

# Host Suitability and Gas Exchange Response of Grapevines to Potato Leafhopper (Hemiptera: Cicadellidae)

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J. Econ. Entomol. 104(4): 1316–1322 (2011); DOI: 10.1603/EC11064

**ABSTRACT** Although potato leafhopper, *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae), is highly polyphagous, classic host studies do not recognize grapevines (*Vitis* spp.), as suitable hosts. Recently, injury has been reported and reproduction documented within grape vineyards, suggesting a host expansion for the leafhopper. To document this apparent expansion in host use, we determined whether grape plants were suitable hosts for potato leafhopper reproduction, measured the consequence of feeding injury on gas exchange rates of grape leaves, and compared the susceptibility to feeding injury among cultivars. We found that potato leafhopper adults survived equally well on grape (*Vitis vinifera* L.), alfalfa (*Medicago sativa* L.), and fava bean (*Vicia faba* L.). The total number of offspring was greater on fava bean but did not differ between alfalfa and grape. Injury to grapevines was assessed by measuring gas exchange responses of leaves in field cages and in greenhouse tests. We found marginally significant declines in photosynthesis and transpiration rates in the field (9.6 and 13.2%, respectively), and much stronger effects in greenhouse tests (ranging between 22 and 52%). Our results verify that *Vitis* is a suitable host, and that potato leafhopper is capable of injuring its gas exchange physiology. We discuss possible explanations for the host expansion, and its potential to damage commercial grapevines.

**KEY WORDS** *Empoasca fabae*, photosynthesis, transpiration, host plant expansion

Potato leafhopper, *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae), has been documented to feed and reproduce on >200 species of plants in 26 families. It is a pest of many plants grown in eastern North America, including legumes; solanaceous crops, such as potatoes (*Solanum* spp.); and maple (*Acer* spp.) trees and other horticultural crops (Lamp et al. 1994). Ecological characteristics, including high vagility, polyphagy, and rapid rate of population increase, result in high densities during the summer (Hogg and Hoffman 1989). Potato leafhopper is also a pest because of the unique plant response to feeding injury. The leafhopper feeds by rapid, repeated penetration of its stylets into the vascular tissue, from which plant material is ingested (Backus and Hunter 1989). Through a combination of mechanical and salivary stimuli, potato leafhopper feeding enhances a wound response that changes the vascular tissue around the feeding site (Ecale and Backus 1995). When this occurs, photoassimilates transported through the phloem build up around the injured site (Hibbs et al. 1964; Nielsen et al. 1990, 1999), and rates of photosynthesis are reduced (Womack 1984, Flinn et al. 1990, Lamp et al. 2004). In addition, stomatal conductance and internode elongation are reduced (Lamp et al. 2004), resulting in the apparent stunting of plants. Thus, leaf-

hopper feeding initiates a cascade of changes (Backus et al. 2005) that is ultimately expressed as hopperburn, an often characteristic discoloration and malformation of leaves, and delayed plant maturity, reduced nutritive components, stunted growth, and reduced yields (e.g., Hutchins and Pedigo 1989).

In spite of the extensive historical research on potato leafhopper, only one research article documents the reproduction of this species on grapevines (*V. vinifera*, Bostanian et al. 2003), and one article describes its injury to grapevines (Lenz et al. 2009). In their extensive work on host plants of *Empoasca* in the 1930s and 1940s, Poos and Wheeler (1943, 1949) did not find *E. fabae* reproducing on any member of the Vitaceae, although they did record collecting adults from grapes (species not listed). Studies documenting pests of grapes within the range of potato leafhopper do not mention this species as a pest (Still and Rings 1973, Demaree and Runner 1942), with the exception of Bostanian et al. (2003), who documented both adults and nymphs on grapevines during 1997–1999. In contrast, the eastern grape leafhopper, *Erythroneura comes* (Say), is a well known pest of grapes (Demaree and Runner 1942, Martinson et al. 1997). In spite of the lack of documentation within research literature, extension entomologists are familiar with the presence of potato leafhopper in vineyards. For example, Jordan et al. (1980) includes a photo of injury caused by

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potato leafhopper in their general guide for commercial vineyards. Extension websites from Ohio (<http://www.oardc.ohio-state.edu/grapeipm/leafhoppers.htm>), New York (<http://www.nysipm.cornell.edu/factsheets/grapes/pests/ghh/ghh.asp>), Connecticut (<http://www.ct.gov/caes/cwp/view.asp?a=2815&q=377722>), Massachusetts (<http://www.umass.edu/fruitadvisor/nesfpmg/095.pdf>), Michigan (<http://www.ipm.msu.edu/pdf/GrapePocketPages.pdf>), and Pennsylvania (<http://ento.psu.edu/extension/factsheets/potato-leafhopper>) mention *E. fabae* as a pest of grapes; however, there is no mention of potato leafhopper presence on grapes on extension websites from other states (including Maine, West Virginia, Virginia, North Carolina, and Delaware). Recently, Lenz et al. (2009) have described research on the growth response of grapevines to potato leafhopper injury, including descriptions of injury symptoms and analysis of leaf growth thresholds.

Thus, the status of potato leafhopper as a pest of grapevines is unclear. We sampled grapevines in Maryland during 2004–2006, demonstrating the presence of potato leafhopper adults and nymphs (W.O.L., personal observations). Here, we report research to determine the potential of potato leafhopper as a pest of grapes. Our objectives were to determine whether grape plants are suitable hosts for potato leafhopper, to measure the consequence of injury on gas exchange rates of grape leaves, and to determine whether grape cultivars vary in their level of susceptibility.

### Materials and Methods

**Host Plant Suitability of Grapes.** Female potato leafhoppers were collected from a field of alfalfa, *Medicago sativa* L., at the Western Maryland Research and Education Center (WMREC), near Keedysville, MD, in August, 2005, and placed in a cage with potted alfalfa overnight in a walk-in chamber. Three plant species were tested: 'Cabernet Sauvignon' grape, grown from cuttings and trimmed to fit in the cage; 'Winsor' fava bean, grown from seed, 21 d after planting; and 'WL323' alfalfa, established in June 2004 and cut back 21 d before the experiment. Individual pots of each plant species were placed separately in 25- by 30- by 38-cm wood frame cages with organdy screening and a Plexiglas front for access. Four replicates of the plant species were used in a randomized complete block design. Five females were placed in each cage. After 5 d, the females were counted for survival and removed from cages. After 12 d, plants were destructively sampled and all nymphs counted. Data were analyzed using analysis of variance (ANOVA) (Proc ANOVA, SAS Institute 1997).

**Field Measurement of Injury to Grape Leaves.** The experiment was conducted at WMREC in a vineyard planted in 1998 with two grape cultivars: 'Chardonnay', a European vinifera type cultivar; and 'Chambourcin', a European-American hybrid. Cultivars were grown in 73-m (240-foot) rows with plants 3 m apart, 5 m between rows, and planted as a randomized block design with five blocks. Three plants were se-

lected for testing within each block and cultivar during 2004.

Adults were collected from an adjacent alfalfa field using a D-Vac suction device. Two grape leaves were selected per plant, representing fully-expanded development but also near the end of the vine. Cloth bags (15 by 20 cm) with drawstrings were placed over each leaf, and four adult leafhoppers were placed in one of the two bags. We attempted to include equal numbers of males and females in bags but were uncertain of the exact ratio. After 2 d, bags were removed from the leaves and gas exchange measurements were made using a LI-6400 Photosynthesis Measurement System (LI-COR Inc., Lincoln, NE). The LI-6400 was set for standardized levels of light ( $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $\text{CO}_2$  concentration ( $400 \mu\text{mol CO}_2 \text{mol}^{-1}$ ). Net photosynthesis, transpiration, and stomatal conductance were measured on a 6-cm<sup>2</sup> area of the leaf. Data were analyzed using ANOVA (Proc Mixed, SAS Institute 1997), with cultivar as a main plot treatment and leafhopper injury as a subplot treatment, whereas blocks and plants within subplots were random effects. Gas exchange measurements were repeated on the same leaves after 5 d. Data from two leaves were deleted from the analysis because of cage malfunction.

**Greenhouse Experiment 1.** Four grape cultivars were used: 'Liné', Cabernet Sauvignon, Chardonnay, and 'Cynthia'. Plants had been grown from cuttings for 12 wk in 15-cm-diameter plastic pots with standard greenhouse potting mixture. Pots were arranged in a randomized complete block design with five blocks, for a total of 20 plants. Two leaves were selected on each plant; one served as a control, whereas the other was exposed to the leafhopper. Clear plastic boxes (12 by 9 by 3.5 cm) that could be opened from the side served as cages. On the top and bottom faces, holes were cut and covered with mesh to allow ventilation. On one of the front faces, a 21-mm hole in the middle was cut for the stem of the leaf, whereas an 8-mm hole off center on the other side was cut to introduce the leafhoppers. Each of the side holes was covered with a piece of foam. Each leaf was placed inside a cage, and four leafhoppers per cage were introduced to one of each pair of cages.

After 3 d, cages and leafhoppers were removed and measurements were taken on each caged leaf using the Li-Cor 6400 Photosynthesis Measurement System. The LI-6400 was set for standard levels of light ( $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $\text{CO}_2$  concentration ( $400 \mu\text{mol CO}_2 \text{mol}^{-1}$ ). Chlorophyll levels in each leaf were measured using a SPAD meter (SPAD 502 chlorophyll meter, Spectrum Technologies, Plainfield, IL). Five measurements were averaged for each leaf. Data were analyzed using ANOVA (Proc Mixed, SAS Institute 1997), with cultivar as a main plot treatment and leafhopper injury as a subplot treatment, whereas blocks and plants within subplots were random effects. Chlorophyll measurements were correlated with gas exchange measurements, with and without leafhopper injury.

**Greenhouse Experiment 2.** Three grape cultivars were used: Cynthia, Chardonnay, and Cabernet Sau-

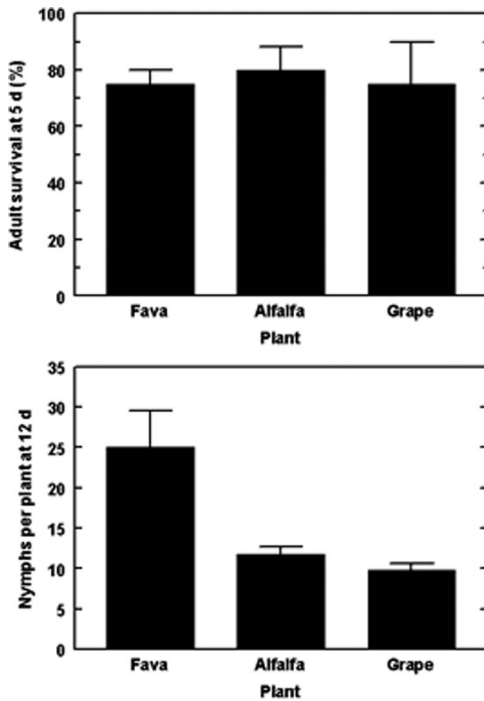


Fig. 1. Mean  $\pm$  SE of adult survival at 5 d and nymphs produced from oviposition by potato leafhopper onto fava, alfalfa, and grape plants.

vignon. Plants were grown as described above. Plants were arranged in a randomized complete block design with five replications. Two leaves were selected for caging on each plant as described above, with one serving as a control and the other exposed to the leafhopper. Three leafhoppers were introduced to the proper cages. After 3 d, cages and leafhoppers were removed and measurements were taken on each caged leaf using the Li-Cor 6400 Photosynthesis Measurement System. Chlorophyll levels in each

leaf were measured using a SPAD meter (SPAD 502 chlorophyll meter, Spectrum Technologies, Plainfield, IL). Five measurements were averaged for each leaf. Signs of yellowing, discoloration, desiccation, curling, and any other symptoms were recorded three times a week during the following 2 wk. Gas exchange measurements were repeated 14 d after cage removal. Data analysis was similar to that for greenhouse experiment 1.

## Results

**Host Plant Suitability of Grapes.** Adult survivorship for 5 d did not differ between the three plant species ( $F_{2,9} = 0.08$ ;  $P = 0.92$ ) (Fig. 1). Mean survivorship on fava bean, alfalfa, and Cabernet Sauvignon grape was 76.7%. The number of nymphs produced through oviposition on each plant species did differ significantly ( $F_{2,9} = 9.5$ ;  $P < 0.01$ ); however, oviposition occurred on all species (Fig. 1). Using least significant difference (LSD) test for planned comparisons, nymph production was significantly higher on fava bean than on the other two plant species ( $P < 0.05$ ). Nymph production was similar on alfalfa and grape ( $P > 0.05$ ).

**Field Measurement of Injury to Grape Leaves.** The exposure of grape leaves to injury by four leafhoppers for 2 d resulted in a significant reduction in all three gas exchange measurements: net photosynthesis (9.6% reduction), transpiration (13.2%), and stomatal conductance (18.8%) (Tables 1 and 2). The two cultivars responded similarly to the injury, as shown by the insignificant interaction effects. Gas exchange rates were not significantly different between healthy and injured leaves 5 d after removal. No injury symptoms were observed at the time of cage removal, and although injured leaves were largely symptomless after 5 d, two leaves (of 30) had brown, necrotic tissue along the leaf edge and one leaf had yellow discoloration. Uninjured leaves were without such symptoms.

Table 1. ANOVA for gas exchange rates in the field study for individual leaves of two grape cultivars, injured by four potato leafhoppers, and measured just after cage removal and 5 d later

Days after cage removal	Parameter	Source	df	F	Pr > F
0	Net photosynthesis	Cultivar (C)	1, 24.3	3.26	0.08
		Injury (I)	1, 27.9	4.10	0.05
		C $\times$ I	1, 27.9	0.04	0.85
	Transpiration	Cultivar	1, 24.4	1.03	0.32
		Injury	1, 27.8	4.65	0.04
		C $\times$ I	1, 27.7	0.10	0.76
	Stomatal conductance	Cultivar	1, 24.5	1.42	0.24
		Injury	1, 27.8	4.77	0.04
		C $\times$ I	1, 27.8	0.03	0.87
5	Net photosynthesis	Cultivar (C)	1, 23.8	0.97	0.34
		Injury (I)	1, 27.5	2.36	0.14
		C $\times$ I	1, 27.5	0.91	0.35
	Transpiration	Cultivar	1, 24.3	0.04	0.84
		Injury	1, 27.3	0.63	0.44
		C $\times$ I	1, 27.3	0.60	0.44
	Stomatal conductance	Cultivar	1, 24.2	0.14	0.71
		Injury	1, 27.3	1.35	0.26
		C $\times$ I	1, 27.3	0.25	0.62

**Table 2.** Means and SEs for gas exchange rates in the field study for individual leaves of two grape cultivars, injured by four potato leafhoppers, and measured just after cage removal and 5 d later

Parameter	Cultivar	Days after cage removal			
		0		5	
		Healthy	Injured	Healthy	Injured
Photosynthesis <sup>a</sup>	Chamborcin	12.2 ± 0.6	11.1 ± 0.6	11.0 ± 0.7	9.3 ± 0.7
	Chardonnay	13.5 ± 0.6	12.1 ± 0.6	11.0 ± 0.7	10.6 ± 0.7
Transpiration <sup>b</sup>	Chamborcin	4.4 ± 0.3	3.9 ± 0.3	3.2 ± 0.2	3.2 ± 0.2
	Chardonnay	4.8 ± 0.3	4.1 ± 0.3	3.0 ± 0.2	3.3 ± 0.3
Stomatal conductance <sup>c</sup>	Chamborcin	0.18 ± 0.02	0.15 ± 0.02	0.18 ± 0.02	0.19 ± 0.02
	Chardonnay	0.20 ± 0.02	0.17 ± 0.02	0.17 ± 0.02	0.19 ± 0.02

<sup>a</sup> Units are micromoles of CO<sub>2</sub> per square meter per second.  
<sup>b</sup> Units are moles of H<sub>2</sub>O per square meter per second.  
<sup>c</sup> Units are moles of H<sub>2</sub>O square meter per second.

**Greenhouse Experiment 1.** The exposure of grape leaves to injury by four leafhoppers for 3 d resulted in a significant reduction in all three gas exchange measurements: net photosynthesis (22.3% reduction), transpiration (37.6%), and stomatal conductance (45.4%) (Tables 3 and 4). Cultivars did not differ in their response to injury as indicated by insignificant interaction terms. Chlorophyll content did not differ at the end of the experiment among the cultivars ( $F_{3, 16} = 0.32; P = 0.80$ ) or as result of injury ( $F_{1, 16} = 0.02; P = 0.90$ ). However, although net photosynthesis was significantly correlated with chlorophyll content in healthy leaves ( $r = 0.50, P = 0.03$ ), it was not significantly correlated with chlorophyll content in injured leaves ( $r = 0.36, P = 0.12$ ).

**Greenhouse Experiment 2.** The exposure of grape leaves to injury by three leafhoppers for 3 d resulted in a significant reduction in all three gas exchange measurements: net photosynthesis (44.8% reduction), transpiration (51.7%), and stomatal conductance (57.6%) (Tables 5 and 6). Although cultivars did significantly vary in gas exchange measurements, cultivars did not differ in their response to injury as indicated by insignificant interaction terms. At 14 d after cage removal, gas exchange measurements did not differ between healthy and injured leaves. Chlorophyll content was significantly reduced at cage removal as result of injury (7.6% decline of SPAD values) and more after 14 d (8.4% decline of SPAD values). Nevertheless, no clear symptoms were observed on the injured plants after 14 d.

**Discussion**

Our research demonstrates that potato leafhopper occurs on Maryland grapevines, that grapevines are

**Table 3.** ANOVA for gas exchange rates in greenhouse Experiment 1 for individual leaves of four grape cultivars, injured by four potato leafhoppers, and measured just after cage removal

Parameter	Source	df	F	Pr > F
Net photosynthesis	Cultivar (C)	3, 12	1.36	0.30
	Injury (I)	1, 16	13.16	0.002
	C × I	3, 16	0.71	0.56
	Cultivar	3, 12	0.54	0.67
Transpiration	Injury	1, 16	15.17	0.001
	C × I	3, 16	0.46	0.71

suitable as host plants, and that the physiology of grapevines is affected adversely by feeding injury. However, the lack of reports from the 1900s of *E. fabae* reproducing on grapevines raises several questions about the potential for a recent host expansion: 1) did early researchers simply overlook potato leafhoppers on grapevines, 2) has there been a genetic change in potato leafhopper to allow host expansion, or 3) has there been a change in grapes to make them suitable as hosts? We briefly address each of these possibilities.

The possibility that potato leafhoppers on grapevines were overlooked is unlikely, because of the lack of potato leafhopper collection records in spite of searches conducted in eastern United States by grapevine researchers during the 1900s (Demaree and Runner 1942, Gleissner 1943, McGrew and Still 1968) and by *Empoasca* researchers (Poos and Wheeler 1943, 1949). Poos and Wheeler (1943) did report adults on grapes but did not record nymphs. Their searches were conducted from 1929 to 1942 in habitats that certainly included grapes. Other leafhopper researchers (DeLong (1931, 1938)) also did not record grapes as hosts. In Europe and Africa, other *Empoasca* species

**Table 4.** Means and SEs for gas exchange rates in greenhouse experiment 1 for individual leaves of four grape cultivars, injured by four potato leafhoppers, and measured just after cage removal

Parameter	Cultivar	Healthy leaf	Injured leaf <sup>a</sup>
Net photosynthesis <sup>b</sup>	Cabernet	6.9 ± 0.9	5.7 ± 0.5
	Sauvignon		
	Chardonnay	7.4 ± 1.5	6.4 ± 1.5
	Cynthia	5.6 ± 1.0	4.1 ± 0.9
	Liné	8.8 ± 1.0	6.1 ± 1.0**
Transpiration <sup>c</sup>	Cabernet	2.86 ± 0.51	2.14 ± 0.26
	Sauvignon		
	Chardonnay	3.40 ± 1.06	2.43 ± 0.62
	Cynthia	2.71 ± 1.01	1.28 ± 0.35*
Chlorophyll <sup>d</sup>	Liné	3.65 ± 0.47	2.03 ± 0.46*
	Cabernet	32.7 ± 1.8	34.3 ± 2.8
	Sauvignon		
	Chardonnay	33.3 ± 1.4	32.4 ± 0.9
	Cynthia	32.4 ± 1.5	29.9 ± 2.6
	Liné	30.7 ± 1.8	32.9 ± 2.6

<sup>a</sup> LSD comparison of healthy and injured leaf: \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ .  
<sup>b</sup> Units are moles of CO<sub>2</sub> per square meter per second.  
<sup>c</sup> Units are moles of H<sub>2</sub>O per square meter per second.  
<sup>d</sup> Units are SPAD.

**Table 5.** ANOVA for gas exchange rates in greenhouse experiment 2 for individual leaves of three grape cultivars, injured by three potato leafhoppers, and measured just after cage removal and after 14 d

Days after cage removal	Parameter	Source	df	F	Pr > F
0	Net photosynthesis	Cultivar (C)	2, 8	1.35	0.31
		Injury (I)	1, 12	67.58	0.0001
		C × I	2, 12	1.60	0.24
	Transpiration	Cultivar	2, 8	3.73	0.07
		Injury	1, 12	29.04	0.0002
		C × I	2, 12	0.03	0.97
	Chlorophyll	Cultivar	2, 8	4.85	0.04
		Injury	1, 12	11.21	0.01
		C × I	2, 12	0.35	0.71
14	Net photosynthesis	Cultivar	2, 8	1.04	0.40
		Injury	1, 12	2.51	0.14
		C × I	2, 12	1.06	0.38
	Transpiration	Cultivar	2, 8	4.67	0.05
		Injury	1, 12	0.52	0.48
		C × I	2, 12	1.31	0.31
	Chlorophyll	Cultivar	2, 8	5.51	0.03
		Injury	1, 12	19.08	0.0009
		C × I	2, 12	0.56	0.59

have long been recognized as pests of grapevines, yet Bournier (1976) did not mention potato leafhopper in his review.

The second explanation suggests that host expansion may be the result of a genetic change in potato leafhopper populations. Yet, the polyphagy and mobility of the leafhopper (Lamp et al. 1994, Sidumo et al. 2005) promote dispersal and high gene flow among populations in different locations and on different hosts, preventing local adaptation (Lenormand 2002). Suitable hosts are common and grapes are much less used than legumes and other host plants in the landscape (W.O.L., personal observations). Related to this question, is the grape "*E. fabae*" a different species or host race? *Empoasca* is a large genus with many morphologically similar species identified by male geni-

ta (DeLong 1931). Our collection of adult males from grape vineyards verified that these specimens are taxonomically identical to *E. fabae*. Furthermore, the migration patterns of the leafhopper suggest that new populations in the northeastern and north central United States come from colonists arriving from southern states (Sidumo et al. 2005). This fact further compounds the difficulty in race formation within the species. Because the leafhopper does not overwinter in the northeastern United States, populations generated on grapes in the northeastern states presumably mix with other migrating populations, and thus are less likely to significantly alter the population genetics of the species. Indeed, in an allozyme study, Taylor et al. (1995) found no genetic differences among potato leafhoppers collected from multiple host plants (pines

**Table 6.** Means and SEs for gas exchange rates in greenhouse experiment 2 for individual leaves of three grape cultivars, injured by three potato leafhoppers, and measured just after cage removal and after 14 d

Days after cage removal	Parameter	Cultivar	Healthy leaf	Injured leaf <sup>a</sup>
0	Net photosynthesis <sup>b</sup>	Cabernet Sauvignon	12.0 ± 0.4	4.8 ± 1.0***
		Chardonnay	12.8 ± 0.4	8.3 ± 1.0**
		Cynthia	12.0 ± 0.6	7.2 ± 1.0**
	Transpiration <sup>c</sup>	Cabernet Sauvignon	4.63 ± 0.38	1.44 ± 0.51**
		Chardonnay	6.22 ± 0.42	3.25 ± 0.73**
		Cynthia	6.56 ± 0.44	3.72 ± 0.75*
	Chlorophyll <sup>d</sup>	Cabernet Sauvignon	29.2 ± 1.2	27.3 ± 1.1
		Chardonnay	26.0 ± 0.9	23.3 ± 2.1
		Cynthia	23.8 ± 1.0	22.4 ± 1.3
14	Net photosynthesis <sup>b</sup>	Cabernet Sauvignon	10.7 ± 0.8	8.2 ± 1.0
		Chardonnay	11.4 ± 0.4	10.8 ± 0.4*
		Cynthia	10.5 ± 1.1	10.4 ± 0.5
	Transpiration <sup>c</sup>	Cabernet Sauvignon	3.04 ± 0.47	2.20 ± 0.34
		Chardonnay	4.29 ± 0.47	4.08 ± 0.52
		Cynthia	3.54 ± 0.52	3.92 ± 0.29
	Chlorophyll <sup>d</sup>	Cabernet Sauvignon	32.6 ± 0.7	29.4 ± 0.9**
		Chardonnay	28.4 ± 0.5	26.7 ± 1.1
		Cynthia	28.4 ± 0.5	25.8 ± 0.8*

<sup>a</sup> LSD comparison of healthy and injured leaf: \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

<sup>b</sup> Units are micromoles of CO<sub>2</sub> per square meter per second.

<sup>c</sup> Units are moles of H<sub>2</sub>O per square meter per second.

<sup>d</sup> Units are SPAD.



[*Pinus* pp.], *Vicia* spp., alfalfa, *Acer* spp., *Ulmus* spp., and *Myrica* spp.), states (Alabama, Georgia, Louisiana, New York, North Carolina, South Carolina, Wisconsin), or years, and concluded that potato leafhopper consists of populations with little or no genetic differentiation.

We propose that plant breeding that has caused a loss of the natural resistance found in native vitaceous plants is the most likely explanation for the host expansion by the potato leafhopper. It is generally thought that feeding acceptance of a host plant by an insect is caused by the combination of stimulation by phagostimulants and chemoreception of feeding deterrents (Dethier 1980). Tallamy et al. (1999) propose that host expansion to novel hosts (and even novel hosts of distant phytochemistry) can result from "loose gustatory receptors." Early introductions of the European "vinifera" grapevines were unsuccessful because of grape phylloxera and a number of plant diseases (Weaver 1976). Private breeding programs in the late 1940s and 1950s brought European/North American hybrids into production in the 1960s, such that "in 1968... the wine revolution in America... had its start" (p. 49, Morton 1985). Thus, the introduction of germplasm from Europe into grape breeding programs in the United States may have caused in the loss of natural resistance in grapevines and allowed for potato leafhopper host expansion. A comparison of native and cultured *Vitis* spp. as hosts for potato leafhopper is needed to test this hypothesis. We did not find any significance among injury to American versus European varieties of grapes, although there has been considerable mixing of all varieties in breeding programs.

The damage that potato leafhopper is capable of causing on grapevines probably depends on local conditions for leafhopper outbreaks and the stage of vine development. Our research supports that of Lenz et al. (2009), suggesting that potato leafhopper is capable of physiological injury to grapes, leading to disruption of normal gas exchange processes (our data) and reduced leaf, shoot, and root growth (Lenz et al. 2009). Yet, injured leaves are capable of repairing themselves within 5 d. In addition, the carbohydrate source-sink relationships in grapevines are such that the vines are capable of tolerating leafhopper injury at certain times of the season (Mercader and Isaacs 2003). Indeed, injury of grapes in Europe by *Empoasca vitis* Goethe, which causes similar hopperburn injury to potato leafhopper, is capable of stimulating the growth of lateral leaves that replace the function of the injured leaf tissue (Candolfi et al. 1993). As a result, we agree with Lenz et al. (2009) that young developing grapevines are probably at greater risk of damage than production-aged grapevines. In spite of significantly impacting gas exchange rates, potato leafhopper injury was relatively symptomless, suggesting the importance of monitoring of leafhopper populations during times of local outbreaks of potato leafhopper instead of depending on visual inspections of leaves. Thus, timing and size of the colonizing population, as well as the

developmental stage of the grapevine, are probably important factors in decision making.

### Acknowledgments

We thank J. Fiola and G.R. Welsh for help at the Western Maryland Research and Education Center. In addition, we thank Richelle Green assistance for greenhouse studies. Portions of the research were conducted as part of an Undergraduate Research Assistant Project from the University of Maryland. Support for this research was provided in part by USDA-Cooperative State Research, Education, and Extension Service project MD-H-176 (NC-193) and USDA Northeastern Regional IPM project 93-34103-8418.

### References Cited

- Backus, E. A., and W. B. Hunter. 1989. Comparison of feeding behavior of the potato leafhopper *Empoasca fabae* (Homoptera: Cicadellidae) on alfalfa and broad bean leaves. *Environ. Entomol.* 18: 473-480.
- Backus, E. A., M. S. Serrano, and C. M. Ranger. 2005. Mechanisms of hopperburn: an overview of insect taxonomy, behavior, and physiology. *Annu. Rev. Entomol.* 50: 125-151.
- Bostanian, N. J., C. Vincent, H. Goulet, L. Lesage, J. Lasnier, J. Bellemare, and Y. Mauffette. 2003. The arthropod fauna of Quebec vineyards with particular reference to phytophagous arthropods. *J. Econ. Entomol.* 96: 1221-1229.
- Bournier, A. 1976. Grape insects. *Annu. Rev. Entomol.* 22: 355-376.
- Candolfi, M. P., M. Jermini, E. Carrera, and M. C. Candolfi-Vasconcelos. 1993. Grapevine leaf gas exchange, plant growth, yield, fruit quality and carbohydrate reserves influenced by the grape leafhopper, *Empoasca vitis*. *Entomol. Exp. Appl.* 69: 289-296.
- DeLong, D. M. 1931. A revision of the American species of *Empoasca* known to occur north of Mexico. U.S. Dep. Agric. Tech. Bull. 231. USDA, Washington, DC.
- DeLong, D. M. 1938. Biological studies on the leafhopper *Empoasca fabae* as a bean pest. U.S. Dep. Agric. Tech. Bull. 618. USDA, Washington, DC.
- Demaree, J. B., and G. A. Runner. 1942. Control of grape diseases and insects in eastern United States. U.S. Dep. Agric. Farmers Bull. 1893.
- Dethier, V. G. 1980. Evolution of receptor sensitivity to secondary plant substances with special reference to deterrents. *Am. Nat.* 115: 45-66.
- Ecalle, C. L., and E. A. Backus. 1995. Mechanical and salivary aspects of potato leafhopper probing in alfalfa stems. *Entomol. Exp. Appl.* 77: 121-132.
- Flinn, P. W., A. A. Hower, and D. P. Knievel. 1990. Physiological response of alfalfa to injury by *Empoasca fabae* (Homoptera: Cicadellidae). *Environ. Entomol.* 19: 176-181.
- Gleissner, B. D. 1943. Biology and control of berry moth in the Erie grape belt with notes on other grape insects. Penn. St. Coll. Agric. Exp. Stn. Bull. 451. The Pennsylvania State University, University Park, PA.
- Hibbs, E. T., D. L. Dahlman, and R. L. Rice. 1964. Potato foliage sugar concentration in relation to infestation by the potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae). *Ann. Entomol. Soc. Am.* 57: 517-521.
- Hogg, D. B., and G. D. Hoffman. 1989. Potato leafhopper population dynamics. In E. J. Armbrust and W. O. Lamp [eds.], *History and perspectives of potato leafhopper*

- (Homoptera: Cicadellidae) research. Misc. Publ. Entomol. Soc. Am. 72: 26–34.
- Hutchins, S. H., and L. P. Pedigo. 1989. Potato leafhopper-induced injury on growth and development of alfalfa. *Crop Sci.* 29: 1005–1011.
- Jordan, T. D., R. M. Pool, T. J. Zabadal, and J. P. Tomkins. 1980. Cultural practices for commercial vineyards. Cornell Univ. Misc. Bull. 111. Cornell University, Ithaca, NY.
- Lamp, W. O., G. R. Nielsen, and S. D. Danielson. 1994. Patterns among host plants of potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae). *J. Kans. Entomol. Soc.* 67: 354–368.
- Lamp, W. O., G. R. Nielsen, C. B. Fuentes, and B. Quebedeaux. 2004. Feeding site preference of potato leafhopper (Homoptera: Cicadellidae) on alfalfa and its effect on photosynthesis. *J. Agric. Urban Entomol.* 21: 25–38.
- Lenormand, T. 2002. Gene flow and the limits to natural selection. *Trends Ecol. Evol.* 17: 183–189.
- Lenz, M. S., R. Isaacs, J. A. Flore, and G. S. Howell. 2009. Vegetative growth responses of Pinot Gris (*Vitis vinifera* L.) grapevines to infestation by potato leafhoppers (*Empoasca fabae* Harris). *Am. J. Enol. Viticult.* 60: 130–137.
- Martinson, T. E., R. Dunst, A. Lakso, and G. English-Loeb. 1997. Impact of feeding injury by Eastern grape leafhopper (Homoptera: Cicadellidae) on yield and juice quality of Concord grapes. *Am. J. Enol. Vitic.* 48: 291–302.
- McGrew, J. R., and G. W. Still. 1968. Control of grape diseases and insects in the eastern United States. U.S. Dep. Agric. Farm. Bull. 1893.
- Mercader, R. J., and R. Isaacs. 2003. Phenology-dependent effects of foliar injury and herbivory on the growth and photosynthetic capacity of nonbearing *Vitis labrusca* (Linnaeus) var. Niagara. *Am. J. Enol. Viticult.* 54: 252–260.
- Morton, L. T. 1985. Winegrowing in Eastern America. Cornell University Press, Ithaca, NY.
- Nielsen, G. R., W. O. Lamp, and G. W. Stutte. 1990. Potato leafhopper (Homoptera: Cicadellidae) feeding disruption of phloem translocation in alfalfa. *J. Econ. Entomol.* 83: 807–813.
- Nielsen, G. R., C. Fuentes, B. Quebedeaux, Z. Wang, and W. O. Lamp. 1999. Alfalfa physiological response to potato leafhopper injury depends on leafhopper and alfalfa developmental stage. *Entomol. Exp. Appl.* 90: 247–255.
- Poos, F. W., and N. H. Wheeler. 1943. Studies on host plants of the leafhoppers of the genus *Empoasca*. U.S. Dep. Agric. Tech. Bull. 850.
- Poos, F. W., and N. H. Wheeler. 1949. Some additional host plants of three species of leafhoppers in the genus *Empoasca*. *Proc. Entomol. Soc. Wash.* 51: 35–38.
- SAS Institute. 1997. SAS/STAT software: changes and enhancements through release 6.12. SAS Institute, Cary, NC.
- Sidumo, A. J., E. J. Shields, and A. Lembo, Jr. 2005. Estimating the potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae) overwintering range and spring premigrant development by using geographic information system. *J. Econ. Entomol.* 98: 757–764.
- Still, G. W., and R. W. Rings. 1973. Insect and mite pests of grapes in Ohio. Ohio Agric. Res. Dev. Ctr. Res. Bull. 1060.
- Tallamy, D. W., C. A. Mullin, and J. L. Frazier. 1999. An alternate route to insect pharmacophagy: the loose receptor hypothesis. *J. Chem. Ecol.* 25: 1987–1997.
- Taylor, P. S., E. J. Shields, and J. I. Davis. 1995. *Empoasca fabae* (Homoptera: Cicadellidae) identification and population studies with allozyme electrophoresis. *Environ. Entomol.* 25: 1109–1114.
- Weaver, R. J. 1976. Grape growing. Wiley, New York.
- Womack, C. L. 1984. Reduction in photosynthetic and transpiration rates of alfalfa caused by the potato leafhopper (Homoptera: Cicadellidae) infestations. *J. Econ. Entomol.* 77: 508–513.

Received 3 March 2011; accepted 8 May 2011.