

Simultaneous effects of food limitation and inducible resistance on herbivore population dynamics

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Abstract

Many herbivore populations fluctuate temporally, but the causes of those fluctuations remain unclear. Plant inducible resistance can theoretically cause herbivore population fluctuations, because herbivory may induce plant changes that reduce the survival or reproduction of later-feeding herbivores. Herbivory can also simply reduce the quantity of food available for later feeders and this, too, can cause population fluctuations. Inducible resistance and food limitation often occur simultaneously, yet whether they jointly facilitate or suppress herbivore fluctuations remains largely unexplored. We present models that suggest that food limitation and inducible resistance may have synergistic effects on herbivore population dynamics. The population-level response of the food plant to herbivory and the details of how inducible resistance affects herbivore performance both influence the resulting herbivore dynamics. Our results identify some biological properties of plant–herbivore systems that might determine whether or not cycles occur, and suggest that future empirical and theoretical population dynamics studies should account for the effects of both food limitation and inducible resistance. © 2007 Elsevier Inc. All rights reserved.

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1. Introduction

Herbivore cycles have long captivated ecologists (Elton, 1924; Varley et al., 1973; Berryman, 1987; Turchin, 2003) and have commonly been ascribed to environmental forcing (Elton, 1924; Andrewartha and Birch, 1954; Hunter and Price, 1998), fitness effects that carry over across several generations (Ginzburg and Taneyhill, 1994), interactions with natural enemies (Southwood and Comins, 1976; Lawton and McNeill, 1979; Berryman, 1996; Brodmann et al., 1997; McCann et al., 2000; Maron et al., 2001; Dwyer et al., 2004), or interactions with the host plant (Lack, 1954; Benz, 1974; Keith and Windberg, 1978; Fischlin and Baltensweiler, 1979; Haukioja, 1980;

Bryant, 1981; Haukioja et al., 1983; Fox and Bryant, 1984; Rhoades, 1985; Myers, 1988). Empirical studies have motivated several distinct hypotheses for how herbivore cycles might be driven by interactions with the host plant. When a herbivore feeds on a plant, it reduces the value of that plant for future herbivores in two possible ways. First, the consumption of plant tissue may limit the quantity of food available to later-feeding herbivores. Here, we refer to this process as “food limitation”. Second, herbivore damage may elicit inducible resistance in the plant that reduces the nutritional quality of the unconsumed tissue (Karban and Baldwin, 1997; Tollrian and Harvell, 1999). Both of these pathways could play important roles in the long-term population dynamics of herbivores. For example, if food limitation causes herbivore performance to be density-dependent, it may lead to cyclic or even chaotic fluctuations in herbivore density over time (Hassell, 1975; May and Oster, 1976; Hassell et al., 1976; Abbott and Dwyer, 2007). Induced resistance alone can also drive fluctuations in herbivore density under certain conditions

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(Fischlin and Baltensweiler, 1979; Edelstein-Keshet, 1986; Edelstein-Keshet and Rausher, 1989; Lewis, 1994; Lundberg et al., 1994; Underwood, 1999b). In reality, food limitation and inducible resistance will often occur simultaneously (Morris, 1997; Agrawal, 2004), yet virtually all previous population dynamic models have examined only one of these processes acting in isolation (but see Ludwig et al., 1978 for a suggestion about how to link the two). The goal of this paper is to explore the joint influence of food limitation and inducible resistance on temporal fluctuations in herbivore population densities.

Although it is true that both food limitation and inducible resistance have the potential to drive herbivore fluctuations, they do not invariably do so (Hassell, 1975; Edelstein-Keshet and Rausher, 1989; Abbott and Dwyer, 2007). Thus when both processes occur simultaneously, they might act in a non-additive fashion, either enhancing or decreasing each other's ability to drive herbivore fluctuations. Here, we investigate the joint influence of food limitation and inducible resistance on herbivore population dynamics. We begin by building single-species population models for herbivores that include one or both processes, but in which plant biomass regrows to its carrying capacity each year, as in agricultural systems. We then extend the models to include population dynamics of plant biomass. We use our models to address three specific questions. First, do food limitation and inducible resistance have non-additive effects on herbivore population dynamics? Second, when population fluctuations are possible, what features of the herbivore (such as its feeding rate and finite rate of population increase) influence whether the population is cyclic or stable? Third, because different plant species employ different types of inducible responses (Karban and Baldwin, 1997), does the type of inducible resistance used by the plant alter its impact on herbivore dynamics?

2. Models

To understand how food limitation and inducible resistance interact to influence herbivore population dynamics, we present a series of models that make different biological assumptions about the plants and herbivores. The advantage of this broad approach is that it allows us to distinguish general patterns from results that arise due to specific model assumptions. Furthermore, our different models are appropriate for describing different natural systems and allow us to determine when we should expect to see particular population dynamical patterns in nature.

Each model presented here is built from a set of rules for how food-limitation acts (the “food limitation submodel”) and how inducible resistance works (the “inducible resistance submodel”), as described below. All models assume a univoltine specialist insect feeding on an annual plant. We choose this scenario partly for analytical convenience, but also because many temperate-zone insect herbivores, including important agricultural pests such as

the Colorado potato beetle (*Leptinotarsa decemlineata*; Hare, 1990), fit this scenario throughout all or parts of their range. Our models track population densities at the end of each generation, after food limitation and inducible resistance have had their effects on survival and immediately prior to reproduction.

Due to the large number of models considered, all models described in this section are summarized in Table 1. In the text, we show fully dimensional models so that the relationships among them are clear. To perform analyses, however, we rescale all models using non-dimensionalization and these rescaled models are shown in Table 1. All algebraic substitutions used to derive the equations in Table 1 from those in the text are shown in Table 2. For clarity, we consistently use tildes (“~”) over unscaled state variables, whereas rescaled state variables lack tildes. Furthermore, we use lowercase Latin letters for the parameters in the unscaled models, and lowercase Greek letters to represent composite parameters in the rescaled models. The biological meaning of each parameter is summarized in Table 2.

Each season, we assume that the density of herbivores relative to plant biomass translates to a given amount of plant tissue damage according to a saturating function, such that

$$d_t = \frac{\tilde{H}_{t-1}/\tilde{P}_{t-1}}{c + \tilde{H}_{t-1}/\tilde{P}_{t-1}} = \frac{\tilde{H}_{t-1}}{c\tilde{P}_{t-1} + \tilde{H}_{t-1}}, \quad (1)$$

where d_t represents the fraction of plant biomass damaged during generation t , $\tilde{P}_{t-1}$ is plant biomass at the end of the preceding generation, and $\tilde{H}_{t-1}$ is the herbivore density. c is a constant determining the steepness of the saturating curve. Low values of c indicate that each herbivore can cause a large amount of damage. The amount of damage inflicted on plants determines the severity of both food limitation and inducible resistance in a given year.

2.1. Food limitation submodels

We present two different models of food limitation that differ with respect to the host plant. In the single-species model, we assume the plant attains its carrying capacity at the start of each growing season prior to the period of herbivore attack. Plant biomass may then decline within the season due to herbivory, but will begin the subsequent season back at carrying capacity regardless of the extent of herbivory. In the two-species model, the plant's population dynamics are explicitly included in the model. In this case, plant recruitment is density-dependent, and the quantity of plant biomass does not necessarily attain its carrying capacity in a given season but instead, its level depends on the previous year's herbivore damage and density of plant biomass. The single-species model is appropriate for systems in which plants are limited by resources and not affected at the population level by herbivory, or for crops that are planted annually. The two-species model is

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