Variation in Tolerance and Resistance to the Leafhopper *Empoasca fabae* (Hemiptera: Cicadellidae) Among Potato Cultivars: Implications for Action Thresholds

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ABSTRACT The potato leafhopper, *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae), is an emerging pest of potato and insecticide applications to control this insect have increased in recent years. Based on field observations of leafhopper–crop dynamics, however, currently recommended action thresholds seem to be overly conservative. As a result, we initiated two experiments designed to quantify the impact of leafhoppers on potato yield, and determine how the magnitude of this effect changes among cultivars. In experiment 1, leafhoppers were manipulated (control versus insecticide-treated plots) on 17 potato varieties. In experiment 2, three cultivars (Superior, Atlantic, and Snowden) were planted representing early-, mid-, and late-season maturing lines, and six insecticide spray regimes were imposed (early-, late-, and full-season applications at high and low rates). In both experiments, leafhopper abundance, plant damage, and potato yield were measured. Overall, leafhoppers reduced yield in control plots by 15.7% relative to insecticide-treated plots. Leafhopper impact, however, varied among cultivars; a significant effect of leafhoppers on yield was detected in 6, 12, and 59% of cultivars tested in each of three trials. Of the 44 cases in which leafhoppers exceeded action thresholds, yield loss was only documented in 13 cases. Data from these experiments provide evidence that such variable effects of leafhoppers on yield are explained by cultivar-specific resistance and tolerance traits. Our results suggest that potato growers can accept higher leafhopper densities than current thresholds recommend, particularly when cultivating resistant and/or tolerant varieties.

KEY WORDS host plant resistance, tolerance, potato leafhopper, sap-feeding insect, economic threshold

The potato leafhopper, *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae), is a sap-feeding insect that attacks a variety of plants in the eastern United States, including several crop plants of economic importance [e.g., potato, *Solanum tuberosum* L.; alfalfa, *Medicago sativa* L.; and soybean, *Glycine max* (L.) Merr.] (Lamp et al. 1994). The pest status of this insect on potato is particularly noteworthy because, historically, leafhoppers were considered secondary pests that rarely reached outbreak densities in potato fields (Dively et al. 1999). Foliar insecticide treatments to control the Colorado potato beetle *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae), largely considered the most devastating insect pest of potato, incidentally suppressed leafhoppers, and thus insecticide applications specifically targeting leafhoppers were infrequent (Ferro 1986, Hare 1990, Dively et al. 1999). This situation changed abruptly in 1995 when the new systemic insecticide imidacloprid (Admire) was registered and rapidly replaced all other means of chemical control (Dively et al. 1999). Imidacloprid is extremely effective against Colorado potato beetle and has some activity against potato leafhoppers if used at planting time at the high-label rate (Olson et al. 2000). However, because of its expense most potato growers apply imidacloprid in-furrow at the low-label rate for Colorado potato beetle. Thus, its residual systemic activity is ineffective when leafhoppers colonize potato fields in June (e.g., Nault et al. 2004).

With the adoption of imidacloprid and commensurate decreases in foliar insecticide used for Colorado potato beetle management, economic problems with potato leafhoppers have drastically increased (Dively et al. 1999). Because of the unpredictable risks of crop loss and lack of decision rules for potato varieties grown in the mid-Atlantic area, growers have adopted a conservative program of applying foliar insecticides at the early signs of leafhopper activity. In 1997 and 1998, potato leafhopper populations reached record high levels in the northeastern United States, and many potato fields were treated multiple times with insecticides (Dively et al. 1999). In 1998, for example, the entire acreage produced by the Ruf Potato Company in Maryland was treated three times for leafhoppers (G.P.D., unpublished data).

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Currently, leafhopper action thresholds, based on sweep-net sampling of adults and visual counts of nymphs, are used in scouting programs (Walgenbach et al. 1985, Dively et al. 1995). Such programs typically use the widely recommend threshold of one adult per sweep, one nymph per 10 leaves, or both (Ferro 1986, Maryland Cooperative Extension 2006). These guidelines, however, have been derived from data collected on potato varieties grown in the North Central states and from experimentation established on the basis of worst-case scenarios (Cancelado and Radcliffe 1979, Walgenbach and Wyman 1985). Ongoing research in Maryland suggests that certain potato varieties may tolerate far greater densities than these thresholds suggest. Thus, the primary objective of this study is to experimentally evaluate the impact of leafhoppers on commonly planted potato cultivars and to ultimately compare these results with the currently endorsed action thresholds.

Materials and Methods

Experiment 1. During summers 1999 and 2000, experiments were initiated to 1) assess the impact of different potato varieties on leafhopper abundance and plant damage (i.e., determine varietal differences in *resistance* to leafhoppers), and 2) measure the effect of leafhoppers on potato yield across varieties (i.e., assess varietal differences in tolerance to leafhoppers). 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). Each plot was separated from neighboring plots by 2 m to minimize interplot dispersal by adult leafhoppers. In 1999, this experiment was conducted at the Wye Research and Education Center (Queenstown, MD) (hereafter referred to as Wye), with four replicates of each treatment combination. In 2000, the experiment was again conducted at the Wye ($n = 4$ replications) and also at the Lower Eastern Shore Research and Education Center (Salisbury, MD) (hereafter referred to as LESREC; $n = 4$ replications). One of the four blocks at LESREC was inadvertently destroyed in late-July thus leaving four replications for an assessment of early-season leafhopper abundance data, but only three replications for a determination of plant damage ratings and yield later in the season.

In 1999, we selected 16 commonly planted potato varieties, and in 2000 we included an additional cultivar resulting in 17 total varieties (see figure legends for a list of varieties). 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 sprays. Thus, 128 plots (=16 potato varieties × leafhoppers present/absent × 4 replicates) were established in 1999, and 136 plots (=17 potato varieties × leafhoppers present/absent × 4 replicates) were created at each field site in 2000. The insecticide permethrin (Ambush, Syngenta Crop Protection, Inc., Greensboro, NC) was applied as a foliar treatment (56 g [AI]/ha) by using a boom sprayer delivering 27 liters/ha spray volume.

Foliar sprays were largely successful at suppressing leafhopper populations. Densities of adults and nymphs were near zero in treated plots, despite sampling several days after insecticide applications. 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 a perimeter three-row border of potato plants surrounding the field with insecticide (permethrin). This procedure killed most of the immigrating adults and any colonists were removed by hand. As a result, our insecticide-treated plots primarily manipulated the abundance of leafhoppers and minimized confounding effects attributable to other insects.

Once a week from early June through 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 also were visually rated for evidence of leafhopper damage (% cupping, yellowing, and necrosis) by two separate observers. The average of these two observations was used as the plot mean. In early August, potato tubers were harvested from the ground, weighed, and the total yield for each plot was calculated.

Because leafhoppers and their associated damage did not occur in sprayed plots, we only used abundance and plant damage data from control plots to assess varietal effects. The impact of potato variety on leafhopper abundance (adults and nymphs) and plant damage (cupping, yellowing, and necrosis) was assessed using analysis of variance (ANOVA) (PROC MIXED; all statistical analyses were performed using SAS, version 9.1). For these analyses, plant variety was considered a fixed effect whereas block was a random effect. Only the date when leafhoppers occurred at peak density (early-mid July) was used for statistical analyses. We used a peak-density approach instead of repeated-measures analyses because leafhopper densities were relatively low during nonpeak sampling dates. Because leafhopper densities and environmental conditions differed drastically between sites and years, we separately analyzed treatment effects at each farm in 1999 and 2000. Counts of adults and nymphs were square-root transformed and the proportion of plant foliage expressing damage symptoms was arcsine square-root transformed to satisfy ANOVA assumptions.

The effects of plant variety and leafhopper injury on potato yield were assessed using two-way ANOVA with plant variety and insecticide treatment as fixed effects, and block as a random effect (PROC MIXED). The pdiff option in SAS was used to compare least-squares means between control and insecticide-treated plots for each variety. Percent yield loss due to leafhoppers was calculated as $[(Y_S - Y_C)/Y_S] \times 100$, where Y_S is the yield in sprayed plots (leafhoppers

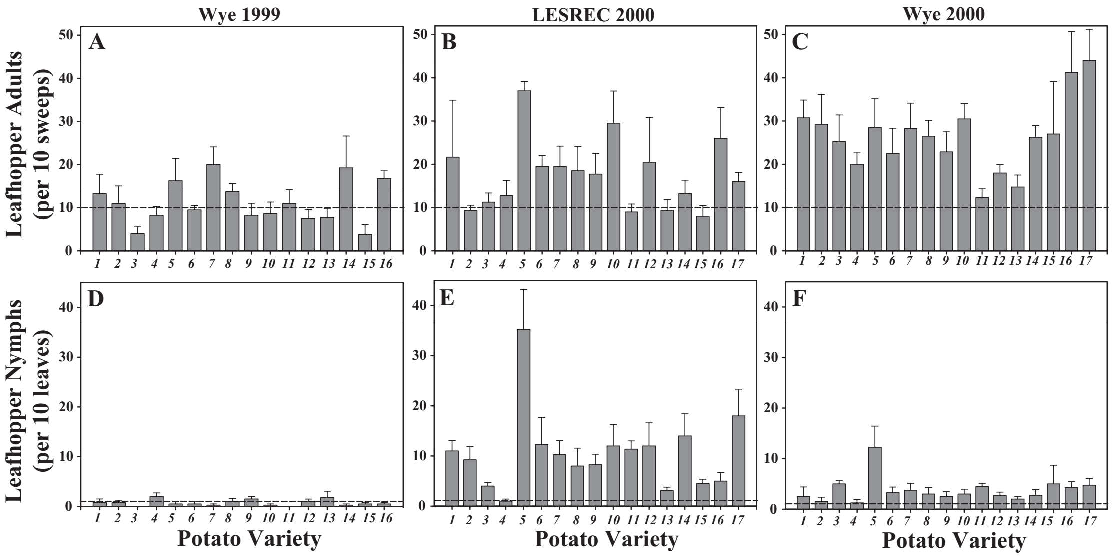

Fig. 1. Peak abundance of the adults (A–C) and nymphs (D–F) of *E. fabae* at Wye in 1999, LESREC in 2000, and Wye in 2000, respectively. Means + SE. Dashed lines indicate the current action thresholds for potato leafhopper adults and nymphs used throughout the eastern United States. Potato cultivated varieties: 1, Andover; 2, Caribe; 3, BelRus; 4, Chieftan; 5, Norkotah; 6, Reba; 7, Yukon Gold; 8, Katahdin; 9, Superior; 10, Superior NewLeaf (Bt); 11, Atlantic; 12, Atlantic NewLeaf (Bt); 13, Snowden; 14, Kennibec; 15, Red Norland; 16, Red Pontiac; 17, Green Mountain.

removed) and Y_C is the yield in control plots (leafhoppers present).

Because the above-mentioned analyses do not specifically address the issue of plant tolerance to leafhopper feeding (i.e., varietal differences in leafhopper impact on yield could result from variation in resistance, tolerance, or both), we performed a series of regressions with leafhopper abundance as the predictor variable and plant yield as the response variable (PROC REG). Because leafhopper nymphs were found at very low densities in 1999 we used adult density as the predictor variable. Separate regressions were conducted for each variety, and we analyzed data separately from different sites and years because environmental factors often strongly affect the degree of plant tolerance to insect herbivory (Wise and Abrahamson 2005).

Experiment 2. In summer 1998, we conducted an experiment at the Wye research site that was similar in design to the above-described experiment. However, instead of 17 varieties, this experiment focused on three specific potato varieties that were selected because of differences in growth. 'Superior,' 'Atlantic,' and 'Snowden' are early-, mid-, and late-season maturing cultivars, respectively. Therefore, we hypothesized that phenological differences in plant–pest dynamics may result in differential effects of leafhoppers on yield among these three cultivars. Also, unlike the above-mentioned experiment in which leafhoppers were manipulated at two levels (sprayed and unsprayed), this experiment varied the insecticide spraying regime at a much finer scale. Specifically, there were six levels of leafhopper manipulation: 1) untreated control, 2) early-season low rate, 3) early-season high rate, 4) late-season low rate, 5) late-season high rate, and 6) full-season high rate. The insecticide permethrin was applied as a foliar spray once a week at either high (56 g [AI]/ha) or low (5.6 g [AI]/ha) rates. Although the high rate applications likely killed all exposed leafhoppers, low rate applications also may have induced sublethal effects on the behavior of surviving leafhoppers (i.e., seizure of feeding). Early-season spray regimes lasted for the 2 wk when leafhoppers first began colonizing potato fields (last 2 wk of June). Late-season spray regimes occurred during the first 3 wk of July, and the full-season treatment lasted for the entire 5-wk period.

Plant variety (three levels) and leafhopper manipulation (six levels) were fully crossed in a factorial design (18 total treatment combinations), and plots were organized using a randomized, complete block arrangement ($n = 6$ plot replications of each treatment combination). As in experiment 1, leafhoppers (adults and nymphs) and plant damage (% cupping, yellowing, and necrosis) were estimated weekly. The only methodological difference was that six sweeps per plot were used for sampling adult leafhoppers in this experiment instead of the 10 sweeps used in experiment 1. Potato tubers were harvested in late July, and total yield was calculated for each plot.

The effects of potato variety and insecticide spray regime were assessed using a two-way ANOVA with variety and spray regime as fixed effects and block as a random effect (PROC MIXED). Peak leafhopper abundance (adults and nymphs), plant damage (% cupping, yellowing, and necrosis), and potato yield were used as response variables. Counts of adults and nymphs were square root transformed, and the pro-

Table 1. ANOVA results (exp 1) assessing the impact of potato variety on leafhopper abundance (adults and nymphs) and plant damage (% cupping, yellowing, and necrosis) at two study sites (Wye and LESREC) and years (1999 and 2000)

	Wye 1999			LESREC 2000			Wye 2000		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
Leafhopper abundance									
Adults	2.37	15, 44	**0.014**	3.20	16, 46	**0.001**	2.72	16, 48	**0.004**
Nymphs	1.37	15, 45	0.205	4.45	16, 47	**<0.001**	2.26	16, 48	**0.015**
Plant damage									
% cupping	13.64	14, 42	**<0.001**	13.51	16, 32	**<0.001**	3.30	16, 47	**<0.001**
% yellowing	5.39	14, 42	**<0.001**	1.93	16, 32	0.056	5.43	16, 47	**<0.001**
% necrosis	27.78	15, 44	**<0.001**	3.88	16, 32	**<0.001**	7.65	16, 47	**<0.001**

Significant *P* values (<0.05) are in bold.

portion of foliage displaying damage symptoms was arcsine square root transformed before statistical analyses. Fisher least significant difference (LSD) test was used to statistically distinguish differences in yield between each treatment.

Results

Experiment 1. The peak abundance of leafhoppers was highly variable across potato cultivars at each site and year (Fig. 1; Table 1). The only exception occurred at the Wye site during 1999 where nymphs were unaffected by plant variety (Fig. 1D), although this result is likely attributable to the unusually low ambient densities that occurred in this year. Leafhoppers in unsprayed control plots exceeded their action threshold in 75% (12/16) of the varieties cultivated in 1999 and 100% (17/17) of the varieties in 2000.

Similarly, leafhopper damage symptoms (foliar cupping, yellowing, and necrosis) were highly variable among cultivars (Fig. 2; Table 1). However, the expression of plant damage symptoms was not always

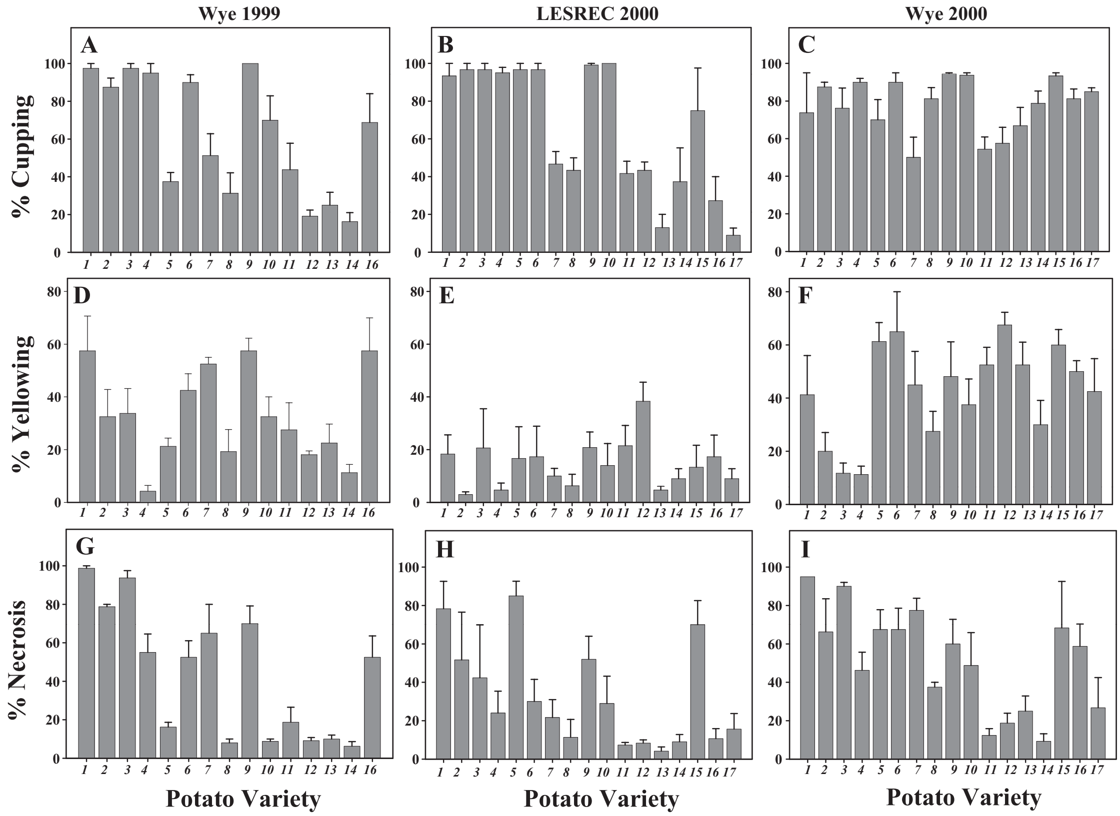

Fig. 2. Percentage of potato foliage displaying damage symptoms from *E. fabae* injury, including cupping (A-C), yellowing (D-F), and necrosis (G-I) at Wye in 1999, LESREC in 2000, and at Wye in 2000, respectively. Means + SE. Potato cultivated varieties: 1, Andover; 2, Caribe; 3, BelRus; 4, Chieftan; 5, Norkotah; 6, Reba; 7, Yukon Gold; 8, Katahdin; 9, Superior; 10, Superior NewLeaf (Bt); 11, Atlantic; 12, Atlantic NewLeaf (Bt); 13, Snowden; 14, Kennibec; 15, Red Norland; 16, Red Pontiac; 17, Green Mountain.

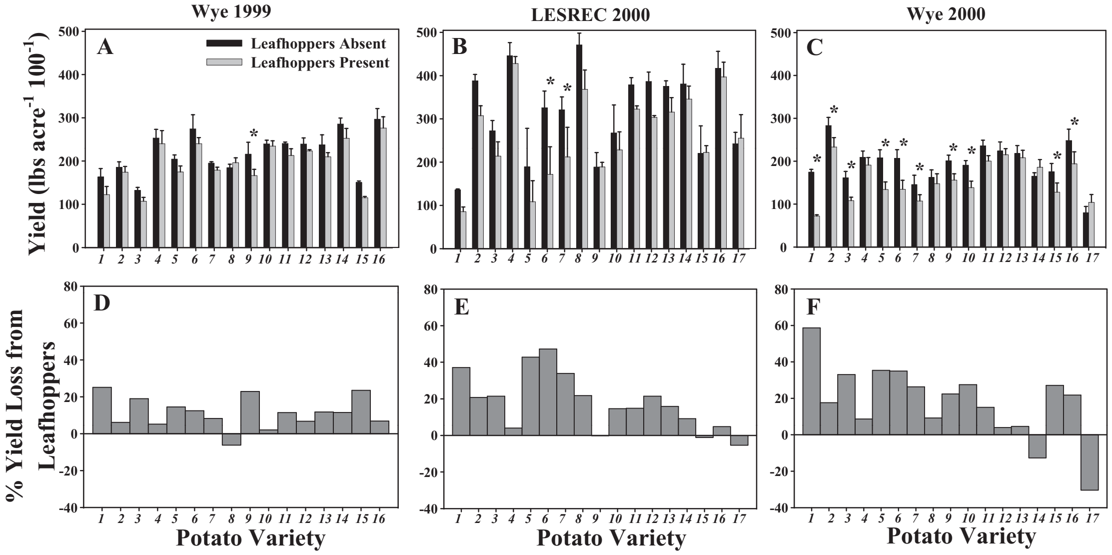

Fig. 3. The impact of *E. fabae* on the yield of 17 potato varieties at two different sites and years, including Wye in 1999 (A and D), LESREC in 2000 (B and E), and at Wye in 2000 (C and F). Means + SE. *, significant effect of leafhopper presence on potato yield ($P < 0.05$). Potato cultivated varieties: 1, Andover; 2, Caribe; 3, BelRus; 4, Chieftan; 5, Norkotah; 6, Reba; 7, Yukon Gold; 8, Katahdin; 9, Superior; 10, Superior NewLeaf (Bt); 11, Atlantic; 12, Atlantic NewLeaf (Bt); 13, Snowden; 14, Kennibec; 15, Red Norland; 16, Red Pontiac; 17, Green Mountain.

directly associated with leafhopper abundance (i.e., certain varieties expressed damage differently while hosting the same density of leafhoppers). In the 1999 experiment at Wye, for example, the densities of leafhoppers on varieties one and eight were extremely similar (Fig. 1A and D). Yet nearly 100% of the leaves in plots of variety 1 expressed necrosis, whereas <10% of foliage in variety 8 displayed necrosis (Fig. 2G).

The overall impact of leafhoppers on potato yield was significant at each site and year, demonstrating that leafhoppers generally reduced yield (Wye 1999: $F = 18.09$; df = 1, 93; $P < 0.001$; Wye 2000: $F = 74.24$; df = 1, 98; $P < 0.001$; LESREC 2000: $F = 17.47$; df = 1, 66; $P < 0.001$) (Fig. 3). Average yield loss attributable to leafhoppers was 11, 18, and 18% at Wye in 1999, at LESREC in 2000, and at Wye in 2000, respectively. This adverse effect, however, varied among cultivars and ranged from ≈60% yield loss (Fig. 3F, variety 1) to ≈30% yield gain (Fig. 3F, variety 17). Leafhoppers significantly reduced yield in 6% (1/16) of cultivars at Wye in 1999, 12% (2/17) of cultivars at LESREC in 2000, and 59% (10/17) of cultivars at Wye in 2000.

As expected, plant cultivar affected potato yield (Wye 1999: $F = 19.67$; df = 15, 93; $P < 0.001$; LESREC 2000: $F = 12.46$; df = 16, 66; $P < 0.001$; Wye 2000: $F = 22.92$; df = 16, 98; $P < 0.001$). Also, the interaction between leafhopper treatment and potato cultivar was significant in one of the three trials (Wye 1999: $F = 0.46$; df = 15, 93; $P = 0.954$; LESREC 2000: $F = 0.67$; df = 16, 66; $P = 0.811$; Wye 2000: $F = 3.11$; df = 16, 98; $P < 0.001$).

Overall, leafhopper density was a poor predictor of plant yield (Fig. 4), suggesting that most potato cultivars are relatively tolerant of leafhoppers. Notably, only 6% of all regressions of leafhopper abundance on plant yield were significant (3/50 regressions; Wye 1999, variety 5: slope = −1.779, SE = 0.694, $P = 0.043$; LESREC 2000, variety 2: slope = −9.094, SE = 2.168, $P = 0.014$; Wye 2000, variety 1, slope = −2.981, SE = 0.491, $P < 0.001$).

Experiment 2. Insecticide spray regimes were successful at creating a gradient of leafhopper densities within each potato variety (Superior, Atlantic, and Snowden), although leafhopper abundance did not differ among the three varieties (Fig. 5; Table 2). Leafhoppers exceeded action thresholds in the untreated control and early-season insecticide treated plots; in many cases, the densities in these plots were at least double or even triple the recommended action thresholds (i.e., nymphs attained peak densities up to 20× the threshold, and adults reached densities up to 7× the threshold).

Insecticide regimes also generated variation in leafhopper damage symptoms that were expressed in potato foliage (Fig. 6; Table 2). Interestingly, the interaction between insecticide treatment and plant cultivar was significant for all three damage ratings, suggesting again that cultivars respond very differently to leafhopper injury.

Insecticide treatments affected the yield of Atlantic ($F = 3.01$; df = 5, 25; $P = 0.029$) (Fig. 7A) and Snowden varieties ($F = 6.27$; df = 5, 25; $P < 0.001$) (Fig. 7B). The yield of Superior, however, was unaffected by insecticides ($F = 2.35$; df = 5, 25; $P = 0.070$) (Fig. 7C), although this effect approached significance. Notably, Atlantic was the only cultivar in which yield from the untreated control plots did not differ from yield in full-season insecticide-treated plots.

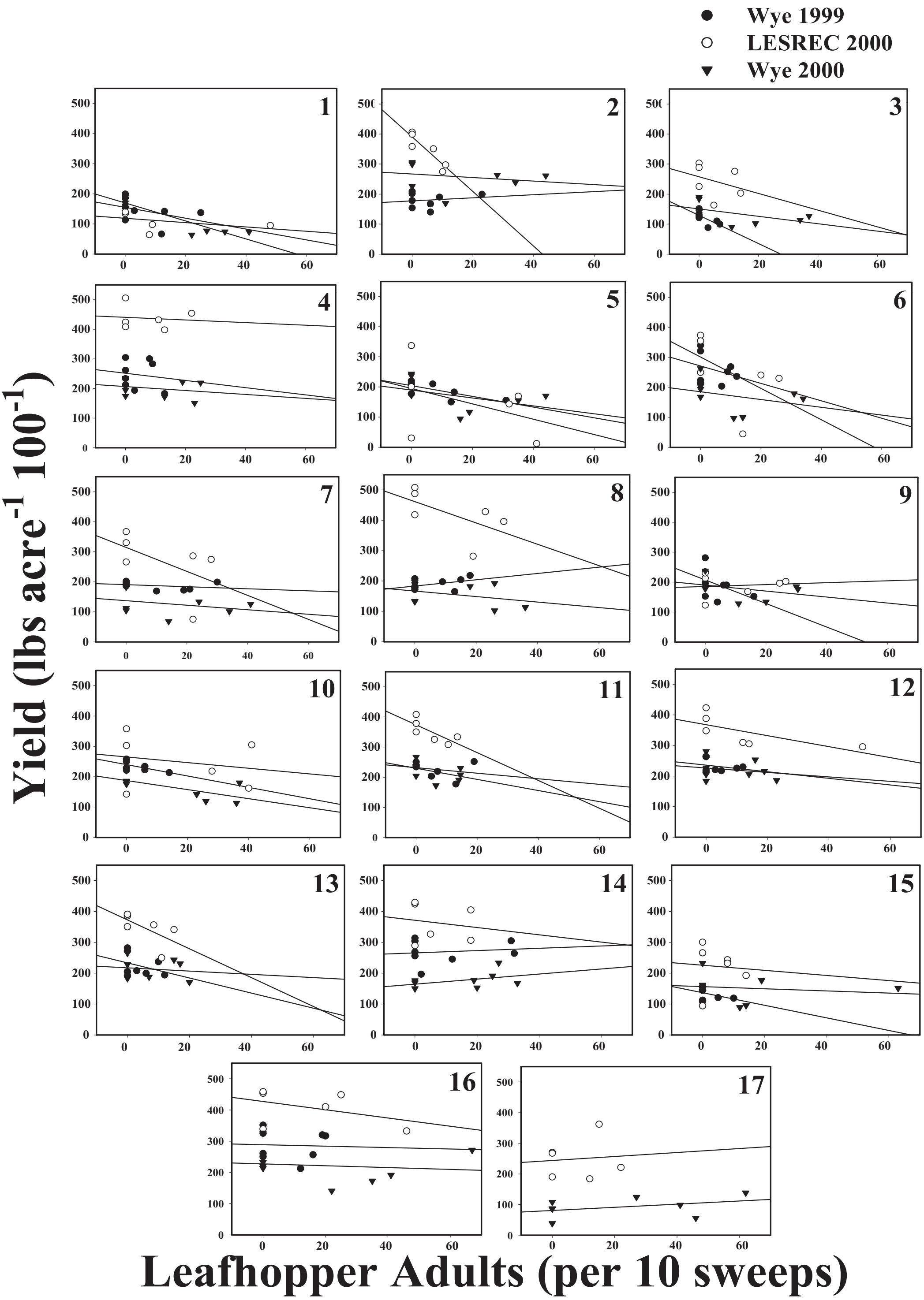

Fig. 4. Relationship between the peak density of *E. fabae* adults and potato yield per plant variety. Data points represent the abundance/yield for each plot and separate regression lines are plotted for each site (Wye and LESREC) and year (1999 and 2000). Only three of the 50 regressions were significant (Wye 1999, variety 5; LESREC 2000, variety 2; Wye 2000, variety 1). Potato cultivated varieties: 1, Andover; 2, Caribe; 3, BelRus; 4, Chieftan; 5, Norkotah; 6, Reba; 7, Yukon Gold; 8, Katahdin; 9, Superior; 10, Superior NewLeaf (Bt); 11, Atlantic; 12, Atlantic NewLeaf (Bt); 13, Snowden; 14, Kennibec; 15, Red Norland; 16, Red Pontiac; 17, Green Mountain.

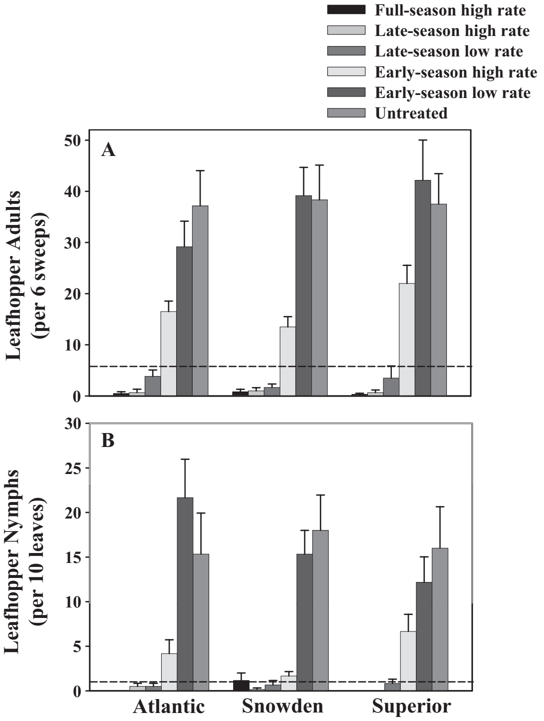

Fig. 5. Peak abundance of the adults (A) and nymphs (B) of *E. fabae* on three potato cultivars (Atlantic, Snowden, and Superior) and under six insecticide spray regimes. Means + SE. Dashed lines indicate the established action thresholds for potato leafhopper adults and nymphs used throughout the eastern United States.

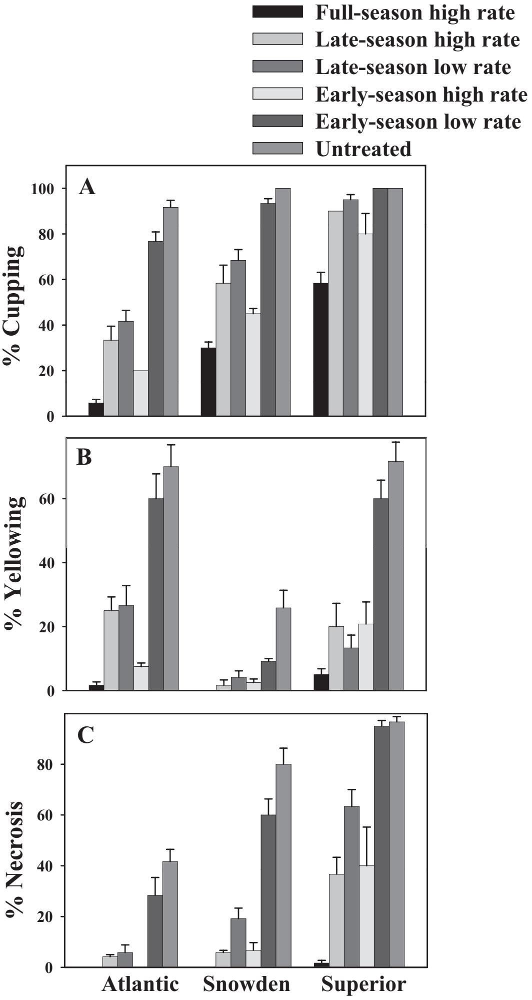

Fig. 6. Percentage of potato foliage displaying damage symptoms from *E. fabae* injury, including cupping (A), yellowing (B), and necrosis (C) on three potato cultivars (Atlantic, Snowden, and Superior) and under six insecticide spray regimes. Means + SE.

Discussion

The dynamics of crop–pest interactions and their impact on plant yield are often highly variable and contingent upon crop variety (Kennedy and Barbour 1992). In potato–leafhopper interactions, we documented substantial variation among plant cultivars in their risk of attack. The abundance of leafhopper nymphs, for example, varied >30-fold between the most and least resistant varieties. Studies on other crop plants, including alfalfa (Danielson et al. 1991, Elden and McCaslin 1997, Ranger and Hower 2001, Shockley et al. 2002) and bean (Lindgren and Coyne 1995, Gonzales et al. 2004) have similarly documented cultivar-based variation in resistance to *E. fabae.* Generally, the mechanism of leafhopper resistance was attributed to glandular trichomes that are expressed on leaves and stems (Elden and McCaslin 1997, Ranger

Table 2. ANOVA results (exp 2) assessing the effects of potato variety and insecticide regime on leafhopper abundance (adults and nymphs) and plant damage (% cupping, yellowing, and necrosis)

	Plant variety			Insecticide			Variety × insecticide		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
Leafhopper abundance									
Adults	0.44	2, 85	0.648	123.57	5, 85	**<0.001**	0.83	10, 85	0.597
Nymphs	0.18	2, 85	0.839	80.72	5, 85	**<0.001**	1.67	10, 85	0.101
Plant damage									
% cupping	141.39	2, 85	**<0.001**	98.39	5, 85	**<0.001**	3.22	10, 85	**0.001**
% yellowing	70.10	2, 85	**<0.001**	65.83	5, 85	**<0.001**	3.66	10, 85	**<0.001**
% necrosis	124.26	2, 85	**<0.001**	115.95	5, 85	**<0.001**	5.22	10, 85	**<0.001**

Significant *P* values (<0.05) are in bold.

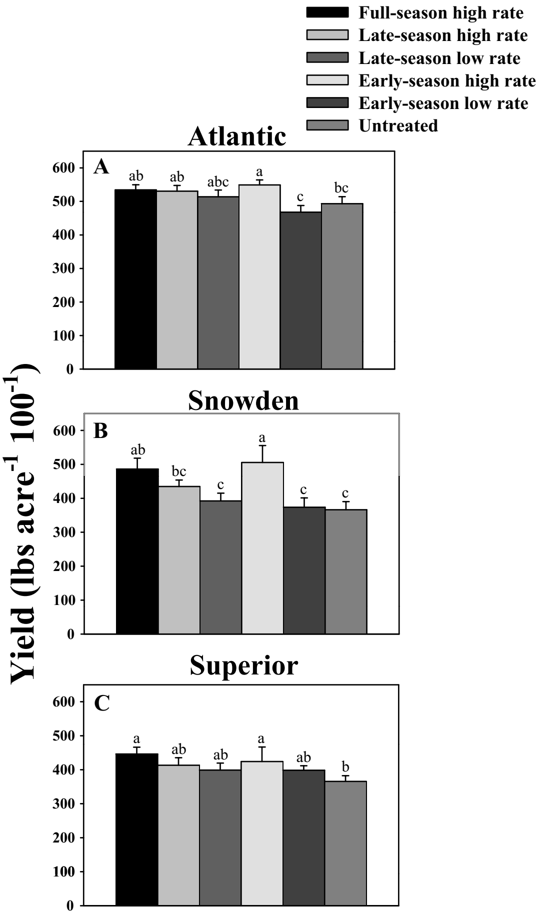

Fig. 7. Yield for three potato cultivars, including Atlantic (A), Snowden (B), and Superior (C), under six insecticide spray regimes. Means + SE. Treatments with different letters are significantly different ($P < 0.05$).

and Hower 2001, Shockley and Backus 2002), including studies on potato and other *Solanum* spp. (Medeiros et al. 2005, Medeiros and Tingey 2006). Potato plants possess both glandular and nonglandular trichomes, although the density of these trichomes varies substantially among cultivars (300–1,600 trichomes/cm^2; G.P.D., unpublished data). At least some evidence exists that intraspecific variation in trichome density explains some of the variation in resistance to leafhoppers documented in this study (I.K., unpublished).

Given that leafhopper abundance differed among cultivars, one might logically expect that symptoms of leafhopper injury (e.g., leaf cupping, yellowing, necrosis) also vary among cultivars. Although plant damage ratings were highly variable and dependent upon crop variety, their expression did not perfectly mirror leafhopper populations. In our second experiment, for example, the main effect of plant variety and the insecticide × variety interaction were nonsignificant for leafhopper adults and nymphs (Table 2), indicating that leafhopper abundance was similar in each treatment. These same main and interactive effects, however, were highly significant for all damage ratings measured (Table 2). Thus, the same density of leafhoppers elicited very different plant responses in each cultivar. The leaves of certain plant varieties began expressing "hopperburn" symptoms almost immediately after leafhoppers colonized and fed on plants, whereas other varieties seemed unresponsive to leafhoppers until they attained very high densities. This distinction is important because the severity of hopperburn is often assumed to correlate directly with leafhoppers and thus yield (Backus et al. 2005).

Genotypic variation in plant tolerance to leafhoppers is not as well investigated as the above-mentioned resistance traits, but one recent study demonstrated plant genetic variation in tolerance to *E. fabae* on alfalfa (Lamp et al. 2007). We found that most potato varieties were relatively tolerant as leafhopper density was a poor predictor of plant yield. Environmental resource levels, however, may dictate the degree of tolerance expressed in plants (Wise and Abrahamson 2005). At Wye in 1999 and at LESREC in 2000, for example, leafhoppers adversely affected yield in <10% of the cultivars tested, whereas ≈60% of the varieties were affected by leafhoppers at Wye in 2000. This result is partially explained by variation in pest abundance (i.e., leafhopper populations were very low in 1999), but not entirely. The two sites studied in 2000 had comparable leafhopper densities, but plants at the LESREC site were far more tolerant than plants at Wye. Future studies that explore precisely which abiotic resources (e.g., soil moisture, nitrogen availability, etc.) most strongly influence tolerance to leafhoppers are warranted.

Perhaps most importantly, our study demonstrates that current action thresholds for *E. fabae* on potato are extremely conservative. Under certain circumstances, leafhoppers reduce potato yield; the maximum yield loss documented in our experiments was ≈60%. Generally, however, leafhopper populations greatly exceeded the established action thresholds (one adult per sweep, one nymph per 10 leaves) without a corresponding loss of yield. In experiment 2, the high rate of insecticide applied during the first 2 wk of leafhopper infestation significantly reduced populations of both adults and nymphs, but peak densities were still at least three-fold higher than the action thresholds, without significant yield loss in the three cultivars (Superior, Atlantic, and Snowden). Thus, action thresholds for leafhoppers on potato can likely be elevated beyond their current levels, particularly when cultivating resistant and/or tolerant varieties. Based on our findings, the cultivars most susceptible to yield loss from leafhoppers are 'Andover,' 'Reba,' and 'Yukon Gold.' The cultivars least susceptible to leafhopper-induced yield loss are 'Atlantic,' 'Green Mountain,' 'Katahdin,' 'Chieftan,' and 'Kennibec.' The effects of leafhoppers on yield for the remaining varieties were inconsistent across sites and years.

Elevating the action threshold for leafhoppers and cultivating tolerant/resistant varieties would be beneficial in several respects. Aside from the obvious economic and potential environmental benefits of reducing insecticide applications in the potato system, minimizing the frequency of chemical inputs aimed at leafhoppers is likely to improve the natural control of other insect pests in the system (e.g., Colorado potato beetle). The most commonly used insecticides for potato leafhopper suppression are dimethoate and pyrethroids, which are disruptive to the natural enemy complex (Hilbeck and Kennedy 1996). Consequently, minimizing such insecticide applications may improve the biological control of Colorado potato beetles and potentially other insects such as aphids that are known to attain pest status on potato. Similarly, recent studies have demonstrated that leafhopper feeding induces resistance to co-occurring Colorado potato beetles (Lynch et al. 2006, Kaplan et al. 2007). Because Colorado potato beetle is largely considered the primary insect pest on potato (Ferro 1986, Hare 1990), it may be beneficial to allow leafhopper populations to develop (presuming that their direct impact on yield is minimal) because of the potential indirect benefits resulting from lower beetle populations.

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