



Density dependence in insect performance within individual plants: induced resistance to *Spodoptera exigua* in tomato

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Net intraspecific density dependence experienced by insect herbivores at the scale of single plants can be a function both of induced resistance in the plant and other interactions among individual herbivores. Theory suggests that non-linearity in the form of this density dependence can influence the effects of plants on herbivore population dynamics. This study examined both net density dependence at the scale of single plants, and changes in plant quality with herbivore density for *Spodoptera exigua* caterpillars on tomato plants. One experiment measured the growth of caterpillars moving freely about the plant at different densities, the distribution of damage by these caterpillars, and the quality of the plant as food for caterpillars (growth of caterpillars on undamaged leaf tissue excised from the plant). A second experiment measured plant quality for plants with different amounts of damage by caterpillars confined to particular leaves in mesh bags. Growth of *S. exigua* caterpillars was found to be negatively density dependent, and this was in part due to decreases in plant quality both as herbivore density increased and as the amount of damage increased. The response of plant quality to herbivores was found to have non-linear features; there was both a threshold below which no significant decreases in quality (as measured by herbivore growth) occurred, and the decrease in herbivore performance saturated at the highest damage levels. In addition, it was found that caterpillar damage was significantly more aggregated than expected when multiple caterpillars occupy a single plant. This study confirms that host plants have the potential to be a source of density dependence that affects herbivore performance.

Although density dependence is necessary for population regulation (Turchin 2003), there has been substantial debate about the importance of intraspecific density dependence for the regulation of insect herbivore populations, which are strongly influenced by abiotic factors (Andrewartha and Birch 1954, White 2001) and often appear to have an abundance of potential food (Hairston et al. 1960). In the last several decades evidence has accumulated showing that insects can exhibit intraspecific competition through interactions on and with their host plants (Denno et al. 1995). They may thus be subject to intraspecific density dependence generated at the scale of single plants, as well as at larger scales (Schultz 1988, Ray and Hastings 1996). In particular, induced plant resistance (an increase in plant chemical or physical traits that reduce herbivore feeding or performance) may contribute density dependent feedback to herbivore populations when the level of resistance depends on the amount of damage received. While many studies have shown that induced resistance increases with increasing damage (Karban and Baldwin 1997), relatively few studies address key aspects of the form of density dependence at the scale of individual plants. A better understanding of density dependence at this scale should help us understand the potential for plant-mediated density dependence to influence herbivore populations at larger scales.

Models of effects of induced resistance on herbivore population dynamics indicate that the shape of the relationship

between the number of herbivores attacking a plant (or amount of damage to the plant) and plant resistance can be important in determining the influence of induced resistance on herbivore populations (Lundberg et al. 1994, Underwood 1999, Underwood et al. 2005, Abbott et al. 2008). In particular, non-linear aspects such as a threshold level of damage required to induce a response or saturation of plant response at high damage levels, should influence the likelihood that induced resistance can generate fluctuations in herbivore populations (Underwood et al. 2005, Abbott et al. 2008, see also Murdoch et al. 2003 for work on non-linear density dependence in consumer–resource interactions in general). Although many previous studies have found that induced resistance increases with herbivore damage or density (see Karban and Baldwin 1997, Table 4.5 for examples) few studies have examined these non-linear aspects of the induced response (but see Karban 1987).

The net negative feedback to herbivore performance as herbivore density on a plant increases could involve not just changes in plant quality but also herbivore behavior and (at the highest densities) food limitation. For example, mobile herbivores may avoid some of the effects of induced resistance when resistance is unevenly distributed within the plant (Orians et al. 2000). Herbivores may disperse their damage in response to plant resistance (Edwards and Wratten 1983, Schultz 1983), and the pattern of herbivore damage across the plant may in turn influence further induction

of plant resistance (Rodriguez-Saona and Thaler 2005). Herbivores may also be subject to density effects not mediated by the plant but arising from direct interactions among individuals, either antagonistic or cooperative.

Net density dependence at the scale of a single plant can be measured in several ways. Some studies have manipulated the amount of damage the plant receives (using artificial damage or confined herbivores) and measured induced resistance either with chemical assays (Baldwin and Schmelz 1994, Thaler et al. 1996) or bioassays (Underwood 2000). This method is useful for efficiently creating a range of damage levels, but excludes the possibility of density dependence mediated by herbivore behavior or interactions among herbivores. It is thus possible that studies manipulating damage, rather than herbivore densities, could overestimate density dependent feedback (if insects avoid plant resistance by moving), underestimate density dependent feedback (if insects are subject to density dependence from sources other than plant quality), or inaccurately estimate plant responses if the spatial distribution of damage is important for feedback between insects and plants. Alternatively, studies may manipulate herbivore density directly, allowing the insects (or mites) to move freely, and measure herbivore performance (Karban 1987, Harrison 1994, Fordyce 2003, Rotem and Agrawal 2003). This captures the net density dependent feedback from the plant and other sources (although sometimes excluding predators), but does not isolate the contribution of changes in plant resistance.

In this study I measured both net density dependence and the change in plant quality in experiments manipulating damage and herbivore density at the scale of a single plant. I used tomato (*Lycopersicon esculentum* var. Castlemart) and the beet armyworm (*Spodoptera exigua*) to address the following questions about within-plant density dependence:

1. Is the individual growth of herbivores that move freely about the plant density dependent?
2. Is density dependence mediated by induced resistance in the plant?
3. Do caterpillars respond behaviorally to increasing density by changing their distribution of damage within a plant?
4. How does plant quality change over a range of damage levels? Are there qualitatively non-linear aspects of the induced response to damage (e.g. threshold or saturation)?

Methods

Study system

Tomato is a model system for the study of induced resistance, and a great deal is known about mechanisms of induction (Howe and Ryan 1999), how induced resistance is distributed through a plant (Orians et al. 2000), and the effects of induced resistance on herbivores (Thaler et al. 2001). *Spodoptera exigua* is a broad generalist and can be an economic pest on tomato (Lange and Bronson 1981). Tomato variety Castlemart (used in this study) is known to have resistance that is induced by *S. exigua* feeding (Broadway

et al. 1986, Stout et al. 1996, Thaler et al. 1996), with significant increases in resistance within 24 h after the onset of damage and peak resistance at three days after damage (Edwards et al. 1985). In tomato, leaves at different distances from a damaged leaf achieve different levels of resistance, creating a great deal of within-plant heterogeneity in resistance (Orians et al. 2000). In this study, it was not possible to keep the distance between damaged and sampled leaves constant; instead, sampled leaves are considered a sample of plant quality rather than representative of the whole plant. Plants for the experiments described here were grown in the Florida State University greenhouses in FSU potting mix in 5 inch (1.68 l) pots with water and fertilizer provided as needed. *Spodoptera* were reared in Percival growth chambers with 12:12 day length at 28°C and fed artificial diet.

Experiment 1

Experiment one examined how the density of freely moving *S. exigua* on a plant influenced the growth of these ‘damaging caterpillars’, the quality of the plant as measured by the growth of caterpillars placed on excised undamaged leaves (‘bioassay caterpillars’), and the dispersion of damage across the plant. Plants with four fully expanded true leaves were used for this experiment. The most recently fully expanded leaf on each plant was first covered with a mesh bag tied around the petiole, protecting that leaf from damage. Each entire plant was then covered with a large mesh sleeve taped to the rim of the pot. Plants were assigned to receive one of five numbers of second instar caterpillars: 0, 1, 2, 5 or 10; there were 10 plants per treatment in each of four temporal blocks for a total of 40 plants per treatment. Because all plants were approximately the same size, different numbers of caterpillars reflect different densities per plant. Because individual damaging caterpillars could not be tracked through the experiment, they were weighed collectively, and released on the soil surface at the base of the plant. Caterpillars were allowed to feed and move for three days. After three days, the mesh sleeves were removed and the damaging caterpillars were re-weighed. Per-capita relative growth rate (RGR: $\ln(\text{weight after}/\text{weight before})/\text{number of caterpillars}$) was calculated to assess their performance. The experiment was carried out in four temporal blocks, with 10 plants per treatment per block.

Forty-eight hours after the damaging caterpillars were removed, the undamaged leaf (protected by the small bag) was harvested from each plant with a razor at the petiole and used in a growth bioassay to determine the potential for plant-mediated density dependent feedback independent of herbivore movement, interactions, or food limitation (caterpillars did not run out of leaf material during the assays). Each undamaged leaf was placed in a 2 oz cup with a damp piece of filter paper. Individual third instar bioassay caterpillars were starved for one hour, weighed, and added to the cups. Forty-eight hours later these caterpillars were starved for one hour, re-weighed and their relative growth rate was calculated. Induced resistance would be indicated by lower RGR’s for caterpillars feeding on damaged versus undamaged plants.

Finally, digital images were taken of all leaves and Sigma Scan was used to measure the total proportion damage to

the plant and the distribution of damage across the plant. The distribution of damage was characterized by the coefficient of variation of damage across leaves (CV) within a plant, where a lower CV indicates a more even distribution of damage.

Experiment 2

Experiment two determined how different levels of damage to the plant (rather than different numbers of caterpillars) affected the growth of caterpillars on undamaged excised leaves. This experiment used a wider range of damage levels than was generated during experiment one. Plants were grown until they had four fully expanded leaves. Leaf area for each plant was determined by estimating the length of the midrib of each leaflet (average midrib length approximately 6 cm). Each plant was then assigned to one of six different damage levels: 0, 5, 20, 40, 60 and 80% of leaf area damaged. Damage was imposed by putting small mesh bags around the appropriate number and size of leaflets and placing 3rd instar *S. exigua* in the bags. Enough caterpillars were used to completely consume the bagged leaflets within 24 h (caterpillars were added or removed to achieve the correct level of damage). The most recently expanding leaf on each plant was left undamaged. After 24 h the damaging caterpillars were removed. Two days later the most recently expanded leaf was harvested and used for a growth bioassay following the same protocol as in experiment one. There were six replicates of each percent damage level in each of four temporal blocks (total of 24 plants / damage level) except for controls for which there were 30 plants per block.

Analyses

Questions 1 and 4 ask whether caterpillar growth is density dependent, and whether there is evidence for qualitatively non-linear features of this density dependence (threshold and a saturation of plant response). I approached these questions by analyzing the data for both experiments using ANOVAs with caterpillar density (experiment 1) or percent damage (experiment 2) included in the models as a categorical variable. This tests for any relationship between density or damage and caterpillar performance, linear or non-linear, without constraining the model to a particular non-linear form. Planned contrasts were used to look for the presence of the non-linear features of interest (threshold and saturation of response). As a simple check of the hypothesis that at least one non-linear function is a better fit than a linear one I also examined ANCOVAs with density or damage as a continuous variable, including both linear and quadratic terms, for tests with at least five levels of density/damage (less than five levels is too few to reliably detect non-linearity). This is a weak test because even if a quadratic term does not improve fit some other non-linear form could still be a better fit than a linear model, however the number of levels of density and damage in these experiments was too low to estimate the fits of more complex non-linear relationships with confidence.

For experiment one, I used ANOVA to assess the effect of caterpillar density on two response variables: relative growth rate (RGR) of damaging caterpillars and plant quality as measured by the RGR of bioassay caterpillars. In both

cases the initial model included caterpillar density, temporal block, and their interactions. The RGR of damaging caterpillars was natural log-transformed to make variances homogeneous; inequality of variances in the raw data likely arose from the difference in number of caterpillars per treatment (individual variation in growth rate is more influential for the lowest density treatment than for high densities where the growth of many individuals was averaged for each data point). Relative growth rates of bioassay caterpillars were not transformed and had normally distributed residuals and equal variances. Planned comparisons of least squared means were used to test for differences between neighboring densities for each response variable, providing qualitative information on the existence of a threshold or saturation of response. To test explicitly for a non-linear relationship I also ran an ANCOVA including density, density², block and all interactions for RGR of bioassay caterpillars. I also calculated the average percent damage per plant for each density of damaging caterpillars in experiment one, so that results of experiment one could be compared with those of experiment two, where percent damage was manipulated directly. The effect of percent leaf area damaged on plant quality in experiment two was assessed by modeling the RGR of bioassay caterpillars as a function of percent damage, temporal block, and their interaction. Residuals met the assumptions of the test without transformation. Planned comparisons of least squared means were used to test for differences between neighboring percent damages. Again, to test explicitly for a non-linear relationship I also ran an ANCOVA including percent damage, percent damage², block and all interactions.

I examined the distribution of damage across the plant in experiment one in two ways. First, I used ANOVA to model the CV of damage among leaves for each plant as a function of caterpillar density, block and their interaction to determine how density affected the overall variability in levels of damage. Coefficients of variation were log-transformed to provide normally distributed residuals and homogeneous variances. Second, I asked whether the distributions of damage for each density differed from the distribution expected if each caterpillar had damaged leaves independently. This is a conservative indicator of whether caterpillar movement differed among densities, as caterpillars could move among leaves without leaving measurable damage. Distributions of damage across all plants in a treatment were described as the probability that leaves received proportion damages from 0 to 1 in increments of 0.05. I used this distribution of damage from the single caterpillar treatments to calculate the expected distributions of damage for multiple caterpillars. For example, the probability that a leaf received a given amount of damage from each of two independent caterpillars is the product of the probabilities of those damage levels from a single caterpillar. Because of the extremely large number of possible combinations of damage from 10 caterpillars (21^{10}), the expected distribution for this density was estimated from 10^7 random samples rather than enumerating all possibilities. I constructed the expected distributions using two different assumptions about how herbivores feed. I considered both an additive model, where the proportion damaged by one caterpillar was added to the proportion damaged by another (truncated at 100% damage), and a multiplicative

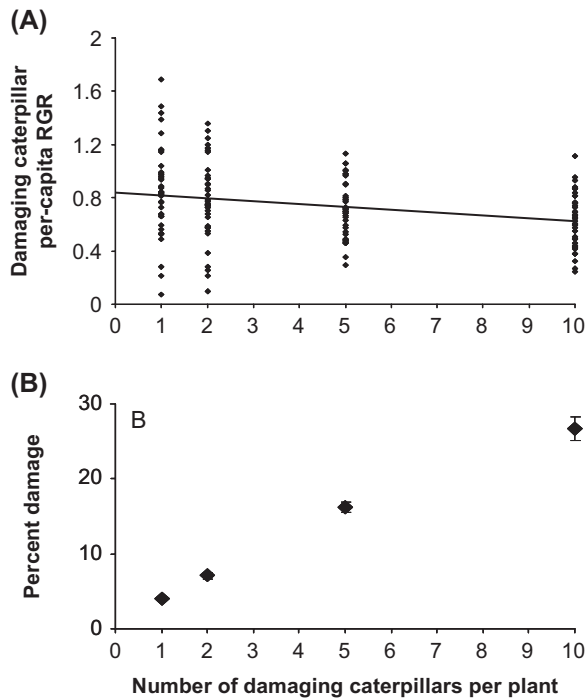


Figure 1. (A) Per-capita relative growth rate (RGR) of *S. exigua* caterpillars feeding at different densities on tomato plants (experiment 1). Each point represents growth of caterpillars on a single plant. $R^2=0.075$, slope=-0.02. (B) Percent damage on plants with different densities of caterpillars in experiment 1. n for each point=40, error bars indicate ± 1 SE.

model where each caterpillar damaged a proportion of leaf left after feeding by previous caterpillars. I used G-tests to ask if the observed distributions of proportion damages for each density differed from the expectations calculated assuming independently moving caterpillars. Despite slight differences in the expected distributions between the additive and multiplicative models, the qualitative and quantitative results for the G-tests did not differ, so I present only results for the additive model. To summarize the distributions for presentation, I calculated the coefficients of variation for both observed and expected distributions (Fig. 3).

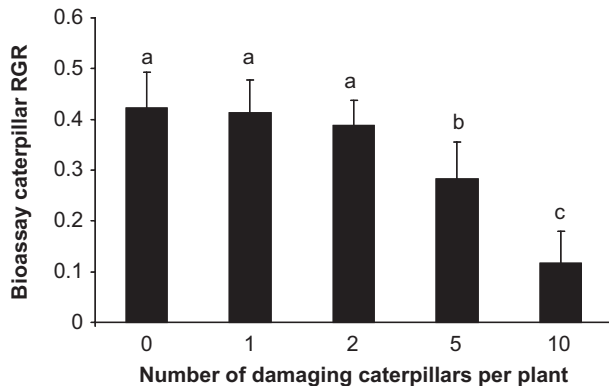


Figure 2. Relative growth rate (RGR) of 'bioassay' *S. exigua* caterpillars feeding on an undamaged leaf from tomato plants subject to damage by different numbers of damaging caterpillars (experiment 1). n for each bar=40, error bars indicate 1 SE. Different letters indicate significant differences between means with $p < 0.05$.

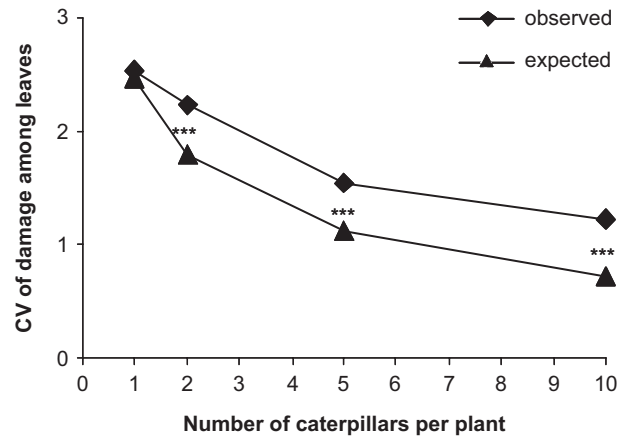


Figure 3. Coefficient of variation (CV) of damage among leaves within plants subject to damage by different numbers of caterpillars per plant (observed data, diamonds), and the expected CV of damage if caterpillars had fed independently as opposed to simultaneously (expected data, triangles). n for observed points=40. Asterisks indicate a significant difference between expected and observed distributions of damage (CV's presented as a summary of the distributions), $p < 0.001$.

Results

Experiment 1

The per-capita relative growth rate of damaging caterpillars decreased significantly with increasing caterpillar density ($F_{3,143}=8.57$, $p < 0.0001$, Fig. 1A) and this relationship varied among blocks (interaction between density and block, $F_{9,143}=1.96$, $p=0.048$), with one block showing no relationship while all others showed a decreasing relationship. The mean amount of plant damage in experiment one ranged from 4% for one caterpillar to 27% for ten caterpillars (Fig. 1B). Plant quality (as measured by the RGR of bioassay caterpillars) declined overall with increasing caterpillar density ($F_{4,172}=10.00$, $p < 0.0001$, Fig. 2), and this effect varied with block (interaction of density and block, $F_{12,172}=2.11$, $p=0.02$), being negative in all cases but significantly so for two of the four blocks. Significant induced resistance (difference of bioassay caterpillar RGR from the control) was observed for five and ten caterpillars (planned comparisons of means $p=0.0124$ and $p < 0.0001$ respectively) but not for smaller numbers of caterpillars. Plant quality was also significantly lower with 10 damaging caterpillars than with five ($p=0.007$). Significant departure from a linear relationship was indicated by a significant three-way interaction of density, density² and block in ANCOVA ($F_{3,176}=2.76$, $p=0.04$) as well as marginally significant two-way interactions of density \times block ($F_{3,176}=2.59$, $p=0.05$) and density² \times block ($F_{3,176}=2.60$, $p=0.05$). All other effects in this model were not significant.

Overall, the CV of proportion of leaves damaged declined with increasing caterpillar density ($F_{3,152}=30.71$, $p < 0.0001$), indicating that damage is more evenly distributed as densities increase (Fig. 4, solid symbols). The decrease in CV with increasing caterpillar density was more linear for some blocks than others (block by density interaction: $F_{9,152}=4.09$, $p < 0.0001$), but all showed a

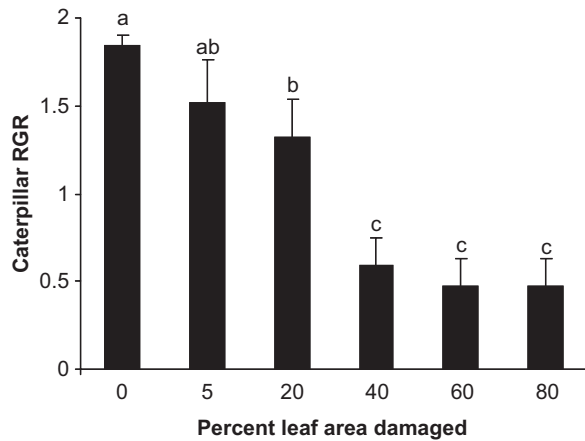


Figure 4. Relative growth rate (RGR) of bioassay *S. exigua* caterpillars feeding on an undamaged leaf from tomato plants subject to different percent leaf areas damaged (experiment two). n for each bar = 24 for all damage levels except 0, where $n = 120$. Error bars indicate 1 SE. Different letters indicate significant differences between adjacent bars with $p < 0.05$.

decreasing pattern. The observed distributions of damage for all densities (two through ten caterpillars per plant) were significantly less even than the expected distributions if caterpillars moved independently (Fig. 4; for two caterpillars: $G = 71.1$, for five caterpillars $G = 240.8$, for ten caterpillars $G = 580.5$, all $p < 0.0001$).

Experiment 2

The relative growth rate of bioassay caterpillars declined with increasing percent leaf damage ($F_{5,91} = 43.23$, $p < 0.0001$), and differed among blocks ($F_{3,91} = 28.11$, $p < 0.0001$), but the relationship between percent damage and larval RGR was the same for all blocks (no block by percent damage interaction). There was a significant decline in plant quality for all treatments above 5% damage, and no difference in quality between 40, 60 and 80% damage (Fig. 5). Significant departure from a linear relationship was indicated by significant linear and non-linear terms in ANCOVA (effect of percent damage: $F_{1,109} = 55.6$, $p < 0.0001$, and percent damage²: $F_{1,109} = 15.16$, $p = 0.0002$); this model also had a significant main effect of block ($F_{3,91} = 32.79$, $p < 0.0001$), but no block by percent damage or percent damage² interactions.

Discussion

The growth of *Spodoptera exigua* caterpillars on tomato plants was significantly slower with increasing caterpillar density, even over a brief feeding period of three days, which is a single instar or less under the conditions of this experiment (Fig. 1). This result is consistent with the few other studies that have looked for within-plant density dependence in herbivore performance (e.g. studies with mites: Karban 1987, Brown et al. 1991, Rotem and Agrawal 2003, Lepidoptera: Harrison 1994 and Hemiptera: Miller 2007), with the exception of studies of group-feeding caterpillars for which density generally has a positive effect on larval performance (Fordyce 2003, but see Inouye and Johnson 2005).

Density dependence in the growth of damaging caterpillars was clearly due at least in part to feedback through systemic induced resistance in the plant. Bioassay caterpillars feeding on undamaged leaves grew more slowly as the density of damaging caterpillars increased (Fig. 2). Increases in induced plant responses have previously been observed both with increasing herbivore density (Underwood 2000), and with increasing damage to plants (Williams and Myers 1984, Baldwin and Schmelz 1994). Many previous studies of this relationship have used artificial damage and measured some aspect of plant chemistry as the response to leaf damage. Measuring the effect of insect damage on insect performance, as in this study, provides less information about the mechanism of plant response but gives a more direct measure of net density dependence, including both plant-mediated effects and other possible positive or negative density effects such as direct interactions among individuals. This study does not allow direct comparison of the magnitude of effects of density through the plant alone and the net effects of density allowing for herbivore movement and direct interactions among individuals. Because the bioassay occurred after the damaging caterpillars were removed from the plant, and it is known that induced resistance changes over time within a plant (Edwards et al. 1985, Underwood 1998), differences in growth rates between damaging and bioassay caterpillars might be due in part to temporal changes in the plant. However, this study does demonstrate that density dependent feedback through induced resistance occurs, even when herbivores can move freely within the plant.

Results of experiment one suggest that caterpillar movement is influenced by intraspecific interactions. As caterpillar density per plant increased, damage became more evenly distributed among leaflets (Fig. 4). This is to be expected because more caterpillars will collectively make more movements among leaflets and thus increase the spread of damage. However, the observed distribution of damage with multiple caterpillars was much more aggregated than expected if caterpillars moved independently. This suggests that caterpillars respond positively either to each other (conspecific attraction) or to each other's damage. As the distribution of damage within the plant can influence the degree of subsequent plant induction (Rodriguez-Saona and Thaler 2005), it would be interesting to determine if this increased aggregation ameliorates or exacerbates negative density dependence due to induced resistance.

Models suggest that the form of density dependence in plant induced resistance should affect how plants influence herbivore population dynamics (Abbott et al. 2008). In particular, even a fairly low threshold below which plant responses do not occur can in theory exacerbate the effects of time lags that can lead to population cycles or influence spatial distributions of herbivores among plants, while saturation of the response might limit the ability of the plant to regulate herbivore populations (Underwood 2000, Underwood et al. 2005). Both thresholds and saturation have been observed previously (Karbon 1987, Underwood 2000), but the form of the plant response has so far been examined in very few systems. Results of experiment one suggest that at low levels of damage and/or low herbivore densities there was little feedback from the plants to the insects. As measured by the growth of bioassay caterpillars, there was no significant

systemic induced resistance with damage from only one or two caterpillars (Fig. 2). Similarly, in experiment two there was no significant induced response at the lowest percent leaf damage (5%, Fig. 4). Although these results do not tell us that there is no plant response at low damage levels, they do suggest that there are damage levels at which the plant response does not significantly affect the herbivores, suggesting a functional threshold. There is no indication of saturation of the plant response in experiment one (Fig. 2), but the range of percent leaf area damaged was relatively small – up to 27% leaf area loss (Fig. 1B). In experiment two the maximum damage level was 80% and there is clear evidence of saturation, with treatments above 40% damage all eliciting the same degree of induced resistance (Fig. 4). This qualitative evidence for a threshold and saturation of response, together with significant polynomial terms in ANCOVAs relating caterpillar growth to density or percent damage, clearly indicate some non-linearity in within-plant density dependence in this system. Because the present study measures effects on only a short portion of the herbivore life-cycle in the laboratory, its results can only indicate the potential for linear or non-linear density dependence for actual herbivore populations in the field; determining how observed non-linearities matter for real populations would require further study. While these results suggest that models of induced resistance and herbivore dynamics should consider non-linear density dependence, to accurately model the consequences of these non-linearities for any particular system would require fitting models with explicit thresholds and asymptotes to the data. This wasn't done in the present study due to limited numbers of experimental densities (or percent damages), but would be an important next step in scaling up from laboratory studies such as these to predictions for real populations.

There has been considerable debate about the importance of density dependence in herbivore population dynamics. This study confirms that host plants can be a source of density dependence that affects herbivore performance. This effect is likely to be common, since induced resistance is found in most plants that have been examined, but measurements of net plant-mediated density dependence are still rare. As we strive to understand more mechanistically how interactions with plants may influence herbivore populations, we will need to consider the form of density dependence arising from plant-mediated interactions (Abbott et al. 2008), as well as the ways in which herbivore movement may change as a function of density. For herbivores that move among plants, studies will also need to scale up from interactions within individual plants to patterns across plants (Underwood et al. 2005).

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