# VARIATION IN PLANT QUALITY AND THE DYNAMICS OF INSECT HERBIVORE POPULATIONS

by

# SANDRA ELIZABETH HELMS SPIRES

(Under the direction of Mark Hunter)

# ABSTRACT

Herbivore population dynamics can be influenced significantly by heterogeneity in plant quality. Birth and death rates of herbivores are influenced by plant-induced changes in parameters such as growth, survival, and fecundity. Variation in plant quality can also have a profound influence on herbivore populations through changes in rates of movement, mortality due to natural enemies, and rates of competition. We should also expect that the strength of density dependence, and herbivore population dynamics, will vary with host plant quality. This thesis examines the impact of variable plant quality on the dynamics of an insect herbivore population. This is done using both aphid population data collected from a common garden of six different species of *Asclepias* plants and some simple models of hypothetical populations to further explore the consequences of variable plant quality.

INDEX WORDS: Aphis nerii, Asclepias, Density dependence, Lysiphlebus testaceipes,
 Milkweed, Parasitism, Plant-insect interactions, Plant quality, Population
 dynamics, Spatial Scale, Tri-trophic interactions

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#### CHAPTER 1

# INTRODUCTION AND LITERATURE REVIEW

Since Hairston *et al.* (1960) proposed "the world is green" hypothesis arguing that herbivores could not be food limited due to the fact that the earth is covered with plants, scientists have become increasingly aware of how inedible the plant world really is for herbivores. Ehrlich and Raven (1964) first set forth the idea that most plants are unpalatable to all but a select group of herbivores. Chemical and physical defenses are widespread in the plant world. Toxins, digestibility reducers, and physical defenses such as thorns and trichomes cause herbivores to be limited in the plants that they are able to utilize as food resources.

Herbivore population dynamics can be influenced significantly by heterogeneity in plant quality (Hunter 1997, Hunter *et al.*, 2000). Plants of different quality can cause differential birth and death rates for herbivores, leading to differences in equilibrium population sizes as well as the period and magnitude of fluctuations around this equilibrium as demonstrated by Underwood and Rausher (2000). Birth and death rates of herbivores are influenced by plant-induced changes in parameters such as growth, survival, and fecundity. Variation in plant quality can also have a profound influence on herbivore populations through changes in rates of movement, mortality due to natural enemies, and rates of competition (Price et al. 1980; Denno and McClure 1983; Denno et al. 1995; Abrahamson and Weis 1997; Lill et al. 2002). We should also expect that the strength of density dependence, and herbivore population dynamics, will vary with host plant quality (Hunter et al. 2000; Hunter 2001).

This thesis examines the impact of variable plant quality on the dynamics of an insect herbivore population. This is done using both aphid population data collected from a common garden of six different species of *Asclepias* plants and some simple models of hypothetical populations to further explore the consequences of variable plant quality. This introductory chapter summarizes our current knowledge of the impact of plant quality on insect herbivore populations. The literature review begins by defining what we mean by plant quality and then examines the different ways in which plant quality can influence herbivore populations.

## **Plant Quality**

Plant quality can be defined as phenotypic traits of a plant that influence the ability of an herbivore to consume that plant. Several different characteristics of plants comprise the broad category of plant quality. Nutritional chemistry, typically measured as carbon-nitrogen ratios, affects the nutritional value gained by an herbivore (Mattson 1980). Historically, from the apparency theory of plant chemical defense, defensive chemistry has been grouped into two categories: toxins and digestibility reducers (Feeny 1976, Rhoades and Cates 1976). Toxins are thought to be energetically expensive for the plant, but make it unpalatable to all but a few herbivores. Digestibility reducers, such as tannins and lignin, are less expensive to the plant but do not completely deter feeding by herbivores. Instead, these compounds make it more difficult for herbivores to consume and draw nutrients from this plant material.

Apparency theory is part of the optimal defense hypothesis of plant chemical defense, which suggests that plants evolve to allocate defenses in a way that maximizes fitness (Feeny 1976, Rhoades and Cates 1976). This means that resources are diverted to chemical defenses at the expense of growth and reproduction. However, the predictions of apparency theory have not

always been proven with empirical evidence. For example phenolic compounds, which are traditionally thought to act as digestibility reducers, can act more like toxins by generating oxygen radicals in the guts of caterpillars (Barbehenn et al. 2005).

Other theories of plant chemical defense have also been suggested to explain patterns of variation of plant defenses; namely the carbon nutrient balance hypothesis (Bryant et al. 1983), the growth rate (resource availability) hypothesis (Coley et al. 1985), and the growth-differentiation balance hypothesis (Herms and Mattson 1992). The carbon nutrient balance hypothesis attempts to explain the influence of soil nutrients and light availability on plant defenses during the lifetime of an individual plant. The growth rate hypothesis looks at the evolution of the allocation of resources to plant defense based on resource availability (again based on nutrient and light availability). The growth-differentiation balance hypothesis places plants on a continuum based on resource availability to predict whether a plant should invest more in growth or differentiation (which includes defense). Unfortunately, no single hypothesis has emerged as the "winner" in explaining variation in plant defenses as none of these four hypotheses is without flaws (Stamp 2003).

Perhaps of greatest potential importance to the dynamics of insect herbivores is the existence of inducible defenses. Inducible defenses are defenses produced in response to herbivore damage such that defenses are reduced when herbivores are absent and increased when herbivores are present (Rhoades 1979). For example, potato and tomato plants have been shown to respond to herbivore damage by producing proteinase inhibitors which inhibit digestive enzymes in the midgut of insect herbivores (Green and Ryan 1972). The existence of inducible defenses provides a mechanism whereby plant quality can impact herbivore population dynamics: the strength of induced resistance produced by a single plant can depend on the

density of attacking herbivores and therefore can be a potential source of density-dependence for insect herbivore populations (Underwood and Rausher 2002). For example, induced changes in plant quality have long been the primary explanation for cycles of larch budmoth in the Swiss Alps (Baltensweiler and Fischlin 1998). In this system, heavy defoliation during budmoth population peaks induces changes in plant quality. Reduced plant quality has a strong effect on budmoth survival and reproduction, and it takes two or more years for plant quality to recover allowing for the possibility that plant quality can induce budmoth population cycles. However recent evidence suggests that parasitoid-budmoth interactions account for more variation in population growth rates and appears to be the dominant factor driving budmoth population cycles (Turchin et al. 2003). Work by Nora Underwood has demonstrated the ability of induced resistance traits in plants to influence density dependence and temporal population dynamics of insect herbivores (Underwood and Rausher 2000, 2002).

Mechanical defenses are another category of plant traits that influence plant quality. These include various types of surface protection such as thorns, trichomes, and resins. Thorns are typically defensive against only larger herbivores (Cooper and Owen-Smith 1986). They influence herbivore bite size and therefore feeding rate, making the plant less profitable (in terms of energy gain per unit time) for the herbivore. Trichomes work through a similar mechanism for smaller herbivores (Gutschick 1999). Many insect herbivores are deterred by trichomes because they make the plant difficult to navigate and many trichomes emit repellant chemicals or sticky substances that trap insects (Duffey 1986). Mechanical defenses are typically less expensive to plants, but they only afford surface protection and may not be as effective against a wide range of herbivores as chemical defenses.

Variation in these plant characteristics occur both among and within plant species and can have important consequences for the population dynamics of insect herbivores. Furthermore, plant quality is not static over time. Many aspects of plant quality have been shown to vary during the growing season. For example, the nutritional value of leaves generally declines with age (Mattson 1980) and concentrations of cardenolides in species of *Asclepias* are known to vary through time (Nelson *et al.* 1981).

# **Influence of Plant Quality on Insect Herbivore Populations**

Variation in plant quality can have a profound influence on herbivore populations through changes in fecundity, survival, movement, mortality due to natural enemies, and rates of competition (Price *et al.* 1980; Denno and McClure 1983; Denno *et al.* 1995; Abrahamson and Weis 1997; Lill *et al.* 2002).

#### Fecundity and Survival

Host plant quality can have both direct and indirect effects on the fecundity and survival of insect herbivores. Direct effects are fairly easy to interpret. For example, increased nutritional quality of a plant (i.e., increased nitrogen content) likely leads to increased fecundity and increased levels of defensive chemistry likely lead to reduced survival rates (Awmack and Leather 2002). However, for many specialist herbivores, particularly those that sequester defensive compounds, increasing levels of defensive chemistry in a host plant may have the opposite effect on survival. In this case, the plant chemistry may have no direct effect on the herbivore, but leads to higher survival rates through increased protection from natural enemies (Hunter 2003).

Indirect effects of plant quality on fecundity and survival include changes in development time, body size, and reproductive strategies. Poor plant quality can lead to increases in juvenile development times, essentially exposing the herbivore to natural enemies for a longer period of time, which can decrease survival rates (slow-growth-high-mortality hypothesis; Clancy and Price 1987). However, there is not strong support for this hypothesis – there are just as many studies showing this not to be the case as there are in support of this hypothesis (Hunter 2003). There have also been numerous studies that show a positive correlation between pupal or adult body size and fecundity and linking reduced body sizes to poor host plant quality (Awmack and Leather 2002).

Modification of oviposition behavior is another response insect herbivores may exhibit when faced with plants of poor quality. The female may reduce the number of eggs laid on each plant, adjust the size or nutritional content of the eggs, or resorb the eggs (Awmack and Leather 2002). Egg size and nutritional content have the potential to influence offspring fitness, and hence influence both survival and fecundity. For example, Leather (1985) showed that the pine beauty moth lays fewer but larger eggs on poor quality host plants than on high quality host plants. This oviposition behavior represents a trade-off between fecundity and survival – on poor quality hosts, there is reduced fecundity, but the larger eggs allow for greater survival rates than would be achieved on the same plant with smaller eggs.

A trade-off between fecundity and survival is also suggested for the resorption of eggs by insects when host plant quality is poor. Ohgushi (1996) found that female ladybeetles feeding on thistle were able to increase their probability of survival through an increase in egg resorption.

## Movement

Host plant quality can also influence herbivore population dynamics through its influence on the spatial distribution of herbivores and the influence on migration rates. For example, Howard & Dixon (1992) showed that decreased host plant quality led to increased production of alates in aphid populations, and hence increased emigration rates. Denno *et al.* (1985) found a significant crowding by host plant nutrition interaction on the production of migratory planthoppers, suggesting that the density dependent migration response typically observed at high densities is dampened if the planthoppers are feeding on a high quality host plant. As both immigration and emigration can influence population dynamics, these are also important factors to consider. Unfortunately, it seems that migration is frequently ignored in studies of population dynamics. This is primarily due to our definition of populations – we often try to identify populations by minimizing rates of movement across boundaries.

However, movement within our population boundaries may still be important to consider, particularly if we are looking at insects that are able to move among host plants of differing quality. The impacts of this might be most clearly seen with source-sink dynamics (Pulliam 1988) or use of herbivore refuges from natural enemies (Murdoch 1994). In the former case, we have higher quality plants that support population growth and lower quality plants that are not capable of sustaining population growth on their own. The influence of source-sink dynamics due to varying plant quality is to create density dependence in the population as a whole.

#### Mortality due to Natural Enemies

Variation in plant quality also has the potential to affect the mortality of insect herbivores due to natural enemies. In such tri-trophic systems, plant traits can influence the interaction

between herbivores and natural enemies by acting both directly and indirectly on herbivores and their natural enemies (Price *et al.* 1980). Plant characteristics such as toxins and digestibility reducers can influence prey quality, abundance, and distribution which in turn affect natural enemies of the herbivore. Plant allelochemicals sequestered by an herbivore may affect growth parameters of a predator (Barbosa *et al.* 1982, Turlings and Benrey 1998 and references therein, Francis *et al.* 2001) or act as a feeding deterrent for predators (Sword 2001). In addition, plant properties may act directly on natural enemies of the herbivore. Chemical cues given off by certain plants may attract natural enemies of an herbivore to that plant (Turlings and Benrey 1998 and references therein, Dutton *et al.* 2002). The role of plant chemistry in herbivorepredator interactions is dependent on the specific allelochemical and its abundance (Barbosa *et al.* 1991). Physical plant structure is important as well. For example, predation and parasitism rates have been shown to be influenced by stem toughness (Moon and Stiling 2000) and vegetation structure (Denno *et al.* 2002).

#### Rates of Competition

Rates of competition among insect herbivores may differ based on host plant quality as variation in plant nutrition and allelochemistry can alter the intensity and/or frequency of competitive interactions (Denno *et al.* 1995). Species that are superior competitors on certain plants may be the inferior competitor on other plants based solely on differences in host plant quality. For example, Fritz (1990) found that competition coefficients of 3 species of sawfly differed significantly among different willow genotypes. Additionally, several studies have also demonstrated that the susceptibility of a host plant determines the outcome of a competitive interaction between two herbivore species (Mopper *et al.* 1990; Moran and Whitham 1990). In

both of these studies, competition occurred only on susceptible genotypes. In fact, it has been suggested that variation in host plant quality may cause herbivores to concentrate on optimal feeding sites, which would suggest that we should expect a higher frequency or more intense competitive interactions on high quality host plants as compared to lower quality plants (Denno *et al.* 1995).

### Strength of Density Dependence

Since both competition for limited resources and mortality imposed by natural enemies have the potential to act in a density-dependent fashion, it might be expected that the expression of density dependence, and herbivore population dynamics, should vary among host plants (Hunter *et al.* 2000; Hunter 2001).

For example, host plant genotype, which influences phenotypic variation in plant quality traits (Underwood and Rausher 2000; McIntyre and Whitham 2003), including plant secondary chemistry (Hunter *et al.* 1996; Larsson *et al.* 2000) has been shown to influence herbivore population dynamics. The strength of density dependence can have considerable impact on population dynamics as its value determines the difference between exponential and density dependent growth. Several recent studies have demonstrated that the strength of density dependence can vary among host plants (Underwood and Rausher 2000, 2002; Rotem and Agrawal 2003).

#### CONCLUSIONS

It is clear that variation in plant quality has the potential to influence the population dynamics of insect herbivores. However, we still do not fully understand how and to what extent

plant quality can influence population dynamics and there is very little empirical evidence. This thesis explores the impact of variable plant quality on dynamics of insect herbivores.

An observational study was conducted using a common garden experiment in which natural populations of aphids were monitored on six different species of *Asclepias*. Plants in the genus *Asclepias* vary in their quality for insect herbivores based, in part, on concentrations of cardenolides in their tissues (Malcolm *et al.* 1989). Furthermore, concentrations of cardenolides are known to vary both within and among species (Malcolm *et al.* 1989), among plant parts, and through time (Nelson *et al.* 1981). In addition to counting aphid numbers on each plant in the common garden, rates of parasitism (through counts of aphid mummies) were also measured.

Chapter 2 analyzes the data collected from this common garden within a single growing season. This chapter examines variation in the power of density-dependent parasitism acting on an insect herbivore feeding on different host plant species. The research addresses two specific questions; 1) does the form and strength of density-dependent parasitism vary among plant species, and 2) can within-season growth of an aphid population be limited by parasitism?

Using some simple models and analyses, Chapter 3 examines the consequences of variation in the strength of density dependence among host plants. This chapter uses both hypothetical examples and data collected from the common garden experiment. Chapter 4 draws some general conclusions from the results of chapters 2 and 3.

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# CHAPTER 2

# EFFECTS OF VARIATION AMONG PLANT SPECIES ON THE INTERACTION

# BETWEEN AN HERBIVORE AND ITS PARASITOID<sup>1</sup>

<sup>1</sup>Helms, S.E. , S.J. Connelly, and M.D. Hunter. 2004. Ecological Entomology 29, pp. 44-51

**ABSTRACT.** 1. Previous studies have demonstrated that phenotypic traits of plants have the potential to affect interactions between herbivores and their natural enemies. Consequently, the impact of natural enemies on herbivore vital rates and population dynamics may vary among plant species. This study was designed to investigate the potential for density-dependent parasitism of an aphid herbivore feeding on six different host plant species.

2. Population densities of the aphid *Aphis nerii* B de F (Homoptera: Aphididae) and its parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) were recorded within a single growing season on six different species of milkweed in the genus *Asclepias* L. (Asclepiadaceae). *Asclepias* species are known to vary in their quality as food for herbivores. Although data on plant quality were not available in this study, population data were analyzed to determine the effects of different *Asclepias* species on rates of parasitism and aphid population growth.

3. Parasitism rates of *A. nerii* varied among *Asclepias* species but were temporally density dependent over at least some range of aphid density on all plant species. Aphid population growth rates also varied among *Asclepias* species, and declined with an increase in the maximum parasitism rates among plant species. However, in no case was density-dependent parasitism sufficient to prevent exponential population growth of aphids within the growing season. The results serve to emphasize that, if natural enemies are to regulate herbivore populations, density-dependent mortality is a necessary, but not sufficient, condition for regulation.

**Key words**. *Aphis nerii*, *Asclepias*, density dependence, *Lysiphlebus testaceipes*, milkweed, parasitism, plant-insect interactions, population dynamics, tritrophic interactions

# **INTRODUCTION**

All populations, if left unchecked, have the potential to grow exponentially (Malthus, 1798). Density dependent processes may limit exponential growth by acting to reduce population growth rates as densities rise (Varley *et al.*, 1973). Both competition for limited resources and mortality imposed by natural enemies have the potential to act in a density-dependent fashion. For insects that feed on plants, variation in plant quality can have a profound effect on both levels of competition and mortality from natural enemies (Price *et al.*, 1980; Denno *et al.*, 1995; Abrahamson & Weis, 1997; Lill *et al.*, 2002). As a consequence, it might be expected that the expression of density dependence, and herbivore population dynamics, should vary among host plant species (Hunter *et al.*, 2000; Hunter, 2001).

The role of density dependent parasitism in aphid population dynamics has been examined in a number of studies. Results have been variable, leading to no general consensus. Parasitism of aphids has been shown to be density dependent (Walker *et al.*, 1984; Murphy & Volkl, 1996; Colfer & Rosenheim, 2001), inversely density dependent (Walker *et al.*, 1984; Zhang & Chen, 1993), and density independent (Zhang & Chen, 1993; Ferguson & Stiling, 1996; Murphy & Volkl, 1996), varying with the species and system under study. Differences in these results may be due to a number of factors including competition from other aphid predators, intraguild predation, and variation in plant quality.

This study was designed to examine variation in the power of density-dependent parasitism acting on an insect herbivore feeding on different host plant species. The research was designed to address two specific questions; 1) does the form and strength of density-dependent parasitism vary among plant species, and 2) can within-season growth of an aphid population be limited by parasitism? The study was conducted by counting populations of the aphid, *Aphis* 

*nerii* B de F (Homoptera: Aphididae), and parasitism by *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae), on six species of plants in the genus *Asclepias* L. (Asclepiadaceae) growing in a common garden.

#### System of Study

Plants in the genus *Asclepias* vary in their quality for insect herbivores based, in part, on concentrations of cardenolides in their tissues (Malcolm *et al.*, 1989). Cardenolides are a group of cardiac-active steroids that act by blocking the  $Na^+/K^+/ATP$  se system which transports ions across cell membranes (Horisberger, 1994). Concentrations of cardenolides are known to vary both within and among species (Malcolm *et al.*, 1989), among plant parts, and through time (Nelson *et al.*, 1981).

*Aphis nerii*, or the oleander aphid, is an aposematic phloem-feeding specialist of oleander (*Nerium oleander* L. (Apocynaceae)) and species of *Asclepias*. These insects have bright yellow coloration with black legs, antennae, cauda, and cornicles. Aphids reproduce parthenogenetically and are not particularly mobile; individuals appear to stay on suitable host individuals, although winged forms are produced in response to crowding or declines in host quality (Groeters, 1989). *A. nerii* occur as highly aggregated colonies on host plants and have been shown to sequester cardenolides from their host plants (Rothschild *et al.*, 1970; Malcolm, 1990). Malcolm (1990) found that aphids sequestered almost all of the types of cardenolide present in the host plant *A. curassavica* L. and so the cardenolide concentrations in the aphids co-vary with the host. There are apparently no large-scale fitness trade-offs from feeding on different hosts for *A. nerii*, suggesting that they possess a sequestration mechanism that renders them fitness insensitive to cardenolide variation among hosts (Groeters, 1993). This is consistent with the findings of

Malcolm (1992) that, in the absence of predators, aphid populations grow at the same exponential rate on high and low cardenolide plants.

*Lysiphlebus testaceipes* is the major parasitoid of *A. nerii* and has a wide distribution in Nearctic America, into Neotropical America, and the Mediterranean (Stary, 1976). *L. testaceipes* was imported into North America and the Mediterranean as a biological control agent and so likely has its origins in South America (Stary, 1970). It lays a single egg in the body of an aphid and, upon hatching, the larva feeds internally on the living aphid, causing it to appear swollen. After the death of the aphid, the aphid's cuticle turns brown to form a typical aphid *mummy*. The wasp pupates inside the aphid mummy and then emerges by cutting a circular hole in the top of the mummy (Stary, 1988). Hall and Ehler (1980) found that parasitism by *L. testaceipes* of *A. nerii* populations feeding on *Nerium oleander* was inversely density dependent.

Although the effect of cardenolides on aphid parasitoids has not been examined, cardenolides have been shown to affect the fitness of several enemies of *A. nerii*: coccinellids (Pasteels, 1978), lacewings (Malcolm, 1992), and spiders (Malcolm, 1989). Pasteels (1978) found that cardenolides disrupted wing development in coccinellids and Malcolm (1989) demonstrated that spiders fed *A. nerii* built severely disrupted webs and attacked fewer non-toxic, control aphids. Survival of lacewing larvae is much lower when feeding on *A. nerii* with high cardenolide content (Malcolm, 1992). It has been demonstrated that variable cardenolide content can also influence the mortality of *A. nerii* by influencing predation: aphid populations were smaller and more influenced by predation on a low cardenolide milkweed than on a high cardenolide milkweed (Malcolm, 1992).

# MATERIALS AND METHODS

#### *Field samples*

From July through to October 2001, *Aphis nerii* populations were counted on six species of *Asclepias* in a common garden located beside the University of Georgia's Botany Greenhouses, Athens, Georgia. Plants are grouped by species in blocks of 25 plants each, with one meter between plants and between blocks. There are four blocks (100 plants) each of *A. exaltata* L., *A. speciosa* L., *A. tuberosa* L., and *A. viridis* L.; and two blocks (50 plants) each of *A. incarnata* L. and *A. sullivantii* L. The plants were watered for two hours, twice a week, as weather dictated. To control fire ants, Orthene was applied to ant mounds as they appeared. Grass between plants was mowed every two to three weeks.

Plant biomass estimates, number of aphids, and number of aphid mummies were recorded from each plant in the garden every two weeks from July 14 to October 22. At the beginning of November, plants senesced and aphid populations dropped to zero on all plants. Biomass estimates of the plants were made by measuring stem height and counting the number of leaves, and then scaling these numbers to dried weights of collected plant material. Aphid densities were then calculated as the number of aphids on an individual plant on a given date divided by the biomass estimate of that plant on that date.

#### Data Analysis

Growth Rate of Aphid Populations. Preliminary observations suggested that aphid populations grew exponentially on all Asclepias species (Fig. 2.1) until the plants senesced at the end of the growing season. Therefore, to approximate the per capita rate of increase (r) of aphids on each plant species, a linear model was found for each individual plant using the natural log of

aphid density against time period (Berryman, 1999). The slope of this line is *r* for aphid growth on that plant. Differences in *r* among plant species were determined by ANOVA (SAS, 1999), using individual plants within each species as replicates. Although there were either 50 or 100 individual plants for each *Asclepias* species in the field, only plants that hosted aphids for at least four consecutive sampling dates were used in the analysis, causing variation among species in sample size (Table 2.1).

Temporal Density Dependent Parasitism. Population data were examined for evidence of both temporal and spatial density-dependent parasitism. Temporal density dependence describes how, as a prey population increases over time, its mortality changes for a single point in space. Spatial density dependence describes how, as average prey density varies among patches, prey mortality changes for a single point in time (Stewart-Oaten & Murdoch, 1990). Percent parasitism was found by dividing the number of mummies by the total number of parasitised and unparasitised aphids on each plant at each time period. To examine temporal density dependence, average values of percent parasitism on each sampling date were regressed against the density of aphids independently for each plant species. The resulting points were graphed as percent parasitism against aphid density. To estimate the shape of parasitism response curves, the resulting data points for each species were fit to several potential equations, namely those of the forms represented in Fig. 2.2. Data were fit to equations (Table 2.2) using the Proc NonLin procedure is SAS (1999). These equations can be described as a linear function (Fig. 2.2, line A), two alternative forms of a saturation curve (Fig. 2.2, line C), and a parabolic curve (Fig. 2.2, line D). The null hypothesis of density independence is represented by line B. Biologically, a linear function represents a density dependent response to prey populations. Saturation curves represent initial density dependence falling to density independence at higher aphid densities. A parabolic

curve represents initial density dependence to some threshold, followed by inverse density dependence beyond that threshold, presumably resulting from limitations on the numerical or behavioral responses of parasitoids (Holling, 1959).

Spatial Density Dependent Parasitism. To assess the evidence for spatial density dependence, average values of percent parasitism for each individual plant (across all sampling dates) were regressed against aphid density, independently for each plant species. These data were graphed as percent parasitism against aphid density and examined for significant relationships between aphid density and percent parasitism.

*Effects of Parasitism on Per Capita Rates of Aphid Population Growth.* Using parasitism rates from the analysis of temporal density dependence, regressions between mean growth rate of *A. nerii* populations and the maximum observed percent parasitism experienced on different plant species were examined. Linear and non-linear regressions using the Proc NonLin procedure in SAS (1999) were compared.

### RESULTS

#### Aphid Population Growth Rate

Aphid population growth was approximately exponential on all *Asclepias* species and showed no signs of decline prior to senescence of host plants in the fall of 2001 (Fig. 2.1b). Plant species identity was a significant predictor of aphid per capita growth rate (r) (F = 10.65, d.f. = 5,247, P<0.0001; Table 2.1). Aphid population growth rate on *A. exaltata* was significantly higher than on all other species, and aphid growth on *A. sullivantii* was significantly higher than that on *A. tuberosa* (Table 2.1).

# Temporal Density Dependent Parasitism

There was evidence of temporal density dependent parasitism over at least some range of aphid densities on all plant species (Fig. 2.3). In other words, there was an initial increase in percent parasitism with aphid density on all host plants. However, the exact form of density dependence among plant species remains equivocal. Figure 2.3 suggests that parasitism on *A. incarnata* and *A. speciosa* might best be described by saturation curves (parasitism reaching a plateau, Fig. 2.2, line C). On the four other host species, percent parasitism appears to decline at high aphid densities, suggesting a switch from density-dependent to inverse density-dependent parasitism (Fig. 2.3). Regression analyses (Table 2.2) suggest that both saturation curves (density dependence falling to density independence) and parabolic curves (density dependence falling to inverse density dependence) provide good descriptions of the data, although r-squared values are generally higher for the parabolic curves. In either case, parasitism of *A. nerii* by *L. testaceipes* is clearly limited at high aphid densities, which may explain why aphid population growth remains exponential (Fig. 2.1b) through the end of the season. In addition, there is obvious variation among host plant species in the form and strength of density dependent parasitism (Fig. 2.4).

#### Spatial Density Dependent Parasitism

There was no evidence that aphid parasitism rates were spatially density dependent on any of the plant species (Fig. 2.5).

## Effects of Parasitism on Per Capita Rates of Aphid Population Growth

The mean population growth rate of *A. nerii* was negatively correlated with the maximum observed parasitism on each *Asclepias* species. Figure 2.6 shows the points for each species with the regression line which best describes this relationship ( $y = 245.1 - 244.5x^{0.000807}$ , *P*=0.0435).

### DISCUSSION

As in many aphid-parasitoid systems (Walker *et al.*, 1984; Murphy & Volkl, 1996; Volkl & Stechmann, 1998), parasitoids did not play a significant role in regulating population growth of *A. nerii* on *Asclepias* species. Aphid densities continued exponential growth up to the end of the growing season (Fig. 2.1b). Aphid parasitoids often exploit a small number of available hosts, and parasitism rates tend to range between 1% and 10% (Mackauer & Volkl, 1993). Although parasitism rates reached over 30% on some host plants in this study (Fig. 2.3), these rates were still not sufficient to regulate aphid population growth within the season.

In contrast to Hall and Ehler (1980), who found parasitism rates of *A. nerii* on *Nerium oleander* to be inversely density dependent, the results of this study found a density dependent response by *L. testaceipes* to *A. nerii* population levels over at least some range of aphid densities on all *Asclepias* species. Therefore, while *L. testaceipes* could potentially regulate aphid densities, its density dependent response was not sufficient to regulate aphid populations. A similar result has been observed in other studies examining the relationship between aphids and their parasitoids. Murphy and Volkl (1996) found density dependent parasitism of aphid populations, however the parasitoid populations remained low and never increased sufficiently to regulate the growth of aphid populations. Several potential factors leading to reduced parasitoid efficiency in regulating aphid populations have been suggested: hyperparasitism (Walker *et al.*,

1984), predation of parasitized aphids (Ferguson & Stiling, 1996), and parasitoid foraging behavior (Mackauer & Volkl, 1993).

Variation among plant species appears to have an influence on the interaction between *A*. *nerii* and *L. testaceipes* since species identity was a significant predictor of aphid growth rate (Table 2.1) and parasitism (Fig. 2.4). These differences among plant species may result from both indirect and direct influences of the host plant on *L. testaceipes* populations.

There does not seem to be much support for *Asclepias* plants indirectly influencing parasitoid populations by influencing aphid abundance or distribution. While previous studies have found that growth rates of *A. nerii* are higher on high cardenolide plants than on low cardenolide plants, it is thought to be the result of higher predation and parasitism rates on the low cardenolide plants (Malcolm, 1992). It has also been suggested that there is no fitness cost to *A. nerii* from variation in cardenolide content of host plants (Groeters, 1993) and that *A. nerii* growth rates are not affected by variation in cardenolide content (Malcolm, 1992). However, *L. testaceipes* populations may still be indirectly influenced by host plant mediated changes in prey quality.

Asclepias plants may influence parasitoids through aphid honeydew. Malcolm (1990) found that the honeydew secreted by *A. nerii* consists of 46% cardenolides. These cardenolides may be recognizable as cues to parasitoids and lead to differential oviposition rates on different plant species. Evidence from the literature seems to suggest that host plant mediated changes in prey quality and direct effects on *L. testaceipes* populations through variation in plant quality may be more important than indirect effects mediated through changes in growth rates of *A. nerii*. Future work will investigate the role of plant chemistry in this interaction and test these predictions.

This study has focused on within-year population dynamics of *A. nerii* populations. While important regulatory processes operate on short term time scales, such as those examined in this study, there may also be population regulation acting over yearly time scales (Sequeira & Dixon, 1997). Overall abundance in one year may be influenced by abundance in the previous year. Aphid populations observed in this study showed no evidence population regulation. However, if these populations were observed on a yearly time scale, evidence of population regulation may be seen.

This study adds to the growing body of knowledge that variation in plant quality can affect the population ecology of parasitoids and the impact of parasitoids on herbivore populations (Price *et al.*, 1980; Abrahamson & Weis, 1997; Hunter, 2003). Moreover, the data serve to emphasize the point that, if parasitoids are to regulate the populations of insect herbivores, density-dependent parasitism is a necessary, but not sufficient, condition for population regulation.

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**Table 2.1.** Mean per capita rate of increase (r) of *Aphis nerii* on six species of *Asclepias* in acommon garden in Athens, Georgia. Means with the same letter are not significantly different.

Species	Mean <i>r</i>	Standard	Ν	Tukey
		Error		Grouping
A. exaltata	1.107	0.031	34	А
A. sullivantii	0.983	0.031	32	В
A. speciosa	0.903	0.021	73	ВC
A. incarnata	0.894	0.026	46	ВC
A. viridis	0.884	0.040	20	ВC
A. tuberosa	0.840	0.026	48	С

**Table 2.2.**  $R^2$  and *P*-values for the regression equations describing temporal density dependent parasitism of *A. nerii* by *L. testaceipes* on six species of *Asclepias* in a common garden in Athens, Georgia. Refer to Fig. 2.2 for a visual representation of these equations. Equations are of the following forms: Linear  $(y = a^*x)$ , Saturation I  $(y = \frac{a^*x}{a+x})$ , Saturation II  $(y = a + b^*x^q)$ 

where q<1), and Parabolic  $(y = a * x^2 + b * x)$ .

Species	Linear	Saturation I	Saturation II	Parabolic
	(Fig. 2A)	(Fig. 2C)	(Fig. 2C)	(Fig. 2D)
A. exaltata	$R^2 = 0.1244$	$R^2 = 0.8175$	$R^2 = 0.9075$	$R^2 = 0.8406$
	<i>P</i> =0.3915	P=0.0008	P=0.0638	P=0.0040
A. incarnata	$R^2 = 0.2910$	$R^2 = 0.6665$	$R^2 = 0.9033$	$R^2 = 0.9158$
	<i>P</i> =0.1676	P=0.0073	P=0.0299	P=0.0006
A. speciosa	$R^2 = 0.8063$	$R^2 = 0.5456$	$R^2 = 0.9456$	$R^2 = 0.9649$
-	P=0.0025	P=0.0230	P=0.0122	<i>P</i> <0.0001
A. sullivantii	$R^2 = 0.1176$	$R^2 = 0.6778$	$R^2 = 0.7613$	$R^2 = 0.9284$
	P=0.4056	P=0.0064	P=0.2560	<i>P</i> =0.0004
A. tuberosa	$R^2 = 0.0458$	$R^2 = 0.5711$	$R^2 = 0.6789$	$R^2 = 0.9351$
	<i>P</i> =0.6108	<i>P</i> =0.0185	P=0.3766	<i>P</i> =0.0003
A. viridis	$R^2 = 0.5097$	$R^2 = 0.4800$	$R^2 = 0.8501$	$R^2 = 0.9738$
	P=0.0467	P=0.0386	P=0.0677	<i>P</i> <0.0001

**Figure 2.1.** a) Numbers per plant, and b) densities per gram of plant tissue of *Aphis nerii* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Data are the means of 100 plants (*A. exaltata, A. speciosa, A. tuberosa,* and *A. viridis*) or 50 plants (*A. incarnata* and *A. sullivantii*).

Figure 2.1 A



B



**Figure 2.2.** Possible forms of the relationship between densities of *Aphis nerii* and percent parasitism by *Lysiphlebus testaceipes*. Letters represent the following relationships: a) linear density dependence, b) density independence (Holling Type I), c) density dependence at low aphid densities and density independence at high aphid densities, and d) density dependence at low aphid densities and inverse density dependence at high aphid densities (Holling Type III).

Figure 2.2



**Figure 2.3.** Temporal density-dependent parasitism of *Aphis nerii* by *Lysiphlebus testaceipes* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Each data point represents a single sample date and is the mean of 100 plants (*A. exaltata, A. speciosa, A. tuberosa*, and *A. viridis*) or 50 plants (*A. incarnata* and *A. sullivantii*) (horizontal and vertical bars indicate 95% CI).

Figure 2.3



**Figure 2.4.** A comparison of parasitism of *Aphis nerii* by *Lysiphlebus testaceipes* on six species of Asclepias growing in a common garden in Athens, Georgia. Each data point represents a single sample date and is the mean of 100 plants (*A. exaltata*, *A. speciosa*, *A. tuberosa*, and *A. viridis*) or 50 plants (*A. incarnata* and *A. sullivantii*).

Figure 2.4



**Figure 2.5.** Spatial density-dependent parasitism of *Aphis nerii* by *Lysiphlebus testaceipes* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Each data point represents an individual plant and is the mean of 7 sampling dates. No statistically significant relationships exist.

Figure 2.5



**Figure 2.6.** Regressions between the per capita rate of increase of *Aphis nerii* and maximum observed parasitism by *Lysiphlebus testaceipes* on six species of *Asclepias* growing in a common garden in Athens, Georgia. Data points represent individual *Asclepias* species and are the means of per capita rates of increase calculated from between 20 and 73 individual plants per species (see text for details).

Figure 2.6



# CHAPTER 3

# VARIATION IN PLANT QUALITY AND THE POPULATION DYNAMICS OF HERBIVORES: THERE IS NOTHING AVERAGE ABOUT APHIDS<sup>1</sup>

<sup>1</sup>Helms, S.E. and M.D. Hunter. 2005. Oecologia (in press)

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# ABSTRACT

In the attempt to use results from small scale studies to make large scale predictions, it is critical that we take into account the greater spatial heterogeneity encountered at larger spatial scales. An important component of this heterogeneity is variation in plant quality which can have a profound influence on herbivore population dynamics. This influence is particularly relevant when we consider that the strength of density dependence can vary among host plants and that the strength of density dependence determines the difference between exponential and density dependent growth. Here, we present some simple models and analyses designed to examine the impact of variable plant quality on the dynamics of insect herbivore populations, and specifically the consequences of variation in the strength of density dependence among host plants. We show that average values of herbivore population growth parameters, calculated from plants that vary in quality, do not predict overall population growth. Furthermore, we illustrate that the quality of a few individual plants within a larger plant population can dominate herbivore population growth. Our results demonstrate that ignoring spatial heterogeneity that exists in herbivore population growth on plants that differ in quality can lead to a misunderstanding of the mechanisms that underlie population dynamics.

# **Key Words**

Density Dependence; Plant-insect Interactions; Plant Quality; Population Dynamics; Spatial Scale

# **INTRODUCTION**

Ecologists are often interested in answering large scale questions while conducting experiments at small scales. The general approach is to assume that results of small scale studies can be used to make larger scale predications. However, as we make predictions about processes on larger spatial scales, we are incorporating greater spatial heterogeneity. Inherent in this heterogeneity is variation in plant quality both within and among plant species (Hunter et al. 1996).

Variation in plant quality can have a profound influence on herbivore populations through changes in fecundity, survival, movement, mortality due to natural enemies, and rates of competition (Price et al. 1980; Denno and McClure 1983; Denno et al. 1995; Abrahamson and Weis 1997; Lill et al. 2002). We should also expect that the strength of density dependence, and herbivore population dynamics, will vary with host plant quality (Hunter et al. 2000; Hunter 2001). For example, host plant genotype, which influences phenotypic variation in plant quality traits (Underwood and Rausher 2000; McIntyre and Whitham 2003), including plant secondary chemistry (Hunter et al. 1996; Larsson et al. 2000) has been shown to influence herbivore population dynamics. The strength of density dependence can have considerable impact on population dynamics as its value determines the difference between exponential and density dependent growth. Several recent studies have demonstrated that the strength of density dependence can vary among host plants (Underwood and Rausher 2000, 2002; Rotem and Agrawal 2003).

Here, we present some simple models and analyses designed to examine the impact of variable plant quality on the dynamics of insect herbivore populations. Specifically, we concentrate on the consequences of variation in the strength of density dependence among host

plants. We illustrate that a) average values of herbivore population growth parameters, calculated from plants that vary in quality, do not predict overall population growth, and b) the quality of a few individual plants within a larger plant population can dominate herbivore population growth.

#### **MATERIALS AND METHODS**

Field observations of aphid populations (Helms et al. 2004) have served as the basis for many of the ideas presented in this paper. In a common garden of *Asclepias* plants in Athens, GA, we have observed exponential growth of *Aphis nerii* populations within a single growing season despite considerable variation in the strength of density dependence among individual plants. We explore this phenomenon here with a series of population models. The initial models are extremely simple, to make some general points. We then increase model complexity and incorporate some real data from our common garden.

Because aphids have overlapping generations, continuous time models have been used. Specifically, these models are all variations of the basic form:

$$\frac{dN}{dt} = N * (r + b * N) \tag{1}$$

where *N* is the size of the population, *r* is the maximum per capita growth rate, and *b* is the strength of density dependence. The quantity (r + b\*N) is the R-function and represents the realized reproductive rate (or per-capita population growth rate) (Berryman 1999). If we make the assumption that *r* is non-zero and positive, the behavior of the population is dependent on *b*. In this case, we can have three outcomes:

- (i) b > 0: The population will experience inverse density dependence and exhibit hyper-exponential growth.
- (ii) b = 0: The population will be density independent and exhibit exponential growth.

(iii) b < 0: The population will experience density dependence and will reach a stable equilibrium.

#### A Simple Model

Our first step in examining the effect of variation in plant quality is to consider a very simple hypothetical system in which there are 10 individual plants hosting aphid populations. We assume that the aphid populations experience the same arbitrary maximum growth rate (r = 0.9) on each plant; however aphids realize exponential growth (b = 0) on one of these plants while experiencing density dependence (we have arbitrarily chosen b = -0.005) on the other 9 plants. These 10 individual populations are each simulated using equation (1). When the 10 plants are considered together as one large population, total population growth is the sum of the population densities from each of the individual plants at each time step.

## Variable Growth Parameters

To make the simple model used above slightly more realistic, we can allow the growth parameters to vary randomly among host plants. These parameters are estimated from the following normal distributions:  $r \sim N(0.9, 0.0025)$  and  $b \sim N(-0.005, 0.000025)$ , where the first value in the bracket is the average parameter estimate, and the second value is the variance around the mean. Note that the average of *b* favors density dependent growth (b < 0). Ten values for each parameter are generated at random from these distributions and used to simulate populations on each of the 10 individual plants using equation (1). Once again, we can sum the densities on individual plants to find total aphid population size. We can compare the model output from runs with variable parameters with a simple model that uses the average parameter

values from all 10 plants. In this case, we calculated mean parameter values from the 10 variable parameter simulations, and used these to simulate an average population.

### Hierarchical Bayesian Parameter Estimation

Rather than assuming that all variation around a mean estimate of a parameter value is due simply to sampling error and will tend to zero as sample size increases, hierarchical Bayesian methods allow for some of this observed variation to be real biological variation among individuals (see Clark 2003, Sauer and Link 2002). Hierarchical Bayesian methods were used to estimate the parameters *r* and *b* from aphid population data. Population densities of the aphid *Aphis nerii* growing in a common garden of *Asclepias* plants in Georgia were monitored from July to October 2001. The common garden consisted of between 50 and 100 plants of each of 6 different *Asclepias* species.

Naturally occurring aphid densities (calculated as number of aphids per gram of plant tissue) were recorded from each plant in the garden every two weeks from July 14 to October 22. Again, aphids have overlapping generations, with a generation time of approximately 1 week. Complete details of our sampling protocols are provided in Helms et al. (2004).

Values for *r* and *b* were estimated by fitting linear regressions between the realized growth rate (*R*) and the population density on individual *Asclepias* plants (i.e., (*x*,*y*) coordinates are  $(N_t, \ln(N_{t+1}/N_t))$ ). The intercept of this line represents *r*, while the slope is the value for *b*, such that R = r + b \* N. Only plants that hosted aphids for at least four consecutive sampling dates were used in the analysis, giving a total of 171 individual plants.

The observational data collected from the field,  $R_{i,j}$  (where i = 1, 2, ..., 171 denotes individual plants, and j = 1, 2, ..., 5 denotes time period) is assumed to follow a normal distribution such that  $R_{i,j} \sim N(\mu_{i,j}, \sigma^2)$  and  $\mu_{i,j} = r_i + b_i * N_{i,j}$  and  $\sigma^2$  follows a flat inverse gamma distribution. Both  $r_i$  and  $b_i$  are given normal prior distributions:  $[r_i | \mu_r, \tau^2_r] \sim N(\mu_r, \tau^2_r)$  and  $[b_i | \mu_b, \tau^2_b] \sim N(\mu_b, \tau^2_b)$ .

Hyperpriors (distributions of the parameters of the distribution of  $r_i$  and  $b_i$ ) have been defined as diffuse normal distributions for the means (i.e.,  $[\mu_r] \sim N(0.0, 1000^2)$  and  $[\mu_b] \sim N(0.0, 1000^2)$ ) and flat inverse gamma distributions for the variances (i.e.,  $[\tau^2_r] \sim Inv$ gamma(0.1, 0.1) and  $[\tau^2_b] \sim Inv$ -gamma(0.1, 0.1)). In all cases, standard non-informative priors and hyperpriors for Bayesian analysis have been used (Spiegelhalter et al. 1999). The program WinBUGS (Spiegelhalter et al. 1999) was used to complete this analysis. After specifying the model, the program carries out the Bayesian analysis with a Markov chain Monte Carlo (MCMC) procedure.

As a comparison to Hierarchical Bayesian methods, standard statistical methods were also used to examine the values of r and b. These parameters were first estimated by using pooled data for all 171 plants. Pooling these data gave 761 data points consisting of the realized growth rate and population density. A linear regression, as well as mean estimates and standard deviations of r and b, for the pooled data were determined using PROC REG in SAS (1999). Values for r and b were also estimated by fitting a linear regression between the realized growth rate and population density for each individual plant and then averaging the resulting parameter values over all 171 plants.

# Models with Movement

Most insect herbivores have the ability to move among plants either within or between generations, and so we added migration to our original models. The results of aphid movement can be considered analytically. Here, we consider only two populations: one that supports exponential growth and one that has density dependent growth. The two-patch model considered here is very similar to models in Underwood (2004), Holt (1985), Hastings (1993), and Freedman & Waltman (1977).

Let N be the population with density dependent growth and P be the population with exponential growth.

Then,

$$\frac{dN}{dt} = N * (r_1 + b * N) - m_1 * N + m_2 * P$$
(2)

$$\frac{dP}{dt} = r_2 * P - m_2 * P + m_1 * N \tag{3}$$

Here,  $r_1$  and  $r_2$  are the maximum growth rates of *N* and *P*, respectively. The strength of density dependence is *b* (here b = 0 for *P*), and  $m_1$  and  $m_2$  are the rates of movement of individuals from populations *N* and *P*, respectively. The following set of assumptions will be made:

- (i)  $r_2 > 0$  (necessary for exponential growth)
- (ii)  $m_1, m_2 > 0$
- (iii) b < 0 (necessary for density dependent growth)

This set of equations (equations (2) and (3)) was solved to find the conditions necessary for equilibrium (i.e.  $N^* > 0$  and  $P^* > 0$ ).

# RESULTS

## A Simple Model

In a deterministic model with aphids on 9 plants exhibiting density-dependent growth and aphids on one plant exhibiting exponential growth, the total population exhibits exponential growth (Figure 3.1). This rather obvious result stems from the fact that exponential growth on a single plant comes to dominate the whole population over time.

#### Variable Growth Parameters

When average population growth is density dependent (b < 0), but is varied randomly from a normal distribution of the type described above, total population growth is exponential (Figure 3.2; Because the parameter values for each individual plant are generated from a normal distribution, it should be noted that the run of this model shown in Figure 3.2 is representative of other runs of this model). Although individual plants exhibit either exponential or density dependent growth, the sum of the population shows exponential growth. Furthermore, by averaging the parameter values over the 10 variable parameter simulations, the parameters are those of density dependent growth. These results indicate that total population growth can be exponential even when average parameter values favor density dependent growth.

This process can occur in nature. Figure 3.3 shows the behavior of *Aphis nerii* populations on 15 different *Asclepias* plants in Georgia (recalculated from data in Helms et al. 2004) as well as the sum of these populations. Once again, there exist both density dependent and exponential growth on the individual plants, but the sum of the population shows exponential growth.

The level of variance in parameter values among populations on different host plants will likely have a significant impact on the dynamics observed in the population as a whole. This variance represents the variation in plant quality that is central to our current discussion. The effect of increasing variance in the parameter b (strength of density dependence) can be examined by plotting the probability of observing exponential growth in the total aphid population (i.e., b is non-negative) against the variance.

Under a normal distribution, as variance in the estimate of the strength of density dependence (b) increases, so does the probability of generating a plant upon which aphids will exhibit exponential growth. The probability of exponential growth also depends on the mean of the parameter b; as the mean of b decreases, so does the probability of exponential growth. This effect can be seen in Figure 3.4. In other words, the greater the variation among individual plants, the more likely it is that overall population growth will be determined by a few plants exhibiting exponential growth.

#### Hierarchical Bayesian Parameter Estimation

Using Bayesian analysis, we have generated distributions for the parameter values *r* and *b* from *Aphis nerii* populations growing in a common garden of *Asclepias* plants in Georgia. The mean value for r is 1.174 with a 95% credible interval (1.004, 1.336) and the mean value for b is -0.004 with a 95% credible interval (-0.01, 0.006). A 95% credible interval is the interval that contains 95% of the data. The values for these parameters approximate the following normal distributions:  $r \sim N(1.174, 0.064^2)$  and  $b \sim N(-0.004, 0.006^2)$ . Using the marginal distribution for *b*, the probability of observing a specific number of individual plants on which aphid populations grow exponentially is shown in Figure 3.5. According to this table, in a population of 10 plants

with the distribution of parameter values found here, there will be one or more plants supporting exponential growth in 93.6% of cases, despite average parameter values favoring density dependent growth.

A comparison of estimated values for r and b from the Hierarchical Bayesian analysis with the standard statistical methods used is shown in table 3.1. The pooled data linear regression gave a mean value for r of 1.05 with a 95% confidence interval of (0.992, 1.108) and a mean value for b of -0.0017 with a 95% confidence interval of (-0.0021, -0.0013). Averaging the parameter estimates for linear regressions on each individual plant gave a mean value for r of 1.183 with a 95% confidence interval of (1.102, 1.263) and a mean value for b of -0.002 with a 95% confidence interval of (-0.006, 0.002).

## Models with Movement

Upon solving equations (2) and (3) to find the conditions necessary for equilibrium (i.e.  $N^* > 0$  and  $P^* > 0$ ), we found that both of the following conditions must be met in order for this system to have an equilibrium:

$$r_1 > \frac{r_2 * m_1}{r_2 - m_1} \tag{4}$$

$$r_2 < m_2 \tag{5}$$

If condition (5) is violated, then there is no equilibrium for this system and both plants experience exponential growth. So if population growth rate on the exponential plant is larger than the rate of emigration from that exponential plant, both populations will grow exponentially (see Fig. 3.6a,  $r_1 = r_2 = 0.9$ , b = -0.005,  $m_1 = m_2 = 0.1$ ). If condition (5) holds and  $r_1 > 0$ , there is always an equilibrium for this system. Populations on both plants will reach a stable population size, with the exponential population  $\frac{-m_1}{r_2 - m_2}$  times larger than the density dependent population (see Fig. 3.6b,  $r_1 = 0.9$ ,  $r_2 = 0.8$ , b = -0.005,  $m_1 = 0.5$ ,  $m_2 = 0.9$ ).

However, if condition (5) holds and  $r_1 < 0$ , condition (4) can be re-written as

$$\frac{r_2}{r_1} < \frac{r_2 - m_2}{m_1} \tag{6}$$

If (6) is true, we will see an equilibrium similar to that in Fig. 3.6b. This demonstrates that plants that are unable to sustain positive aphid growth ( $r_1 < 0$ ) can still exhibit equilibrium aphid densities as a result of immigration from plants supporting exponential growth. However, if (6) is false, then both populations will go extinct (see Fig. 3.6c,  $r_1 = -0.2$ ,  $r_2 = 0.5$ , b = -0.005,  $m_1 = 0.1$ ,  $m_2 = 0.8$ ).

In summary, to prevent exponential aphid growth on all plants, aphid population growth rate on the exponential plant must be less than the rate of emigration from the exponential plant. Furthermore, if aphid growth rate on the exponential plant is less than the rate of aphid emigration from that plant and the second plant is a sink, i.e. unable to sustain population growth (r < 0), then populations on both plants will go extinct unless condition (6) holds.

## DISCUSSION

The spatial scale at which insect herbivore populations are examined can have considerable influence on the assessment of factors underlying population dynamics. Using a simple deterministic model, we have demonstrated that exponential growth by an herbivore on a single plant in a population will dominate the whole population over time, even when the other plants favor density-dependent growth by the herbivore population (Fig. 3.1). While this simple example may seem obvious, it underscores an important point – when individual plants vary in quality for herbivores, the dynamics of the herbivore population as a whole can be driven by the quality of a few individual plants. As a consequence, average growth parameters calculated from the entire plant population may be poor predictors of overall population growth.

In nature, both the strength of density dependence, *b*, and the maximum per capita growth rate, *r*, of herbivores can vary among host plants (Underwood and Rausher 2000, 2002; Rotem and Agrawal 2003; Figure 3.3). When we allowed these parameters to vary around a given mean, such that the average parameter values favored density dependent growth, we found either density dependent or exponential growth on individual plants, but exponential growth for the herbivore population as a whole (Figure 3.2). Furthermore, as variability around the mean value of *b* increased, we were more likely to observe one or more plants supporting exponential growth (Figure 3.4) while the growth of the whole herbivore population was determined by these few plants. What we have not explored here is the potential for aphid populations on an individual plant to vary between exponential and density-dependent growth over time. Temporal changes in the quality of individual plants might cause such changes in aphid growth and will be considered in future work.

Given that variation among host plants in both the maximum per capita growth rate and the strength of density dependence of insect herbivores should be common (Hunter et al. 2000; Hunter 2001) and has been demonstrated experimentally (Rotem and Agrawal 2003; Underwood and Rausher 2000, 2002), we should begin exploring the use of statistical methods that allow for such variability in parameters to be expressed as "real" variation among individuals rather than

as measurement error. Using standard statistical procedures, measurement error declines towards zero as sample size increases.

Standard statistical analyses conducted on data from *Aphis nerii* populations on *Asclepias* plants showed the strength of density dependence estimated from the smaller spatial scale of individual plants (Table 3.1, "average") to be only slightly stronger than that from pooled data over the entire field. However, there was a fairly large difference in the 95% confidence intervals between the two methods. Using the pooled data, the 95% confidence interval for *b* contains only negative values, while that for the average of individual plants allows for both negative and positive numbers. However, this may just be an artifact of the differences of sample size (N=761 for pooled data versus N=171 for average of individual plants).

Instead of all variance being due to measurement error and decreasing towards zero as sample size increases, Hierarchical Bayesian analysis allows for some variation to be real variation among individuals. While variance due to measurement error does decline as sample size increases, Hierarchical Bayesian statistics also allows estimation of real variance that exists among plants. For the data from *Aphis nerii* populations on *Asclepias* plants, not only does the Hierarchical Bayesian analysis detect a much stronger average value of density dependence (-0.004), but the 95% credible interval contains both negative and positive values for *b* and allows for much more variability than does either of the standard statistical methods used in this paper. An added strength of Hierarchical Bayesian analysis is the generation of distributions of the values of *r* and *b* for each individual plant (not shown here). With standard statistical methods, treating each plant individually would only allow for a point estimate for each of the values of *r* and *b*. In addition, with the Hierarchical Bayesian analysis, we find that in a population of 10 plants, we will observe exponential growth for the whole population 93.6% of the time (Figure

3.5), despite the average value of *b* favoring density dependent growth. These results are supported by our field observations (Helms et al. 2004) where we found the total population exhibiting exponential growth, but aphid populations on individual host plants exhibiting either density dependent or exponential growth (Fig. 3.3).

Standard statistical approaches such as those used in this paper are likely to be inappropriate for scaling up from small studies to larger studies, where true variation among plants is likely to increase with spatial scale (Hunter et al. 1996). Hierarchical Bayesian methods should provide a better approach to parameter estimation (Clark 2003, Sauer and Link 2002) because they produce distributions of parameters rather than simple mean estimates. These distributions encompass real variation among individuals, can be used to make predictions about local dynamics (Figure 3.5) and may be useful tools in the attempt to scale up results from small scale studies to large scale predictions.

There are an increasing number of studies suggesting that measures of spatial variance are essential to understanding processes that determine population dynamics. Including measures of spatial variance and covariance can give qualitatively different results than simply using mean values estimated from a single spatial scale (Inouye 2004, Melbourne & Chesson 2004, Underwood 2004). Spatial variance has been shown to explain coexistence of competing species that exhibit strong competitive interactions at smaller spatial scales (Inouye 2004) and to influence population abundance for insect herbivores (Underwood 2004).

Shima and Osenberg (2003) demonstrated an analogous situation in populations of reef fish. They found that differences in patch quality caused an underestimation of the effect of density dependence. Aggregation of data over large spatial scales in this study underestimated the strength of density dependence by approximately 97%. Because habitat quality co-varies

with population density, the strength of density dependence becomes obscured in a heterogeneous habitat. Shima and Osenberg (2003) termed this phenomenon "cryptic density dependence." Further support for the existence of cryptic density dependence in reef fishes has been provided by Forrester and Steele (2004) and is likely to be found in many other systems. Several studies of insect herbivores have found that the detection of density dependence is only possible at smaller spatial scales (Hassell et al. 1987, Jones et al. 1987, Southwood et al 1989). Hastings (1993) showed in a two-patch model that the degree of coupling between the dynamics of the two patches will influence the detection of density dependence at larger spatial scales. If the dynamics in the two patches are weakly coupled, then density dependence will be much less apparent at the level of the whole population even though there is clear density dependence at the level of a patch.

Consistent with the results of the two-patch model of Hastings (1993), the effect of exponential growth on a single plant dominating the dynamics of the whole population will decline if the rate of emigration from the exponential population is large in relation to its maximum population growth rate. In this case, sufficient emigration from the exponential population causes the whole population to exhibit either density dependent growth or go extinct depending on values of the other model parameters (Figs 3.6b, c). In our *Asclepias-Aphis nerii* system, movement among plants is sufficiently rare within a growing season and the estimated parameter values for r are sufficiently high (Table 3.1) such that exponential aphid growth on some individual plants does indeed dominate the dynamics of the whole population (Figure 3.3). However, the production of alate aphids at very high density (Groeters 1989) might alter the effects of the plants that support exponential growth on the entire aphid population. The final

outcome will depend upon the relative values of dispersal and population growth rate (equation 5).

Other recent studies have also demonstrated that for herbivores that move among plants, variability in plant quality can influence herbivore population dynamics (Underwood 2004). Specifically, this study showed that increasing variance in quality among host plants leads to increasing effects on herbivore population size. Furthermore, Underwood (2004) found that herbivore mobility increased the effect of variance in plant quality. It is clear that variation in rates of movement among individual plants should be considered along with variation in rates of increase and density dependence if we wish to understand the role of variable plant quality in population dynamics (Pulliam 1988; Gilpin and Hanski 1991).

An appreciation for the role of variation in plant quality in the population dynamics of herbivores is growing (Foster et al. 1992; Rossiter 1994; Belovsky and Joern 1995; Larsson et al. 2000; Underwood and Rausher 2000, 2002; Helms et al. 2004; Rotem and Agrawal 2003). As we have demonstrated in this paper, ignoring the spatial heterogeneity that exists in herbivore population growth on plants that differ in quality can lead to a misunderstanding of the mechanisms that underlie observed population dynamics. Counting herbivores on plants and taking averages of population size, per capita growth rate, and the strength of density dependence is simply not sufficient (Hunter et al. 2000). Plant-derived variation in herbivore population parameters should be described explicitly, using appropriate statistical techniques, and incorporated directly into population models. Until this becomes the rule rather than the exception, our basic understanding of herbivore population ecology will continue to be inadequate.

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**Table 3.1**. Comparison of estimates for r (maximum per capita growth rate) and b (strength of density dependence) using Hierarchical Bayesian analysis (HB), a linear regression for the pooled data (pooled), and an average of values from linear regressions on each individual plant (average). 95% CI is the 95% credible interval for the HB analysis and the 95% confidence interval for the pooled and average analyses.

	Mean	Standard Deviation	95% CI
R			
HB	1.174	0.0640	(1.004, 1.336)
Pooled	1.050	0.8182	(0.992, 1.108)
Average	1.183	0.5403	(1.102, 1.263)
В			
HB	-0.0040	0.0060	(-0.01, 0.006)
Pooled	-0.0017	0.0055	(-0.0021, -0.0013)
Average	-0.0020	0.0310	(-0.006, 0.002)

**Figure 3.1.** Aphid population growth as simulated using a deterministic model (equation 1) for (a) the mean of 9 plants with density dependent growth, (b) one plant with exponential growth, and (c) the total aphid population on these ten plants.





Figure 3.2. Aphid population growth with the parameters r (maximum population growth rate) and b (strength of density dependence) varying randomly among host plants. Individual plants exhibit either density dependent growth or exponential growth (solid lines). The dashed line represents the totals of these populations. The dotted line represents the output of a model that uses the average parameter values from all 10 plants.

Figure 3.2



**Figure 3.3.** Population growth of *Aphis nerii* on 15 different *Asclepias* plants growing in a common garden in Athens, Georgia in 2001 (recalculated from data in Helms et al. 2004).

Figure 3.3



**Figure 3.4.** The probability of observing a plant upon which aphids will exhibit exponential growth as the variance in the estimate of the strength of density dependence (*b*) increases. The parameter *b* is assumed to follow a normal distribution, and these results are shown for 3 different values of the mean of *b*: -0.005, -0.05, -0.5.

Figure 3.4



**Figure 3.5.** The probability that, in a population of 10 *Asclepias* plants, there will be a given number of plants on which *Aphis nerii* populations grow exponentially despite average growth parameters favoring density dependence. For example, there is a 20% probability of one plant supporting exponential aphid growth and only a 6.4% probability that all plants will exhibit density-dependent growth.

Figure 3.5



Figure 3.6. Aphid population growth as simulated using a deterministic model (equations 2 and 3) which allows aphids to move among host plants. Here we assume that there are two host plants, one with density dependent growth (solid line, b = -0.005) and one with exponential growth (dashed line, b = 0). Possible outcomes of this model are represented by the following combinations of parameter values: (a)  $r_1 = r_2 = 0.9$ , b = -0.005,  $m_1 = m_2 = 0.1$ , (b)  $r_1 = 0.9$ ,  $r_2 = 0.8$ , b = -0.005,  $m_1 = 0.5$ ,  $m_2 = 0.9$ , and (c)  $r_1 = -0.2$ ,  $r_2 = 0.5$ , b = -0.005,  $m_1 = 0.1$ ,  $m_2 = 0.8$  (see text for details).

Figure 3.6



## CHAPTER 4

## CONCLUSIONS

In general the results of this thesis demonstrate that consideration of variable plant quality and the effects of plant quality on herbivore populations is essential to understanding the population dynamics of insect herbivores. An appreciation for the role of variation in plant quality in the population dynamics of herbivores is growing (Foster et al. 1992; Rossiter 1994; Belovsky and Joern 1995; Larsson et al. 2000; Underwood and Rausher 2000, 2002; Rotem and Agrawal 2003). We add to the conclusions of other studies and suggest that ignoring the spatial heterogeneity that exists in herbivore population growth on plants that differ in quality can lead to a misunderstanding of the mechanisms that underlie observed population dynamics.

Using a common garden experiment, we examined the hypothesis that aphid population growth rates and rates of parasitism would vary among host plant species (Chapter 2). Both aphid growth rates and parasitism rates were found to vary among plant species. Furthermore, we found that although parasitoids exhibited a density dependent response to aphid populations over at least some range of aphid densities, this was not sufficient to regulate aphid populations. This emphasizes the point that, if parasitoids are to regulate the populations of insect herbivores, density-dependent parasitism is a necessary, but not sufficient, condition for population regulation.

Since our common garden experiment showed that parasitism rates varied among host plant species and therefore we should also expect that the strength of density dependence will vary with host plant quality (Hunter et al. 2000; Hunter 2001), we used some simple models

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to further examine the consequences of variation in the strength of density dependence among host plants on herbivore population dynamics. We show that average values of herbivore population growth parameters, calculated from plants that vary in quality, do not predict overall population growth. Furthermore, we illustrate that the quality of a few individual plants within a larger plant population can dominate herbivore population growth. This means that the standard practice of counting herbivores on plants and taking averages of population size, per capita growth rate, and the strength of density dependence is simply not sufficient (Hunter et al. 2000). Plant-derived variation in herbivore population parameters should be described explicitly, using appropriate statistical techniques, and incorporated directly into population models.

We have shown that variable plant quality can influence the population dynamics of insect herbivores. The influence of plant quality on herbivore populations should be measured in field studies and explicitly included in models of insect herbivore population dynamics.

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