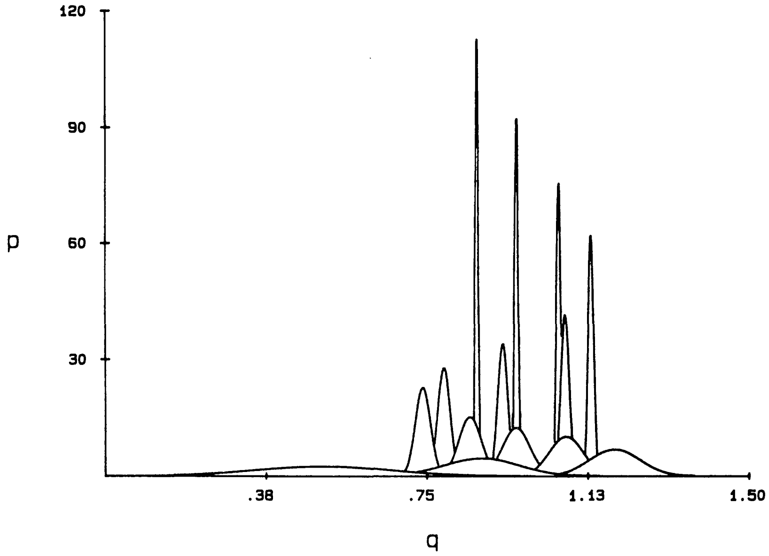

FIG. 6.—Computer-generated plots of the frequency distribution of plant defenses in the vegetation for 14 successive time intervals. Shown here is $p(q, t_i)$ versus q for $t_i = 0, 1, \ldots,$ 14 dimensionless time units, for the model consisting of equations (2) and (3) with the plant and herbivore responses f and with R given by the right-hand side of equations (18). The partial and ordinary differential equations were solved numerically along characteristics using a predictor-corrector method. The initial distribution, represented by the curve at the right, was Gaussian. Values of the parameters used were $\alpha = 0.2$, $b = 0.5$, $\kappa = 2.5$, $r = 3.0$. This case corresponds to the situation in which a limit cycle exists in the h/H_0-$\bar{Q}/q_c$ plane (see fig. 5*a*). Thus, the mean value of q ($\bar{Q}$), located at the peak of each distribution, undergoes oscillations, first shifting to the right, then to the left, then to the right. The variance of the distribution continually decreases, as predicted by the model. Eventually, the plant population would be homogeneous in its level of defenses, which would continue cycling. The herbivore density, also cycling between low and high values, is not shown in this graph.

sufficient density-dependent mortality to regulate an herbivore population. In essence, our model says that increases in herbivore density lead to an increase in the average level of defenses in the vegetation. This increased level of resistance in plants in turn lowers the population growth rate of the herbivore, either directly through toxicity or indirectly by increasing the susceptibility of the herbivores to other density-independent mortality factors. (We do not imply or suggest that inducible defenses are necessarily directly toxic, or that predators and parasites are not important components of the entire regulatory process.)

Several factors influence the steady-state herbivore population density when it is regulated primarily by inducible defenses. From equation (15) it follows that low equilibrium herbivore populations tend to occur if the rate of decay of defenses is low (low a), if the defense is effective or toxic at a relatively low level (low q_c), if the rate of induction of the defense by herbivores is high (high $K_{\max}$), or if the "sensitivity" of induction is high, that is, if the level of herbivory necessary to trigger induction at a given rate is low (low k_n).

2. Inducible defenses can significantly lower the size at which other density-

dependent agents regulate the herbivore population. Inspection of figure 4 indicates that the magnitude of this type of effect increases (h_{ss} decreases) as the null cline corresponding to $d\bar{Q}/dt = 0$ moves to the left and upward. Examination of equation (15) in turn reveals that this occurs under the same condition favoring low herbivore populations when density dependence is provided solely by induced defenses. Equations (15) and (17) indicate that herbivore equilibrium levels are influenced primarily by characteristics of the inducible defense. They do not appear to be influenced by characteristics of the herbivore (e.g., intrinsic birth and death rates, externally imposed carrying capacity [H_0]), contrary to the suggestion of Rhoades (1985).

A long-standing problem in ecology has been that of understanding how herbivore populations, particularly those of insects, are regulated at levels that do not cause appreciable defoliation of their host plants (i.e., why the world is green; Hairston et al. 1960; Murdoch 1966; Ehrlich and Birch 1967; Slobodkin et al. 1967; Crawley 1983; Strong et al. 1984). In general, ecologists have tended to favor the explanation that predators, parasites, and climatic factors regulate herbivore populations far below the level at which they may cause significant defoliation (Southwood 1975; Strong et al. 1984). Some workers, however, have at least hinted at the possibility that plant defenses may also provide such regulation (Feeny 1975; Rhoades 1985). Conclusions 1 and 2 provide theoretical support for such a possibility by indicating that inducible defenses acting alone or in conjunction with predators and parasites may maintain herbivores at low endemic levels.

3. Fluctuations in continuous herbivore populations caused by induced defenses are rarely stable oscillations. By analogy with the simplest Lotka-Volterra model of predator-prey population dynamics (Lotka 1925; Volterra 1926; see also Emlen 1984), it might be expected that inducible defenses alone can lead to persistent oscillations in both the mean level of inducible defenses and the size of the herbivore population. In both case 1 and case 2, however, the models predict convergence to stable equilibrium levels of inducible defenses and herbivore density. The convergence may be accompanied by transient decaying oscillations, but no stable cycles occur. In case 3, the persistent stable oscillations depend on the assumption that the herbivore growth rate exhibits an Allee effect, and even then, such cycles are found only with a restricted range of parameter values.

It has been proposed (Benz 1974; Fischlin and Baltensweiler 1979; Fox and Bryant 1984; Rhoades 1985) that inducible defenses are responsible for the fluctuations seen in some herbivore populations. Our model would lead to the conclusion that such systems differ in some basic way from those considered here. Such factors as seasonal or temporally discrete herbivore generations would certainly lead to a greater propensity for oscillation whether or not induced defenses are involved (see May and Oster 1976). Partial or total loss of mobility, increased selectivity of undefended versus defended plants, or a more unusual induction response in plants could be additional influences that lead to cycling. These possibilities bear further investigation.

4. Mobile nonselective herbivores do not maintain heterogeneity in the levels of induced defenses. It has been suggested that herbivores may maintain heterogeneity in the quality of their host plants by causing variation in the expressed

level of inducible defenses (Haukioja and Niemalä 1977; Edwards and Wratten 1983; Schultz 1983). In our models for mobile nonselective herbivores, this is not the case. Equation (9) indicates that when an equilibrium is reached for herbivore population size and mean plant quality, the variance of quality also eventually reaches an equilibrium. At this equilibrium, two forces act to change the variance of the expressed level of inducible defenses. Plants (units of vegetation) with relatively low levels of inducible defenses are stimulated by the herbivores to produce higher levels of defenses ($S(h) > aq$). Plants with a relatively high initial level of the inducible factors experience a net reduction in these factors through the counteracting tendency for spontaneous decay of the defenses ($S(h) < aq$). Together, these two processes would tend to reduce the variance of the level of the defense about its mean value.

In contrast, the addition of new plants, with defenses not yet expressed, into the population tends to increase the variance. A balance between these two forces leads to the equilibrium variance given by equation (9). If there is essentially no turnover in the plant population over a number of herbivore generations ($\bar{B} = 0$), as could occur when the plant is a tree or other long-lived perennial, then this equilibrium variance is zero. In our models it is apparent that heterogeneity persists only because it is restored by plant population recruitment. However, our results depend critically on the assumption that herbivores are mobile and nonselective (i.e., all parts of the vegetation experience the same level of herbivory). Furthermore, the force that leads to a decrease in the variance is the spontaneous rate of decay of the induced defenses (i.e., $\partial f/\partial q = -a < 0$). This effect would not necessarily exist in models for which a different dependence of f on q was assumed.

From equation (9) it can be seen that increasing the rate of decay of the inducible defense (a) tends to decrease the heterogeneity in the plant population. By contrast, increasing the rate of turnover of individuals in the plant population, as reflected by $\bar{B}$, tends to increase the variance of the level of defense. Heterogeneity is also increased by any factor that increases the equilibrium mean level of defense. When herbivore populations are regulated solely by inducible defenses, the primary factor is the critical toxicity level of the defense (q_c): the higher this value, the higher the equilibrium level of q, and hence the greater the variance of q. When herbivores are regulated by a combination of inducible defenses and other factors, increasing heterogeneity in plant quality will be brought about by decreasing q_c, the rate of decay of defense (a), or the sensitivity of the defense (k_n) and by increasing the rate at which it is induced (K_{max}).

SUMMARY

Recent empirical evidence suggests that many plants respond to herbivore damage by producing inducible defenses. Although several workers have suggested that inducible defenses may be responsible for fluctuations in some herbivore populations, little formal justification for this suggestion exists.

We describe here a quantitative framework that may be used for understanding the effects of inducible plant defenses on herbivore populations. In particular, we

use procedures for modeling continuous, structured populations to examine the dynamics of interactions between inducible defenses and mobile herbivores. Our models indicate that inducible defenses can by themselves regulate herbivore populations under a wide variety of conditions and that, in conjunction with other regulatory agents (e.g., predators, parasitoids), they can significantly depress herbivore populations. However, only under unusual conditions can inducible defenses cause persistent fluctuations in herbivore populations. Finally, our model suggests that herbivores cannot maintain heterogeneity in the level of inducible defenses within a plant population. These conclusions may not apply to sedentary or selective herbivores or to herbivores with discrete, nonoverlapping generations.

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APPENDIX A

Derivation of Averaged Equations

Several properties of the population are based on moments of the inducible defense distribution, $p(q,t)$. Assuming that q can take values only between 0 and some maximum, $q_{\max}$, we have

the total plant population size,
$$P = \int_0^{q_{\max}} p(q,t)\,dq\,;$$

the average value of q in the vegetation,
$$\bar{Q} = \frac{1}{P}\int_0^{q_{\max}} q\,p(q,t)\,dq\,;$$

the second moment (average value of q^2),
$$\bar{U} = \frac{1}{P}\int_0^{q_{\max}} q^2 p(q,t)\,dq\,;$$

the variance of q in the vegetation,
$$\bar{V} = \frac{1}{P}\int_0^{q_{\max}} (q - \bar{Q})^2 p(q,t)\,dq = \bar{U} - \bar{Q}^2\,.$$

P, $\bar{Q}$, $\bar{U}$, and $\bar{V}$ are time-dependent variables. Furthermore, the notations $Q = P\bar{Q}$, $U = P\bar{U}$, and $V = P\bar{V}$ denote the cumulative values of $\bar{Q}$, $\bar{U}$, and $\bar{V}$. In the following derivations, all integrals are taken from 0 to $q_{\max}$ and proceed from equation (2).

To find plant biomass, integrate both sides of equation (2):

$$\int \frac{\partial p}{\partial t}\,dq = -\int \frac{\partial (fp)}{\partial q}\,dq - \int \sigma p\,dq\,;$$

then, since $\sigma = \sigma(h, P)$ is independent of q by assumption A,

$$\frac{dP}{dt} = \frac{d}{dt}\int p\,dq = -(fp)_0^{q_{\max}} - \sigma \int p\,dq .$$

Now, if $p(q_{\max}, t) = 0$ (assumption D) and $fp = P\bar{B}$ at $q = 0$ (assumption C),

$$dP/dt = P\bar{B} - P\sigma = P[\bar{B} - \sigma(h,P)],$$

which is equation (7a).

To find the average value of q, multiply equation (2) by q and then integrate:

$$\int q\frac{\partial p}{\partial t}\,dq = -\int q\frac{\partial(fp)}{\partial q}\,dq - \int \sigma q p\,dq ;$$

then,

$$\frac{dQ}{dt} = \frac{d}{dt}\int qp\,dq = -(qfp)_0^{q_{\max}} + \int fp\,dq - \sigma(h,P)\int qp\,dq$$

(by assumption A for σ). Below, we deal more generally with f, such that $f(q,h) = f_1(h) + f_2(h)q$. For the case of inducible defenses, $f_1(h) = S(h)$ and $f_2(h) = -a$. Then,

$$\frac{dQ}{dt} = f_1(h)\int p\,dq + f_2(h)\int qp\,dq - \sigma(h,P)\int qp\,dq$$

$$= f_1(h)P + f_2(h)Q - \sigma(h,P)Q .$$

Furthermore,

$$\frac{d\bar{Q}}{dt} = \frac{d}{dt}\frac{Q}{P} = \frac{1}{P}\frac{dQ}{dt} - \frac{Q}{P^2}\frac{dP}{dt}$$

$$= f_1(h) + f_2(h)\bar{Q} - \sigma(h,p)\bar{Q} - (Q/P^2)P[\bar{B} - \sigma(h,P)]$$

$$= f_1(h) + f_2(h)\bar{Q} - \bar{B}\bar{Q} = S(h) - \bar{Q}(a + \bar{B}),$$

which is equation (7b), the desired result.

To find the variance in q, multiply equation (3) by q^2 and then integrate both sides:

$$\int q^2\frac{\partial p}{\partial t}\,dq = -\int q^2\frac{\partial(fp)}{\partial q}\,dq - \int \sigma q^2 p\,dq .$$

Then,

$$\frac{dU}{dt} = \frac{d}{dt}\int q^2 p\,dq = -(q^2 fp)_0^{q_{\max}} + \int 2qfp\,dq - \sigma(h,P)\int q^2 p\,dq$$

$$= 2f_1(h)Q + U[2f_2(h) - \sigma(h,P)] .$$

Let $\bar{U} = U/P$. Then,

$$\frac{d\bar{U}}{dt} = \frac{d}{dt}\frac{U}{P} = \frac{1}{P}\frac{dU}{dt} - \frac{U}{P^2}\frac{dP}{dt}$$

$$= 2f_1(h)\bar{Q} + \bar{U}[2f_2(h) - \sigma(h,P)] - (U/P^2)P[\bar{B} - \sigma(h,P)]$$

$$= 2f_1(h)\bar{Q} + \bar{U}[2f_2(h) - \bar{B}] .$$

Because $\bar{V} = \bar{U} - \bar{Q}^2$,

$$\frac{d\bar{V}}{dt} = d\bar{U}/dt - 2\bar{Q}d\bar{Q}/dt$$

$$= 2f_1(h)\bar{Q} + \bar{U}[2f_2(h) - \bar{B}] - 2\bar{Q}[f_1(h) + f_2(h)\bar{Q} - \bar{B}\bar{Q}]$$

$$= 2\bar{V}f_2(h) - \bar{V}\bar{B} + \bar{B}\bar{Q}^2,$$

which is equation (8). If $\bar{B} = 0$ (no new plants enter the population),

$$d\bar{V}/dt = 2\bar{V}f_2(h) = -2a\bar{V}.$$

APPENDIX B

DIMENSIONLESS MODEL EQUATIONS

Consider equations (14). Let $\bar{Q} = \hat{Q}Q^*$, $h = \hat{h}h^*$, $t = \tau t^*$, where the asterisks indicate dimensionless variables and the circumflexes indicate constant scale factors carrying the dimensions. Equations (14) may then be written

$$\frac{d(\hat{Q}Q^*)}{d(\tau t^*)} = K_{\max}\frac{\hat{h}h^*}{k_n + \hat{h}h^*} - a\hat{Q}Q^*,$$

$$\frac{d(\hat{h}h^*)}{d(\tau t^*)} = \hat{h}h^*r_0(1 - \hat{Q}Q^*/q_c).$$

Multiplying through by the constant factors $\tau/\hat{Q}$ and $\tau/\hat{h}$ leads to

$$dQ^*/dt^* = \frac{\tau}{\hat{Q}}K_{\max}\left(\frac{h^*}{k_n/\hat{h} + h^*}\right) - a\tau Q^*,$$

$$dh^*/dt^* = h^*r_0\tau[1 - (\hat{Q}/q_c)Q^*].$$

Now choose the appropriate scale factors,

$$\tau = q_c/K_{\max}, \qquad \hat{Q} = q_c, \qquad \hat{h} = k_n,$$

and drop the asterisk notation to obtain

$$d\bar{Q}/dt = h/(1 + h) - \alpha\bar{Q}, \tag{B1a}$$

$$dh/dt = hr(1 - \bar{Q}), \tag{B1b}$$

where $\alpha = aq_c/K_{\max}$, $r = r_0q_c/K_{\max}$ (see eqs. 14).

Similar methods lead from equations (17) to the dimensionless equations

$$d\bar{Q}/dt = h/(\kappa + h) - \alpha\bar{Q}, \tag{B2a}$$

$$dh/dt = hr[(1 - \bar{Q}) - h], \tag{B2b}$$

for $\kappa = k_n/H_0$, and from equations (18) to the dimensionless set

$$d\bar{Q}/dt = h/(\kappa + h) - \alpha\bar{Q}, \tag{B3a}$$

$$dh/dt = hr[(1 - \bar{Q}) - \mu(1 - h)^2]. \tag{B3b}$$

APPENDIX C

STABILITY CALCULATIONS, EQUATIONS (B1)

To avoid carrying numerous parameters, stability calculations are best performed on the dimensionless equations. Accordingly, the Jacobian of equations (B1) at the nontrivial steady state, where $\bar{Q}/q_c = 1$ and $h/H_0 = h_{ss}$, is

$$J = \begin{bmatrix} -\alpha & \dfrac{1}{(1 + h_{ss})^2} \\ -h_{ss}r & 0 \end{bmatrix}.$$

Thus,

$$\beta = \mathrm{trace}(J) = -\alpha < 0,$$

$$\gamma = \det(J) = h_{ss}r/(1 + h_{ss})^2 > 0.$$

In terms of dimensionless units, it is found that, for equations (B1), $h_{ss} = \alpha/(1 - \alpha)$. Since $\beta < 0$ and $\gamma > 0$, this steady state is stable. Decaying oscillations are obtained when $\beta^2 < 4\gamma$, that is, when $\alpha^2 < 4r\alpha(1 - \alpha)$. In terms of the original parameters, this inequality is

$$a < 4r_0/(1 + 4r_0q_c/K_{max}).$$

Making a small increases the likelihood that this inequality is satisfied. For large r_0, the right-hand side of this inequality approaches K_{max}/q_c. Thus, making K_{max} large also increases the likelihood that this inequality is satisfied.

APPENDIX D

STABILITY CALCULATIONS, EQUATIONS (B2)

The Jacobian of equations (B2) at the nontrivial steady state, $\bar{Q}/q_c = \bar{Q}_{ss}$ and $h/H_0 = h_{ss}$, can be expressed as

$$J = \begin{bmatrix} -\alpha & \dfrac{\kappa}{(\kappa + h_{ss})^2} \\ -h_{ss}r & -h_{ss}r \end{bmatrix}.$$

Thus,

$$\beta = \text{trace}(J) = -\alpha - h_{ss}r < 0$$

and

$$\gamma = \det(J) = h_{ss}r[\alpha + \kappa/(\kappa + h_{ss})^2] > 0,$$

implying stability. Decaying oscillations are obtained when $\beta^2 < 4\gamma$, which, after some simplification, leads to

$$(\alpha - h_{ss}r)^2 < 4h_{ss}r\kappa/(\kappa + h_{ss})^2.$$

As the value of h_{ss} approaches one, this inequality becomes

$$(\alpha - r)^2 < 4r\kappa/(\kappa + 1)^2,$$

which is most likely satisfied if r is large.

APPENDIX E

STABILITY CALCULATIONS, EQUATIONS (B3)

The Jacobian of equations (B3) is

$$J = \begin{bmatrix} -\alpha & \dfrac{\kappa}{(\kappa + h)^2} \\ -hr & r[(1 - Q) - \mu(h - 1)^2] - 2hr\mu(h - 1) \end{bmatrix}.$$

Thus,

$$J(0,0) = \begin{bmatrix} -\alpha & 1/\kappa \\ 0 & r(1 - \mu) \end{bmatrix},$$

$$\text{trace}(J) = r(1 - \mu) - \alpha,$$

$$\det(J) = -\alpha r(1 - \mu).$$

This implies that (0,0) is a saddle point whenever $(1 - \mu) > 0$ and that it is stable when $(1 - \mu) < 0$. (In subcases c and d of case 3, the steady state (0,0) is stable.)

A nontrivial steady state has the Jacobian

$$J = \begin{bmatrix} -\alpha & \dfrac{\kappa}{(\kappa + h)^2} \\ -hr & -2hr\mu(h - 1) \end{bmatrix}.$$

Thus,

$$\mathrm{trace}(J) = -[\alpha + 2hr\mu(h - 1)],$$
$$\det(J) = hr[2\alpha\mu(h - 1) + \kappa/(\kappa + h)^2].$$

If $h > 1$, then clearly $\mathrm{trace}(J) < 0$ and $\det(J) > 0$, implying stability. If $h < 1$, the result depends on the relative slopes of the two null clines at their point of intersection (i.e., at the steady state). If the slope of the q null cline is less steep, the steady state is a saddle point. Otherwise, it is an unstable node or focus. (See Edelstein-Keshet 1987 for proof of these assertions in a general model with an Allee effect.)

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