Vegetative Growth Responses of Pinot gris (*Vitis vinifera* L.) Grapevines to Infestation by Potato Leafhoppers (*Empoasca fabae* Harris)

Marcel S. Lenz,[1]* Rufus Isaacs,[2] James A. Flore,[3] and G. Stanley Howell[4]

Abstract: The potato leafhopper (*Empoasca fabae* Harris) can be a damaging pest of vineyards throughout eastern North America, causing leaf curling and yellowing in sensitive cultivars. To determine the relationship between infestations by this insect and vine growth and resource allocation, potted and fruitless Pinot gris (*Vitis vinifera* L.) grapevines grafted to rootstock 1103 Paulsen (*V. berlandieri* Planch. x *V. rupestris* Scheele) were infested for 7 days with 0.0 to 4.5 potato leafhopper (*E. fabae*) nymphs per leaf. Shoot growth, leaf growth, and infestation symptoms of the leaves were quantified before and after the infestation period, and biomass of vegetative vine structures was measured at the end of the experiment. Leaf symptoms of cupping and discoloration were positively correlated with infestation severity, while shoot and leaf growth declined with increasing leafhopper density. Root mass at the end of the experiment was lower in vines with higher infestation levels. Analysis of these results enabled damage symptom and leaf growth thresholds to be determined at between 0.5 and 1.0 *E. fabae* per leaf. However, recovery of vines after infestation was observed in leaf and shoot growth parameters, and vine biomass was reduced only when *E. fabae* densities exceeded 3.0 nymphs per leaf. This study reveals the negative effect of low densities of *E. fabae* on a sensitive grape cultivar and suggests that vines can recover from low infestation levels during the postinfestation period.

Key words: grapevine, potato leafhopper, IPM, tolerance, pest management, source:sink relations

The potato leafhopper, *Empoasca fabae* Harris, can be a pest on a broad range of crops throughout eastern North America, including grapevines. This insect migrates from southern regions of the United States into the upper Midwest region on warm weather fronts each spring and arrives in Michigan during May–June, depending on weather conditions (Carlson et al. 1992). The timing and abundance of this pest vary from year to year, but it often causes injury to grapevines, with potential economic significance to wine and grape producers. Knowing how *E. fabae* populations affect vine function would be useful for integrated vineyard management programs, allowing vineyard managers to make decisions based on the risk to vine productivity and growth, rather than reacting to symptoms. If there is a relationship between the abundance of *E. fabae* and the quantity or quality of grapevine growth, then damage thresholds could be determined. Damage thresholds have been defined as the number of insects necessary to cause measurable loss of host utility (Pedigo et al. 1986), and such thresholds could be used to make control decisions based upon estimated losses in vineyard productivity rather than the mere presence or quantity of this insect. Utilization of such thresholds by vineyard managers could decrease the need for insecticide applications, thus reducing production costs and the environmental impact of viticulture.

Carbohydrate source:sink relationships exert a strong influence on growth of grapevines. For example, reducing carbohydrate source strength of potted Pinot noir (*Vitis vinifera* L.) by defoliation resulted in decreased rates of berry maturation (Petrie et al. 2000a) and reduced biomass accumulation (Petrie et al. 2000b). Increasing vegetative sink size and competition by increasing shoot numbers of potted Chambourcin (Joannes Seyve 26-205) grapevines resulted in shoots that were shorter, had fewer and smaller leaves, and shorter internodes (Miller et al. 1996a). Similarly, increasing reproductive sink strength by retaining higher numbers of clusters on potted Seyval (Seyve-Villard 5-276) grapevines caused decreases in shoot length, leaf area, and cluster weight (Edson et al. 1993). The size of carbohydrate source can also affect vine capacity to tolerate leaf injury, such as that caused by foliar-feeding insects. When potted Niagara (*Vitis labrusca* L.) grapevine leaves were injured to mimic beetle feeding at bloom (low carbohydrate source activity), shoot growth was stunted and root mass was lower compared with undamaged vines. In contrast, the same

[1]Viticulturist, Leelanau Wine Cellars, 7161 N. West Bay Shore Dr., P.O. Box 68, Omena, MI, 49674, [2]Associate professor, Department of Entomology, Center for Integrated Plant Systems, [3]Professor, and [4]Professor emeritus, Department of Horticulture, Plant and Soil Sciences, Michigan State University, East Lansing, MI, 48824.

*Corresponding author (email: lenzmarcels@yahoo.com)

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damage at veraison when the source is high had no such effect (Mercader and Isaacs 2003, 2004).

These studies show that altering carbohydrate source:sink relationships can have profound affects on vine morphology. Decreasing the ratio of carbohydrate source strength to carbohydrate sink strength can lead to deficits in the vine resources available for plant growth and metabolism (Mullins et al. 1992). Since the leaves are the main source of carbohydrate production for grapevines, disruption of leaf function by foliar-feeding insects such as *E. fabae* has the potential to reduce source strength and limit vine growth, productivity, and fruit quality. The magnitude of this effect might be mitigated by inherent vine tolerance to feeding injury and by compensatory growth to produce leaf area in response to feeding injury. Capacity for such mitigation will vary among cultivars and among vines of varying crop load, nutritional status, and so on (Howell 2001).

The physiological effects of *E. fabae* infestation have been studied in detail on various crop plants, but there is relatively little information for grapevines. The photosynthetic activity of alfalfa (*Medicago sativa* L.) and potato (*Solanum tuberosum* L.) leaves showed reduced rates of CO_2 assimilation, transpiration, and stomatal conductance and disrupted translocation of sugars in response to *E. fabae* exposure (Hibbs et al. 1964, Ladd and Rawlins 1964, Womack 1984, Walgenbach and Wyman 1985, Flinn et al. 1990, Nielsen et al. 1990, 1999, Lamp et al. 2001). Infestation of individual alfalfa plants by *E. fabae* resulted in reduced growth (Poos and Johnson 1936, Flinn and Hower 1984, Hower and Flinn 1986), leaf and stem wilting (Harman et al. 1995), and reduced leaf number and decreases in both fresh and dry masses (Poos and Johnson 1936, Flinn and Hower 1984, Hower and Flinn 1986, Flinn et al. 1990, Hutchins and Pedigo 1990).

The studies described above show that *E. fabae* infestations can disrupt leaf function of both alfalfa and potato, thereby reducing the strength of the main source of carbohydrate synthesis, and stunting growth. The mechanisms underlying these effects have been elucidated, revealing a dynamic interaction between complex insect-feeding stimuli and complex plant responses. Feeding by *E. fabae* ruptures plant cells, thereby initiating a wound response that can be enhanced by leafhopper saliva (Backus et al. 2005). The differential sensitivity to the wound response and insect saliva among grape species and cultivars may explain variability in sensitivity to *E. fabae* feeding in *Vitis*. In sensitive grape cultivars, reductions in source strength by *E. fabae* through stimulation of leaf symptoms can result in stunted vine growth (R. Isaacs, personal observation, 2003), yet the relationships between infestation and magnitude of symptoms is not known and the effects on vine growth and resource allocation have not been elucidated.

The goals of this research were to determine the following in *Vitis vinifera* grapevines: (1) whether *E. fabae* infestations on grapevines reduce the quantity of vegetative growth; (2) the relationship between symptoms of infestation and quantity of growth; (3) damage thresholds for changes in vegetative growth in response to *E. fabae* infestation; and (4) whether vines can recover from *E. fabae*-induced growth reductions.

Materials and Methods

Plant material. The vines used for this study were 2-year-old Pinot gris (*Vitis vinifera* L.) grafted to rootstock 1103 Paulsen (*V. berlandieri* Planch. x *V. rupestris* Scheele). The vines were purchased from a nursery and each was weighed and labeled prior to potting, then grown in black plastic pots with 10 L steam-sterilized soil composed of 50% sandy loam, 30% sphagnum peat, and 20% washed sand. The vines were potted on 29 June 2005 (day 1) and, prior to infestation, were normal in appearance with no symptoms of pest damage or nutritional imbalance. A 1.5-m length of bamboo was then inserted into the soil at the edge of each pot for shoot training. Each vine was trained to one shoot.

The vines were grown under natural light in a greenhouse on the main campus of Michigan State University and were watered as needed, usually three times per week. All flower clusters were removed; lateral shoots and any main shoots in excess of the one shoot necessary to conduct the experiment were removed as they appeared. The vines were fertilized monthly with 600 mL of a solution made by mixing five tablespoons (~60 g) of 15-30-15 (N-P-K) fertilizer (Scotts Miracle Grow, Marysville, OH) with 19 L water. This solution contained ~475 mg/L of both nitrogen and potassium, 950 mg/L phosphorus, and trace amounts of boron, copper, iron, manganese, molybdenum, and zinc.

Insect source. Second and third instar *E. fabae* nymphs were used to infest the vines for this study. This life stage was used because it is flightless and because the insects would not lay eggs in the leaves during the period of infestation. Adult *E. fabae* were collected from a field of alfalfa (*Medicago sativa* L.) and clover (*Trifolium pratense* L.) using a canvas sweep net. These insects were placed into collapsible cages that measured 61 x 61 x 61 cm (model 1450D; BioQuip Products, Gardena, CA) and reared indoors on bean plants (*Vicia faba* L.) grown from seed. The second and third instar nymphal offspring of these adults were used for the experiments. To collect nymphs for applying treatments, a piece of white mesh was placed inside the body of an aspirator, then enough nymphs for one vine were aspirated and rendered temporarily immobile using CO_2 gas. While still immobile, the aspirator was dismantled and the fabric containing the nymphs was removed and placed on the soil at the base of the trunk. The vine was then enclosed in a bag made from this same fabric by placing the bottom edge of the open fabric bag over the top edge of the pot and placing a rubber band over the point of intersection. This process was repeated until all the vines received the appropriate number of *E. fabae* nymphs. Each vine was enclosed in a fabric bag; these bags reduced the amount of photosynthetically active radiation by about one-third and reduced air flow only slightly (data not shown).

Leaf symptom measurements. Normally, the central portion of a grapevine leaf is flat and the margin is flat or slightly elevated, compared with curling downward when fed upon by *E. fabae*. Leaf-cupping symptoms were described in terms of relative concavity or convexity and were scored as follows: 1 (normal), 2 (slight cupping), 3 (moderate cupping), or 4 (severe cupping). Leaves were scored as follows: 1 (normal), leaf was the normal flat to slightly concave shape and the leaf margin lay in the leaf plane up to ~10° above the leaf plane; 2 (slight cupping), leaf margin curling downward but not overlapping the abaxial leaf surface, leaf margin between 0° and 45° below the leaf plane; 3 (moderate cupping), margin curling downward to a greater extent than a 2 score, but not overlapping the abaxial leaf surface, the leaf margin is between 45° and 90° below the leaf plane; 4 (severe cupping), margin curling downward and overlapping the central portions of the abaxial leaf surface, the leaf margin is curled at an angle greater than 90° below the leaf plane. The percentage of leaves cupped was quantified as the number of leaves showing any degree of cupping as a proportion of the total number of leaves.

Discoloration was assessed visually and expressed as the percentage of tissue per leaf that was yellow to light green and given a score ranging from 0 to 100% in increments of 10%. The percentage of leaves discolored was recorded as the number of leaves showing any amount of discoloration as a proportion of the total number of leaves. The variable "% nonzero leaf" was the average percent discoloration per leaf of only those leaves that were discolored.

Growth measurements. Internode lengths and midrib lengths were measured with a ruler to the nearest millimeter. The length of an internode was the linear distance between two nodes and the length of a midrib was the linear distance between the basal and apical ends of the primary vein that bisects the leaf blade. Shoot length was the sum of the lengths of all internodes for a given shoot. At the end of the experiment, biomass accumulation was measured as the fresh and dry mass of the leaves, shoots, wood, and roots of each vine. The leaves included both the lamina and petiole, shoot mass included all of the current season's shoot growth except the leaves, roots included all growth from the main trunk axis below the graft union excluding the main axis, and all remaining tissue was categorized as the wood. Total vine biomass was the sum of these four tissue types. Fresh weight measurements were recorded immediately after collection, and dry mass measurements were attained from plant material that was dried in an oven at 49°C until no further reduction in mass occurred.

Measurements and treatment application. This experiment lasted for 114 days. At three times throughout the course of the experiment, the lengths of all internodes and leaf midribs were measured and each leaf was scored for degree of cupping and amount of discoloration. The vines were potted on day 1 (29 June 2005) and data for time-1 were collected on days 27 to 29; included in this data set was the leaf area regression (see section for leaf area analysis). Leaf areas of the experimental vines were measured on day 30 and the vines were arranged into blocks based on leaf area per vine. On the following day, the treatments were randomly applied to each vine within a block, thus initiating the infestation period. There were six treatment levels: 0.0, 0.5, 1.0, 1.5, 3.0, and 4.5 *E. fabae* nymphs per leaf. The infestation period lasted for 7 days, ending on day 38 when all *E. fabae* were aspirated off each vine and counted. Data for time-2 were collected on days 41 to 43, 3 days after the infestation was terminated. Data for time-3 were collected on days 111 to 113, 73 days after the infestation was terminated. On day 114, the vines were destructively analyzed for biomass accumulation.

Leaf area analysis. Leaf area was estimated by determination of the relationship to midrib length. At time-1, midrib length and leaf area were measured on 469 leaves from additional potted Pinot gris vines treated the same as those used in the experiment. For each leaf, midrib length was measured with a ruler and leaf area was measured with a leaf area meter (LI3000; LI-COR, Lincoln, NE). The regression equation between these two variables was used to estimate leaf area from midrib length measurements.

Experimental design and statistical analysis. This experiment was a randomized complete block design with repeated measures. The blocking factor was leaf area and the treatment factor was the number of *E. fabae* nymphs per leaf. All midrib and internode length data were analyzed using a linear mixed model with treatment level and time as fixed effects and block as a random effect (PROC MIXED, SAS version 8.0; SAS Institute, Cary, NC). The Shapiro–Wilk test was used to determine whether the residuals were normal; in cases where the residuals were not normal, the data were transformed. Log transformations were performed on shoot length and leaf area to normalize the residuals. Leaf cupping and discoloration data were analyzed using a linear mixed model with treatment level as a fixed effect and block as a random effect. Biomass data were analyzed using analysis of covariance (ANCOVA) with preplanting vine mass used as the covariate and with treatment level used as a fixed effect and block as a random effect. A log transformation was performed on the root fresh mass to normalize the residuals. Multiple comparison tests at the 5% level were used to examine pairwise differences among all means for all of the analyses using least significant difference tests. All statistical analyses were performed using SAS version 8.0. All figures were created using SigmaPlot 8.0, including best-fit equations and R^2 values (Systat Software, Richmond, CA).

Pest control. A minor outbreak of powdery mildew (*Uncinula necator* Schw.) occurred and the vines were sprayed on days 56 and 62 with Compass (trifloxystrobin) and Terraguard (triflumizole), respectively. Later in the season, the vines were showing mild symptoms of two-spotted spider mite (*Tetranychus urticae* Koch) infestation and were sprayed with Floramite (bifenazate) on day 90.

Results

A regression was performed between midrib length and leaf area for 469 leaves in order to calculate leaf size and leaf area/vine (data not shown). This relationship was significant at the 0.1% level with an adjusted $R^2 = 0.84$; the equation was $y = 0.0125x^{1.9955}$ where x = midrib length (mm) and y = leaf area (cm^2).

Leaf symptoms. At time-1, all leaves were normal in shape and color (data not shown). After exposure to *E. fabae*, leaf assessments taken at time-2 showed that symptoms of *E. fabae* infestation were apparent and were directly related to infestation level. As infestation severity increased, so too did the amount of cupped leaves. As few as 0.5 *E. fabae*/leaf resulted in significantly more cupped leaves than the control. The range in the number of cupped leaves per vine was from 1.5 for the control to 12.6 for the leaves receiving 4.5 *E. fabae*/leaf. In terms of percentage of leaves per vine that were cupped, the range was 5.3 to 58.7%. At the higher levels of *E. fabae* infestation, symptoms were severe with leaves discolored and cupped after exposure to the insects for one week. Discoloration typically appeared as light yellow or light green wedge-shaped areas in the leaf tissue, with the wide end at the leaf margins. Cupping symptoms were downward with the abaxial surface on the inside of the cupped leaf. A nonlinear regression between *E. fabae* per leaf and percent of leaves cupped was significant at the 0.1% level with an adjusted $R^2 = 0.82$ (Figure 1A). The average score for the degree of leaf cupping was 2.0 (slight) for the control vines and increased up to 3.1 (moderate) for the vines receiving 4.5 *E. fabae*/leaf. Linear regressions between *E. fabae* per leaf and all leaf-cupping variables were significant at the 0.1% level.

Leaf discoloration was directly related to infestation severity. The number of leaves that were discolored per vine ranged from 0.0 for the control to 6.6 for the 4.5 *E. fabae*/leaf level, or 0.0 to 30.7% of the total leaves on these vines. A nonlinear regression between *E. fabae* per leaf and percent leaves discolored was significant at the 0.1% level with an adjusted $R^2 = 0.82$ (Figure 1B). The average percent discoloration of the discolored leaves ranged from 0% of the leaf area on control vines to 33.1% on vines exposed to 4.5 *E. fabae*/leaf.

Shoot and leaf growth. Prior to exposure to *E. fabae* (time-1), there were no significant differences among treatments in terms of internodes per vine, leaves per vine, leaf size, or leaf area per vine (Table 1). Although there were slight differences among treatments in terms of internode length, no level differed significantly from the control. Shoot length on vines receiving 0.5 *E. fabae*/vine were shorter than the control vines, but not significantly different from other vines exposed to *E. fabae*.

Three days after the end of the infestation period, every variable for leaf and shoot growth showed significant differences among treatments (Table 1). In addition, each variable showed an inverse linear relationship to the number of *E. fabae* per leaf. Infestation by this insect resulted in fewer leaves per vine, less leaf area per vine, and smaller leaves. Shoot growth was also reduced by infestation, with higher levels of *E. fabae* infestation causing reduced shoot length, fewer internodes per vine, and shorter average internode lengths (Table 1).

Ten weeks after the end of the infestation period, comparison among treatments revealed a different trend than immediately after the infestation (Table 1). Although significant differences still existed among treatments for internodes per vine, leaves per vine, leaf size, and leaf area per vine, there were no longer differences among treatments in terms of internode length and shoot length. Where significant differences were found, it was typically one of the middle treatment levels that showed growth stimulation, and in all cases the control vines did not differ

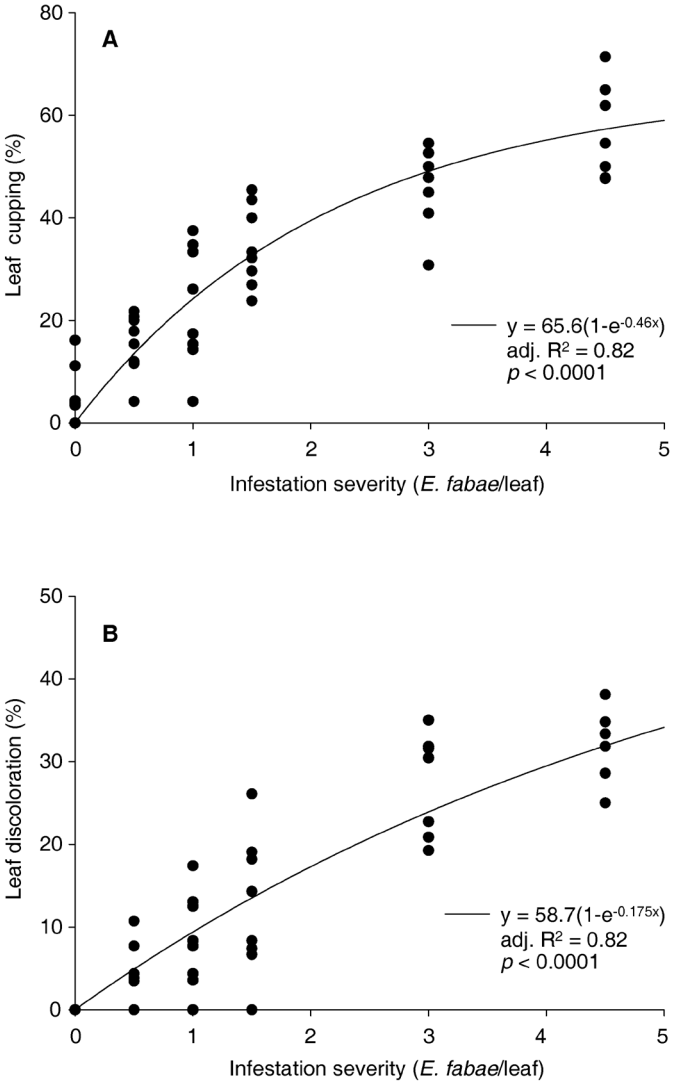

Figure 1 Relationship between level of infestation of Pinot gris grapevines by *E. fabae* and the level of leaf cupping (**A**) or leaf discoloration (**B**). Data points are the percentage of the total number of leaves that exhibited downward cupping or discoloration in response to *E. fabae* infestation. Equations show best fit lines and their correlation coefficients.

Table 1 Leaf and shoot production of Pinot gris grapevines: time-1, before *E. fabae* infestation; time-2, three days after *E. fabae* infestation; time-3, 10 weeks after *E. fabae* infestation.

E. fabae/leaf	Leaves/ vine	Leaf area/ vine (cm^2)	Leaf size (cm^2)	Shoot length (mm)	Internodes/ vine	Internode length (mm)
Time-1						
0.0	17.0[a]	731	31.8	854 a	21	42 ab
0.5	18.0	680	29.8	769 b	20	39 ab
1.0	17.0	728	33.3	801 ab	20	41 ab
1.5	17.0	729	32.9	805 ab	20	40 ab
3.0	18.0	700	29.9	795 ab	21	37 b
4.5	17.0	728	31.7	816 ab	20	42 a
F values[b]	ns	ns	ns	*	ns	*
Time-2						
0.0	27 a	1,576 a	47.4 a	1,328 a	30 a	45 a
0.5	26 ab	1,329 b	41.9 bc	1,108 b	28 ab	40 b
1.0	24 b	1,415 b	45.5 ab	1,089 b	27 ab	40 b
1.5	25 ab	1,362 b	43.1 abc	1,075 bc	28 ab	39 b
3.0	22 c	1,124 c	39.8 c	942 d	26 b	37 b
4.5	22 c	1,182 c	41.7 bc	971 cd	24 c	41 b
F values[b]	***	***	**	***	***	***
Linear R^2	0.78***	0.79***	0.63**	0.84***	0.81***	0.81**
Quadratic R^2	ns	0.83**	0.67*	0.90***	ns	0.86**
Time-3						
0.0	34 c	2,599 b	74.9 ab	1,738	37 d	48
0.5	36 ab	2,645 b	71.3 bc	1,707	38 bcd	44
1.0	38 a	3,069 a	78.1 a	1,850	41 a	46
1.5	36 ab	2,725 b	73.4 ab	1,762	39 abc	45
3.0	37 a	2,639 b	68.0 c	1,787	40 ab	44
4.5	35 bc	2,547 b	70.4 bc	1,736	37 cd	47
F values[b]	***	***	***	ns	***	ns
Linear R^2	ns	ns	ns	ns	ns	ns
Quadratic R^2	0.48**	0.33*	ns	ns	0.55**	ns

[a]Means separated by LSD; values within a column followed by the same letter are not significantly different at the 5% level.
[b]Significant F values and R^2 values shown at 5% (*), 1% (**), 0.1% (***), or not significant (ns); regressions for each parameter were plotted against *E. fabae*/vine.

from the 4.5 *E. fabae*/leaf vines in terms of these growth parameters. For all variables where significant differences were found, the 1.0 *E. fabae*/leaf level was consistently among the highest values.

Biomass accumulation. There was no clear trend toward lower fresh weight of vine vegetative tissues with increasing *E. fabae* infestation, although vines receiving 1.0 *E. fabae*/leaf had the highest fresh mass of leaves, shoots, and the total vine (Table 2). These data are a reflection of these vines having the longest shoots, largest leaves, and most leaves per vine (Table 1). In contrast, those vines exposed to 4.5 *E. fabae*/leaf had the lowest fresh root mass and lowest total vine fresh mass.

A similar pattern of response was seen in the dry mass data (Table 2). Vines exposed to 1.0 *E. fabae*/leaf had the highest leaf, shoot, and root dry mass, and they also had the highest total vine mass. Vines exposed to 4.5 *E. fabae*/leaf were the smallest among treatments and had significantly less biomass than the vines receiving 0.0, 0.5, or 1.0 *E. fabae*/leaf.

Discussion

These experiments show that *E. fabae* infestation reduces vegetative growth of potted Pinot gris grapevines and also suggest that vines have some capacity to recover from this injury. The levels of leaf cupping and yellowing symptoms were both positively correlated with the number of *E. fabae* per vine. As the number of *E. fabae* per vine increased, infestation caused transient decreases in internodes per vine, average internode length, shoot length, leaves per vine, leaf size, and leaf area per vine. Biomass data collected from vines sampled 10 weeks after the exposure to leafhoppers showed that leaf and shoot mass of vines receiving 1.0 *E. fabae*/leaf were largest and root mass of the vines exposed to 4.5 *E. fabae*/leaf was the lowest. These data agree with other recent studies on *V. labrusca* cv. Niagara response to feeding by beetles, indicating that vines can tolerate and compensate for foliar herbivory (Mercader and Isaacs 2003, 2004).

Decreased shoot length observed in response to *E. fabae* feeding was due to both reduced internode lengths and

Table 2 Biomass production of Pinot gris grapevines 10 weeks after exposure to varying levels of *E. fabae* infestation: fresh biomass and dry biomass (time-3).

	Mass (g)					
***E. fabae*/leaf**	**Initial**	**Leaves**	**Shoots**	**Wood**	**Roots**	**Total**
Fresh biomass						
0.0	72.4 a[a]	51.5 b	32.2 b	64.8 ab	81.7 ab	230.2 ab
0.5	56.5 b	55.1 b	33.8 ab	69.0 a	85.3 ab	243.1 a
1.0	68.2 ab	61.8 a	37.0 a	59.4 b	89.7 a	247.9 a
1.5	66.9 ab	54.2 b	33.9 ab	60.2 b	71.7 bc	220.0 b
3.0	56.1 b	55.9 b	34.1 ab	61.0 b	75.5 abc	226.4 ab
4.5	66.9 ab	53.6 b	35.3 ab	60.2 b	61.1 c	210.2 b
F values[b]	*	***	*	*	***	**
Linear R^2	ns	ns	ns	ns	0.29**	0.18*
Quadratic R^2	ns	ns	ns	ns	ns	ns
Dry biomass						
0.0		17.0 b	17.6	37.2 ab	44.4 ab	116.1 ab
0.5		17.9 b	18.3	38.9 a	41.4 ab	116.5 ab
1.0		20.1 a	19.9	33.7 b	48.3 a	122.1 a
1.5		17.4 b	18.4	34.6 ab	38.3 bc	108.6 bc
3.0		17.9 b	18.3	34.7 ab	41.2 ab	112.1 abc
4.5		17.3 b	18.9	34.0 b	33.6 c	103.8 c
F values[b]		**	ns	*	**	***
Linear R^2		ns	ns	ns	0.26**	0.19*
Quadratic R^2		ns	ns	ns	ns	ns

[a]Means separated by LSD; values within a column followed by the same letter are not significantly different at the 5% level.
[b]Significant F values and R^2 values shown at 5% (*), 1% (**), 0.1% (***), or not significant (ns); regressions for each parameter were plotted against *E. fabae*/vine.

fewer internodes per vine immediately after vine exposure to this insect (time-2). After 10 weeks of growth in the absence of infestations (time-3), shoot length was no longer significantly different among treatments. Average internode length showed no significant differences among treatments, although there were some differences among treatments in terms of internodes per vine. Our observations that vines receiving 1.0 *E. fabae*/leaf had the most internodes might indicate compensatory or stimulatory growth in response to low levels of infestation. Both leaves per vine and average leaf size were significantly reduced after one week of exposure to *E. fabae*, and both parameters likely contributed to the reduced leaf area observed in this study. By the end of 10 weeks, however, treatment differences in leaf area, leaf size, and leaves per vine were less pronounced than after infestation. Leaf measurements showed that low infestation levels resulted in larger leaves, greater numbers of leaves per vine, and higher overall leaf area per vine, further suggesting that there was a recovery from growth reductions induced by *E. fabae*.

Vine infestation by *E. fabae* resulted in a reduction in shoot length and leaf area of the vines combined with symptoms of leaf discoloration, leading to stunted growth. Thus, the size of carbohydrate source tissues was reduced with increasing infestation. In the absence of any compensatory mechanisms such as enhanced photosynthetic rates of the remaining leaf area, this could translate into a reduction in carbohydrate source strength of infested vines. Reducing the carbohydrate source could limit the vine's ability to meet the growth and productivity requirements of the carbohydrate sink tissues, depending on the strength of those sinks. The grape leafhopper (*Empoasca vitis* Goethe), a close relative of *E. fabae*, has been shown to reduce the rates of assimilation, transpiration, mesophyll conductance, and stomatal conductance of Merlot (*Vitis vinifera* L.) leaves (Candolfi et al. 1993). Related research on the effects of *E. fabae* infestation on vine photosynthesis indicates a linear reduction in carbon assimilation by Pinot gris vines with increasing leafhopper infestation (Lenz 2007). Such impacts on photosynthesis are expected to result in reductions in source strength with increasing infestation severity, ultimately causing the differences observed in shoot and leaf growth.

If the findings from this study are consistent with the response found in a vineyard situation, similar reductions in carbohydrate source and vine growth from leafhopper infestation on sensitive cultivars would be expected to force growers to accept lower yields or yields of reduced fruit maturity (Mansfield and Howell 1981, Petrie et al. 2000a). However, at infestation levels ranging from 0.5 to 1.5 *E. fabae*/leaf for 7 days, shoot and leaf growth may be stimulated if other stresses are absent. Abundance of *E. fabae* in vineyards in Michigan rarely exceeds 1.0 per leaf, but their infestations may be present for longer than one week if not controlled promptly (R. Isaacs, personal observation, 2003). Further research that varies infestation duration will

be needed to determine whether more chronic exposure to leafhoppers prevents vines from compensating. The combined effect of a fruit sink for carbohydrates and infestation by *E. fabae* in sensitive cultivars may also produce a more pronounced effect on vine growth and ability to compensate (Howell 2001), and this effect should be the strongest at veraison when the fruit becomes the dominant sink (Mullins et al. 1992).

Compensation for aboveground herbivory may be driven by root storage carbohydrates, as indicated by the root mass of the 4.5 *E. fabae*/leaf vines being much lower than the other treatments (Table 2). Alternatively, recovery in growth by leaves and shoots at time-3 might have been achieved by vines allocating fewer carbohydrate resources to the roots to recover from loss of functional leaf area because of insect infestation. Such a phenomenon has been noted in other studies of source/sink relations for grapevines (Candolfi-Vasconcelos et al. 1994, Edson et al. 1995, Miller et al. 1996b).

The results from this experiment suggest that thresholds for visible symptoms may be much lower than those for growth symptoms. Threshold levels for leaf symptoms all occurred at 0.5 and 1.0 *E. fabae*/leaf. Cupped leaves per vine, the percentage of leaves that were cupped, and the average discoloration per discolored leaf became significantly higher than the control by 0.5 *E. fabae*/leaf, whereas the average score per cupped leaf, total number of discolored leaves, and percentage of leaves that were discolored became significantly greater than the control by 1.0 *E. fabae*/leaf. Shoot length, average internode length, average leaf size, and leaf area per vine all decreased significantly relative to the control by 0.5 *E. fabae*/leaf; leaves per vine decreased by 1.0 *E. fabae*/leaf while the number of internodes per vine did not significantly decrease until 3.0 *E. fabae*/leaf. In contrast, effects on vine biomass were found only at 4.5 *E. fabae*/leaf, a high level that is equivalent to 74.8 *E. fabae*/vine, or 12,456 *E. fabae* hr/vine. In order to equilibrate these treatment levels to existing and/or future studies, these per leaf values can be translated into other units. Multiplying *E. fabae* per leaf by leaves per vine gives the number of *E. fabae* per vine. Another unit that can be used to report treatment levels is *E. fabae* hr/leaf or *E. fabae* hr/vine; this is the product of the number of *E. fabae* and the number of hours that the insects were allowed to feed, which was 168 hr for this experiment.

Compensatory increases in photosynthetic rates for grapevine leaves in response to *E. fabae* infestation have not been documented, but studies on grapevines and cherry have demonstrated that partial defoliation can result in increased rates of assimilation for the remaining leaves (Layne and Flore 1992, 1995, Petrie et al. 2000c) by altering the ratio of carbohydrate sources and sinks. Grapevines possess compensatory photosynthetic mechanisms which respond to changing source/sink relationships, and the data from time-3 indicate that growth rates of leaves and shoots were enhanced for some infestation levels relative to the control (Table 1). It is likely that remobilization of storage carbohydrates from the roots is part of this mechanism, since vines have the ability to remobilize stored carbohydrates in order to meet sink demands (Candolfi-Vasconcelos et al. 1994).

Compensatory responses in perennial fruit crops have been observed in cases where plants experience sudden decreases in source strength. In several experiments, partial defoliation did not significantly affect boll number, mean boll weight, or lint yield of cotton plants (Wilson et al. 2003). Other studies showed that partial defoliation of cherry can result in enhanced rates of carbon assimilation for the remaining leaf tissue (Layne and Flore 1992, 1993, 1995). It was demonstrated that partial defoliation of nonfruiting grapevines resulted in higher carbon assimilation for the remaining leaves (Petrie et al. 2000c), and similar responses may occur in response to *E. fabae* infestation. Walgenbach and Wyman (1985) observed partial recovery of assimilation rates for potato (*Solanum tuberosum* L.) following *E. fabae* infestations, and Zhou and Backus (1999) revealed eventual phloem regrowth in alfalfa whereby new sieve tubes circumvented damaged areas of phloem.

Conclusion

Caution should be exercised when extrapolating the results of this study to an established vineyard situation where vines have larger carbohydrate reserves and fruit as a carbohydrate sink. However, our findings provide insight for vineyard management during the period of establishment when fruit is typically removed from vines to allow vegetative growth to dominate. Our results suggest that even highly sensitive cultivars such as Pinot gris can tolerate infestation by *E. fabae* if they have time to recover. Another practical application of this study is to refine management strategies for *E. fabae*, given that relatively small populations of *E. fabae* may not cause significant reductions in vine growth. Further research in mature and establishing commercial vineyards is needed to quantify the impact of *E. fabae* on vine growth and productivity and to determine under what conditions vines can compensate for low infestations of *E. fabae*.

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