Oecologia (2002) 131:220–226
DOI 10.1007/s00442-002-0871-2

PLANT ANIMAL INTERACTIONS

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Fitness consequences of cotyledon and mature-leaf damage in the ivyleaf morning glory

Received: 10 November 2001 / Accepted: 17 December 2001 / Published online: 14 February 2002
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Abstract To understand the evolutionary and ecological consequences of natural enemy damage to plants, it is essential to determine how the fitness effects of damage differ depending on the tissues damaged and the subsequent pattern of damage. In a field experiment with the ivyleaf morning glory, the direct and indirect effects on fitness of herbivore damage to cotyledons and mature leaves was evaluated. Damage to mature leaves had negligible direct effects on fitness and no indirect effects on fitness through other correlated traits. Damage to cotyledons also did not directly affect fitness, but did so indirectly through its effects on plant size. These findings suggest that increased resistance to cotyledon damage or increased compensatory growth following cotyledon damage could be effective strategies for plants of this species to counteract the negative effects of herbivory.

Keywords *Ipomoea hederacea* · Herbivory · Juvenile resistance · Path analysis · Indirect effects

Introduction

Although there is consensus that the effects of herbivore and pathogen damage on plant fitness are usually negative (e.g., Crawley 1983; Burdon 1987; Marquis 1992), this consensus has largely been achieved through the study of natural enemy damage to mature tissues. As a consequence, relatively few data exist on whether fitness consequences of damage to juvenile tissues are similar to the well-described fitness consequences of damage to mature tissue. These data are essential, however, before conclusions can be reached about what types of damage are the most important for plant ecological and evolutionary dynamics, what forms of resistance and tolerance are most likely to be subject to natural selection, and even which life stages or tissues biologists should consider when designing studies of plant-herbivore interactions.

Comparing the fitness consequences of natural enemy damage to cotyledons and mature leaves represents a promising area to investigate this question because it is unclear which type of damage will have more severe fitness effects. On one hand, because plants at the cotyledon stage are making the transition from heterotrophism to autotrophism, it is likely that damage to cotyledons will have significant fitness consequences. Furthermore, damage at this life-history stage can have potentially deleterious effects on fitness through its correlated effects on juvenile survivorship, overall plant size, or the onset of reproduction. Because damage to cotyledons occurs early in the plant's life cycle, it is also likely that the plant will suffer subsequent damage that could modify or alter the fitness consequences of cotyledon damage (e.g., Strauss 1991; Pilson 1996; Wise and Sacchi 1996). On the other hand, it is possible that damage to mature leaves has larger fitness effects because nutrients necessary for compensation may have already been allocated to other plant functions (e.g., flower, pollen or ovule production, fruit maturation) or because there is insufficient time for compensation prior to the end of the growing season.

Unfortunately, there are no data from the literature to indicate whether damage to cotyledons or mature leaves is likely to have more severe fitness effects. However, there have been several studies of early and late season damage to vegetative tissue upon which one might base a prediction, with the implicit assumption that early season damage to mature tissue is qualitatively similar to damage to cotyledons, which also occurs early in the season. Even if this assumption is valid, the available studies are inconclusive about which of the preceding alternatives is more likely. For example, both Maschinsky and Whitham (1989) and Lennartsson et al. (1998) found that plants could tolerate or compensate for damage early in the season, but could not do so when damage occurred

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later in the season. Maschinski and Whitham (1989) and Lennartsson et al. (1998) studied plants that form a basal rosette and have a single, apically dominant meristem (*Ipomopsis arizonica* and *Gentianella campestris*, respectively). After the apical meristem is damaged in these plants, many lateral meristems are activated, each of which supports flowers. Seed set in the flowers of these lateral meristems compensates for the deleterious effects of herbivores on fitness. Damage later in the season is likely to have more negative effects on fitness in these plants because fewer undifferentiated meristems remain later in the season, nutrient availability is reduced, and there is less time for meristem activation, flowering, and seed maturation before the end of the growing season (Maschinksi and Whitham 1989; Lennartsson et al. 1998).

In many plant systems, however, damage does not have the effect of producing larger, bushier plants. For example, Fritz et al. (2001), found that slug damage early in the season to juvenile willows greatly reduced biomass and performance, though the effects of this damage on lifetime reproductive success in this system are unknown. Moreover, larger, bushier plants do not always have higher fitness: Doak (1991) described a case where early damage to apical meristems in dwarf fireweed increased branch biomass, but *decreased* seed set. For systems such as these, damage early in the season might have the effect of reducing plant size or delaying the onset of reproduction, and thus have greater fitness effects than later season damage.

Given these contrasting results, it remains an empirical question as to whether damage to cotyledons or damage to mature leaves generally has greater effects on fitness, and whether the effects of early season damage to cotyledons are qualitatively similar to the effects of early-season damage to vegetative tissues. In this article, I present results of a study that evaluates the effects of cotyledon and mature leaf damage on fitness in the ivyleaf morning glory (*Ipomoea hederacea*). In particular, I evaluated the following questions: (1) Does damage to cotyledons have more or less severe effects on fitness than mature-leaf damage? (2) Does herbivore damage affect fitness directly, or indirectly because of its effects on other traits correlated with fitness? and (3) What is the relative magnitude of direct and indirect effects of damage on fitness? In contrast to patterns that might be predicted from studies of early and late season damage to mature tissue (Maschinski and Whitham 1989; Lennartsson et al. 1998), I find that damage to cotyledons has significant, deleterious effects on fitness, while damage to mature tissue has negligible effects.

Materials and methods

Natural history and study system

The ivyleaf morning glory, *Ipomoea hederacea* (L.) Jacquin (Convolvulaceae), is a twining annual vine common to agricultural fields and roadsides in the southeastern United States. Seeds typically germinate in early June or July when soil is disturbed (e.g., by plowing or other agricultural activities). Plants begin flowering 4–6 weeks after germination, and seeds mature approximately 4 weeks later. Though visited by bumblebees, the selfing rate has been estimated at 93% (Ennos 1981).

A taxonomically diverse natural enemy fauna, including insect, mammalian, and fungal enemies, attacks *I. hederacea* (Bright 1998; Stinchcombe 2001). Insect herbivores commonly include grasshoppers (Orthoptera: Acrididae), fleahoppers (Hemiptera: Miridae), and lepidopteran larvae; mammalian herbivores such as deer (*Odocoileus virginianus*) also impose severe damage (Stinchcombe 2001). A white rust [*Albugo ipomoeae-panduranae* (Oomycetes: Peronosporales: Albuginaceae)] and an orange rust [*Coleosporium ipomoea* (Uredinales: Coleosporaceae)] are also commonly found on the underside of plant leaves (Bright 1998). Natural damage during the experiment reported here was limited to insect herbivores and fungal pathogens.

Experimental design

Experimental seeds were produced by letting parents from 20 inbred lines self-fertilize, thereby mimicking the natural mating system of *I. hederacea*. Before planting, seeds were nicked with a razor blade to facilitate germination. Experimental seeds were planted on 17 July 1999 into a recently plowed field in the Duke University Botany Research Plot. A large fence around this research site fully excludes deer from experimental populations. A total of 600 seeds, drawn in equal numbers from the 20 inbred lines, were planted in five spatial blocks. Rows and columns of plants were spaced 1 m apart; each plant that germinated was given a 2 m wooden garden stake to twine around.

Germination success was measured 4 days after planting. During the survey of germination success, I measured insect damage to cotyledons using the following categorical scale: 0% damage, 1–25% damage, 26–50% damage, 51–75% damage, 76–100% damage; for analysis, I assigned the last four categories the midpoint percentage values (e.g., 0.13, 0.38, 0.63, 0.88). White and orange rust damage were not observed on cotyledons and were first observed on mature leaves at 3 weeks; flowering commenced at 4 weeks.

Here I am primarily interested in comparing the fitness effects of damage to cotyledons and damage to mature leaves; however, few plants in natural populations escape damage by mammalian herbivores, and mammalian herbivory might alter the fitness effects of insect or pathogen damage to cotyledons and mature leaves. Therefore, to mimic patterns of mammalian herbivore damage, I removed with scissors 30% of the leaves on half of the plants to simulate natural levels of deer damage (Stinchcombe 2001). Prior to clipping, I recorded the total number of leaves on all plants in the clipping treatment to ensure that the correct number of leaves was removed. This treatment was imposed approximately 5 weeks after germination; leaf removal was evenly distributed across the height of the plant. On control plants, I handled, but did not cut, approximately 30% of the leaves.

Seven weeks after emergence, and prior to leaf senescence, I measured damage on all plants. To do this, I chose four leaves ("focal leaves") that were evenly spaced along the height of the plant. To measure damage, I placed a clear plastic grid over the four focal leaves, measured leaf length, the amount of leaf area missing due to insect herbivore damage, and the amount of leaf area covered by each pathogen. Percent leaf area missing was used as a measure of insect damage, and percent leaf area covered by spores used as a measure of pathogen damage. As the median number of leaves per plant at the time of the damage survey in this experiment was 18, this sampling procedure typically resulted in detailed measurements of slightly more than 20% of the leaves per plant. Although this procedure does not provide detailed information on the spatial and temporal patterns of herbivore damage, it provides a "whole-plant" average for damage to mature leaf tissue. I converted leaf length to leaf area with the use of a regression equation, and then multiplied the average leaf area of the four focal leaves by the total number of leaves on the plant to calculate

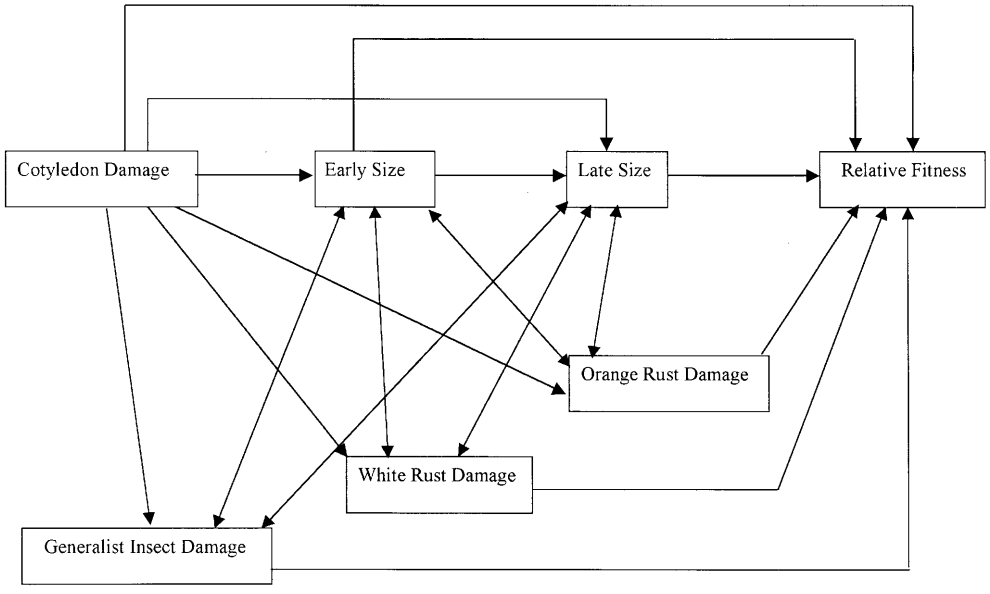

Fig. 1 Path diagram representing the hypothesized causal relationships between early damage, plant size, late-season damage by natural enemies, and relative fitness

total leaf area. Estimates of total leaf area calculated from this sampling procedure are highly correlated with estimates calculated from counts of every leaf (r=0.96; Stinchcombe 2001).

Leaf senescence and seed set began at 8 weeks, and a killing-frost ended the experiment in the 2nd week of November. Seeds were collected on a daily basis. Individuals that survived to the damage survey but set no seeds were assigned a fitness value of zero. I calculated relative fitness by dividing total viable seed set of each plant by the mean viable seed set of all plants. Viability was assessed according to criteria described in Stinchcombe and Rausher (2001).

Statistical methods

Analysis of genetic variation for susceptibility to damage

For categorical variables such as cotyledon damage, I evaluated whether families differed in the proportion of individuals in each damage category with a likelihood ratio test (FREQ procedure, SAS 1990). A significant likelihood ratio test indicates that the distribution of individuals in the different cotyledon damage categories differed by inbred line, indicating genetic variation for susceptibility to damage. Because likelihood ratio tests may not be valid when the expected value for a cell in a chi-square table is less than 5 (Zar 1999), I also performed these analyses on data in which damage was pooled into 0%, 1–50%, and 51–100% categories.

For continuous response variables such as damage by insect herbivores or fungal pathogens, I used ANCOVA to assess whether genetic variation for susceptibility to damage existed. In these analyses block, inbred line, clipping treatment, inbred line × block, and the inbred line × clipping treatment interaction were included as independent variables. In these analyses, a significant inbred line, inbred line × clipping, or inbred line × block interaction indicates the presence of significant genetic variation for how much damage plants suffered – either in the experiment as a whole, one of the clipping treatments, or some of the spatial blocks. Preliminary analyses indicated that inclusion of other damage terms as covariates in these analyses altered neither the pattern nor significance of these results.

Effects of the clipping treatment

To assess the consequences of removing 30% of mature leaves on insect herbivore damage, orange rust damage, and white rust damage, I evaluated the significance of the clipping and inbred line×clipping interaction terms in the models described above. For response variables such as fitness and total leaf area, I considered the significance of the clipping treatment and inbred line × clipping treatment interaction in two additional models that also contained block effects.

Structural equation modeling

I used structural equation modeling (SEM) to examine the direct and indirect effects of damage on fitness. SEM is a generalized approach to path analysis (Kingsolver and Schemske 1991; Mitchell 1992). I chose SEM instead of multiple regression and ANCOVA because of its ability to accommodate complex networks of causal relationships between variables (Scheiner et al. 2000). Given an a priori hypothesis of the causal relationships and correlations between variables, SEM calculates partial regression coefficients that describe the effects of one variable on another in standard deviation units, while holding all other variables constant. By comparing the observed correlations between variables to the correlations that would be expected according to the specified model, SEM assesses the goodness of fit of a given model. The difference between the expected and observed correlations between variables is expressed as a χ^2 statistic (Mitchell 1992). A significant χ^2 statistic indicates a poorly fitting model – the observed correlations between variables are significantly different from the correlation structure specified by the model. Provided they are nested, competing models can be tested: the difference between the χ^2 statistics of different models is also χ^2 distributed, with degrees of freedom equal to the difference between the degrees of freedom in the two models (Mitchell 1992). If the models are significantly different, the model that provides a better fit to the data is preferred; if the models are not significantly different, the simplest model is preferred on the basis of parsimony.

The a priori model I evaluated is portrayed in Fig. 1; in this figure paths between variables with single arrow-heads indicate hypothesized causal relationships between variables; paths with double arrow-heads indicate correlations between variables without a hypothesized causal relationship. The model describes several possible characteristics of plant-herbivore interactions. In particular, damage by one natural enemy can increase or decrease the amount of damage caused by subsequent natural enemies (Karban and Baldwin 1997). Furthermore, natural enemy damage and plant size are potentially correlated, either because damage reduces plant size or because natural enemies prefer larger plants (e.g.,

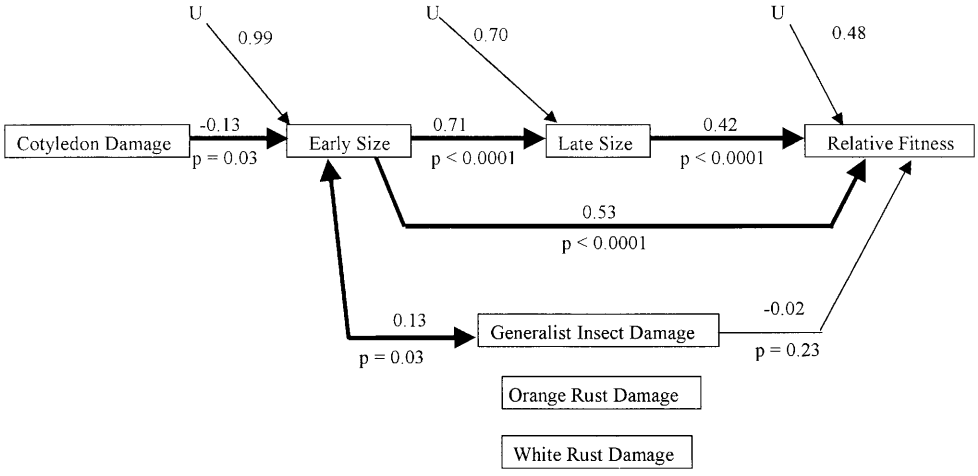

Fig. 2 Most parsimonious path diagram representing the relationships between cotyledon damage, plant size, generalist insect damage, and relative fitness. Significant paths are shown by the *bold arrows*; estimated path coefficients are presented above the *arrow* and *P*-values below the *arrow*. Indirect and total effects of natural enemy damage on fitness were calculated according to standard methods (see text). The variable *U* represents unexplained influences on the measured variables, and was calculated as the square-root of ($1–R^2$); *U* could not be estimated for Generalist Insect Damage because there are no causal paths leading to this variable

Type of Damage	Direct Fitness Effect	Indirect Fitness Effect	Total Fitness Effect
Cotyledon Insect	0	-0.11	-0.11
Mature-leaf Insect	-0.02	0	-0.02
Mature-leaf Orange Rust	0	0	0
Mature-leaf White Rust	0	0	0

Price 1991). Finally, natural enemy damage can affect fitness directly, or indirectly through its effects on other correlated traits (see below).

I evaluated this model for the clipping treatment only for two reasons. First, prior to the implementation of the clipping treatment I recorded the total number of leaves, providing an estimate of early plant size. These data were not available for the control treatment, thus precluding attempts to fit the same initial model to both treatments. Second, I evaluated multiple models in which I substituted a proxy for early size for each individual (e.g., block or inbred line means for early size), but all of these models produced a poor fit to the data when applied to the control treatment. Although it would be ideal to fit the model described by Fig. 1 to both treatments, it is likely that the clipped treatment is a representative sample of the experimental population as a whole. As the clipping treatment was imposed on a random sample on half the plants in each inbred line, it represents an unbiased sample of all of the experimental plants. In addition, as described below, the clipping treatment had no effect on any of the variables measured during the experiment and included in the path model, suggesting that differences between experimental treatments in the most parsimonious path model are unlikely.

I performed the SEM with the maximum likelihood estimation option of the CALIS procedure of SAS (SAS 1990). I compared the full model portrayed in Fig. 1 to a series of alternative models in which a greater number of path coefficients were constrained to equal zero. I repeated this procedure in an iterative fashion until I arrived at the most parsimonious model that could be used to estimate direct and indirect effects of damage. I calculated indirect effects of damage on fitness by multiplying the intervening path coefficients. Total effects of damage on fitness were calculated as the sum of direct and indirect effects.

Although this procedure defines direct and indirect effects statistically, one could argue that because no damage to reproductive tissues was observed, all effects are "indirect" in a biological sense. To alleviate this potential confusion, I use the term "direct effect" to describe situations where natural enemy damage is negatively or positively related to fitness, presumably because some aspect of damage affects the plant's ability to produce flowers, viable ovules or pollen, or to mature seeds. I use the term "indirect effect" to describe situations where natural enemy damage alters some other aspect of the plant (e.g., size), that itself affects the plant's ability to produce flowers, viable ovules or pollen, or to mature seeds.

Results

Genetic variation for susceptibility to damage

The experimental population exhibited marginally significant genetic variation for susceptibility to cotyledon damage in the experiment (χ^2=92.54. *df*=76, *P*=0.096). These results do not appear to be artifacts of small expected values for cells in the chi-square table analysis of the pooled data also suggested that genetic variation for susceptibility to cotyledon damage existed (χ^2=58.04, *df*=38, *P*=0.020).

In contrast, there was no significant genetic variation for susceptibility to mature-leaf insect damage, or either form of fungal damage in the experimental population (*F*<1.32, *P*>0.12 for inbred line, inbred line × block, and inbred line × clipping interactions).

Effects of clipping treatment

The clipping treatment had no detectable effects on any of the response variables measured (*F*<1.46, *P*>0.23 for all clipping and inbred line × clipping interactions). Based upon these data, it appears that the clipping treatment did not affect insect herbivore, white rust, or or-

ange rust damage to mature leaves, or total size or relative fitness. Therefore, it is likely that the path model fitted to the clipping treatment (see below) is representative of the experimental population as a whole.

Structural equation modeling

The basic model (Fig. 1) provided a good fit to the data (χ^2=1.45, *df*=3, *P*=0.69), but 13 of the 18 path coefficients were not significantly different from zero. The most parsimonious model that provides a good fit to the data is presented in Fig. 2 (χ^2=11.99, *df*=9, *P*=0.21). Although the reduced model does not appear to fit the data as well as the full model (i.e., the χ^2 value is higher and the *P*-value lower), this is probably because the reduced model has appreciably fewer parameters. Indeed, the Akaike Information Criterion is lower for the reduced model than for the full model (–6.01 versus 4.54 for the full model), indicating that the reduced model fits the data better after adjusting the model likelihood for differences in the number of parameters (Hilborn and Mangel 1997).

In contrast to the full model, five of the six estimated paths in the most parsimonious model are significantly different from zero. Removing the remaining non-significant path from generalist insect damage to fitness reduces model fit (though not significantly), and would preclude estimating the indirect effects of early damage on fitness through its subsequent effects on early size and generalist insect damage.

Cotyledon damage by insect herbivores does not directly affect fitness, but has potentially large consequences for fitness through its effects on other, intervening traits. In general, cotyledon damage had the effect of reducing early size; early size, in turn, was positively correlated with fitness and late size. Late size was also positively correlated with fitness. Cotyledon damage by herbivores also had a weak, but positive indirect effect on relative fitness through its intervening effects on generalist insect damage to mature leaves: cotyledon damage reduced early plant size, early plant size increased the susceptibility to generalist insect damage, and generalist insect damage decreased relative fitness.

In contrast to the results for cotyledon damage, mature-leaf damage by insect herbivores and fungal pathogens has negligible consequences on plant fitness, either directly or indirectly. The direct effects, indirect effects, and total effects of herbivore damage on relative fitness are presented in Fig. 2.

Discussion

Previous investigations have documented that plant interactions with natural enemies differ earlier and later in the season, and between juvenile and adult phases of a plant's life cycle. For example, plant resistance to herbivore and pathogen damage, herbivore performance, the population dynamics and abundance of herbivores, and the species richness of the herbivore community have all been shown to differ between juvenile and adult phases (Leonard and Thompson 1976; Zagory and Libby 1985; Price et al. 1987; Kearsley and Whitham 1989; Waltz and Whitham 1997; Karban and Thaler 1999). These studies, however, have often failed to measure relative fitness of the plants (though see Maschinski and Whitham 1989; Lennartsson et al. 1998; Tiffin 2002). It has therefore been difficult to understand the evolutionary consequences of these temporal and developmental changes in plant-natural enemy interactions.

The data presented here suggest that *I. hederacea* is able to completely compensate for both artificial damage and natural herbivore and pathogen damage to mature leaves, but is unable to compensate for damage during the juvenile phase to cotyledons. These results stand in contrast to the findings of Maschinski and Whitham (1989) and Lennartsson et al. (1998) on early and late season damage to vegetative tissues. One possible explanation for this discrepancy is that these investigations examined damage to apical meristems rather than to cotyledons, and that damage early versus late in the season to the apical meristem of *I. hederacea* would have produced effects similar to those described by Maschinski and Whitham (1989) and Lennartsson et al. (1998). An alternative explanation is that the discrepancy between these contrasting results is not due to the different tissues attacked, but is instead related to the different patterns of growth and plant architecture between these systems. For example, unlike *Ipomopsis* and *Gentianella*, *Ipomoea hederacea* does not form a basal rosette, and it is common for secondary meristems to be activated and support flowers even in the absence of damage to the apical meristem. Clearly differentiating between these possibilities will require further experimental work, but at minimum they suggest that the patterns of early and late season damage described by Maschinski and Whitham (1989) and Lennartsson et al. (1998) may not apply to all systems or tissue types.

For *I. hederacea*, these results suggest that selection should favor either increased resistance to damage early in the season (juvenile resistance) or increased compensatory growth following damage. For example, avoidance of cotyledon damage would reduce its negative consequences on plant size traits that are positively related to fitness. The presence of genetic variation for susceptibility to cotyledon damage also indicates that it is likely that there would be a response to selection on traits such as resistance that minimize the susceptibility of plants to cotyledon damage. In like fashion, genotypes that are better able to minimize the effects of damage on early plant size (i.e., exhibit compensatory growth) should also be favored by selection. Though these data clearly indicate that damage by herbivores early in the life cycle can have appreciable fitness effects, they do not illustrate why reduced plant size is deleterious for fitness. Several potential mechanisms could explain these data. One is that reduced size might put individuals at a

competitive disadvantage with larger, neighboring inter- or intra-specific competitors. If the competition hypothesis holds for the present experiment, it is likely to be due to interspecific competition, because experimental plants were relatively well-spaced (1 m) compared to natural populations (personal observation) and by the end of the growing season the area between experimental plants had been extensively covered by colonizing vegetation.

Alternatively, reduced photosynthetic area might reduce the number of flowers produced, or the ability of plants to mature seeds, or delay the onset of reproduction. In *I. hederacea*, a delayed onset in reproduction appears to be one of the likely mechanisms, as suggested by two studies of the closely related congener *I. purpurea*. When artificially damaged at the cotyledon stage in the greenhouse, individuals of this species showed both reduced plant size and increased time to first flower (J.M. Kniskern, unpublished data). Furthermore, natural damage to cotyledons of *I. purpurea* grown in the field is associated with increased time to flowering (P. Tiffin, unpublished data).

The effects of early damage on fitness, as mediated by plant size or time to flowering, are likely to vary greatly from year to year as determined by the length of the growing season. For example, if the growing season had been longer, previously damaged plants might have been able to achieve equal size and set enough seeds to reduce or eliminate the negative effects of early-season damage and its attendant reduction in early plant size, especially if undamaged plants were phenologically more advanced and had begun to senesce. Though the killing frost that ended my experiment occurred approximately a week after the average for this area of N.C. (Perry 1996), in past years the growing season at this field site has lasted for an additional 4 weeks (personal observation), so these scenarios are not unreasonable. In contrast, if the growing season had been significantly shorter, it is likely that the direct and indirect effects of cotyledon damage on plant size would have been greater, and thus the fitness costs of damage early in life and early plant size would have been more pronounced.

A major caveat applies to these results. Path analyses are often based upon phenotypic data and as such are potentially prone to bias due to environmental covariances between traits and fitness (Rausher 1992; Mauricio and Mojonnier 1997; Stinchcombe et al. unpublished manuscript). In many cases this potential problem can be eliminated by replacing phenotypic measurements of traits with estimates of family means or estimates of breeding values for those traits, which yields unbiased estimates of the pattern of natural selection. As path analysis is extremely sensitive to small sample sizes, using family means would require a large number of families – ideally, 10 times as many families as there are paths to be estimated (Mitchell 1993; Kline 1998). As such, the results presented here should be viewed mainly as hypotheses that need subsequent evaluation with genotypic means or breeding values analysis. Nevertheless, as described above, the path analysis portrayed in Fig. 2 suggests two potentially important traits for such a genotypic path analysis or selection analysis: resistance to juvenile damage and compensatory growth ability once damaged as juvenile plant.

Acknowledgements I thank J.L. Stone and B. Calhoun for help in securing a field site. L.C. Moyle, J. Thaler, P. Tiffin, I. Baldwin, and two anonymous reviewers made numerous helpful comments on a previous version of the manuscript. Discussions with M.T. Rutter and R.A. Zufall were also especially helpful, and J. Kniskern and P. Tiffin kindly allowed me to cite unpublished data. I gratefully acknowledge the financial support of Sigma Xi, the Society for Integrative and Comparative Biology, and the Harry S. Truman Scholarship foundation.

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