

The costs of anti-herbivore defense traits in agricultural crop plants: a case study involving leafhoppers and trichomes

IAN KAPLAN,¹ GALEN P. DIVELY, AND ROBERT F. DENNO²

Department of Entomology, University of Maryland, College Park, Maryland 20742 USA

Abstract. The expression of plant defenses is thought to entail costs (e.g., the allocation of resources away from growth or reproduction) that constrain the evolution of plant genotypes maximally defended against herbivores. Although central to the ecological theory underlying plant–insect interactions at large, the concept of defense costs is particularly evident in agricultural crops where plants may be under simultaneous selection for enhanced growth and/or reproduction (i.e., yield) and anti-herbivore resistance traits that deter pests. In this study we investigate the role of trichomes as a resistance mechanism against a sap-feeding insect (the leafhopper, *Empoasca fabae*) on potato. Natural variation in trichome density among 17 potato cultivars was used to test for the role of trichomes as a putative defense against leafhoppers, and evidence of costs in trichome expression. Two different types of costs were explored: (1) allocation costs (i.e., the relationship between trichomes and yield), and (2) costs involving trade-offs with alternative defense strategies (e.g., tolerance). Although leafhopper abundance did not decrease as trichome density increased, leafhopper injury to potato plants (foliar necrosis) was negatively correlated with trichome density. As a result, the per capita effect of leafhopper adults and nymphs on foliar damage was lower on plants with high trichome densities. We found no evidence, however, for costs of expressing this resistance trait; trichomes were not correlated with either potato yield or tolerance to herbivory. Thus, selection for multiple plant defenses to alleviate the impact of pests in agronomic crops may indeed be possible without inherent losses in plant yield.

Key words: costs of defense; ecological trade-offs; *Empoasca fabae*; herbivory tolerance; host-plant resistance; leafhopper; optimal defense theory; potato; *Solanum tuberosum*; trichomes.

INTRODUCTION

Plants in natural populations possess varying levels of defense against their herbivores, with some individuals relatively resistant and others more susceptible (Krischik and Denno 1983, Kennedy and Barbour 1992, Osier and Lindroth 2006, Donaldson and Lindroth 2007). Yet plants often experience substantial fitness gains when they avoid herbivore damage (Bardner and Fletcher 1974, Marquis 1992). This observation has led evolutionary ecologists to question why all plants are not maximally defended against herbivores and why susceptible genotypes persist in populations. The most widely cited explanation for this paradox is that expressing defenses entails costs that are imposed on other physiological and biochemical processes (Parker 1992, Simms 1992, Bergelson and Purrington 1996, Strauss et al. 2002). Building defenses, for example, may require allocation of valuable nutrient reserves, such that well-defended plants grow slower, produce fewer progeny,

and are weaker competitors against neighboring plants (Herms and Mattson 1992, van Dam and Baldwin 1998, Agrawal et al. 1999, Zavala et al. 2004). This juxtaposition between growth and defense as fundamentally conflicting processes is pervasive in the ecological literature (e.g., Coley et al. 1985, Herms and Mattson 1992, Stamp 2003).

Although defense costs have traditionally been viewed in the context of trade-offs with plant growth, more recent assessments of the issue emphasize a diverse range of other potential costs (e.g., genetic and ecological constraints; Iwao and Rausher 1997, Stinchcombe and Rausher 2001, Strauss et al. 2002, Wise 2007). For instance, the expression of one defense may result in a concomitant decrease in the expression of a second defense (Koricheva et al. 2004). Most notably, anti-herbivore resistance and tolerance traits have been suggested to represent potentially redundant, and thus alternative, plant defense strategies (van der Meijden et al. 1988, Fineblum and Rausher 1995).

Agricultural crop plants provide an intriguing perspective on defense costs because crops can be under selection for both defense and yield. In fact, one explanation for why herbivores are more abundant and damaging in agricultural compared with natural systems is that crop plants have been bred to maximize yield, resulting in varieties that are poorly defended, and

Manuscript received 24 September 2007; revised 28 August 2008; accepted 19 September 2008. Corresponding Editor: R. A. Huffbauer.

¹ Present address: Department of Entomology, 4142 Comstock Hall, Cornell University, Ithaca, New York 14853-2601 USA. E-mail: ikaplan@cornell.edu

² Deceased.

thus high in susceptibility to pest outbreaks (Bottrell and Adkisson 1977, Smedegaard-Petersen 1985, Welter and Steggall 1993). Thus, host-plant resistance is expected to be negatively correlated with plant growth. Among tobacco varieties, for example, leaf nicotine content is inversely related to yield (Vandenberg and Matzinger 1970). Similarly, because herbivores can counter, and thus “defeat,” the defenses of their host plant, selecting for crop varieties that possess multiple defense mechanisms may represent a more effective long-term pest management strategy (Bolter and Jongsma 1995, Karban and Agrawal 2002). Given the aforementioned constraints, however, the relationship between multiple plant defenses and crop yield remains unclear, despite the undisputable importance of this relationship in sustainable agriculture.

We investigated the association between resistance to herbivores, tolerance to herbivory, and yield in potato (*Solanum tuberosum*), focusing exclusively on interactions involving the potato leafhopper (*Empoasca fabae*), a key insect pest in this system. Although absent from potato-growing regions in western North America, potato leafhoppers are abundant in the eastern United States and frequently attain pest status in potato fields (Cancelado and Radcliffe 1979, Walgenbach and Wyman 1985). Our previous research in this system has demonstrated that leafhoppers cause a 15–20% yield loss, on average, and can inflict as much as 60% yield loss on certain cultivars (Kaplan et al. 2008; see Plate 1). Trichomes (i.e., small hairs that protrude from the surface of plant leaves and stems), however, have been implicated as a resistance trait that may protect potato plants from leafhopper injury (Tingey 1991, Flanders et al. 1992, Medeiros et al. 2005, Medeiros and Tingey 2006). Thus, the goal of our study was to use intraspecific variation in trichome density among potato cultivars to assess the impact of trichomes on leafhopper abundance, leafhopper-induced damage, plant yield, and plant tolerance to herbivory. Understanding the relationships among these variables is central to the development of plant cultivars that can simultaneously resist herbivores and tolerate damage while maintaining yield.

METHODS

During the summers of 1999 and 2000, experiments were initiated to quantify the impact of trichomes on leafhoppers, and measure the potential costs of expressing trichomes. Both plant variety and potato leafhopper presence were manipulated in a randomized complete block design, and each treatment combination was assigned at the plot level (plot size = two 6 m long rows spaced 0.9 m apart = 20 plants). In 1999, this experiment was conducted at the Wye Research and Education Center, Queenstown, Maryland, USA (hereafter referred to as Wye), with four replicate blocks. In 2000, the experiment was repeated at the Wye ($n = 4$ replications), and was also conducted at the Lower

Eastern Shore Research and Education Center, Salisbury, Maryland, USA (hereafter referred to as LES-REC; $n = 4$ replications).

In 1999, we selected 16 commonly planted potato varieties, and in 2000 we included an additional cultivar resulting in 17 total varieties (Appendix A). These cultivars have not specifically been bred for increased trichome density and thus any variation in trichomes among cultivars is incidental. In each replicate block, two plots were cultivated for each variety, one a control plot that leafhoppers naturally colonized, and the other an experimental plot where leafhoppers were excluded using weekly insecticide spraying. Thus, 128 plots (16 potato varieties \times leafhoppers present/absent \times four replicates) were established in 1999, and 136 plots (17 potato varieties \times leafhoppers present/absent \times four replicates) were created at each field site in 2000. The insecticide permethrin (Ambush, Syngenta Crop Protection, Greensboro, North Carolina, USA) was applied as a foliar treatment (56 g a.i./ha) using a boom sprayer delivering 27 L/ha spray volume. The only other insect found at a high density in potato fields at our study sites was the Colorado potato beetle. However, beetles were prevented from colonizing plots by spraying the perimeter border of potato plants surrounding the field with insecticide. This procedure killed most of the immigrating adults and any colonists were removed by hand.

Once a week from early June through late July, plots were sampled for leafhopper adults and nymphs. Adult density was estimated using sweep net sampling (10 sweeps per plot), whereas the density of nymphs was measured by visually searching foliage (10 leaves per plot; Walgenbach et al. 1985). Plants were also visually rated for evidence of leafhopper damage (percentage of total leaf surface area exhibiting foliar necrosis) by two separate observers. The average of these two observations was used as the plot mean. Because necrotic lesions can easily be distinguished from healthy leaf tissue, it is unlikely that our visual assessment of damage was affected by trichome density. In early August, potato tubers were harvested from the ground, weighed, and the total yield for each plot was calculated.

At the Wye site in 2000, leaves were collected from each of 17 potato cultivars and used to quantify trichome densities. Three leaves were randomly selected from different plants in each cultivar and three disks (3 cm diameter) were removed from each leaf using a cork borer. Trichomes on the undersides of leaf disks (where leafhoppers primarily reside and feed) were counted using a dissecting microscope, and the average count for the three disks was used as an estimate of trichome density. Although potato plants possess both glandular and non-glandular trichomes, we analyzed the total number of trichomes (i.e., glandular + non-glandular) because the two trichome types are highly correlated ($r = 0.7490$, $P < 0.0001$). Separate analyses using each trichome type (data not shown) produced similar

TABLE 1. Main and interactive effects of trichomes and site/year on the abundance of adult and nymph leafhoppers (*Empoasca fabae*), their per capita damage to potato (*Solanum tuberosum*), and potato necrosis, yield, and tolerance to herbivory by leafhopper adults and nymphs.

Effects	Trichomes			Site/year			Trichomes × site/year		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Leafhopper abundance									
Adults	18.68	1, 176	<0.0001	5.94	2, 176	0.0032	0.04	2, 176	0.9594
Nymphs	3.80	1, 177	0.0527	5.38	2, 177	0.0054	3.34	2, 177	0.0378
Foliar necrosis (%)	17.71	1, 175	<0.0001	2.74	2, 175	0.0672	1.48	2, 175	0.2307
Per capita damage									
Adults	25.95	1, 174	<0.0001	9.11	2, 174	0.0002	3.14	2, 174	0.0459
Nymphs	12.56	1, 175	0.0005	9.64	2, 175	0.0001	0.08	2, 175	0.9227
Plant yield	0.19	1, 176	0.6668	16.40	2, 176	<0.0001	6.73	2, 176	0.0015
Plant tolerance									
Adults	2.84	1, 44	0.0988	3.03	2, 44	0.0585	1.02	2, 44	0.3674
Nymphs	1.58	1, 30	0.2185	8.52	1, 30	0.0066	6.43	1, 30	0.0167

patterns to the analysis with total number of trichomes presented here. In addition, we repeated trichome counts using a subset of potato varieties grown in a different year and location (August 2008, in Freeville, New York, USA) to assess the consistency of trichome expression among cultivars in time and space. Our earlier trichome counts from experimental field plots were positively correlated with subsequent trichome measurements ($n = 7$ varieties, $r = 0.7642$, $P < 0.05$), and thus it is likely that the spectrum of trichome variation described in this study is genetically, rather than environmentally, driven.

The effect of potato cultivar on trichome density was assessed with ANOVA (Proc GLM; all statistical analyses were performed using SAS, Version 9.1 [SAS Institute 2002]). The impact of trichomes on leafhopper abundance (adults and nymphs), plant damage (percentage necrosis), per capita leafhopper effects, plant yield, and plant tolerance to herbivory was assessed using regression (Proc MIXED). Site and year were included as random effects in our statistical model.

Per capita leafhopper effects were calculated by dividing foliar necrosis by leafhopper abundance. Thus, high per capita values indicate that relatively large amounts of plant damage were inflicted by relatively few leafhoppers.

Tolerance was quantified using a reaction norm approach, which in this case represents the slope of the line relating leafhopper abundance to plant yield (Strauss and Agrawal 1999). The more negative the slope, the less tolerant that variety is to leafhoppers (e.g., Kaplan et al. 2008). This methodological approach (i.e., regressing plant fitness or yield on levels of herbivory) is widely used in studies on plant tolerance to herbivory and the slope value serves as a reliable estimate of tolerance (see Stowe et al. 2000). However, it should be noted that the slope (and thus tolerance) may be sensitive to the yield potential of each variety tested.

Because leafhoppers were not found in insecticide-treated plots we only used abundance and plant damage data from control plots (i.e., those which did not receive

insecticide applications and thus were colonized by naturally occurring leafhopper populations) to assess trichome effects. Similarly, because allocation costs for trichomes can be most accurately measured in the absence of herbivory, we used yield data from insecticide-sprayed plots to investigate the relationship between trichomes and yield. Because leafhoppers have the greatest potential to affect potato yield during outbreak periods in mid-summer, only the date when leafhoppers occurred at peak density (from early to mid-July) was used for statistical analyses. Counts of adults and nymphs were square-root transformed, per capita effect data were log-transformed, and the proportion of plant foliage expressing damage symptoms was arcsine square-root transformed to satisfy the assumptions of parametric statistics.

RESULTS

The density of trichomes on potato leaves varied greatly among cultivars ($F = 6.25$, $df = 16, 50$, $P < 0.0001$), with the most densely covered variety possessing more than five times the trichome density (1621 trichomes/cm²) as the least densely covered variety (307 trichomes/cm²; Appendix A).

The abundance of leafhopper adults was positively associated with the density of trichomes among potato cultivars (Table 1, Fig. 1A). Similarly, the abundance of leafhopper nymphs was positively related to trichomes (Table 1, Fig. 1B), although this effect was marginally significant. Leafhopper-induced foliar necrosis, however, was negatively associated with trichome density, such that high-trichome plants received lower levels of leafhopper injury (Table 1, Fig. 2). As a result, the per capita effect of leafhopper adults (Table 1, Fig. 3A–C) and nymphs (Table 1, Fig. 3D–F) on plant damage decreased with an increase in trichomes. Site and year effects tended to be highly significant, indicating that leafhopper abundance and thus damage are variable across growing seasons and locations (Table 1).

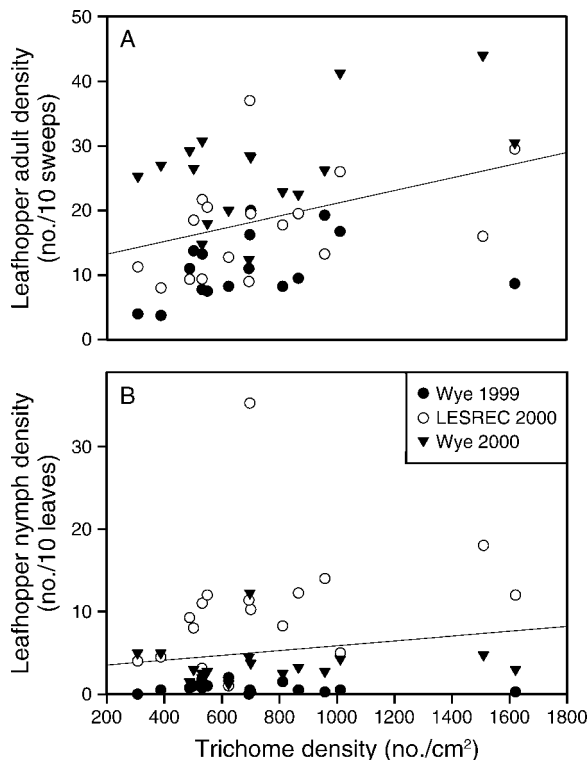


FIG. 1. The relationship between the density of leafhopper *Empoasca fabae* (A) adults and (B) nymphs and trichome density at Wye in 1999, LESREC in 2000, and Wye again in 2000. The abundance of leafhopper adults was positively related to trichome density ($F_{1,176} = 18.68, P < 0.0001$), and a similar, albeit weaker, relationship existed with leafhopper nymphs ($F_{1,177} = 3.80, P = 0.0527$). Each data point represents the mean value for each cultivar within a site. The plotted line represents a fitted regression. See *Methods* for a description of the experimental sites (Wye Research and Education Center, Queenstown, and the Lower Eastern Shore Research and Education Center (LESREC), Salisbury, Maryland, USA).

The expression of trichomes had no impact on potato yield (Table 1, Fig. 4). Trichomes also did not affect tolerance to leafhoppers as evidenced by the nonsignificant relationship between trichome density and tolerance to both leafhopper adults (Table 1, Fig. 5A) and nymphs (Table 1, Fig. 5B). For both insect life stages there were trends for positive associations between trichomes and tolerance, and this relationship approached significance ($P = 0.099$) for adult leafhoppers. Site and year effects were significant for tolerance to nymphs and marginally significant for adults ($P = 0.058$).

DISCUSSION

Trichomes have long been considered to function as a plant resistance mechanism against phytophagous insects (Levin 1973), although their effects are often variable within the herbivore community (van Dam and Hare 1998, Hare and Elle 2002, Andres and Connor

2003, Gruner et al. 2005). Unexpectedly, we found that leafhoppers were more abundant on high trichome-producing potato cultivars (Fig. 1). This result is surprising because previous studies on plant-leafhopper dynamics routinely report negative effects of trichomes, including studies on potato leafhoppers (Tingey 1991, Flanders et al. 1992, Medeiros et al. 2005, Medeiros and Tingey 2006). Although it is unclear which factors contributed to this positive relationship, trichomes are known to interfere with foraging by predators and parasitoids, resulting in weaker top-down suppression of herbivorous pests (Price et al. 1980, Kennedy 2003, Gassmann and Hare 2005). Thus, under certain ecological conditions (i.e., when natural enemies are abundant) trichomes may indeed benefit herbivores. Leafhopper predators (e.g., *Nabis*) were observed in our experimental fields, allowing for this possibility. Moreover, alfalfa trichomes impede the searching of *Anagrus nigriventris*, an egg parasitoid of the potato leafhopper (Lovinger et al. 2000). However, the effects of natural enemies such as *Anagrus* on potato leafhopper population dynamics are poorly described, and therefore it is difficult to estimate the importance of enemy effects in this system. Additionally, several studies that have documented negative effects of trichomes on leafhopper abundance (e.g., Styrsky et al. 2006) compared pubescent with glabrous plants. As a result, the range of trichome densities among the potato cultivars selected for our experiments may simply not have been large enough.

Despite the fact that leafhopper abundance was not reduced by trichomes, the damage inflicted by leafhoppers on potato plants (i.e., foliar necrosis) was negatively correlated with trichomes (Figs. 2 and 3). Although

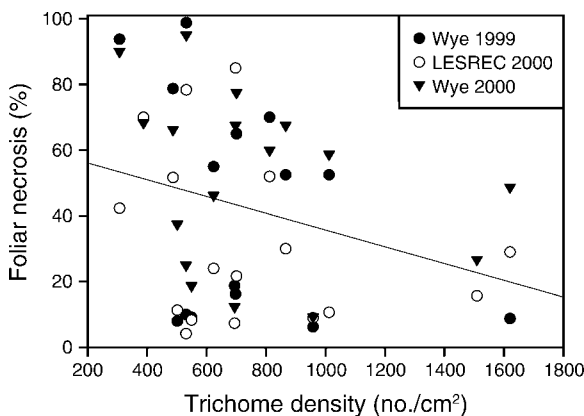


FIG. 2. The relationship between leafhopper-induced foliar necrosis and trichome density at Wye in 1999, LESREC in 2000, and Wye in 2000. Leafhopper-induced foliar necrosis was negatively associated with trichome density such that high-trichome plants received lower levels of leafhopper injury ($F_{1,175} = 17.71, P < 0.0001$). Each data point represents the mean value for each cultivar within a site. The plotted line represents a fitted regression.

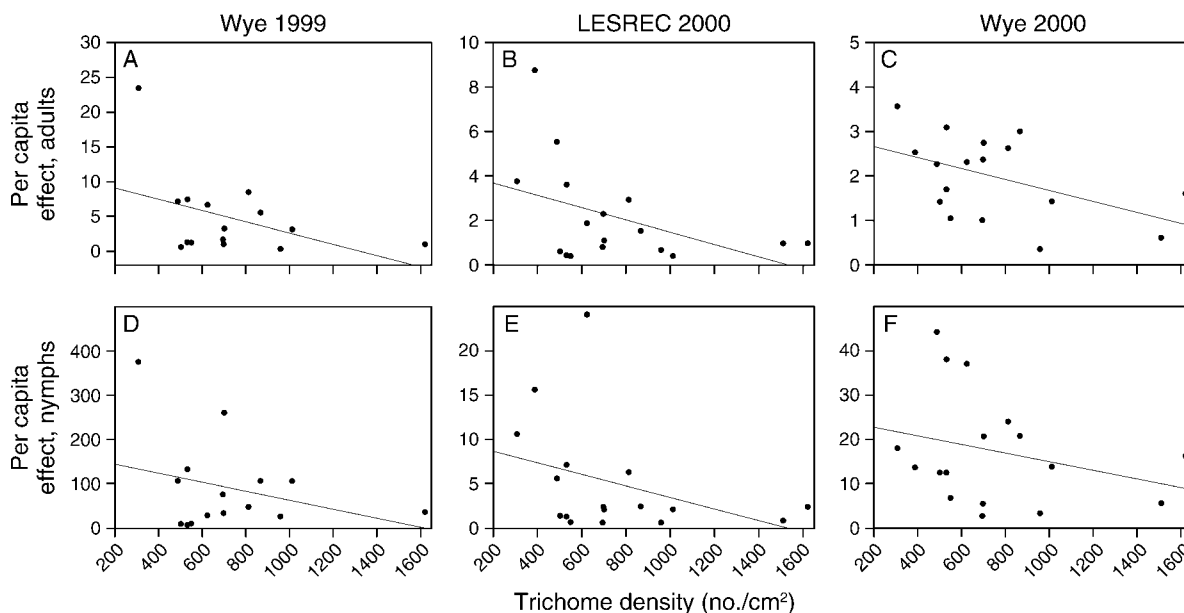


FIG. 3. The relationship between per capita plant damage by leafhopper (A–C) adults and (D–F) nymphs and trichome density at Wye in 1999, LESREC in 2000, and Wye in 2000, respectively. The per capita effect of leafhopper adults ($F_{1,174} = 25.95$, $P < 0.0001$) and nymphs ($F_{1,175} = 12.56$, $P = 0.0005$) on plant damage decreased with an increase in trichomes. The per capita effect was calculated as plant damage (percentage foliar necrosis) divided by leafhopper abundance. Each data point represents the mean value for each cultivar within a site. Plotted lines are fitted regressions.

symptoms of “hopperburn” are varied, necrosis of leaf tissue is considered the most damaging type of leafhopper injury and indicative of excessive consumption by sap-feeding insects (Backus et al. 2005). Importantly, feeding by leafhopper nymphs is thought to inflict greater damage than adults, perhaps explaining the discrepancy between trichome effects on abundance and damage (i.e., the abundance of nymphs was only weakly correlated with trichomes, whereas adults were strongly correlated).

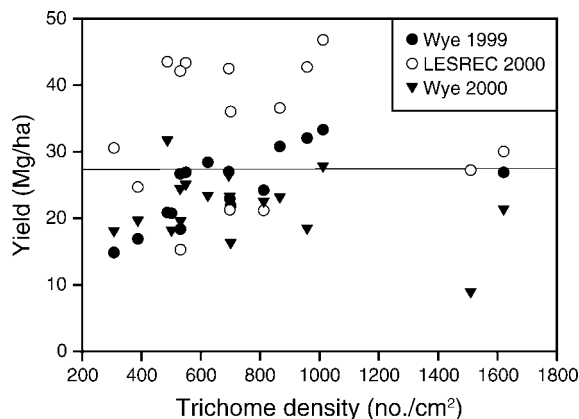


FIG. 4. The relationship between potato yield and trichome density at Wye in 1999, LESREC in 2000, and Wye in 2000. The expression of trichomes had no impact on potato yield ($F_{1,176} = 0.19$, $P = 0.6668$). Each data point represents the mean value for each cultivar within a site. The plotted line represents a fitted regression, which is not significant.

Nymphs are less mobile than adults and more likely to be impeded by trichomes (Medeiros and Tingey 2006). Because a reduction in herbivore damage is the ultimate measure of success for any given plant resistance trait, trichomes protected potato plants from leafhopper injury and thus appear to function in a defensive manner.

The costs of expressing trichomes have been explored in several plant systems and the results from these investigations have been equivocal (Agren and Schemske 1993, 1994, Elle et al. 1999, Hare et al. 2003, Hare and Elle 2004). We found no evidence of allocation costs for trichome production (Fig. 4). Thus, in the potato system tuber yield appears to be independent of foliar defense expression. Agricultural systems in general may be less prone to exhibit trade-offs between defense and growth given that crop plants are typically provided with supplementary water and nutrients. The logic underlying growth–defense trade-offs is largely based on plants having limited quantities of resources to allocate towards both processes. Thus, elevating overall levels of available resources via irrigation and fertilization may weaken the strength of growth–defense trade-offs. Osier and Lindroth (2006), for example, found that allocation costs of phenolic glycosides in aspen trees were only apparent under resource-limiting conditions (i.e., low nutrients and/or light), and not when abiotic resources occurred at high levels.

Similarly, we found no evidence for trade-offs between resistance (i.e., trichomes) and tolerance (Fig. 5). Although earlier studies suggested that resistance and

tolerance may represent alternative plant defense strategies (e.g., van der Meijden et al. 1988, Fineblum and Rausher 1995), more contemporary assessments of the topic have largely failed to confirm this as a universal trade-off in plants (Mauricio et al. 1997, de Jong and van der Meijden 2000, Tiffin 2000, Feroni et al. 2004). Notably, Leimu and Koricheva (2006) recently reviewed the evidence for resistance–tolerance trade-offs and found that the two defense strategies tended to be positively correlated in agricultural crops and negatively correlated in wild plants. We found weak evidence for a positive association between trichomes and tolerance, a trend that approached significance ($P = 0.0988$) for adult leafhoppers (Fig. 5A).

Despite the overall lack of evidence for costs of trichomes in the potato system, we add the caveat that defense costs are likely to be a quantitative phenomenon. Thus, costs will likely become more evident as the expression of that defense increases. The range of trichomes in our cultivars may not have been sufficient for detecting allocation costs. Similarly, the possibility always remains that other unmeasured variables may be contributing to the net effect of trichomes in the potato system. For instance, trichomes may impose ecological costs if they have opposing effects on different members of the potato herbivore community (van Dam and Hare 1998, Hare and Elle 2002, Andres and Connor 2003, Gruner et al. 2005). In other words, the same resistance trait that adversely affects one species may benefit a second co-occurring species. In soybean, for example, trichomes reduce leafhopper abundance, but increase the density of caterpillars (Styrsky et al. 2006). Aside from leafhoppers, the other dominant herbivore in the potato system is the Colorado potato beetle (*Leptinotarsa decemlineata*). Because we excluded beetles from our fields, we could not quantitatively assess the impact of trichomes on resistance and susceptibility to potato beetles. Reports from the literature, however, are mixed, with some studies finding no effects (Douches et al. 2001, Coombs et al. 2003, 2005, Cooper et al. 2007) and others demonstrating adverse effects (Kennedy and Sorenson 1985, Tingey 1991, Flanders et al. 1992, Yencho and Tingey 1994, Pelletier and Dutheil 2006). In a comprehensive field trial of 1686 potato accessions, trichomes were associated with resistance to both leafhoppers and Colorado potato beetles, as well as secondary pests such as aphids and flea beetles (Flanders et al. 1992; also see Tingey 1991). Thus, trichomes at the very least do not appear to directly benefit other herbivores in the potato community, and may in fact generate patterns of cross resistance whereby trichomes provide some baseline level of defense against the assemblage of sap-feeding and leaf-chewing insects.

In a related manner, an increase in trichome production may result in concurrent decreases in the expression of other resistance traits (Koricheva et al. 2004). For instance, Rudgers et al. (2004) found that trichomes and toxic leaf glands were negatively corre-

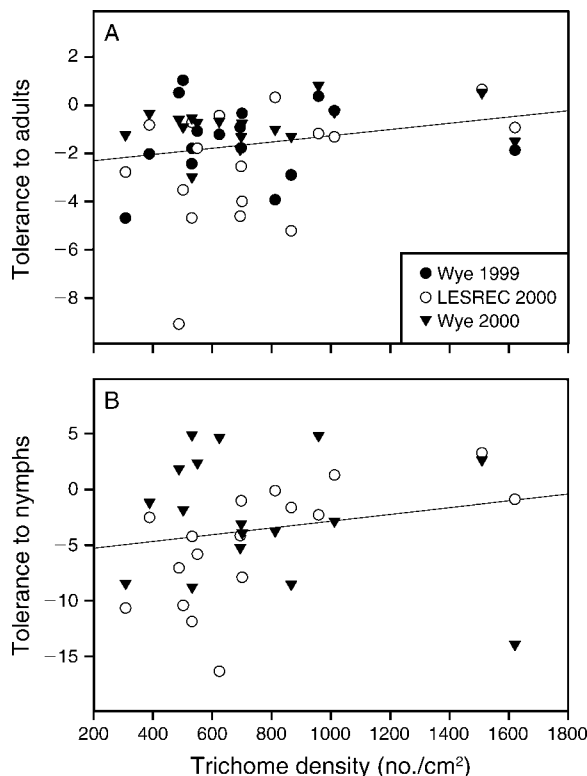


FIG. 5. The relationship between potato tolerance to leafhopper (A) adults and (B) nymphs and trichome density at Wye in 1999, LESREC in 2000, and Wye in 2000. Trichomes did not affect tolerance to either leafhopper adults ($F_{1,44} = 2.84$, $P = 0.0988$) or nymphs ($F_{1,30} = 1.58$, $P = 0.2185$). Tolerance values represent the slope of the line relating leafhopper abundance to plant yield. Each data point represents the mean value for each cultivar within a site. Plotted lines are fitted regressions (not significant).

lated among species in the cotton clade (Gossypieae). Potato plants possess several resistance traits, including secondary chemicals (e.g., glycoalkaloids, protease inhibitors) that can deter herbivorous pests of potato. Given that these compounds are known to play an important role in anti-herbivore defense, it is possible that such traits co-vary with trichome expression.

Conclusions

The importance of defense costs is deeply entrenched in many conceptual aspects of plant–herbivore interactions including optimal defense theory (Zangerl and Bazzaz 1992), constitutive vs. inducible defense strategies (Agrawal and Karban 1999, Heil and Baldwin 2002, Cipollini et al. 2003), and the maintenance of defense polymorphisms in natural plant populations (Kennedy and Barbour 1992, Elle et al. 1999, Hare et al. 2003). Similarly, the success of agricultural crop plants is contingent on their ability to simultaneously grow and defend. Thus, the significance of understanding both the causes and consequences of plant defense costs is a

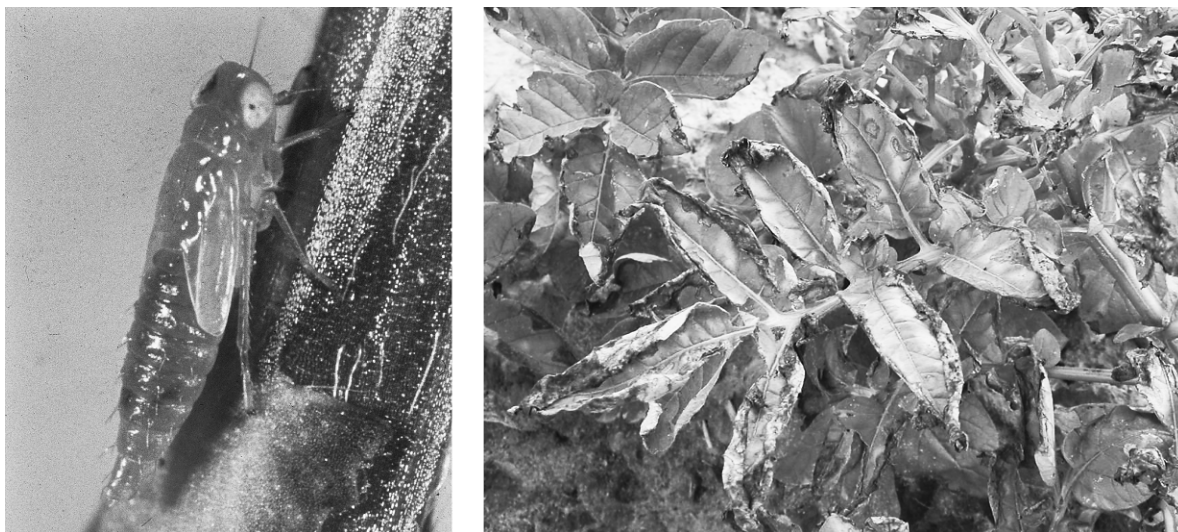


PLATE 1. (Left) A nymph of the leafhopper *Empoasca fabae* residing on the stem of a potato plant. Leafhopper nymphs predominantly feed on plant stems and the undersides of leaves, resulting in cupping, yellowing, and necrosis of foliage. (Right) Damage to potato foliage from excessive feeding by nymphs and adults of the leafhopper *E. fabae*. Heavy infestations of this insect result in "hopperburn" symptoms that lead to the development of necrotic lesions forming from the edges of leaves. Photo credits: G. P. Dively.

critical area of research in both basic and applied ecology. Based on our knowledge of the potato system, plant breeders have been successful in developing cultivars that are relatively well-defended, tolerate damage, and maintain yield. Whether or not these patterns would continue to prevail as plants are selected for increases in trichome density, above and beyond the upper limit tested in this study, is unknown. Ultimately, testing such defense and/or growth limits will provide an important feedback from agricultural science to basic plant–insect interactions and also provide the genetic basis for sustainable crop production.

ACKNOWLEDGMENTS

Stig Larsson and Dan Hare provided valuable comments on later stages of this manuscript. Funding for this research was provided by a USDA Competitive Research Grant (NRICGP, Entomology and Nematology, 00-35302-9334) to R. F. Denno and G. P. Dively.

LITERATURE CITED

- Agrawal, A. A., and R. Karban. 1999. Why induced defenses may be favored over constitutive strategies in plants. Pages 45–61 in R. Tollrian and C. D. Harvell, editors. *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, New Jersey, USA.
- Agrawal, A. A., S. Y. Strauss, and M. J. Stout. 1999. Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. *Evolution* 53:1093–1104.
- Agren, J., and D. W. Schemske. 1993. The cost of defense against herbivores: an experimental study of trichome production in *Brassica rapa*. *American Naturalist* 141:338–350.
- Agren, J., and D. W. Schemske. 1994. Evolution of trichome number in a naturalized population of *Brassica rapa*. *American Naturalist* 143:1–13.
- Andres, M. R., and E. F. Connor. 2003. The community-wide and guild-specific effects of pubescence on the folivorous insects of manzanitas *Arctostaphylos* spp. *Ecological Entomology* 28:383–396.
- Backus, E. A., M. S. Serrano, and C. M. Ranger. 2005. Mechanisms of hopperburn: an overview of insect taxonomy, behavior, and physiology. *Annual Review of Entomology* 50: 125–151.
- Bardner, R., and K. E. Fletcher. 1974. Insect infestations and their effects on the growth and yield of field crops: a review. *Bulletin of Entomological Research* 64:141–160.
- Bergelson, J., and C. B. Purrington. 1996. Surveying patterns in the cost of resistance in plants. *American Naturalist* 148:536–558.
- Bolter, C. J., and M. A. Jongsma. 1995. Colorado potato beetles (*Leptinotarsa decemlineata*) adapt to proteinase inhibitors induced in potato leaves by methyl jasmonate. *Journal of Insect Physiology* 41:1071–1078.
- Bottrell, D. G., and P. L. Adkisson. 1977. Cotton insect pest management. *Annual Review of Entomology* 22:451–481.
- Cancelado, R. E., and E. B. Radcliffe. 1979. Action thresholds for potato leafhopper *Empoasca fabae* on potatoes in Minnesota. *Journal of Economic Entomology* 72:566–569.
- Cipollini, D., C. B. Purrington, and J. Bergelson. 2003. Costs of induced responses in plants. *Basic and Applied Ecology* 4:79–89.
- Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–899.
- Coombs, J. J., D. S. Douches, S. G. Cooper, E. J. Grafius, W. L. Pett, and D. D. Moyer. 2005. Combining natural and engineered host plant resistance mechanisms in potato for Colorado potato beetle: choice and no-choice field studies. *Journal of the American Society for Horticultural Science* 130:857–864.
- Coombs, J. J., D. S. Douches, W. B. Li, E. J. Grafius, and W. L. Pett. 2003. Field evaluation of natural, engineered, and combined resistance mechanisms in potato for control of Colorado potato beetle. *Journal of the American Society for Horticultural Science* 128:219–224.

- Cooper, S. G., D. S. Douches, J. J. Coombs, and E. J. Grafius. 2007. Evaluation of natural and engineered resistance mechanisms in potato against Colorado potato beetle in a no-choice field study. *Journal of Economic Entomology* 100: 573–579.
- de Jong, T. J., and E. van der Meijden. 2000. On the correlation between allocation to defence and regrowth in plants. *Oikos* 88:503–508.
- Donaldson, J. R., and R. L. Lindroth. 2007. Genetics, environment, and their interaction determine efficacy of chemical defense in trembling aspen. *Ecology* 88:729–739.
- Douches, D. S., T. J. Kisha, J. J. Coombs, W. Li, W. L. Pett, and E. J. Grafius. 2001. Effectiveness of natural and engineered host plant resistance in potato to the Colorado potato beetle. *Hortscience* 36:967–970.
- Elle, E., N. M. van Dam, and J. D. Hare. 1999. Cost of glandular trichomes, a “resistance” character in *Datura wrightii* Regel (Solanaceae). *Evolution* 53:22–35.
- Fineblum, W. L., and M. D. Rausher. 1995. Trade-off between resistance and tolerance to herbivore damage in a morning glory. *Nature* 377:517–520.
- Flanders, K. L., J. G. Hawkes, E. B. Radcliffe, and F. I. Lauer. 1992. Insect resistance in potatoes: sources, evolutionary relationships, morphological and chemical defenses, and ecogeographical associations. *Euphytica* 61:83–111.
- Foroni, J., J. Nunez-Farfán, P. L. Valverde, and M. D. Rausher. 2004. Evolution of mixed strategies of plant defense allocation against natural enemies. *Evolution* 58:1685–1695.
- Gassmann, A. J., and J. D. Hare. 2005. Indirect cost of a defensive trait: variation in trichome type affects the natural enemies of herbivorous insects on *Datura wrightii*. *Oecologia* 144:62–71.
- Gruner, D. S., A. D. Taylor, and R. E. Forkner. 2005. The effects of foliar pubescence and nutrient enrichment on arthropod communities of *Metrosideros polymorpha* (Myrtales). *Ecological Entomology* 30:428–443.
- Hare, J. D., and E. Elle. 2002. Variable impact of diverse insect herbivores on dimorphic *Datura wrightii*. *Ecology* 83:2711–2720.
- Hare, J. D., and E. Elle. 2004. Survival and seed production of sticky and velvety *Datura wrightii* in the field: a five-year study. *Ecology* 85:615–622.
- Hare, J. D., E. Elle, and N. M. van Dam. 2003. Costs of glandular trichomes in *Datura wrightii*: a three-year study. *Evolution* 57:793–805.
- Heil, M., and I. T. Baldwin. 2002. Fitness costs of induced resistance: emerging experimental support for a slippery concept. *Trends in Plant Science* 7:61–67.
- Herns, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67:283–335.
- Iwao, K., and M. D. Rausher. 1997. Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *American Naturalist* 149:316–335.
- Kaplan, I., G. P. Dively, and R. F. Denno. 2008. Variation in tolerance and resistance to the leafhopper *Empoasca fabae* (Hemiptera: Cicadellidae) among potato cultivars: implications for action thresholds. *Journal of Economic Entomology* 101:959–968.
- Karban, R., and A. A. Agrawal. 2002. Herbivore offense. *Annual Review of Ecology and Systematics* 33:641–664.
- Kennedy, G. G. 2003. Tomato, pests, parasitoids, and predators: tritrophic interactions involving the genus *Lycopersicon*. *Annual Review of Entomology* 48:51–72.
- Kennedy, G. G., and J. D. Barbour. 1992. Resistance variation in natural and managed systems. Pages 13–41 in R. S. Fritz and E. L. Simms, editors. *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. University of Chicago Press, Chicago, Illinois, USA.
- Kennedy, G. G., and C. F. Sorenson. 1985. Role of glandular trichomes in the resistance of *Lycopersicon hirsutum glabratum* to Colorado potato beetle (Coleoptera, Chrysomelidae). *Journal of Economic Entomology* 78:547–551.
- Koricheva, J., H. Nykänen, and E. Gianoli. 2004. Meta-analysis of trade-offs among plant antiherbivore defenses: Are plants jacks-of-all-trades, masters of all? *American Naturalist* 163:E64–E75.
- Krischik, V. A., and R. F. Denno. 1983. Individual, population and geographic patterns in plant defense. Pages 463–512 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.
- Leimu, R., and J. Koricheva. 2006. A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: combining the evidence from ecological and agricultural studies. *Oikos* 112:1–9.
- Levin, D. A. 1973. Role of trichomes in plant defense. *Quarterly Review of Biology* 48:3–15.
- Lovinger, A., D. Liewehr, and W. O. Lamp. 2000. Glandular trichomes on alfalfa impede searching behavior of the potato leafhopper parasitoid. *Biological Control* 18:187–192.
- Marquis, R. J. 1992. Selective impact of herbivores. Pages 301–325 in R. S. Fritz and E. L. Simms, editors. *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. University of Chicago Press, Chicago, Illinois, USA.
- Mauricio, R., M. D. Rausher, and D. S. Burdick. 1997. Variation in the defense strategies of plants: Are resistance and tolerance mutually exclusive? *Ecology* 78:1301–1311.
- Medeiros, A. H., I. Delalibera, and W. M. Tingey. 2005. Aspects of potato leafhopper (Homoptera: Cicadellidae) biology on *Solanum berthaultii* and other potato genotypes. *Journal of Economic Entomology* 98:1704–1709.
- Medeiros, A. H., and W. M. Tingey. 2006. Glandular trichomes of *Solanum berthaultii* and its hybrids with *Solanum tuberosum* affect nymphal emergence, development, and survival of *Empoasca fabae* (Homoptera: Cicadellidae). *Journal of Economic Entomology* 99:1483–1489.
- Osier, T. L., and R. L. Lindroth. 2006. Genotype and environment determine allocation to and costs of resistance in quaking aspen. *Oecologia* 148:293–303.
- Parker, M. A. 1992. Constraints on the evolution of resistance to pests and pathogens. Pages 181–197 in P. G. Ayres, editor. *Pests and pathogens: plant responses to foliar attack*. BIOS Scientific Publishers, Oxford, UK.
- Pelletier, Y., and J. Duthéil. 2006. Behavioural responses of the Colorado potato beetle to trichomes and leaf surface chemicals of *Solanum tarjense*. *Entomologia Experimentalis et Applicata* 120:125–130.
- Price, P. W., C. E. Bouton, P. Gross, B. A. McPherson, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11:41–65.
- Rudgers, J. A., S. Y. Strauss, and J. F. Wendel. 2004. Trade-offs among anti-herbivore resistance traits: insights from Gossypieae (Malvaceae). *American Journal of Botany* 91: 871–880.
- SAS Institute. 2002. SAS statistical software. Version 9.1. SAS Institute, Cary, North Carolina, USA.
- Simms, E. L. 1992. Costs of plant resistance to herbivory. Pages 392–425 in R. S. Fritz and E. L. Simms, editors. *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. University of Chicago Press, Chicago, Illinois, USA.
- Smedegaard-Petersen, V. 1985. The limiting effect of disease resistance on yield. *Annual Review of Phytopathology* 23: 475–490.

- Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. *Quarterly Review of Biology* 78:23–55.
- Stinchcombe, J. R., and M. D. Rausher. 2001. Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory, *Ipomoea hederacea*. *American Naturalist* 158:376–388.
- Stowe, K. A., R. J. Marquis, C. G. Hochwender, and E. L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology and Systematics* 31:565–595.
- Strauss, S. Y., and A. A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14:179–185.
- Strauss, S. Y., J. A. Rudgers, J. A. Lau, and R. E. Irwin. 2002. Direct and ecological costs of resistance to herbivory. *Trends in Ecology and Evolution* 17:278–285.
- Styrsky, J. D., I. Kaplan, and M. D. Eubanks. 2006. Plant trichomes indirectly enhance tritrophic interactions involving a generalist predator, the red imported fire ant. *Biological Control* 36:375–384.
- Tiffin, P. 2000. Are tolerance, avoidance, and antibiosis evolutionarily and ecologically equivalent responses of plants to herbivores? *American Naturalist* 155:128–138.
- Tingey, W. M. 1991. Potato glandular trichomes: defensive activity against insect attack. *ACS Symposium Series* 449: 126–135.
- van Dam, N. M., and I. T. Baldwin. 1998. Costs of jasmonate-induced responses in plants competing for limited resources. *Ecology Letters* 1:30–33.
- van Dam, N. M., and J. D. Hare. 1998. Differences in distribution and performance of two sap-sucking herbivores on glandular and non-glandular *Datura wrightii*. *Ecological Entomology* 23:22–32.
- Vandenberg, P., and D. F. Matzinger. 1970. Genetic diversity and heterosis in *Nicotiana*. III. Crosses among tobacco introductions and flue-cured varieties. *Crop Science* 10:437–440.
- van der Meijden, E., M. Wijn, and H. J. Verkaar. 1988. Defense and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51:355–363.
- Walgenbach, J. F., and J. A. Wyman. 1985. Potato leafhopper (Homoptera: Cicadellidae) feeding damage at various potato growth stages. *Journal of Economic Entomology* 78:671–675.
- Walgenbach, J. F., J. A. Wyman, and D. B. Hogg. 1985. Evaluation of sampling methods and development of sequential sampling plan for potato leafhopper (Homoptera, Cicadellidae) on potatoes. *Environmental Entomology* 14: 231–236.
- Welter, S. C., and J. W. Steggall. 1993. Contrasting the tolerance of wild and domesticated tomatoes to herbivory: agroecological implications. *Ecological Applications* 3:271–278.
- Wise, M. J. 2007. Evolutionary ecology of resistance to herbivory: an investigation of potential genetic constraints in the multiple-herbivore community of *Solanum carolinense*. *New Phytologist* 175:773–784.
- Yencho, G. C., and W. M. Tingey. 1994. Glandular trichomes of *Solanum berthaultii* alter host preference of the Colorado potato beetle, *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata* 70:217–225.
- Zangerl, A. R., and F. A. Bazzaz. 1992. Theory and pattern in plant defense allocation. Pages 363–391 in R. S. Fritz and E. L. Simms, editors. *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. University of Chicago Press, Chicago, Illinois, USA.
- Zavala, J. A., A. G. Patankar, K. Gase, and I. T. Baldwin. 2004. Constitutive and inducible trypsin proteinase inhibitor production incurs large fitness costs in *Nicotiana attenuata*. *Proceedings of the National Academy of Sciences (USA)* 101: 1607–1612.

APPENDIX

Trichome densities, origin, year, and cross location of each potato cultivar used in experiments (*Ecological Archives* A019-035-A1).