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Density dependent population growth of the two-spotted spider mite, *Tetranychus urticae*, on the host plant *Leonurus cardiaca*

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We observed *Tetranychus urticae* (Koch), a polyphagous spider mite herbivore, on *Leonurus cardiaca* (L.) at several sites in eastern North America at variable density, ranging from extremely dense to sparse. To understand the nature of *T. urticae*'s population dynamics we experimentally manipulated population densities on *L. cardiaca* and assessed per capita growth after 1 to 2 generations in laboratory and field experiments. In particular, we took a 'bottom-up' approach, manipulating both plant size and quality to examine effects on mite dynamics. Per capita growth was strongly dependent on the initial density of the mite population. Spider mite populations grew (1) in a negatively density dependent manner on small plants and (2) unhindered by density dependence on large plants. Mean per capita growth was 59% higher on small plants compared to large plants, irrespective of mite density. We also found evidence for density dependent induced susceptibility to spider mites in small plants and density dependent induced resistance in large plants. Hence, spider mite populations grew at a relatively fast rate on small plants, and this was associated with negative density dependence due to factors that depress population growth, such as food deterioration or limitation. On large plants, spider mite populations grew at a relatively slow rate, apparently resulting in herbivore densities that may not have been high enough to cause intraspecific competition or other forms of negative density dependence.

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It is widely believed that in most animal species, population growth rate is a decreasing function of density (Harrison and Cappuccino 1995, Turchin 1995). Thus, per capita growth rate is negatively associated with present and/or past population densities (negative density dependence). A persistent debate among ecologists has surrounded the question of whether and how herbivore populations are regulated (Strong 1984). Early research focused on whether abiotic or biotic factors controlled populations (Cappuccino 1995). However, regulation was generally viewed as intuitively necessary, preventing populations from becoming infinitely large or extinct (Harrison and Cappuccino 1995). There is a growing body of evidence for density dependence in natural populations, especially from manipulative experiments (Turchin and Karieva 1989, Harrison and Cappuccino 1995, Sequeira and Dixon 1997, Hunter and Elkinton 1999, Karels and Boonstra 2000). Difficulty in the detecting density dependence may be due to the great variance frequently associated with the effect of density on population growth (Strong 1984), as herbivores can be limited by many factors that potentially act in a density dependent manner. These factors include resources, predators, parasitism, disease, competition, and plant resistance, all of which can cause herbivore populations to decrease in size (Karban 1989, Turchin and Karieva 1989, Cappuccino 1992, Harrison and Cappuccino 1995, Hunter and Elkinton 1999, Krebs et al. 2001). Indeed, these multiple factors frequently interact to ultimately determine population

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dynamics (Turchin and Karieva 1989, Harrison and Cappuccino 1995, Hunter and Elkinton 1999, Krebs et al. 2001).

Phytophagous insect populations exist at relatively low to extremely high density. Top-down factors (i.e. natural enemies) can act to depress herbivore population size, usually well below the host-plant's carrying capacity (Price 1987, Turchin and Karieva 1989, Cappuccino 1992, Hunter and Elkinton 1999). Alternatively, bottom-up factors, such as plant defenses, can control herbivore population growth (Hunter and Price 1992). For example, the induced responses of a plant can be dependent on the amount of damage imposed by herbivory. Induced resistance to herbivory was positively correlated with mite density on cotton plants (Karban 1987, Agrawal and Karban 2000) and Mexican bean beetle density on soybean plants (Underwood 2000). Although effects of changes in plant quality on herbivore dynamics have long been theorized (Haukioja and Hakala 1975, Karban and Baldwin 1997), they have only recently received empirical attention and support (Underwood and Rausher 2002). Thus, the role that dynamic changes in plant quality have on herbivore populations, and especially their interactive effects with other factors have been little studied.

We observed the polyphagous two-spotted spider mite, *Tetranychus urticae* (Tetranychidae) on motherwort, *Leonurus cardiaca* (Lamiaceae), at several sites in eastern North America at both extremely high and low densities. In addition, most populations of *L. cardiaca* have abundant small seedlings co-occurring with larger, mature plants that grow from perennial roots. In this study we take a 'bottom-up' approach to examining population regulation of spider mites. In particular, the absolute leaf area available to a mite population, which is inversely proportional to density, may be positively correlated with per capita growth rates (i.e. negative density dependence). In addition, dynamic changes in plant quality following initial attack may contribute to density dependent effects. Thus, we assess the independent and potential interactive effects of plant size and quality on herbivore population dynamics. Specifically, we asked the following three questions in a series of laboratory and field experiments: (1) How does population density affect subsequent performance (per capita growth) of spider mites? (2) What role does host-plant size play in determining the nature of spider mite population growth? (3) Do density dependent changes in plant quality affect spider mite fecundity and do these effects interact with plant size?

Material and methods

Study system and general procedures

We manipulated initial mite population sizes on *L. cardiaca* plants in order to study per capita growth of spider mites and assessed them after a 10 to 14 day test period, spanning 1–2 generations of mites. Adult female spider mites were used as founder individuals in all trials. Spider mite eggs hatch in approximately three days and individuals complete development within $\approx$ 6–10 days. We determined per capita growth based on the change in population size (the sum of births and deaths) and assumed that immigration and emigration did not occur because there was no contact between plants.

We collected *L. cardiaca* seeds from a natural population at King's College Circle, University of Toronto (Toronto, Ontario). Seeds were germinated in a petri dish between two damp sheets of filter paper and then planted in 500 ml pots in 50:50 Sunshine Soil Mix No.1 (Sun Grow Horticulture, Inc., Belleview, WA) and sterilized topsoil mix with approximately 0.6 gram of slow-release Nutricote (Vicksburg Chemical, Vicksburg, MS) fertilizer (13:13:13 N:P:K). Plants were kept in the greenhouse until they were used in the experiments. For experiments employing plants in different size classes, we made use of natural variation between plants. In particular, differences in plant size were caused by variable time to germination and variable growth rates (seeds were sown at the same time). Once inoculated with mites, the plants were haphazardly positioned in rows, at least 30 centimetres away from each neighbour, on a laboratory bench at ambient light and temperature.

Spider mites were obtained from laboratory colonies grown on *L. cardiaca*, except for the field experiment for which we collected mites from naturally infested *L. cardiaca*. Mites were moved using a fine, slightly dampened paintbrush. Mites were generally placed on a single leaf of the plants, but were not restricted from moving around the plant (except as noted). One to two weeks later, we destructively assessed mite populations by removing the leaves of each plant and separately counting adult females, males and immatures (indistinguishable), and eggs using a dissecting microscope. Plants grew minimally over the assay period (2 true leaves expanded) probably because of the low light conditions. In general, we report the effect of our density manipulations on total mite population growth, summing over the different life stages.

Density dependent population growth

The first experiment was designed to quantify the role of leaf area variation in per capita population growth. We imposed a spider mite population treatment as described above, with initial spider mite numbers ranging from 1 to 30 per plant. In addition, we measured the length of the leaves on all plants ($n = 32$), each

having 2 pairs of true leaves. Leaf length is strongly correlated with leaf area (area $= 8.8 \times 10^{-4}$(length)$^2 - 8.9 \times 10^{-5}$, $F_{1,30} = 1354.569$, $r^2 = 0.978$, $P < 0.001$). Mite densities ranged from 0.05–0.60 mites per cm^2. Subsequent procedures were as described above and assessment took place after 14 days.

Our second experiment was designed to assess the relationship between population growth rate and available leaf area, while controlling for differences in the number of mites per plant. Spider mites were inoculated onto plants ($n = 28$) but the number was kept constant at 3 mites per plant. Mite populations were restricted to one leaf of the second true leaf pair on plants with 2 to 5 pairs of true leaves. The second true leaves were fully expanded when used although the size varied considerably between plants. The restriction of mites to single leaves was achieved using a ring of sticky Tanglefoot (Grand Rapids, MI) around the petiole to prevent movement along the stem. In addition, a small "skirt" cut from a spun polyester bag (Fibe-Air, Kleen test products, Brown Deer, WI) was placed between the innoculated leaf and the rest of the plant to prevent mites from moving between leaves. The skirt prevented leaves from touching without covering the leaf surface. Mite densities ranged from 0.1–0.6 mites per cm^2, the same range as achieved in the previous trial. Subsequent procedures were as described above and assessment took place after 10 days.

We next conducted a field test of the role of plant size in the density dependence relationships of spider mites on *L. cardiaca* (experiment 3). Our experiment was conducted at the University of Toronto's Koffler Scientific Reserve at Joker's Hill, near Newmarket, Ontario, Canada (44° 03′ N, 79° 29′ W) in the Oak Ridges Moraine. This experiment tested the effect of mite population density on population growth on small (2 pairs of true leaves) and large (4–5 pairs of true leaves) plants in nature. The plants were grown in a glasshouse and transplanted to the understory of a *Robinia pseudoacacia* (Fabaceae) dominated stand on June 11, 2001. This habitat had many naturally occurring seedling and mature *L. cardiaca* plants. Natural infestations of *T. urticae* at the time of the experiment ranged from 0–4 mites per seedling and 0–25 mites per mature plant. We estimated leaf area of all plants ($n = 18$ of each size) and randomly assigned a small number of mites to the small plants in order to obtain densities of 0–0.5 mites per cm^2 leaf area. We then randomly assigned mite densities to large plants (0–0.15 mites per cm^2) and inoculated the appropriate number of mites using adult female mites collected from natural infestations on *L. cardiaca*. We were unable to collect enough mites in the field to achieve densities up to 0.5 mites per cm^2 on large plants. Plants were not bagged and were completely randomized with respect to size and mite density. We non-destructively measured leaf area and counted adult female mites every seven days for three weeks.

Induced responses to herbivory, plant quality, and density dependence

Our field experiment revealed that plant size may affect the density dependence relationship for spider mites on *L. cardiaca*. In our final experiment, we aimed to explain some of the evident differences between the plant size classes by assessing the effects of mite density on changes in plant quality on small and large plants. We achieved this by matching the density of mites on small (2–3 true leaf pairs, $n = 17$) and large (4 true leaf pairs, $n = 15$) plants from about 0–0.2 mite/cm^2 and assessing the effect of mite damage on plant quality by assaying mite population growth on an undamaged part of the plant. An equal area of about 4 cm^2 was enclosed on one leaf of the second true leaf pair of each plant at the beginning of the experiment. We used a strip of wet cotton shaped into a circle as the enclosure and inoculated damager mites outside the enclosure. Since mites do not cross a wet barrier, the enclosed area was kept undamaged. The wetness of the cotton was maintained using a wick that ran from the cotton on the leaf to a small container filled with water. Damager mites were free to move over the entire plant except for inside the cotton barrier. After 10 days, the changes in plant quality were assayed by introducing 3 mites to the undamaged leaf area inside the cotton enclosure on each plant. On day 14, the total number of offspring inside each circle was counted.

Statistical methods

We assessed density dependence by regressing a measure of per capita growth, the natural logarithm of the number of mites at the end of the test period per initial founder mite, on the initial manipulated population size. Thus, initial spider mite number is a term common to both variables in the regression. Some have argued that statistical significance that is even partially attributable to the presence of a term common to both correlated variables could be a spurious correlation. Prairie and Bird (1989) explain that the claim that these correlations should be rejected is an unfortunate misconception within the ecological literature and there is no theoretical reason for avoiding such calculations, as long as the formulation is deliberate. Cappuccino (1992) has further argued that this issue is not relevant to density manipulation experiments where the initial densities are experimentally imposed.

The primary goal of our experiments was to determine the effect of experimentally imposed mite density

on per capita population growth. In experiments where plant size and mite populations were manipulated simultaneously, we used a factorial ANOVA analysis to assess the role of plant size (discrete) in mediating different relationships between initial populations (continuous) and per capita growth. An interaction between the two indicates a different relationship between initial population size and per capita growth rates for the two size classes of plants. Because interaction terms can be difficult to detect, we additionally performed separate regression analyses for the large and small plant groups and we report the results of both analyses. Per capita population growth rates were adjusted for the number of days in the assay and are thus reported on a per day basis. Neither the normality of the residuals nor r^2 values were improved by including a squared term in the analyses; thus, linear regressions are reported even in cases where there appears to be some non-linearity in the relationships.

Results

Density dependent population growth

Per capita growth rate was negatively correlated with initial spider mite density per plant (Fig. 1A, $F_{1, 30} = 5.587$, $r^2 = 0.160$, $P = 0.025$) and positively correlated with plant leaf area (Fig. 1B, $F_{1, 30} = 5.910$, $r^2 = 0.165$, $P = 0.021$). In this experiment, it is difficult to assess the relative roles of these two factors because, on average, larger plants had lower densities of mites. However, in the second experiment we manipulated mite density while holding the initial mite number per plant constant. This was accomplished by restricting exactly 3 mites to differently sized leaves in the same leaf position on plants. Per capita growth rate per day decreased as a function of initial density of restricted populations (Fig. 1C), ranging from about 2.1 to 0.07 over a range of 0 to 0.6 mites per cm^2 respectively ($F_{1, 26} = 5.556$, $r^2 = 0.176$, $P = 0.026$). The total area of the plant did not predict per capita growth rate ($F_{1,26} = 0.867$, $r^2 = 0.031$, $P = 0.360$).

We conducted the third experiment to test for the role of mite density and plant size simultaneously in the field. Survival after the first week was marginally density dependent on small plants but not on large plants (small: $F_{1, 16} = 3.874$, $r^2 = 0.195$, $P = 0.067$; large: $F_{1, 16} = 1.982$, $r^2 = 0.110$, $P = 0.178$). In a combined analysis using two-way ANOVA, no interaction between plant size and initial density on per capita growth rate was detected ($F_{1, 32} = 1.358$, $P = 0.253$). Nevertheless, two and three weeks after inoculation, per capita growth rate decreased as a function of density on smaller plants but not on large plants (week 2, small: $F_{1, 16} = 6.077$, $r^2 = 0.275$, $P = 0.025$; large: $F_{1, 16} = 0.301$, $r^2 = 0.018$, $P = 0.591$. week 3, small: $F_{1, 16} = 6.932$, $r^2 = 0.302$, $P = 0.018$; large: $F_{1, 16} = 0.880$, $r^2 = 0.052$, $P = 0.362$, Fig. 2A, C). When we restricted our analysis of the small plants to the ones with the same densities as large plants, a similar pattern emerged in week 3 ($F_{1, 5} = 5.768$, $r^2 = 0.536$, $P = 0.061$, Fig. 2B), but not in previous weeks. In a combined analysis using a two-way ANOVA, the interaction between plant size and mite density across equal densities was nearly significant ($F_{1, 34} = 4.229$, $P = 0.074$). In addition, we

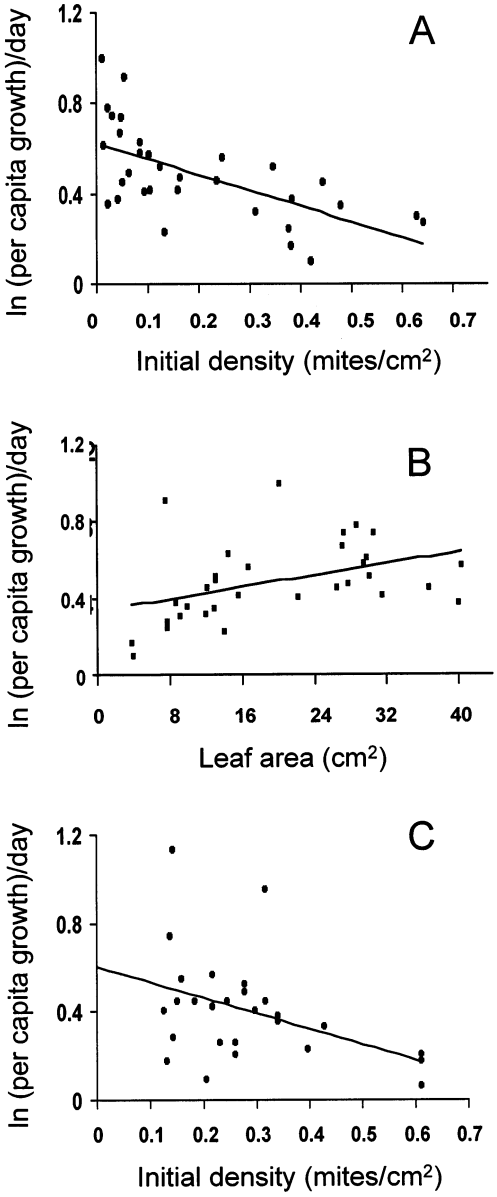

Fig. 1. The effect of (A) initial mite density and (B) and total leaf area on spider mite per capita growth. (C) The effect of initial mite density on spider mite per capita growth. In the latter experiment, mite populations of equal size (3 per leaf) were restricted to single leaves of variable area, so the effects observed are entirely attributable to leaf area available.

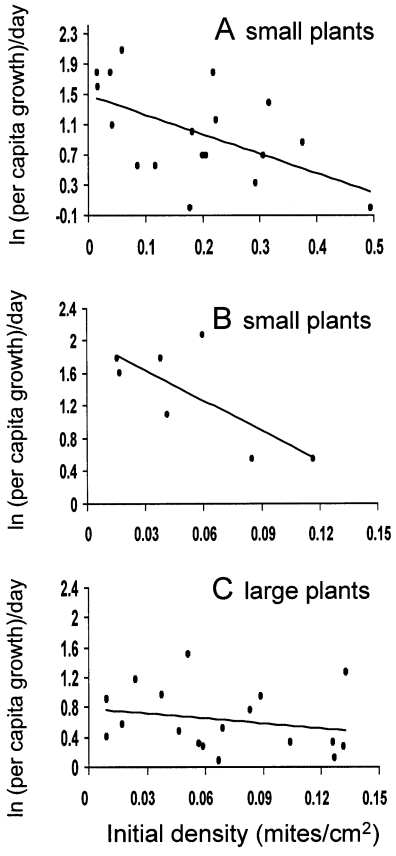

Fig. 2. The effect of initial mite density on subsequent spider mite per capita growth in the field. (A) Plants were relatively small (2 pairs of true leaves) and had mites over a range of 0–0.5 mites/cm^2 and (B) the same small plants plotted over a range of 0–0.15 mites/cm^2, excluding higher densities. (C) Plants were relatively large (4–5 pairs of true leaves) and had mites over a range of 0–0.15 mites/cm^2.

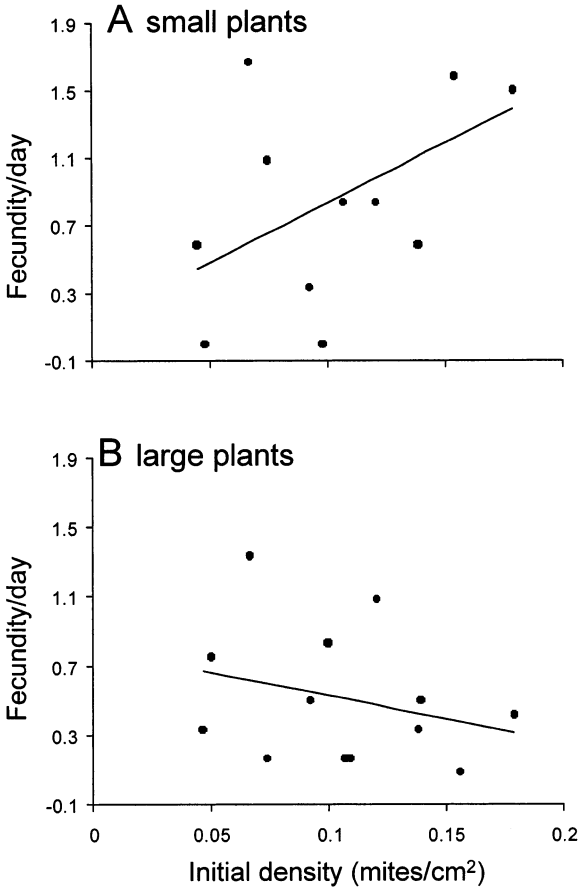

Fig. 3. A test of density dependent induced plant responses. The effect of initial mite density on the daily reproduction of spider mites introduced to an undamaged enclosure after 10 days of initial damage on (A) relatively small plants (2–3 pairs of true leaves) and (B) on relatively large plants (4 pairs of true leaves).

found that across all initial mite densities (from a single week's analysis), mites on small plants had 59% higher per capita growth than those on large plants (e.g. week 3, mean mites per capita per day $\pm$ SE: small 1.007 ± 0.148; large 0.634 ± 0.098, $F_{1, 32} = 5.482$, $P = 0.026$).

Induced responses to herbivory, plant quality, and density dependence

Our final experiment was designed to assess mite density mediated changes in the plant quality and whether these effects interacted with plant size. In a combined analysis using two-way ANOVA, the interaction between plant size and initial density on the total number of offspring in the enclosures was significant (Table 1). The number of offspring per female in the enclosures tended to increase as a function of initial density on small plants, from approximately 0.4 to 1.7 mites per day over a range of 0 to 0.2 mites/cm^2 ($F_{1, 10} = 3.498$, $r^2 = 0.259$, $P = 0.091$, Fig. 3A). Conversely, the number of offspring per female in the enclosures tended to decrease as a function of initial density on large plants,

Table 1. Analysis of variance for the effects of plant size and initial mite density on per capita spider mite reproduction on an undamaged part of the plant.

Source	ss	df	Ms	F	P
Plant size	0.353	1	0.353	1.599	0.220
Initial mite density	0.193	1	0.193	0.872	0.361
Plant size $\times$ Initial mite density	0.972	1	0.972	4.397	0.048
Error	4.641	21	0.221		

from approximately 1.3 to 0.1 mites over an initial density range of 0 to 0.2 mites/cm^2 ($F_{1,\ 12} = 3.972$, $r^2 = 0.249$, $P = 0.069$, Fig. 3B). Thus, plant size interacted with density-mediated induced changes in plant quality (Table 1).

Discussion

Our experiments demonstrate that bottom-up factors associated with plant size and quality interact to produce density dependent population growth of spider mites. In our first experiment, we demonstrated density dependence by manipulating mite populations on plants. Second, we unambiguously implicate mite density per se in density dependence by holding spider mite number constant and restricting mites to single leaves (of variable size) at the same leaf position on plants. This test revealed the importance of population density, irrespective of population size, in determining the rate of per capita growth. Per capita growth decreased as density increased, therefore some mechanism caused the alteration of reproductive output and/or survival of spider mites under more dense conditions. We note that many studies of density dependence simply manipulate population size, while assuming that this corresponds to a manipulation of density. However, our detailed measurements of plant leaf area allowed for the calculation of the true effects of density per se.

At our field station, natural populations of spider mites occur on resident *L. cardiaca* plants. In our experiment, per capita growth of spider mite populations was negatively density dependent on relatively small plants, but not on relatively larger plants over a similar range in densities. These results suggest a possible reversal of density dependence attributable to plant size. Here, smaller plants supported higher per capita growth, supporting a relatively faster growing, more dense, mite population. Several preliminary experiments (K.A. Rotem and A.A. Agrawal, unpubl.) also demonstrated that mite population growth was higher on small plants compared to large plants. Thus, only under conditions of high population growth do mites experience negative density dependence. We posit that the strong density independent influence of plant size interacted with density dependent processes.

Changes in plant quality following herbivory contribute to spider mite reproduction and/or survival and may explain the differential growth of spider mite populations on small and large plants (Karban 1987, Karban and Baldwin 1997). Indeed, differential plant induction based on size and phenology has been previously reported (Stout et al. 1996). The results of our final experiment indicate that *L. cardiaca* responds in a density dependent manner to mite feeding, but that this effect varies with plant size. In these experiments, density per se of the spider mites was matched on small and large plants. Thus, we found evidence of density dependent induced susceptibility to spider mites in small plants and induced resistance in large plants. These finding may be initially counter-intuitive when considered in conjunction with the findings of negative density dependence on small plants and no density dependence on large plants. However, since spider mite populations grow more rapidly on small plants compared to large plants, factors such as food limitation, aggression, and intraspecific competition between adult females could explain the reduction of reproductive output observed in more dense populations. We observed that sufficient amounts of intact tissue were always available for consumption by spider mites and only in rare cases was there more than 50% of plant tissue damaged. In general, less tissue was available on small plants compared to large plants due to the feeding of a more rapidly growing population.

The interaction between rapidly growing populations and less leaf area may explain the greater evidence for negative density dependence on relatively small plants compared to large plants. In other words, small plants show density dependent increases in plant quality (induced susceptibility) resulting in high population growth. In turn, this leads to an overall pattern of negative density dependence, which may be caused by limitation of high quality food. Although large plants showed no density dependence overall, we found evidence for density dependent decreases in plant quality. At such low levels of population growth, densities may not be high enough to cause intraspecific competition or other forms of negative density dependence. Other factors could even cause the fitness of individual spider mites to increase in the presence of others because of some advantage to being in a group (i.e. an Allee effect, Allee et al. 1949, Denno and Benrey 1997). In our experiments, such positive density dependence apparently matched the density dependent induced plant resistance under some conditions.

Depending on the causes of the differences observed in the 3rd and 4th experiment (Figs. 2 and 3), the above logic of induced responses followed by resources limitation may not be required. There were many unmeasured differences between the field (experiment 3) and laboratory experiment (experiment 4).

In their natural habitat we found variably sized populations of spider mites on *L. cardiaca*, ranging from hundreds of mites per leaf to single mites. Because *L. cardiaca* frequently occurs in populations consisting of seedling and mature plants, mite herbivores naturally attack different sized plants. The existence of variably sized mite populations on different sized plants can result in different modes of population growth. We conclude that spider mite population growth on *L. cardiaca* is governed by at least 3 factors: 1) plant size, which when small is likely to result in intraspecific

competition, 2) plant quality: which decreases with plant size, and 3) an interactive effect between density dependent changes in plant quality (induced plant responses) and the available leaf area for consumption.

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