

ABSTRACT

Title of Dissertation / Thesis: HOST PLANT-MEDIATED INTERSPECIFIC
 COMPETITION VIA INDUCED
 RESISTANCE: INTERACTIONS BETWEEN
 THE POTATO LEAFHOPPER AND THE
 COLORADO POTATO BEETLE

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Interspecific competition has seen a renaissance over the last several decades and has become recognized as an important force influencing the structure of phytophagous insect communities. This research examined interspecific competition, mediated through a shared host plant, between the potato leafhopper (PLH) and the Colorado potato beetle (CPB), two important pests on potatoes. In Maryland, PLH colonize fields in advance of CPB due to management practices and differences in the migration behavior of these two herbivores. Results show that previous feeding by PLH adversely affected oviposition preference and larval performance of CPB in both greenhouse and field-cage experiments. Results suggest

that these two herbivores compete through feeding-induced changes in plant physiology or morphology. This research has important implications for the management of agricultural pests such that higher densities of PLH should be tolerated before controls are instigated due to the benefits of CPB reduction that accrue via leafhopper-induced plant resistance.

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RESISTANCE: INTERACTIONS BETWEEN THE POTATO LEAFHOPPER AND
THE COLORADO POTATO BEETLE

By

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INTRODUCTION

Interspecific competition as a force shaping the structure of phytophagous insect communities has experienced a controversial history to say the least (Strong et al. 1984; Damman 1993; Denno et al. 1995). Classical competition theory from the 1960's and 70's was based largely on observational data and suggested that resources were limiting and that two species could co-exist only if they occupied different niches and therefore utilized different resources (McClure and Price 1976; Rathcke 1976; Waloff 1979). Thus, if two species were observed exploiting different habitats or micro-habitats, then interspecific competition was assumed to be the process driving this divergence.

Throughout the next decade, however, classical competition theory was harshly challenged (Lawton and Strong 1981; Lawton 1982; Lawton and Hassell 1984; Strong et al. 1984). Alternative theory emerged suggesting that resources were not limiting and that top-down forces such as predators and parasitoids had a greater influence in determining the distribution and abundance of herbivorous insects (Hairston et al. 1960; Strong 1982). Although this view was also based largely on observational data, it did gain the attention of ecologists in that it identified the need for a more experimental approach to tease apart the importance of multiple factors, including competition, on community structure.

As a consequence, many experimental studies over the last two decades have examined the role of top-down, bottom-up, and lateral forces such as competition, in

structuring insect communities (Karban 1989; Hunter and Price 1992; Forkner and Hunter 2000; Denno et al. 2002, 2003). The result has been a growing body of evidence suggesting that all of these forces act collectively on insect herbivores and a return to the view that interspecific competition can be an important factor contributing to the structure of phytophagous insect communities (Stiling and Strong 1984; Karban 1986; Faeth 1987; Damman 1993; Weeks and Hoffmann 2000, Denno et al. 2000). Notably, a relatively recent review of published experimental studies (Denno et al. 1995) found widespread evidence for interspecific competition among insect herbivores, particularly in species interactions involving herbivores with sucking/piercing mouthparts. In addition, competition was found less often in free-living mandibulate herbivores (chewing insects). However, when interspecific competition did occur between mandibulate herbivores, it occurred indirectly (67% of cases) and was mediated through host plant-related factors. These findings are consistent with the growing appreciation of the importance of indirect effects in species interactions and food web dynamics (Faeth 1992; Wise and Weinberg 2002; Ohgushi 2005).

Host plant-related factors that mediate interspecific competition between insect herbivores include induced resistance (immediate or delayed), host-plant phenology and host-plant dispersion (Denno et al. 1995). Although each of these factors can be important, induced resistance is gaining attention and emerging as an important mechanism mediating herbivore interactions in numerous systems (Karban and Baldwin 1997; Agrawal et al. 1999; Denno et al. 2000; Denno and Kaplan in press). Induced resistance results when herbivore damage produces changes in the host plant that diminish subsequent herbivore attack, either by reducing the preference for or

performance of other herbivores on the induced plant (Karban and Myers 1989; Agrawal 1999). Resistance can result from feeding-induced changes in plant nutrition (McClure 1980; Denno et al. 2000), morphology (Agrawal 1999), allelochemistry (Levin 1976; Faeth 1986; Rausher, Iwao et al. 1993; Agrawal 1998; Agrawal 1999) or a combination of such changes that have negative consequences for other herbivores (Karban and Baldwin 1997; Agrawal 1998; Agrawal 1999; Agrawal et al. 1999).

Depending on the plant and herbivore species involved, induced resistance can be local or systemic (occur throughout the plant), it may arise rapidly or with significant delay, and it may decay either quickly or quite slowly whereby resistance persists for several herbivore generations (Karban and Baldwin 1997; Agrawal et al. 1999; Denno and Kaplan in press). Thus, induced resistance allows for “interspecific competition” to occur indirectly between herbivore species that are spatially and/or temporally separated on the same host plant (McClure 1980; Faeth 1986; Tomlin and Sears 1992b; Inbar et al. 1995; Denno et al. 2000; Wise and Weinberg 2002; Denno and Kaplan in press). Moreover, this evidence certainly challenges the historical paradigm that resource partitioning diminishes the intensity of interspecific competition (Denno and Kaplan in press).

Besides its contribution to the re-emergence of interspecific competition as an important force influencing the dynamics of herbivore populations, the effects of induced resistance are being realized at the community level whereby the effects of previous feeding by an early-season herbivore can cascade to affect the structure of the entire herbivore assemblage (Denno and Kaplan in press; Van Zandt and Agrawal 2004). In

addition, herbivore-induced changes in a shared host plant can affect higher trophic levels and thus affect web-dynamics at large (Ohgushi 2005; Denno and Kaplan in press).

Induced resistance may also have important implications in agriculture where it becomes critical to elucidate factors influencing the density of pest herbivores and thus in the development of Integrated Pest Management programs (Thaler 1999, 2002). The prevalence of insecticide resistance, and the concern over excessive use of pesticides in the environment, demand a better understanding of pest dynamics in agricultural systems (Noronha et al. 2001; Matsumura 2004). One of the most notable cases of insecticide resistance has occurred with the Colorado potato beetle (Forgash 1985), a major pest of potatoes throughout North America (Ferro 1985; Forgash 1985; Hare 1990; Roush et al. 1990; Weber and Ferro 1994). Because potato is among the most important crops in the Northeast region of the United States (USDA 1999), and because it is susceptible to several species of insect pests that feed at different times through the growing season (USDA 2002), this system provides an ideal opportunity to explore the consequences of induced resistance and plant-mediated competition between insect herbivores on the same shared host plant. Moreover, leaf damage in potatoes and related plants in the Solanaceae family results in the induction of proteinase inhibitors (Green and Ryan 1972), glycoalkaloids (Hlywka, Stephenson et al. 1994), amino acids (Tomlin and Sears 1992a) and polyphenol oxidase (Thaler 1999), all compounds with known anti-herbivore effects (Karban and Baldwin 1997; Constabel 1999). Thus, the mechanistic underpinnings for induced resistance occur in the potato system as well.

The two major pests of potatoes in Maryland, the potato leafhopper (*Empoasca fabae*: Hemiptera: Cicadellidae) and the Colorado potato beetle (*Leptinotarsa*

decemlineata: Coleoptera: Chrysomelidae), are temporally separated in potatoes due to their differing overwintering habits, crop colonization phenologies, and current control methods (Dively et al. 1999a). As a result, in some fields, the potato leafhopper migrates into potato fields early in the season whereas the Colorado potato beetle colonizes later, after plants have been previously damaged by potato leafhopper. Using a combination of greenhouse and field-cage experiments, I tested for the possibility of delayed, plant-mediated competition between these two pests such that previous feeding by leafhoppers induces physiological or morphological changes in plants that have adverse effects on the performance of Colorado potato beetles. My objectives were to determine if previous feeding on potato plants by potato leafhoppers had adverse consequences for Colorado potato beetles resulting in (1) reduced oviposition preference for damaged foliage and (2) decreased larval performance (development time, body weight and enhanced larval mortality) on damaged foliage. Although there is a growing body of literature demonstrating that plant-mediated competition can occur between temporally and spatially separated herbivores, only a handful of studies have tested for interspecific competition between insects in two distinct feeding guilds (e.g., sap-feeders and mandibulate herbivores), and no clear pattern has emerged (Denno et al. 1995; Van Zandt and Agrawal 2004). Toward filling this void, this study aims to enhance our understanding of plant-mediated interspecific competition between insect herbivores in different feeding guilds.

STUDY SYSTEM

Potato is the most important agricultural crop in the Northeast region of the United States where over 163,900 acres are grown annually with a gross value of \$295

million (USDA 1999). In Maryland, acreage has grown significantly over the last several years and potatoes are becoming an increasingly important crop. A majority of the production is located on the Eastern Shore where potatoes are grown for both the fresh market and processing (USDA 2002). The Colorado potato beetle has been a significant pest of potatoes throughout the Northeast region of the U.S, including Maryland (Dively et al. 1995; USDA 2002). However, current management practices, which include the use of a systemic insecticide at planting, have resulted in increases of a second pest, the potato leafhopper (Dively et al. 1999a).

The potato leafhopper (*Empoasca fabae*) is a pest in Maryland and the United States where it attacks a wide range of crops and wild plants including several agriculturally important crops such as potato, alfalfa, beans, and soybeans (USDA 2002). Potato leafhopper cannot overwinter in the northern U.S. and migrates up from the south, colonizing potatoes in late May or early June in Maryland (Dively 1986; Lamp et al. 1994). Both adults and nymphs of the potato leafhopper feed on the vascular tissue of the leaves and stems of plants (Walgenbach and Wyman 1985; Ferro 1986; Lamp et al. 1994). With its piercing-sucking mouthparts, it taps into the plant tissue and injects saliva while feeding that causes abnormal cell growth and blocks the transport of phloem sap in the leaf tissue. Symptoms do not appear immediately, but within two weeks plants begin to show signs of “hopper burn” which is characterized by leaf curling, chlorosis, and ultimately necrosis of the leaves (Lamp et al. 1994; Walgenbach and Wyman 1985; Ferro 1986).

The Colorado potato beetle (*Leptinotarsa decemlineata*) is a major pest of potatoes in the U.S. where it can cause severe defoliation (Weber and Ferro 1994; Ferro

1985) leading to potential yield loss. Moreover, it also attacks other solanaceous crops including tomato and eggplant (USDA 1999a). Eggs are deposited on the undersides of foliage and both larvae and adults are voracious defoliators (USDA 2002). Larvae pass through 4 larval instars and a prepupal stage before pupating in the soil (Jacques 1988). Colorado potato beetles have 2 full generations and a partial third per growing season in Maryland, overwinter locally as adults and become active from late April through May (USDA 2002). Contemporary management practices involve the application of a systemic insecticide to the soil at the time potato seed is planted in early March to early April, precluding the first generation of beetles from inflicting significant damage (USDA 2002; Dively et al. 1999a). However, by the time the second generation of beetles emerges in late June-early July, potatoes are no longer protected from the systemic insecticide, and this generation effectively colonizes fields where it can inflict severe damage (USDA 2002; Dively et al. 1999a).

The contemporary use of an early-season systemic insecticide for control has altered herbivore dynamics observed in some Maryland potato fields (USDA 2002; Dively et al. 1999a). Where Colorado potato beetles once colonized fields along with potato leafhoppers, this new soil-treatment approach has resulted in the temporal separation of the two pests whereby potato leafhoppers migrate into fields and begin feeding well before colonization by Colorado potato beetle (USDA 2002; Dively et al. 1999a). Thus, this system provided an ideal opportunity to test for plant-mediated competition between two economically important pests of potato.

METHODS

Study site

This study was conducted over the summers of 2001 and 2002, in both greenhouse and field settings. Greenhouse facilities were located at the University of Maryland, College Park, Maryland. Field experiments were conducted in potato fields on the University of Maryland Farm, Beltsville, Maryland.

Establishing leafhopper-damaged treatment plants

To assess the effects of previous feeding by potato leafhoppers on the oviposition preference and performance of Colorado potato beetles, plants experiencing four levels of damage caused by leafhopper feeding (none, low, medium and high) were established in the summer of 2001 at the field site in Beltsville. In mid May, 512 tuber seed pieces (*Solanum tuberosum* Kennebec variety) were planted in individual pots in standard potting medium, and allowed to grow in the greenhouse until above ground foliage was observed. Potted plants were then transferred to 3.66 m (12 feet) x 3.66 m (12 feet) x 1.83 m (6 feet) frame field cages covered with saran screening (1.3 mm mesh). To establish the four leafhopper damage treatments, groups of 64 potted potato plants were placed into each of eight cages (two cages per damage level) in early June. Plants were allowed to grow in the field cages for one month before the leafhoppers were introduced in early July. Potato leafhoppers (adults and nymphs) were collected in nearby fields using a D-vac suction sampler (Dvac Co., Ventura, CA) and released into the cages at pre-established densities. Treatments were created by releasing leafhoppers into cages at one of four densities (0, 3, 10, and 20 adult leafhoppers per plant), densities spanning the range that occurs naturally in the potato fields (Dively et al. 1999b). Cages were

monitored and leafhoppers were replaced to maintain desired densities for each treatment level. Leafhoppers were allowed to feed for 2 weeks, at which time visual signs of feeding damage were observed. To verify that leafhopper density treatments resulted in differences in leafhopper feeding damage, all plants were removed from cages following exposure to leafhoppers and 20 plants from each of the four density treatments were scored for feeding damage by quantifying leaf curling (%) and leaf necrosis (%) (Dively et al. 1999b). To verify the persistence of the four leafhopper-density treatments, the number of potato leafhopper nymphs per plant was also censused on 20 plants per treatment at the end of the two-week exposure period. The effect of leafhopper feeding at various densities (0, 3, 10, and 20 adult leafhoppers per plant) on leaf curling (%), leaf necrosis (%), and the number of remaining potato leafhopper nymphs were assessed using ANOVA followed by LSD means comparisons (SAS 2001). Based on these data, plants from each of these four leafhopper density levels (0, 3, 10, and 20 adult potato leafhoppers per plant) were then assigned to one of four potato leafhopper damage levels (none, low, medium, and high).

Effect of potato leafhopper feeding on Colorado potato beetle oviposition preference

To determine the effect of previous feeding by potato leafhoppers on the oviposition preference of Colorado potato beetles in the field, five blocks of 16 plants (four from each leafhopper damage level: none, low, medium, and high) were transplanted into the ground in a latin square design at the Beltsville Farm. Within each block, plants were separated by 0.91 meters (3 feet). Saran screen field cages 3.66 m (12 feet) x 3.66 m (12 feet) x 1.83 m (6 feet) were then erected over each block of 16 plants. Thus, there were five blocks with four treatments per block and four replicates per block

of each damage treatment. Sixteen pairs of field-collected Colorado potato beetles were released into each cage (one pair per plant) on 25 July 2001. Beetles were allowed to settle for several days after which time eggs were visually censused on 4 and 8 August 2001 (peak oviposition period) by counting the number of egg masses on each plant. Treatment means were compared on each date using ANOVA followed by LSD means comparisons (SAS 2001).

Effect of potato leafhopper feeding on Colorado potato beetle performance; development time, adult weight and survival

To determine the effect of leafhopper feeding on Colorado potato beetle development time, adult body weight, and survival, both greenhouse and field experiments were conducted. In the summer of 2001, leafhopper-damaged plants were established as described above, and 20 plants from each of the four damage levels were moved into the greenhouse. Four plants from each of the four damage levels were randomly assigned to each of five greenhouse benches (16 plants per bench). One cohort of 15 one-day-old, first-instar Colorado potato beetle larvae (obtained from field-collected eggs at Beltsville) was caged on each plant in an organdy mesh bag on 24 July 2001. Every other day, all sleeve cages were opened to record the developmental stage (instar) for all larvae in each cohort. This procedure was followed until all larvae reached the prepupal stage, at which time prepupae were removed from cages, counted, and then placed in buckets of soil for pupation. After emergence, the weight of all adults was determined. Average development time (days from first instar to second, third and fourth instars and prepupa), larval survival to prepupal stage (proportion of larvae surviving from first instar to prepupal stage), and adult wet weight (g) was determined for each

cohort and treatment means were compared using ANOVA followed by LSD means comparisons (SAS 2001). Data were log-transformed as needed to meet assumptions of normality and homogeneity of variances.

The effects of previous feeding by leafhoppers on the performance of Colorado potato beetles (development time, survival to adult, and adult body weight) was also determined in the field during the summer of 2002 at the Beltsville Farm. Potatoes for this experiment were planted at our field site on 24 April 2002. Plants were grown until above ground foliage was observed. At this time field cages (3.66 m (12 feet) x 3.66 m (12 feet) x 1.83 m (6 feet) frame cages covered with saran screening) were erected over 20 groups of 30 plants, each cage containing 3 rows of 10 plants. Leafhopper damage treatments (none, low, medium, and high) were established by releasing field-collected leafhoppers (adults and nymphs) between 13-18 June into each cage at one of four densities (0, 3, 10, and 20 adult leafhoppers per plant). Five replicates of each treatment were established for a total of 20 field cages. Leafhoppers were allowed to feed on caged plants for two weeks until damage symptoms appeared at which time (28 June -5 July) one cohort of 20 first-instar Colorado potato beetle was placed onto each caged plant. Thereafter, each cage was entered every other day and the larval instar of 30 randomly selected larvae was determined visually. This procedure was followed for 3 weeks until larvae pupated and most adults had emerged, at which point adults were returned to the lab and weighed. To estimate larval survival, all larvae on the center row of plants in each cage were visually censused on 9-16 July (day 11). Treatment effects on development time (days from first instar to second, third, and fourth instar), larval survival (number of larvae per row), and adult body weight (wet weight in g) were

assessed using ANOVA and means were compared using PROC MIXED procedures in SAS (SAS 2001). In addition, pre-planned comparisons in development time from first to second, third, and fourth instar (days) and adult body weight were made between the no leafhopper-feeding treatment and the pooled combination of all leafhopper-feeding treatments (low, medium, and high) using t-tests. Data from the summer of 2002 was not log transformed as all data met assumptions of normality and homogeneity of variances.

RESULTS

Establishing leafhopper-damaged treatment plants

There was a significant effect of the leafhopper density/feeding treatments (0, 3, 10 and 20 adult potato leafhoppers per plant) on damage to potato plants (Table 1.1). Specifically, the percentage of cupped leaves ($F_{3,76}=791.64, p<0.0001$) and necrotic leaves ($F_{3,76}=36.0, p<0.0001$) increased with an increase in leafhopper density. Moreover, there was a significant effect of treatment on the number of leafhopper nymphs remaining at the end of the exposure period ($F_{3,76}=172.10, p<0.0001$; Table 1.1), verifying the persistence of the four leafhopper density treatments. Based on these data confirming the treatment effects, plants from each of the four leafhopper density levels (0, 3, 10, and 20 adult potato leafhoppers per plant) were then assigned to potato leafhopper damage treatment levels none, low, medium, and high, respectively (Table 1.2).

Effect of potato leafhopper feeding on Colorado potato beetle oviposition preference

When given a choice, female Colorado potato beetles deposited at least twice as many egg masses on plants that incurred no to medium levels of leafhopper feeding damage as they did on highly damaged plants. This pattern prevailed when oviposition preference was assessed in field cages on both 4 August ($F_{3,76} = 5.94, p = 0.0011$; Figure 1.1) and 8 August 2001 ($F_{3,76} = 4.10, p = 0.0094$; Figure 1.2).

Effect of potato leafhopper feeding on Colorado potato beetle development time, adult weight and survival

In the greenhouse study, Colorado potato beetle larvae developing on plants experiencing a high level of feeding damage by potato leafhoppers took longer to molt into second and third instars than larvae feeding on plants with no, low, or medium levels of damage (second instars: $F_{3,76} = 4.71, p = 0.0045$, Figure 1.3; third instars: $F_{3,76} = 6.06, p = 0.0009$; Figure 1.4). However, development time from first to fourth instar and the prepupal stage was not significantly protracted by feeding on leafhopper-damage plants, although there was a trend in this direction in this greenhouse study (fourth instar: $F_{3,72} = 1.82, p = 0.1503$, Figure 1.5; prepupa: $F_{3,68} = 0.73, p = 0.5362$, Figure 1.6).

Results from the greenhouse study also showed that survivorship from first instar to the prepupal stage (reported as proportion surviving) was significantly higher for larvae developing on undamaged plants compared to plants experiencing low, medium, or high levels of leafhopper damage ($F_{3,76}=4.64, p=0.0049$; Figure 1.7). Also, larvae developing on plants with low and high levels of leafhopper damage molted into significantly lighter adults than larvae developing on plants experiencing no damage or moderate damage ($F_{3,68}=5.29, p = 0.0024$; Figure 1.8).

When assessed in field cages, there was no effect of the four leafhopper feeding treatments on the development time of Colorado potato beetle larvae from first to the second instar ($F_{3,16}=1.14, p=0.3640$; Figure 1.9), third instar ($F_{3,16}=1.50, p=0.2529$; Figure 1.10) or fourth instar ($F_{3,16}=2.00, p=0.1544$; Figure 1.11). However, in pair-wise comparisons between beetles fed potato foliage that had experienced either no leafhopper damage or some level of damage (pooled combination of low, medium and high treatments), larval development time was extended on damage treatments as assessed by days to second instar ($t_{16}=2.03, p=0.0595$; Figure 1.12), third instar ($t_{16}=2.06, p=0.0561$; Figure 1.13), and fourth instar ($t_{16}=2.35, p=0.0320$; Figure 1.14). Moreover, there was no effect of the four leafhopper damage treatments on the survival of beetle larvae as indexed by the density of larvae per field cage on 9-16 July (day 11) ($F_{3,16}=0.88, p=0.4711$; Figure 1.15). Also, there was no significant effect of treatment (no, low, medium, and high leafhopper feeding damage) on the body weight of adult Colorado potato beetles in the field cage experiment ($F_{3,16}=2.33, p=0.1131$; Figure 1.16). However, in a pair-wise comparison, adult beetles were significantly heavier when they developed on control foliage than when they were raised on leafhopper-damaged potato leaves (pooled combination of low, medium and high treatments) ($t_{16}=-2.39, p=0.0294$; Figure 1.17).

DISCUSSION

Data from greenhouse and field experiments show that previous feeding on potato plants by potato leafhoppers adversely affects both the oviposition preference and larval performance of Colorado potato beetles. Specifically, (1) adult beetles deposit fewer eggs on leafhopper-damaged foliage, (2) larvae develop slower and survive less well

when raised on leafhopper-damaged leaves, and (3) larvae molt into smaller adult beetles. Because leafhoppers and beetles never occupied potato plants at the same time, this represents a clear case of induced resistance, whereby one herbivore species affects another indirectly through feeding-induced changes in plant physiology or morphology (see Karban and Baldwin 1997; Agrawal et al. 1999; Denno and Kaplan in press). Moreover, this becomes one of a growing number of studies demonstrating strong interspecific competitive effects between two distantly related taxa in different feeding guilds, a sap-feeder and a mandibulate herbivore (reviewed in Denno and Kaplan in press). This particular interaction is asymmetric by default, because due to management practices and the annual nature of the potato crop, in many cases, potato leafhoppers may colonize potatoes in advance of Colorado potato beetles. The real-world opportunity for beetles to precede leafhoppers in fields can exist depending upon the management practices that growers choose to use. However, previous research has shown that potato leafhoppers have greater effects on the amino-acid profile of potatoes than Colorado potato beetles suggesting that induced effects on plant nutrition are indeed asymmetric (Tomlin and Sears 1992a). For the most part, however, reciprocal effects are rarely examined in many reports of plant-mediated inter-specific competition, largely because researchers explore the effects of early-season feeders on late-season species (Damman 1993, Denno et al. 1995; Denno and Kaplan in press). Nonetheless, in cases where their colonization phenologies differ, the possibility exists that Colorado potato beetles could induce changes in potato physiology or morphology with adverse effects on leafhoppers.

Although the mechanism for induced resistance by potato leafhoppers remains an open question, several possibilities exist including altered plant nutrition as noted above, allelochemistry, morphology, or some combination of these responses. For example, it is well documented that solanaceous plants such as potatoes contain compounds that have anti-herbivore properties. Natural resistance to herbivores in potatoes has been attributed to glycoalkaloids and proteinase inhibitors (Green and Ryan 1972; Tingey 1984; Sikinyi et al. 1997). Moreover, allelochemical-based resistance has been found in certain wild *Solanum* species that results in negative effects on the survival and fecundity of Colorado potato beetles (Pelletier et al. 1999). Notably, previous feeding by insect herbivores or applications of the elicitor methyl jasmonate result in increased concentrations of proteinase inhibitors and polyphenol oxidases (Green and Ryan 1972; Bolter and Jongsma 1995; Stout and Duffey 1996; Stout et al. 1998), glycoalkaloids (Hlywka et al. 1994), and several amino acids (Tomlin and Sears 1992) in potato. Such compounds should be included as high-probability targets for investigating the mechanism underlying leafhopper-induced resistance in potato. In my study, symptoms of “hopper burn,” such as leaf curling and distortion are indicative of an induced morphological change that may have adverse consequences for Colorado potato beetle. This morphological change more likely influences oviposition preference by adult beetles rather than larval performance because there was no evidence, based on observations, that curled leaves deterred larval feeding. Thus, the induced-resistance effects on Colorado potato beetle performance in this system could have their basis in altered plant chemistry or leaf architecture.

There are numerous examples in other systems in which plant-mediated competition between insect herbivores results from altered changes in plant nutrition

(McClure 1980; Inbar et al. 1995; Denno et al. 2000; Redman and Scriber 2000), allelochemistry (Stout and Duffey 1996; Wold and Marquis 1997; Stout et al. 1998; Inbar et al. 1999a, 1999b; Mayer et al. 2002; Bezemer et al. 2003; Van Zandt and Agrawal 2004), morphology (Agrawal 1998, 1999), or some combination of these mechanisms (Agrawal 1999). Together, these studies underscore the diversity of mechanisms that underlie plant-mediated competition between insect herbivores.

Overall, my research as well as that from other reports suggests that plant-mediated competition between insect herbivores is a widespread phenomenon, one that affects not only species interactions but also community structure (Damman 1993, Denno et al. 1995; Kaplan and Denno in press; Van Zandt and Agrawal 2004). Induced resistance as the underlying mechanism has been shown to influence a diverse range of herbivores in various habitats, and its effects can be seen within and among several feeding guilds (Kaplan and Denno in press). Collectively, the literature and my research show that induced resistance has adverse effects on a diversity of performance and fitness components including development time, survival, oviposition and feeding preferences, and adult body weight and fecundity (Karban and Baldwin 1997; Kaplan and Denno in press). Moreover, the occurrence of systemic induced resistance challenges the paradigms of traditional competition theory in that herbivores can compete indirectly if they occur on a plant at different times, occupy different microhabitats, or occur at relatively low densities (Karban and Baldwin 1997; Kaplan and Denno in press). My research certainly supports the view that seasonally-displaced herbivores can compete via induced resistance. However, unlike other studies where the induced resistance effect occurs at low herbivore densities (Karban and Baldwin 1997), the resistance factor

imposed by potato leafhoppers on Colorado potato beetles appears to be density dependent. For example, in my greenhouse study, high but not low leafhopper density/damage imposed fitness and performance penalties on beetles (Figs. 1.3, 1.4, and 1.7).

Importantly, induced resistance effects extend to higher trophic levels such that herbivores developing on induced plants can experience a higher risk of attack from predators or parasitoids (Thaler 1999, 2002; Kessler and Baldwin 2004; Denno and Kaplan in press). In the greenhouse study, the delay seen in this system occurred early in development, whereby most of the delay occurred from the first to the second instar in the high leafhopper damage treatment. This delay carried through to the fourth instar, which could impact the Colorado potato beetle's susceptibility to predation as well as the type of predator that may impact its survival. In fact, in the potato system, leafhopper-induced developmental delays in the larvae of Colorado potato beetles (Figs. 1.3 and 1.4) result in increased exposure to predaceous stinkbugs and dramatic increases in mortality (Kaplan, Dively and Denno unpublished data). All considered, the effects of induced resistance can cascade to other herbivores and their natural enemies, and thereby affect the structure and dynamics of the entire food web (Van Zandt and Agrawal 2004; Ohgushi 2005). In the context of the rapidly growing and community-wide impacts of induced resistance, the historical view that "interspecific competition" is a weak and infrequent force in the structuring communities of herbivorous insects should be seriously scrutinized. Current data are far more in line with the resurrected notion that interspecific competition, both direct and plant-mediated, is an important factor affecting the structure

and dynamics of herbivorous insect communities (Damman 1993, Denno et al. 1995; Kaplan and Denno in press; Van Zandt and Agrawal 2004).

Induced plant resistance also has important implications for the management of agricultural pests. Economic injury levels (EIL) for potato pest management have been developed primarily for single pest species (Ferro 1986; Mahr et al. 1995). However, potato growers in the mid-Atlantic area of the United States are faced with intra-seasonal decisions concerning the control of both potato leafhopper and Colorado potato beetle (Walgenbach et al. 1985; Dively et al. 1995, 1998). The current management approach assumes that the impacts of both pests are independent, thus control decisions regarding PLH are based on leafhopper densities and current control costs and not on projected costs associated with CPB management. My research has shown that feeding by potato leafhopper has negative consequences on Colorado potato beetle that feeds later in the season. Current management practices for potato leafhoppers include the use of insecticides when potato leafhopper densities reach a certain economic threshold, which has historically been rather conservative (Walgenbach et al. 1985; Dively et al. 1995). Based on my findings, a potato grower should be able to accept a higher level of potato leafhopper injury, if losses due to Colorado potato beetle later in the summer can be prevented at a level high enough to offset the risks of leafhopper damage. Thus, the action threshold for leafhopper control should be higher when the delayed benefits of beetle reduction via induced plant resistance are considered. Importantly, higher action thresholds for potato leafhopper should also increase the chance of maximizing Colorado potato beetle mortality from natural enemies. Ultimately, to establish an effective management strategy for the multiple pests on potato, it will be essential to combine the

positive indirect effects of induced resistance along with the negative direct effects on crop yield.

APPENDIX: TABLES

Table 1.1. Effect of leafhopper density/feeding (0, 3, 10, or 20 leafhoppers per plant) on the percentage of cupped potato leaves, the percentage of necrotic leaves, and the number of leafhopper nymphs/potato plant remaining on the four treatments after a two-week exposure period.

Number of adult potato leafhoppers released per plant	df ¹	<i>Cupped leaves (%)</i>		<i>Necrotic leaves (%)</i>		<i>Number of remaining leafhopper nymphs/plant</i>	
		Mean	±SEM	Mean	±SEM	Mean	±SEM
0	3, 76	2.75 ^a	0.369	0.15 ^a	0.082	0.30 ^a	0.105
3		10.45 ^b	2.035	0.50 ^a	0.115	1.85 ^a	0.264
10		79.50 ^c	2.112	2.25 ^a	0.446	15.20 ^b	1.033
20		94.75 ^d	1.559	11.80 ^b	1.771	29.70 ^c	1.793

1 Degrees of freedom numerator, denominator

Means (± SEM) within columns with different letters are significantly different ($P < 0.05$)

Table 1.2. Assignment of potato leafhopper damage treatment levels based on the number of adult potato leafhoppers released per plant.

Number of adult potato leafhoppers released per plant	Potato leafhopper damage treatment level
0	None
3	Low
10	Medium
20	High

APPENDIX: FIGURES

Figure 1.1. Number of Colorado potato beetle egg masses deposited on plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Oviposition preference was assessed on 4 August 2001 in a field cage at Beltsville, Maryland. Means (\pm SEM) with different letters are significantly different ($P < 0.05$).

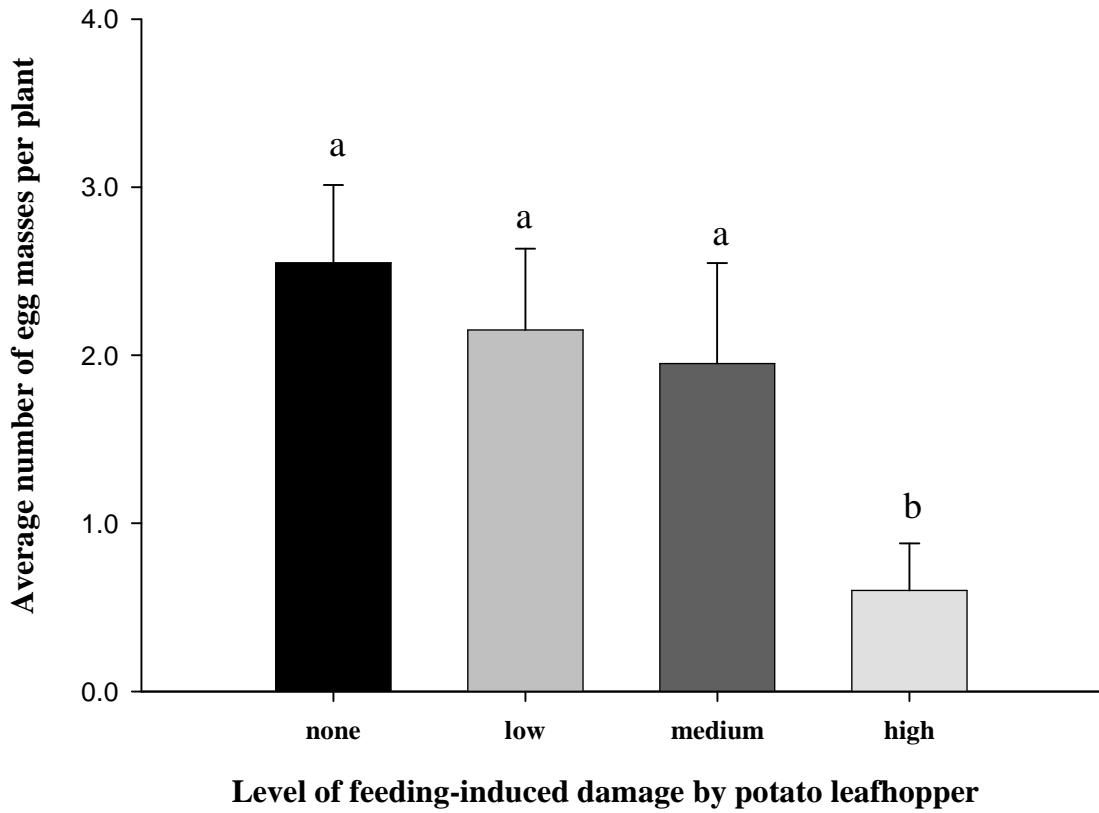


Figure 1.2. Number of Colorado potato beetle egg masses deposited on plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Oviposition preference was assessed on 8 August 2001 in a field cage at Beltsville, Maryland. Means (\pm SEM) with different letters are significantly different ($P < 0.05$).

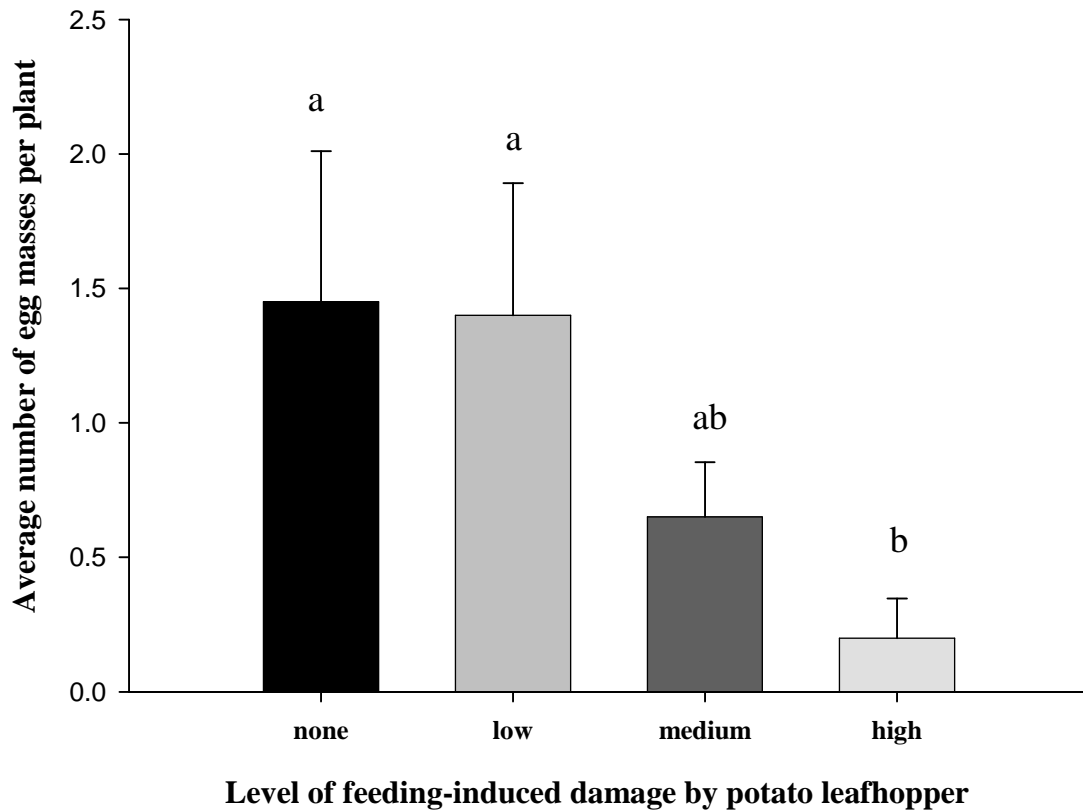


Figure 1.3. Development time to second instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a greenhouse in College Park, Maryland. Means (\pm SEM) with different letters are significantly different ($P < 0.05$).

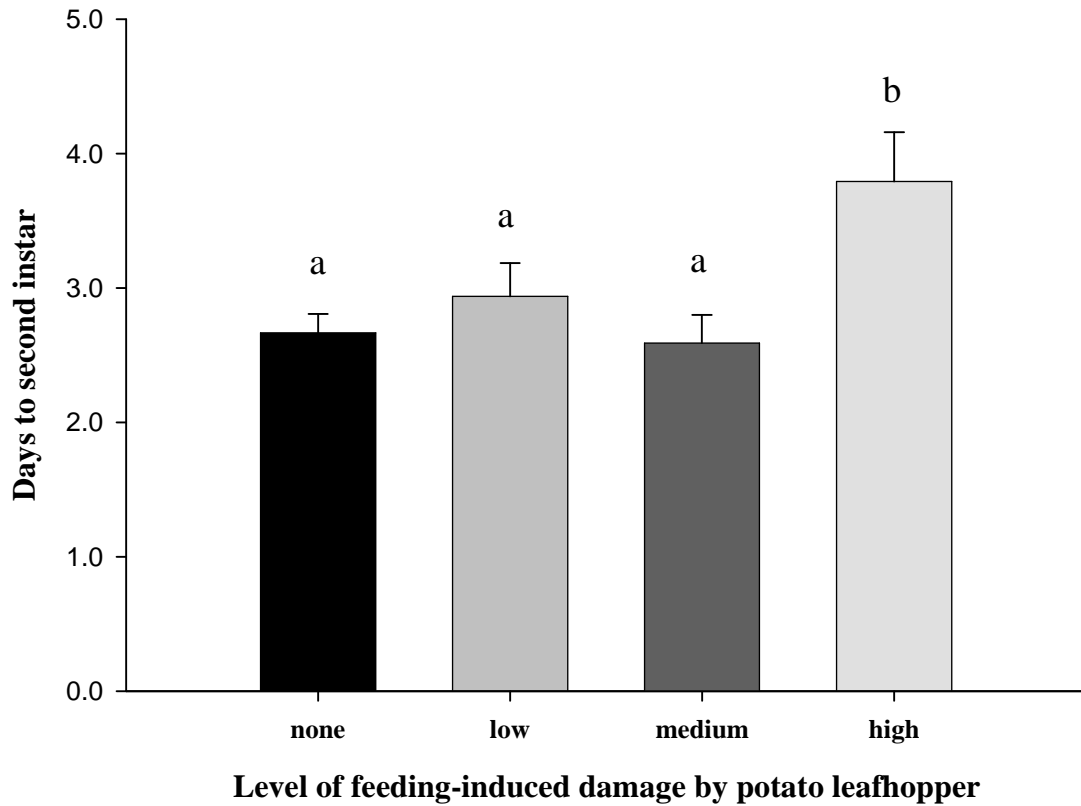


Figure 1.4. Development time to third instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a greenhouse in College Park, Maryland. Means (\pm SEM) with different letters are significantly different ($P < 0.05$).

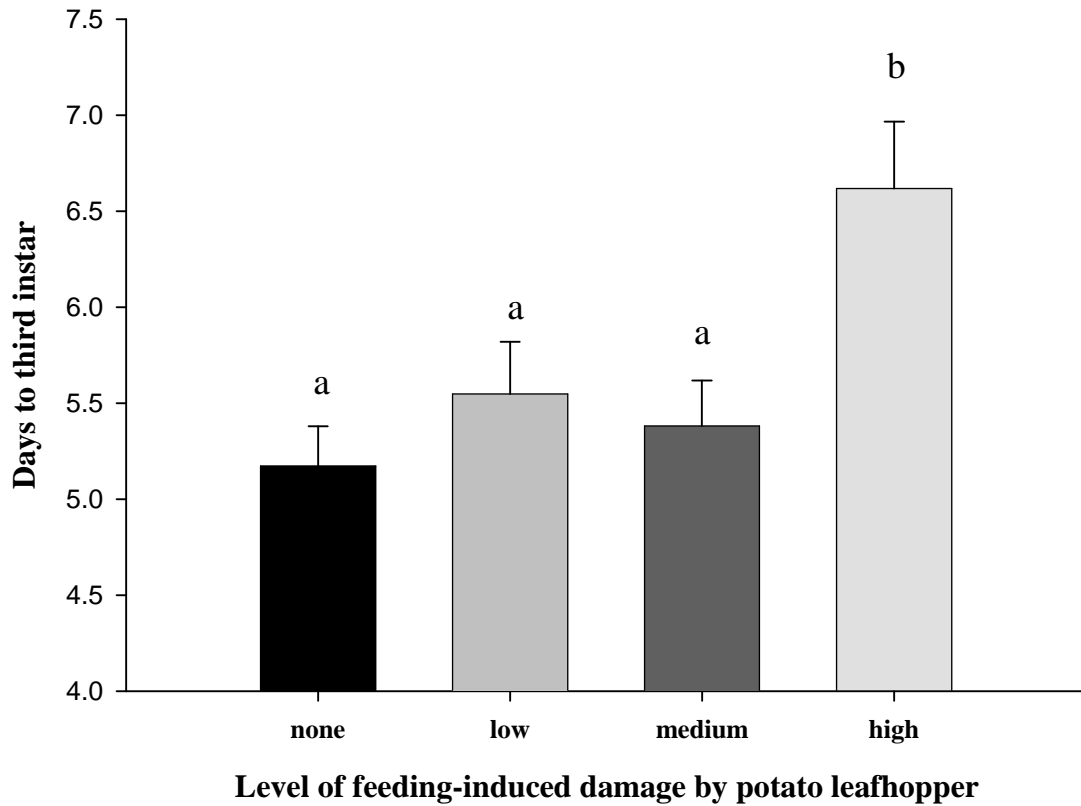


Figure 1.5. Development time to fourth instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a greenhouse in College Park, Maryland. Means (\pm SEM) are shown.

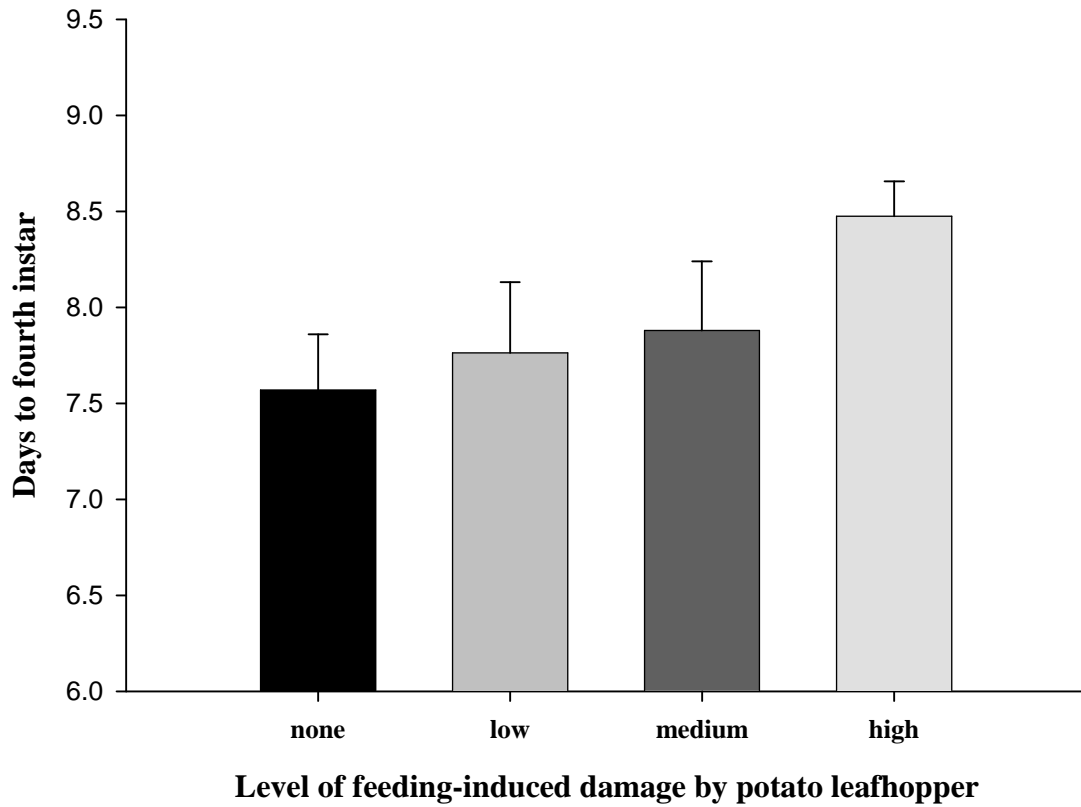


Figure 1.6. Development time to prepupal instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a greenhouse in College Park, Maryland. Means (\pm SEM) are shown.

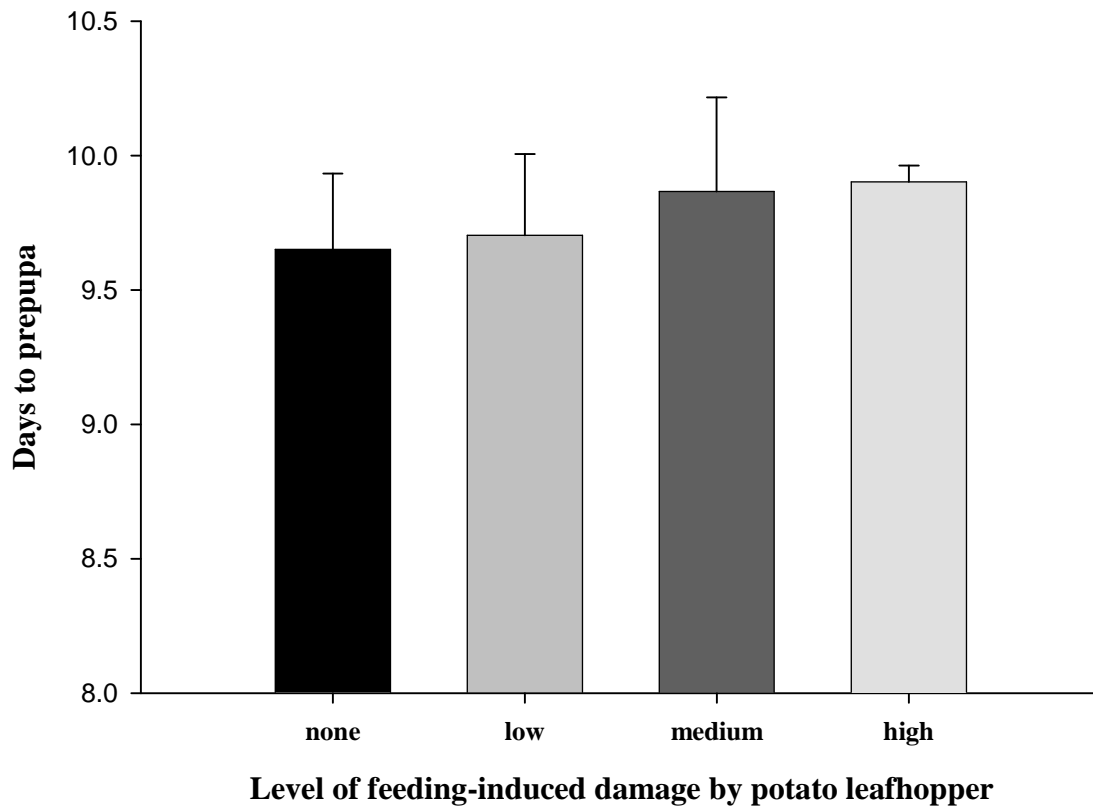


Figure 1.7. Survivorship to prepupal instar of Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a greenhouse in College Park, Maryland. Means (\pm SEM) with different letters are significantly different ($P < 0.05$).

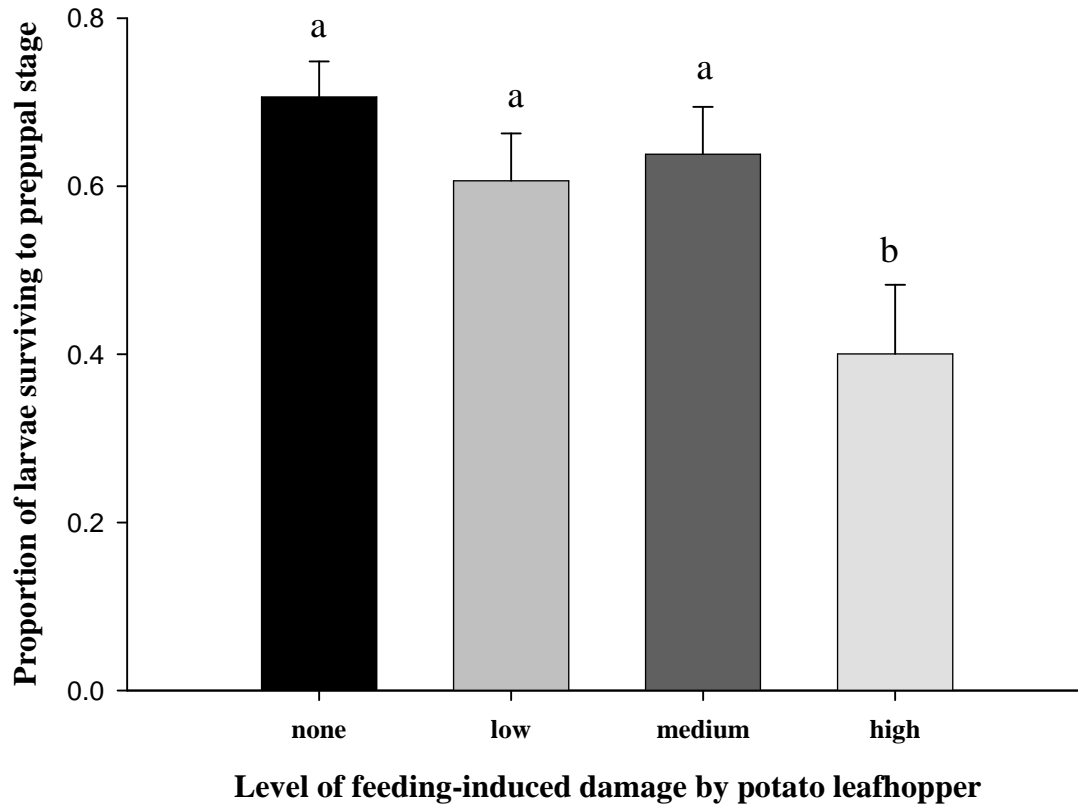


Figure 1.8. Body weight (g) of adult Colorado potato beetles emerging from larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a greenhouse in College Park, Maryland. Means (\pm SEM) with different letters are significantly different ($P < 0.05$).

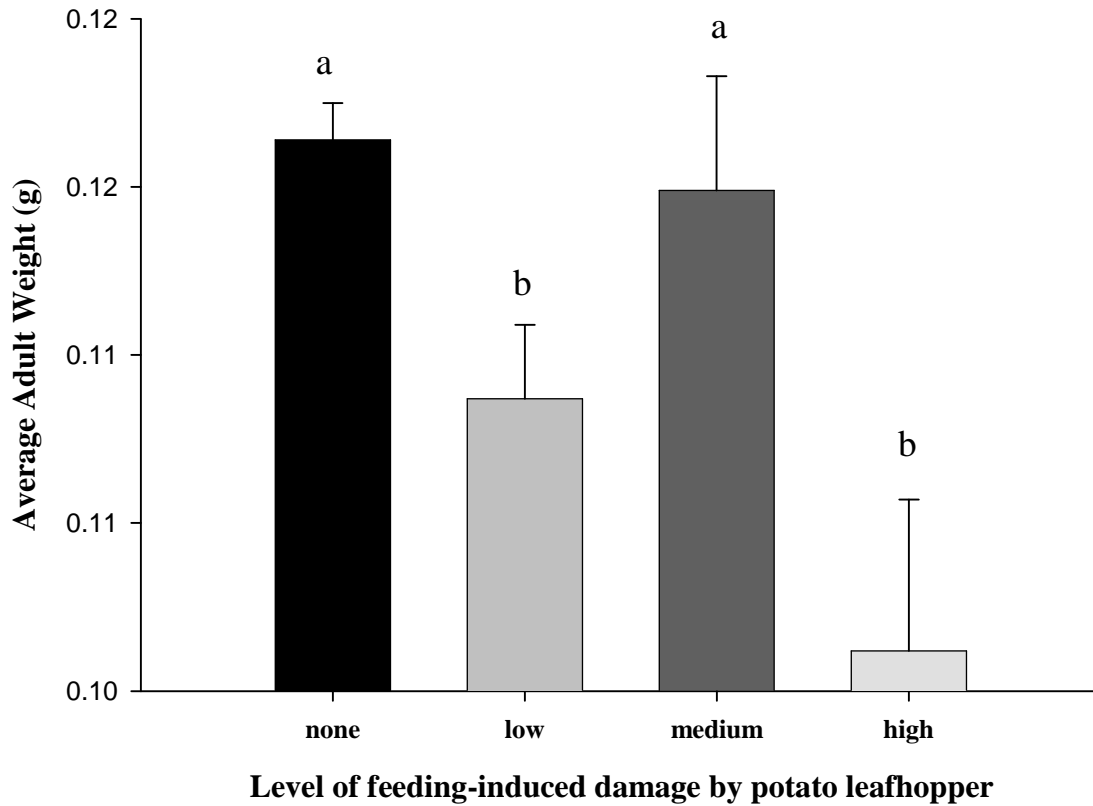


Figure 1.9. Development time to second instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) are shown.

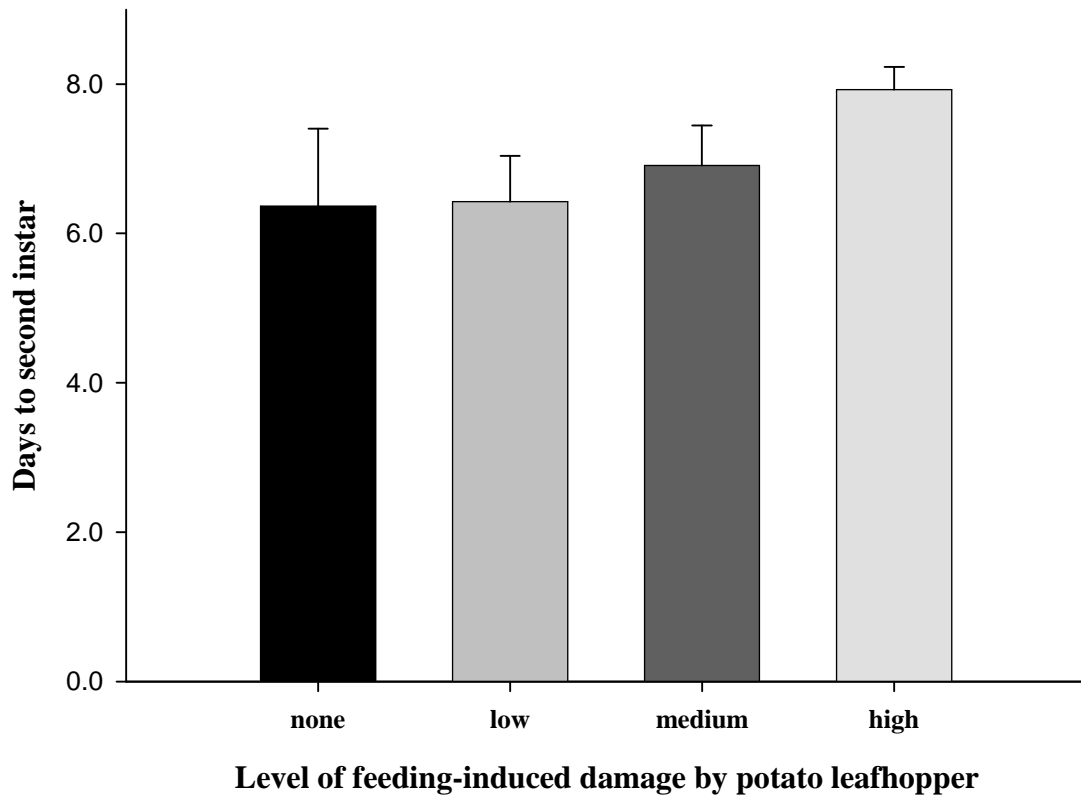


Figure 1.10. Development time to third instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) are shown.

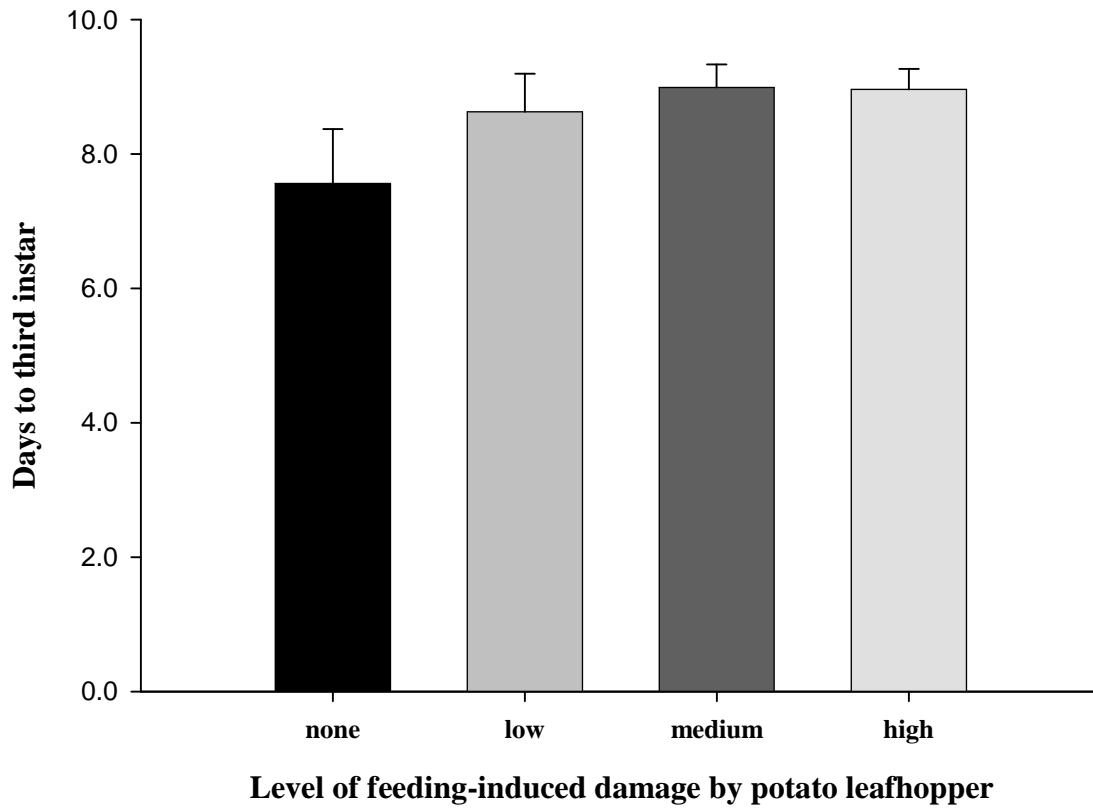


Figure 1.11. Development time to fourth instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) are shown.

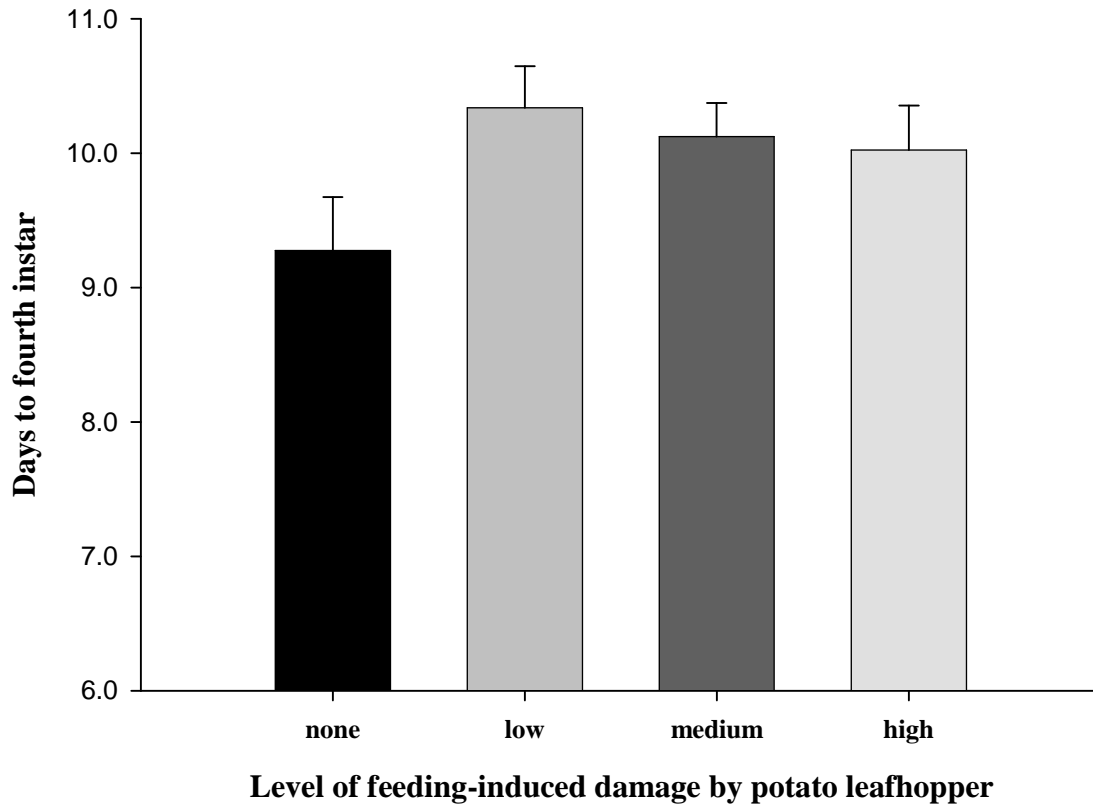


Figure 1.12. Development time to second instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of two levels of damage by potato leafhoppers: none or the pooled combination of low, medium, and high damage. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) with different letters are significantly different ($P \sim 0.05$).

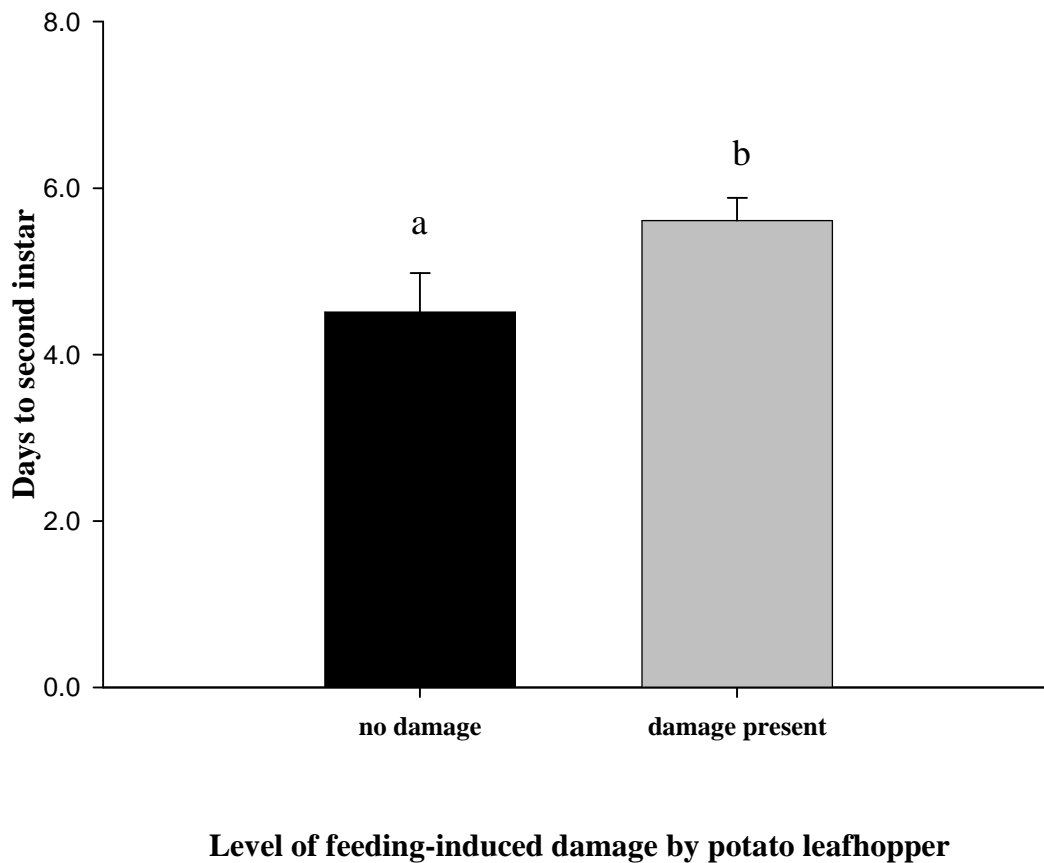


Figure 1.13. Development time to third instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of two levels of damage by potato leafhoppers: none or the pooled combination of low, medium, and high damage. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) are shown.



Figure 1.14. Development time to fourth instar (days) for Colorado potato beetle larvae fed potato plants that experienced one of two levels of damage by potato leafhoppers: none or the pooled combination of low, medium, and high damage. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) with different letters are significantly different ($P < 0.05$).

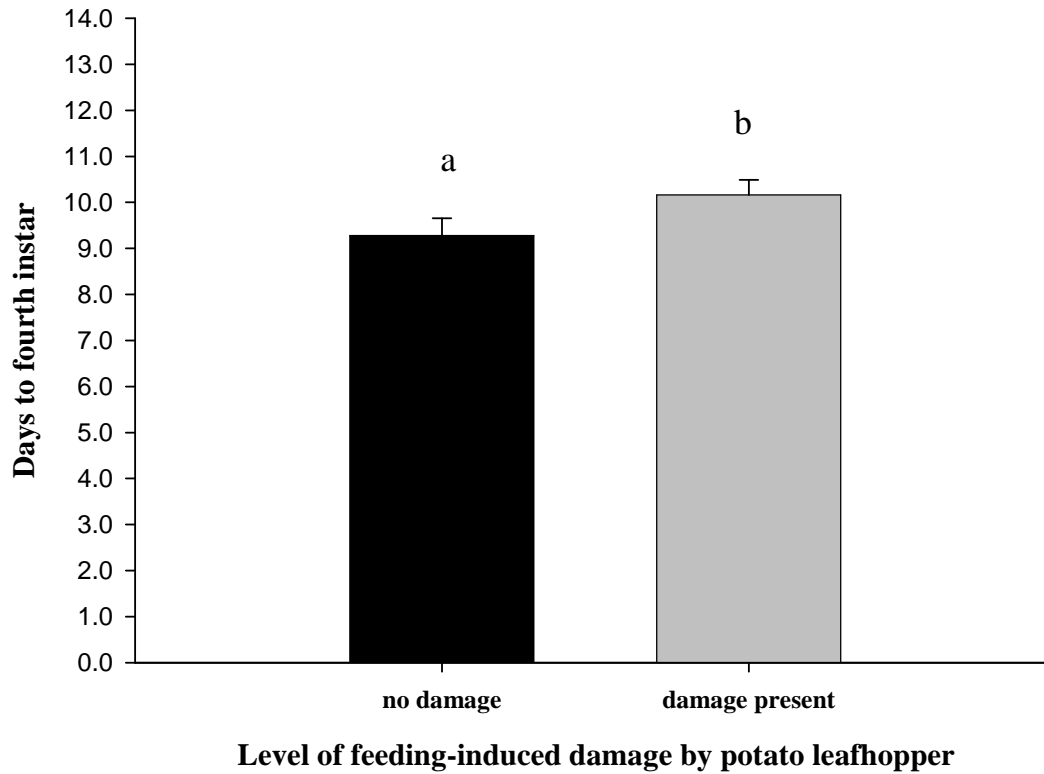


Figure 1.15. Number of surviving Colorado potato beetle larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) are shown.

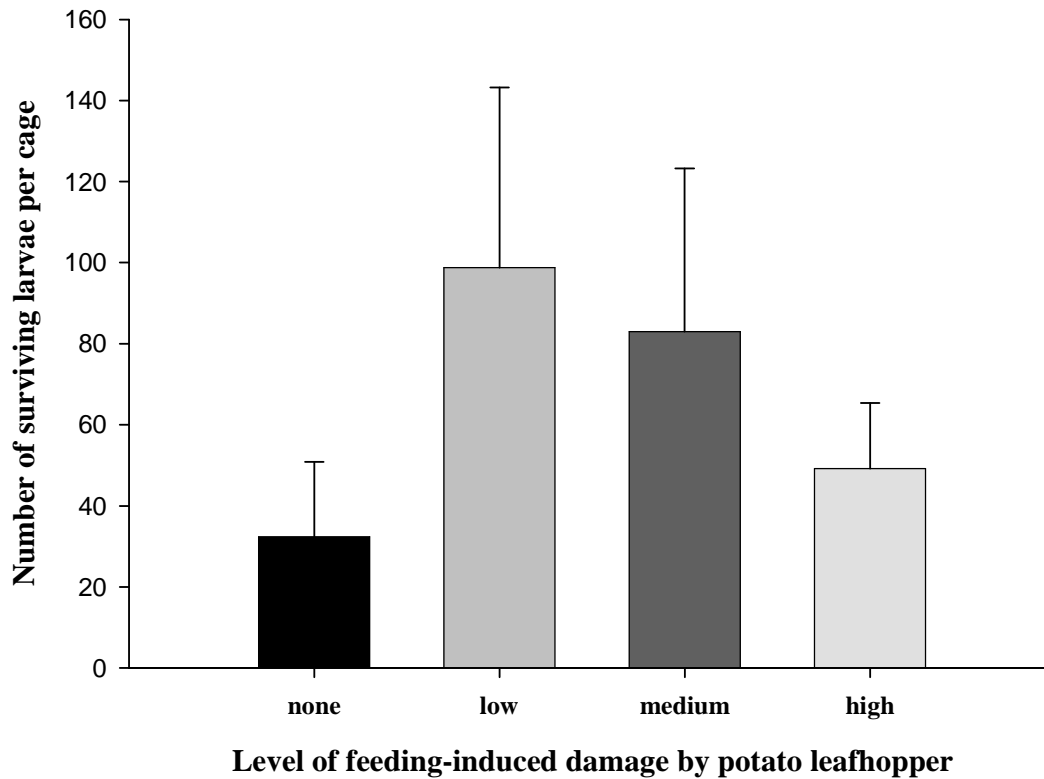


Figure 1.16. Body weight (g) of adult Colorado potato beetles emerging from larvae fed potato plants that experienced one of four levels of damage by potato leafhoppers: none, low, medium, and high. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) are shown.

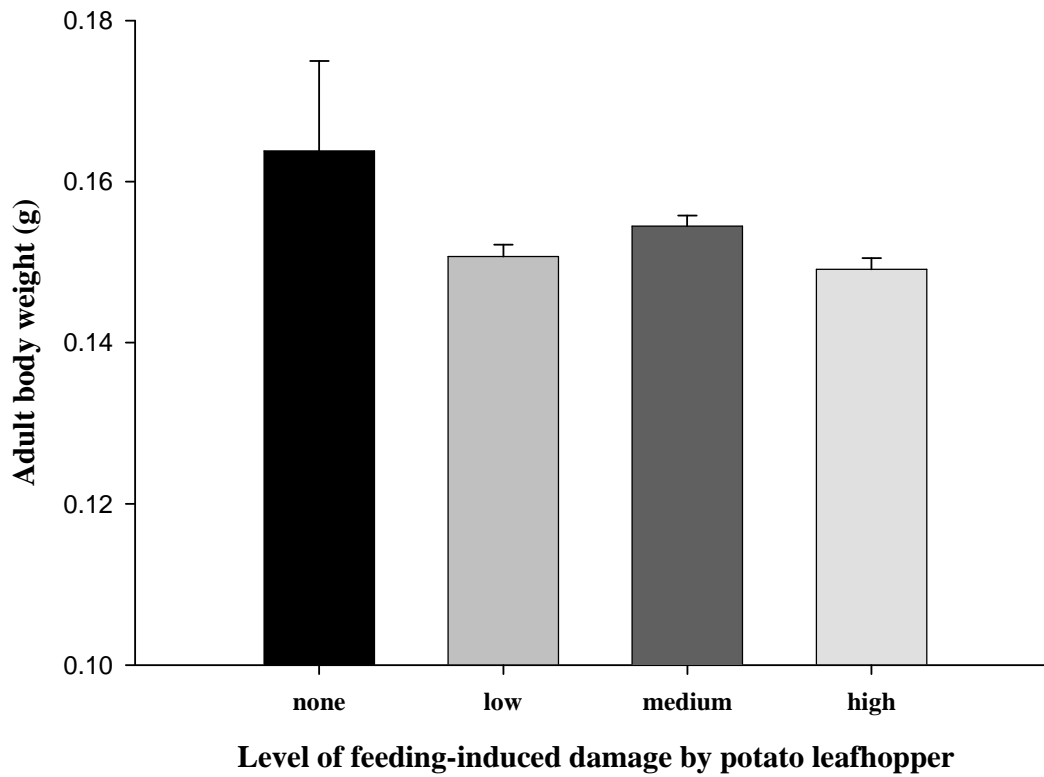
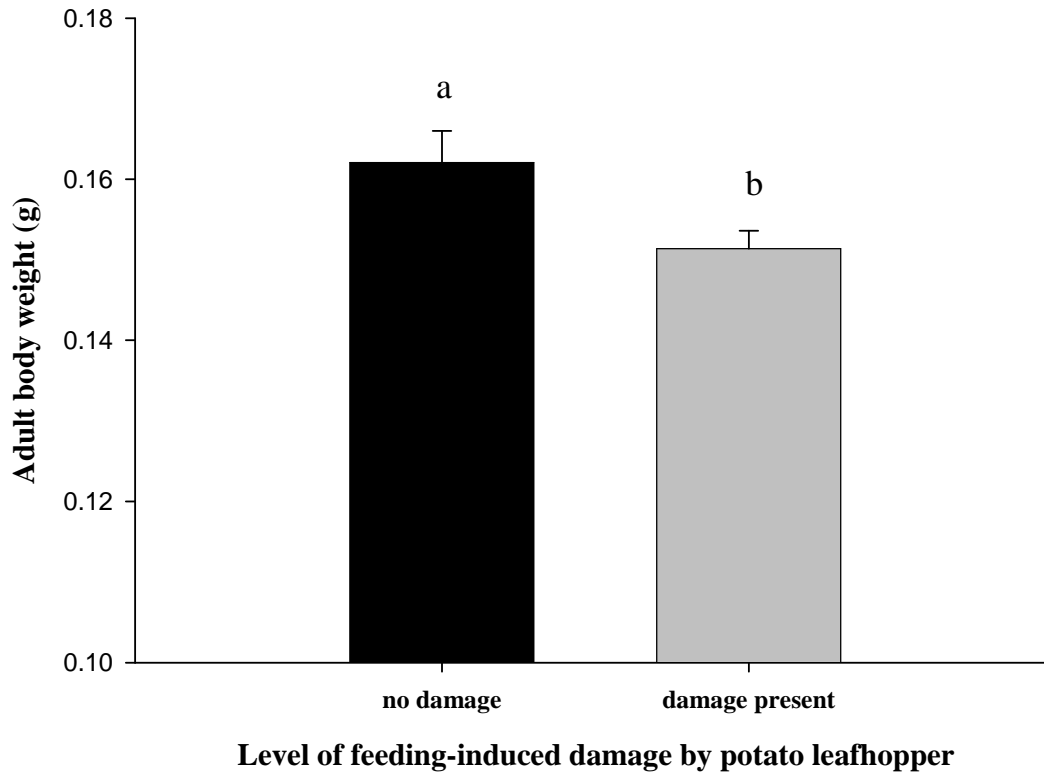


Figure 1.17. Body weight (g) of adult Colorado potato beetles emerging from larvae fed potato plants that experienced one of two levels of damage by potato leafhoppers: none or the pooled combination of low, medium, and high damage. Experiment was conducted in a field cage at Beltsville, Maryland. Means (\pm SEM) with different letters are significantly different ($P < 0.05$).



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