Phenophase-Dependent Growth Responses to Foliar Injury in *Vitis labruscana* Bailey var. Niagara during Vineyard Establishment

Rodrigo J. Mercader[1] and Rufus Isaacs[2]*

Abstract: In comparison to mature vines, the lack of fruit and lower carbohydrate reserves in vines during establishment create a situation in which the lowest source to sink ratios occur early in the season during rapid vegetative growth. This study compared responses of young *Vitis labruscana* Bailey var. Niagara vines to injury applied early in the season (bloom) and/or late in the season (veraison). Different sets of plants were injured with hole punchers to imitate foliar injury by leaf-skeletonizing beetles either during bloom, during veraison, or during both phenophases in 2000 and 2001, using 2 x 2 factorial designs. In 2000, vines were injured during bloom by removing 30% of the total leaf area of each fully expanded leaf and during veraison by removing 30% of the subsequently expanded leaves on 1.5 m of each shoot. During 2001, injury during bloom and veraison consisted of removing 20% of the total leaf area of all fully expanded leaves, thereby removing the same percentage of the source available each time. Injury applied during bloom in 2000 significantly reduced pruning weights, total shoot length, and cane diameters the following season, while veraison injury did not. Vines injured during bloom in 2001 had lower numbers of nodes and mature nodes, lower pruning weights, and lower total cluster weight the following season compared to the uninjured vines, while vines injured solely during veraison showed no significant response to injury. In both years, vines injured during both bloom and veraison had the greatest reduction in vegetative growth. Results indicate that during the establishment phase vines are more tolerant of injury during veraison than during bloom and that foliar injury early in the season can significantly reduce a vine's ability to tolerate subsequent foliar injury.

Key words: tolerance, source to sink ratio, herbivory, defoliation

In recent years, new juice grape (*Vitis labruscana*) vineyards in Michigan have been planted with Niagara grapevines at a faster rate than any other grape variety in the past 20 years (Kleweno and Matthews 2001). The establishment of these vineyards is a critical period in their development, as a poor start can hinder productivity for several years (Zabadal 1997). During establishment, vines typically bear very little or no fruit and the fruit produced is generally removed to improve vegetative growth (Zabadal 1997). Compared to mature vines, the smaller size and lower levels of carbohydrates found in the storage organs of young vines may significantly reduce their ability to compensate for foliar injury. In addition, the lack of fruits as carbohydrate and nitrogen sinks in young vines may create a significantly greater relative source to sink ratio during veraison compared to that of mature vines. Several studies have found that sink demand strongly influences carbohydrate production (Wardlaw 1990) and that potted grapevines without fruit have been reported to have sink limitations during veraison (Miller et al. 1996, Petrie et al. 2000). This potential for a sink limitation during veraison suggests that nonbearing vines may have a high level of tolerance to foliar injury at this time.

There is an increasing need to link current understanding of vine tolerance to herbivory to pest management strategies, as concern over the long-term ecological and health effects of pesticides are leading to increased restriction of pesticide availability for crop protection. In establishing vineyards, plant-protection strategies focus on the protection of vegetative tissues from sucking and chewing insects. In southern Michigan vineyards, as in many vineyards across the eastern United States, vines may be subject to herbivory by two leaf-skeletonizing beetles: the rose chafer, *Macrodactylus subspinosus* (F.), which has adults that are active during bloom, and the Japanese beetle, *Popilia japonica* (Newman), which has a peak of adult beetle activity during veraison. The abundance of these insects varies greatly, particularly in relation to local soil types and weather conditions (Chittenden 1916, Fleming 1972, Vittum et al. 1999). Consequently, the need for insecticidal control to protect vines from economic injury depends upon local beetle densities and the vine's ability to tolerate injury during different phenophases. Integrated pest man-

[1]Graduate Student, [2]Assistant Professor, Department of Entomology, 243 Natural Sciences Building, Michigan State University, East Lansing, MI 48824.

*Corresponding author [Email: isaacsr@msu.edu; tel: (517) 355-6619; fax: (517) 346-7592]

Acknowledgments: Funding for the project was provided by Project GREEEN, The Viticulture Consortium-East through a subcontract with NYSAES, Cornell University and the Michigan Agricultural Experiment Station. This research was in partial fulfillment of the MS degree for RJM.

Our thanks to Bruce Van Den Bosch, Jason Keeler, Kasey Watts, and Kelly Bahns for their work on this project, to Keith Mason for technical assistance, and to all the members of the Small Fruit Entomology laboratory at MSU for their help with mechanical injury treatments. We are grateful to John Wise and the staff at the Trevor Nichols Research Complex for providing vineyard management services and research facilities. We also thank G.S. Howell for valuable advice on viticultural techniques and concepts.

Manuscript submitted February 2003; revised August 2003

agement strategies for eastern United States vineyards could be improved by better understanding of the impact of defoliation in relation to the seasonal variation in source to sink balance. If the periods during which vines are most susceptible to foliar injury were identified, then applications of foliage-protecting insecticides could be limited to those periods when defoliators reach population levels sufficient to compromise sustainable vine productivity (Howell 2001).

This study examined the relative ability of young *V. labruscana* Bailey var. Niagara vines to tolerate foliar injury during bloom and veraison. In particular, this study tested the hypothesis that nonbearing grapevines are more tolerant to injury during veraison than at bloom, as would be expected by the higher source to sink ratio at this time. This was tested in a study during 2000 where similar absolute levels of injury were applied during bloom and/or veraison and in 2001 by damaging 20% of vine's total leaf area at bloom and/or veraison.

Materials and Methods

Plant material. This study was conducted in a *V. labruscana* Bailey var. Niagara vineyard established in spring 1999, at the Trevor Nichols Research Complex in Fennville, Michigan. Two shoots from each of the two canes (total of four shoots) of each vine were trained onto a 1.37-m high bilateral-cordon Hudson River Umbrella trellis system, and all other shoots were removed at the 1- to 3-inch stage (Eichorn-Lorenz stage 9 [Eichorn and Lorenz 1977]). There were seven vines per row, with 1.8 m between vines and 3 m between rows. Fertilizer was applied to the vineyard as urea (46% nitrogen, N) at 52 kg N/ha on 16 March 2000, and 116 kg N/ha on 25 March 2001. All vines received a standard plant-protection program (Gut et al. 2002).

2000 experiment. Sixteen vines with cane height between 0.5 m and 1.0 m were selected to receive mechanical injury treatments during bloom and/or during veraison. Treatments were imposed in a 2 x 2 factorial design with four replicates per treatment combination; vines were injured either at bloom, at veraison, at bloom and veraison, or not injured. Leaf area was removed using single-hole paper punchers (size of holes = 38.5 mm^2). This method was used to avoid all major veins in order to imitate feeding by skeletonizing beetles and to avoid the differential impacts on photosynthetic capacity caused by interveinal injury and by whole-leaf removal, midrib injury, or lateral vein injury (Hall and Ferree 1976, Boucher et al. 1987). Vines injured at bloom had 30% of the total leaf area of every fully expanded leaf removed during 19 to 21 June. Injury during veraison (15 to 16 August) consisted of removing 30% of the leaf area of every fully expanded leaf on 1.5 m of each shoot, starting at the point where the shoots first reached the trellis. To ensure appropriate injury levels were applied, visual aids were made for use while damaging leaves (Figure 1).

During the 2000 growing season, cane diameters were measured between the second and third node of each cane

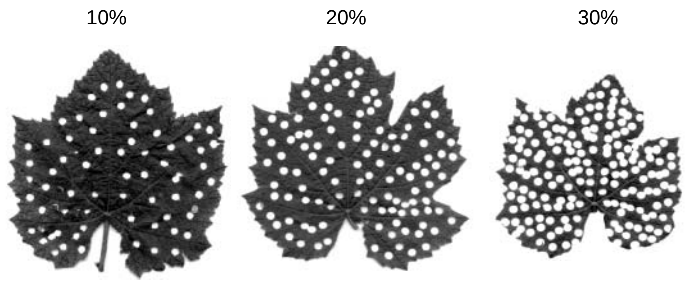

Figure 1 Example leaves of *Vitis labrusca* var. Niagara grapevines after using a hole-puncher to apply mechanical injury treatments to remove either 10, 20, or 30% of the interveinal leaf area. Similar figures were used to guide application of appropriate leaf area injury.

(from the base of the cane) using Vernier calipers, and node numbers were counted at trace bloom (13 to 14 June), at veraison (6 August), and after leaf senescence (21 October) on all experimental vines. In addition, the number of mature nodes was counted and the total shoot length was measured after leaf loss (10 to 11 November).

On 26 January 2001, all vines were pruned to 15 nodes per shoot and the weight of wood pruned off (pruning weights) was determined by immediately tying all the cuttings and weighing them with a digital scale (Stren, Madison, NC) in the vineyard. Prior to bloom in 2001, the diameter of canes (9 May) and the number of nodes remaining dormant after the 16-inch shoot growth stage had been reached (22 May) were recorded on all vines.

Statistical analysis. Measurements taken before veraison injury were analyzed as a one-way ANOVA, with bloom injury as the sole treatment and cane diameter at trace bloom as a covariate. Measurements taken after veraison injury were analyzed by date as a 2 x 2 factorial analysis with cane diameter at trace bloom as a covariate, using SAS statistical software (version 8; SAS Institute, Cary, NC). The analysis of pruning weight data indicated a significant bloom interaction between injury timings; therefore, bloom injury was analyzed separately within veraison injury and veraison injury was analyzed within bloom injury. This was performed using the LSmeans Slice function of the PROC GLM function in SAS.

2001 experiment. On 20 February 2001, 40 vines not previously used for experiments were pruned to 15 nodes on each of two canes and the pruning weights were recorded as described above. The number of shoots on these vines was adjusted to four per cane on 8 May. Due to strong winds between 5 and 11 June, vines lost shoots and only 28 vines were retained for the experiment. Because of this damage, vines were assigned to three blocks according to shoot number left on the vines; Block 1 had 12 vines with 5 shoots, block 2 had 12 vines with 6 shoots, and block 3 had 4 vines with 7 shoots. These vines were mechanically injured during bloom and/or veraison as a balanced 2 x 2 factorial design within each block, with a total of seven replicates per treatment combination. Bloom injury consisted of removing 20% of the total leaf area of all fully expanded leaves between 18 June and June 2001, while veraison injury consisted of removing 20% of the total leaf area of all fully expanded leaves between 21 and 24 August 2001. On vines injured at both times, only leaves that expanded after application of bloom injury were injured at veraison. Therefore, vines injured at veraison and those injured at bloom and veraison had the same absolute level of injury.

Vegetative growth parameters were measured during the 2001 growing season at budburst, bloom, midseason, veraison, and postharvest. On each vine, the length of main shoots (11 to 14 June, 9 to 13 July, 8 to 14 August, 9 to 14 October), the node number of main shoots (11 to 14 June, 9 to 13 July, 8 to 14 August, 9 to 14 October), the node number of lateral shoots per main shoot (18 July, 20 August, 23 October), and cane diameters (14 May, 13 June, 11 to 13 July, 6 August, 25 September) were measured. On 17 and 24 February and 4 and 5 March 2002, the number of mature nodes was recorded on all experimental vines, vines were pruned to 15 nodes per shoot, and the pruning weights were then measured, as described above.

Table 1 Vegetative growth measurements of vines injured during the 2000 growing season. Letters below a column denote significant effects ($p < 0.05$) of injury at bloom (B) and/or veraison (V) in the factorial analysis on the parameter measured.

Injury	Total nodes[a]	Mature nodes[b]	Total shoot length (m)[b]	Pruning wt (g)[c]
No injury	116.0 ± 8.7 a[d]	96.8 ± 8.7 a	14.91 ± 1.6 a	637 ± 92.9 b
Bloom	102.4 ± 5.0 a	86.0 ± 2.4 a	12.31 ± 1.2 a	598 ± 129.7 cb
Veraison	134.3 ± 14.6 a	109.5 ± 10.6 a	17.13 ± 1.5 a	987 ± 64.0 a
Bloom and veraison	107.8 ± 27.4 a	92.3 ± 21.1 a	11.73 ± 3.4 a	342 ± 142.0 c
			B[e]	BV[f]

[a]Measured 21 Oct 2000.
[b]Measured 10-11 Nov 2000.
[c]Measured 26 Jan 2001.
[d]Values in a column with the same letters are not significantly different at the $p < 0.05$ level. Means separation performed by least squares difference using the Tukey-Kramer adjustment method to control for experimentwise error.
[e]Significant effect of injury at bloom ($F_{1,10} = 6.64$, $p = 0.03$). No significant effect of injury at veraison ($F_{1,10} = 0.45$, $p = 0.52$).
[f]There was a significant interaction between bloom and veraison; see text for details.

To determine whether foliar injury treatments affected fruit quality and yield in the third year of establishment, all fruit on the experimental vines was harvested on 22 September 2002. Although spring frosts on 22 to 23 April and 20 to 21 May 2002 drastically reduced crop load in many Michigan vineyards (including the experimental vineyard), crop weights were measured and the berries were frozen. Berries were thawed three weeks later, and the soluble solids (Brix) were recorded from the apical berry of three randomly chosen clusters per vine using a hand-held refractometer (model RHB 32ATC; Westover, Woodinville, WA).

Statistical analysis. Measurements taken prior to veraison injury were analyzed as a blocked one-way ANOVA with bloom injury as the sole treatment and the pruning weights as covariates. Measurements taken after veraison injury were analyzed by date as a blocked 2 x 2 factorial analysis with pruning weights as covariates, using SAS statistical software, version 8. Where F values for a blocking factor were less than 1, the factor was considered to be ineffective and the analysis was performed without it.

Results

2000 experiment. Injury at bloom did not cause any measurable change in average cane diameter or node number when measurements were taken at veraison. No interactions between bloom and veraison injury were detected in the growth parameters measured after leaf senescence. No impact of bloom injury was detected on cane diameters, total node number, or mature node number (Table 1). Injury at veraison also had no impact on the aboveground growth parameters measured. However, injury at bloom had a negative impact upon total shoot length, while injury at veraison did not (Table 1). No differences were found between means for total shoot length due to bloom injury, potentially due to the lower statistical power of the means comparison test.

Although leaf injury had no consistent effect on vegetative growth parameters, injury at both bloom and veraison reduced pruning weights (Table 1). There was a significant interaction of bloom and veraison injury effects on this growth parameter; therefore, bloom injury was analyzed within veraison injury and veraison injury within bloom injury. Within vines not injured at bloom, veraison injury resulted in a 35% increase in pruning weights compared to controls ($F_{1,10} = 10.77$, $p = 0.01$). However, within vines injured during bloom, injury at veraison caused a 46% reduction in pruning weights ($F_{1,10} = 5.79$, $p = 0.04$). Within vines injured at veraison, bloom injury caused a reduction in pruning weights ($F_{1,10} = 41.2$, $p < 0.01$), but within vines not injured at veraison, bloom injury had no detectable impact on pruning weights ($F_{1,10} = 0.61$, $p = 0.45$).

Cane diameters measured prior to bloom in the 2001 growing season were impacted by injury at bloom during the previous season ($F_{1,10} = 6.5$, $p = 0.03$). Vines injured solely at bloom and those injured at bloom and veraison had 15% smaller mean cane diameters than control vines (12.6 ± 0.5 mm, 12.6 ± 0.7 mm, and 14.8 ± 0.2 mm, respectively). Vines injured solely at veraison also had smaller mean cane diameter (13.1 ± 0.7 mm) than control vines, but no significant effect of veraison injury was found ($F_{1,10} = 0.51$, $p = 0.49$). Injury during the previous year had no effect on the number of nodes remaining dormant after the 16-inch shoot growth stage in 2001. This was the case for injury during either bloom ($F_{1,10} = 0.37$, $p = 0.56$) or veraison ($F_{1,10} = 0.05$, $p = 0.82$).

Table 2 Vegetative growth measurements of vines injured during the 2001 growing season. Letters below a column denote significant effects ($p < 0.05$) of injury at bloom (B) in the factorial analysis on the parameter measured. No significant impacts of veraison injury were detected.

Injury	Lateral shoot nodes[a]	Total nodes[a]	Mature nodes[b]	Total shoot length (m)[c]	Pruning wt (g)[b]
No injury	517.7 ± 41.6 ab[d]	725.0 ± 54.0 ab	271.7 ± 14.5 ab	23.17 ± 1.76 a	1035 ± 142 a
Bloom	449.0 ± 35.2 ab	635.1 ± 42.9 ab	218.7 ± 23.0 ab	20.36 ± 1.42 a	617 ± 65 b
Veraison	645.86 ± 75.0 a	831.3 ± 78.0 a	277.3 ± 16.3 a	21.2 ± 2.16 a	862 ± 105 ab
Bloom and veraison	377.9 ± 41.6 b	561.7 ± 19.8 b	201.9 ± 13.5 b	19.15 ± 1.17 a	559 ± 65 b
	B[e]	B[f]	B[g]		B[h]

[a]Measured 9-14, 23 Oct 2001.
[b]Measured 17, 24 Feb, and 4, 5 Mar 2002.
[c]Measured 9-14 Oct 2001.
[d]Values in a column with the same letters are not significantly different at the $p < 0.05$ level. Means separation performed by least squares difference using the Tukey-Kramer adjustment method to control for experimentwise error.
[e]$F_{1,22} = 11.18$, $p = 0.003$.
[f]$F_{1,22} = 10.56$, $p = 0.004$.
[g]$F_{1,21} = 13.68$, $p = 0.001$.
[h]$F_{1,21} = 11.26$, $p = 0.003$.

2001 experiment. When measured at midseason, there was no detectable difference between vines injured at bloom and uninjured vines in their shoot length ($F_{1,23} = 0.29$, $p = 0.60$), total node number ($F_{1,23} = 0.04$, $p = 0.85$), main shoot node number ($F_{1,23} = 1.67$, $p = 0.21$), lateral shoot node number ($F_{1,23} = 0.35$, $p = 0.56$), or cane diameters ($F_{1,23} = 0.12$, $p = 0.73$). However, by veraison, vines injured at bloom had a lower total number of nodes ($F_{1,23} = 6.59$, $p = 0.02$), number of nodes on lateral shoots ($F_{1,23} = 6.32$, $p = 0.02$), and total shoot length ($F_{1,23} = 5.59$, $p = 0.03$). No impact of bloom injury was found on main shoot node number ($F_{1,23} = 1.35$, $p = 0.26$) or cane diameter ($F_{1,2} = 0.61$, $p = 0.44$) at veraison.

Measurements taken postharvest still indicated a significant negative impact of bloom injury on the total number of nodes and number of nodes on lateral shoots, but not on shoot length (Table 2). As found during veraison, no significant impact of bloom injury was found on the number of nodes on the main shoots ($F_{1,22} = 0.59$, $p = 0.45$), or cane diameter ($F_{1,2} = 2.10$, $p = 0.16$). No significant effect of injury at veraison was observed on total node number, lateral shoot node number, shoot length (Table 2), main shoot node number ($F_{1,22} = 0.66$, $p = 0.43$), or cane diameter ($F_{1,21} = 0.02$, $p = 0.89$).

Injury applied at bloom significantly reduced the number of mature nodes and the weight of pruned wood compared to the control vines. In contrast, veraison injury treatments did not have a significant impact on either of these parameters (Table 2).

In 2002, crop weight was found to be significantly reduced in response to bloom injury but not in response to injury at veraison. There was no effect on soluble solids (Brix) of injury applied either at bloom or at veraison (Table 3).

Table 3 Mean yield and Brix of vines injured in the 2001 growing season and harvested on 22 September 2002. There was a significant effect of injury at bloom analyzed as a factorial ANOVA with foliar injury at bloom and/or veraison as treatments.

Injury	Crop wt (g)	Brix
No injury	3602.9 ± 353.4 a[a]	15.9 ± 0.2 a
Bloom	2425.3 ± 398.7 ab	16.4 ± 0.5 a
Veraison	3624.3 ± 714.3 a	15.5 ± 0.3 a
Bloom and veraison	1304.7 ± 457.5 b	16.0 ± 0.2 a

[a]Values in a column with the same letters are not significantly different at the $p < 0.05$ level. Means separation was performed by least squares difference using the Tukey-Kramer adjustment method to control for experimentwise error.

Discussion

The results presented here indicate that young nonbearing *V. labruscana* vines are better able to tolerate foliar injury during veraison than during bloom. In experiments during 2000 and 2001, bloom injury had significant negative impacts upon several of the growth parameters measured, while veraison injury did not affect any of the growth parameters measured. The negative impact of bloom injury on vegetative growth during the 2000 growing season was observed the following season in reduced cane diameters, further emphasizing that within-season effects can be translated to reduced growth in subsequent years.

Vines injured solely at veraison in 2000 had significantly greater pruning weights than all other vines (Table 1). However, an 11.5% reduction in cane diameter was observed in vines damaged only at veraison compared to controls, although this was not statistically significant. These results suggest that a certain level of foliar injury may induce an increase in aboveground growth during the later part of the season. The smaller cane diameter in veraison-injured vines, though not significant, may be an indication that a reallocation of resources caused the increased pruning weights. Alternatively, an increase in sink activity induced by injury may have taken place. Candolfi-Vasconcelos et al. (1994) have demonstrated that defoliation-stressed *Vitis vinifera* vines can re-translocate carbohydrates stored in storage tissues to fruit. In addition, our own studies on potted *V. labruscana* Bailey var. Niagara vines have shown that root weight was significantly impacted by injury at veraison, while no differences in aboveground injury were observed (Mercader and Isaacs 2003).

Increases in individual-leaf carbon assimilation rates have been reported in vines where defoliation has been performed by whole-leaf removal (Hofäcker 1978, Candolfi-Vasconcelos and Koblet 1991). In addition, several studies have reported cases of overcompensation induced by herbivory or mechanically simulated herbivory (Paige 1992, Vail 1992, Hjälten et al. 1993). In these cases, the injury released apical dominance, increasing branching patterns and reducing the between-leaf competition for cytokinins and other root-produced resources, which have been associated with observed increases in single-leaf photosynthetic rates (Wareing et al. 1968, Aarssen and Irwin 1991, Ovaska et al. 1992, Irwin and Aarssen 1996). The mechanical injury applied in this study is unlikely to have caused a release of apical dominance or reduced competition between leaves as no leaves were removed and no apical meristems were injured. Whether the difference observed here is due to an increase in sink activity or to a reallocation of resources is an important consideration, as a reallocation of resources toward aboveground growth may cause a reduction in carbohydrates stored in roots and other tissues, potentially compromising future growth and yield.

Vines injured during both bloom and veraison in 2000 had significantly lower pruning weights than did control vines. This response is opposite to that of vines injured solely at veraison in 2000, indicating that bloom injury compromised the ability of vines to respond to injury at veraison (Table 1). Different types of stresses have been shown to reduce plant compensatory abilities (Trumble et al. 1993), and various studies have found plants unable to tolerate several episodes of injury (Hare 1980, Crawley 1983, Cartwright and Kok 1990). This response to injury suggests that the increase in pruning weights exhibited in vines injured solely at veraison is probably due to a reallocation of resources toward aboveground growth and not to an increase in carbon assimilation due to the injury applied. However, the level of injury applied at bloom in 2000 was high (30% removed of each fully expanded leaf, Figure 1).

Injury at bloom in 2001 had a significant negative effect on total node number, lateral shoot node number, and shoot length at veraison. This contrast to results from vines injured at bloom in 2000 is most likely due to the higher replication and the use of pruning weights as covariates in 2001 and not to a difference between two-year-old and three-year-old vines. Measurements taken at veraison and postharvest indicated no significant difference in main shoot node number between bloom-injured vines and controls. Therefore, bloom-injury treatments primarily affected the production of lateral shoots in these vines. In contrast to results from vines injured in 2000, vines injured solely at veraison in 2001 did not display any significant increase in pruning weights compared to uninjured controls. This difference between 2000 and 2001 may be due to the higher level of injury imposed in 2001; injury at veraison during 2001 was applied on all fully expanded leaves, while veraison injury in 2000 was only applied on 1.5 m of the shoot (average shoot length in 2000 = 3.62 m). Because of vine growth between bloom and veraison, the total amount of injured leaf area at veraison in 2001 was approximately three times greater than that injured at bloom. However, the percent defoliation was 20% at both phenophases, allowing a direct comparison of bloom injury and veraison injury in terms of the vine source to sink ratio at the time of injury. A comparison between bloom and veraison injury in 2001 suggests that the stronger effect of bloom injury on vine growth was not due to the presence of a greater source (leaves) at veraison but was due to a lower relative sink at veraison than at bloom in these fruitless vines.

As previously mentioned, crop level was reduced by the spring frosts in 2002. This makes the lack of a significant impact of either bloom or veraison injury on soluble solids of fruit harvested in 2002 not surprising, as during veraison 2002 there was ample canopy present to ripen fruit. The significant negative impact of injury at bloom on crop weight is a strong indication that injury during bloom induced a significant source limitation. We were unable to measure root growth in these experiments, but root growth was probably reduced in vines displaying compromised aboveground vegetative growth in response to foliar injury. This assumption is based on the significant negative impacts of injury at bloom on mean cane diameter (injured in 2000) and yield (injured in 2001). Future work on tolerance to foliar injury in establishing vineyards would benefit greatly from root-growth measurements.

This study stresses the importance of using vine physiology as a starting point to developing quantitative or qualitative economic injury thresholds for foliar injury. This is illustrated by the higher tolerance to foliar injury during veraison than bloom in young vines indicated here. In Michigan juice grape vineyards, the Japanese beetle is generally a far more abundant pest than the rose chafer, and consumes at least 10 times the amount of leaf area per beetle than the rose chafer (Mercader 2002). This highly apparent foliar damage makes it the target of significant insecticide inputs, but some of these chemical inputs may be unnecessary given the high level of tolerance to injury that nonbearing vines display late in the season. Vines with low or zero crop load occur when vines are first established or when spring frost injury kills primary and secondary buds, a situation not uncommon in cool-climate vineyards. Further experiments and commercial vineyard sampling are currently underway to determine the long-term tolerance of vines to chronic injury by foliar pests.

Conclusion

Results of this study are consistent with the notion that source to sink ratios at the time of injury have a strong impact on a vines ability to tolerate injury. This translates to a higher risk of negative effects on vine establishment because of foliar feeding by beetles early in the growing season rather than late in the growing season in *V. labruscana* vines. In addition, early season damage compromises the ability of vines to tolerate late-season injury. These results suggest that the temporal distribution of foliar injury may have a greater effect on growth of establishing vines than the total amount of injury sustained.

Literature Cited

Aarssen, L.W., and D.L. Irwin. 1991. What selection: Herbivory or competition? Oikos 60:261-262.

Boucher, T.J., D.G. Pfeiffer, J.A. Barden, and J.M. Williams. 1987. Effects of simulated insect injury on net photosynthesis of potted grapevines. HortScience 22:927-928.

Candolfi-Vasconcelos, M.C., and W. Koblet. 1991. Influences of partial defoliation on gas exchange parameters and chlorophyll content of field-grown grapevines: Mechanisms and limitations of the compensation capacity. Vitis 30:129-141.

Candolfi-Vasconcelos, M.C., M.P. Candolfi, and W. Koblet. 1994. Retranslocation of carbon reserves from the woody storage tissues into the fruit as a response to defoliation stress during the ripening period in *Vitis vinifera* L. Planta 192:567-573.

Cartwright, B., and L.T. Kok. 1990. Feeding by *Cassida rubiginosa* (Coleoptera: Chrysomelidae) and the effects of defoliation on growth musk thistle. J. Entomol. Sci. 25:538-547.

Chittenden, F.H. 1916. The Rose Chafer: A Destructive Garden and Vineyard Pest. United States Department of Agriculture Farmer's Bulletin 721:1-8.

Crawley, M.J. 1983. Herbivory: The Dynamics of Animal-Plant Interactions: Studies in Ecology. University of California Press, Berkeley.

Eichorn, K.W., and Lorenz, D.H. 1977. Phänologishche enwicklungsstadien der rebe. Nachrichtenbl. Dtsch. Pflanzenschutzdienstes (Braunschweig) 29:119-120.

Fleming, W.E. 1972. Biology of the Japanese Beetle. Technical Bulletin 1449. United States Department of Agriculture. US Government Printing Office, Washington, DC.

Gut, L.J., R. Isaacs, J.C. Wise, A.L. Jones, A.M.C. Schilder, B. Zandstra, and E. Hanson. 2002. 2002 Fruit Spraying Calendar. Extension Bulletin E-154. Michigan State University Extension, East Lansing, MI.

Hall, F.R., and D.C. Ferree. 1975. Influence of twospotted spider mite populations on photosynthesis of apple leaves. J. Econ. Entomol. 69:245-248.

Hare, J.D. 1980. Impact of defoliation by the Colorado potato beetle on potato yields. J. Econ. Entomol. 73:369-373.

Hjälten, J., K. Danell, and L. Ericson. 1993. Effects of simulated herbivory and intraspecific competition on the compensatory ability of birches. Ecology 74:1136-1142.

Howell, G.S. 2001. Sustainable grape productivity and the growth-yield relationship: A review. Am. J. Enol. Vitic. 52:165-174.

Irwin, D.L., and L.W. Aarssen. 1996. Effects of nutrient level on cost and benefit of apical dominance in *Epilobium ciliatum*. Am. Midl. Nat. 136:14-28.

Kleweno, D.D., and V. Matthews. 2001. Michigan Rotational Survey: Fruit Inventory 2000-2001.

Mercader, R.J., and R. Isaacs. 2003. Phenophase-dependent effects of foliar injury and herbivory on the gowth and photosynthetic capacity of nonbearing *Vitis labrusca* (L.) var. Niagara. Am. J. Enol. Vitic. 54:252-260.

Mercader, R.J. 2002. Phenophase-dependent tolerance to foliar herbivory in grape vines, *Vitis labrusca* var. Niagara (L.). M.S. Thesis, Michigan State University, East Lansing, MI.

Miller, D.P., G.S. Howell, and J.A. Flore. 1996. Influence of shoot number and crop load on potted Chambourcin grapevines. I. Morphology and dry matter partitioning. Am. J. Enol. Vitic. 47:380-388.

Ovaska, J., M. Walls, and P. Mutikainen. 1992. Changes in leaf gas exchange properties of cloned *Betula pendula* saplings after partial defoliation. J. Exp. Bot. 43:1301-1307.

Paige, K.N. 1992. Overcompensation in response to mammalian herbivory: From mutualistic to antagonistic interactions. Ecology 73:2076-2085.

Petrie, P.R., M.C.T. Trought, and G.S. Howell. 2000. Growth and dry matter partitioning of Pinot noir (*Vitis vinifera* L.) in relation to leaf area and crop load. Aust. J. Grape Wine Res. 6:40-45.

Trumble, J.T., D.M. Kolodny-Hirsh, and I.P. Ting. 1993. Plant compensation for arthropod herbivory. Ann. Rev. Entomol. 38:93-119.

Vail, S. 1992. Selection for overcompensatory plant responses to herbivory: A mechanism for the evolution of plant-herbivore mutualism. Am. Nat. 139:1-8.

Vittum, P.J., M.G. Villani, and H. Tashiro. 1999. Turfgrass Insects of the United States and Canada. Cornell University Press, Ithaca, NY.

Wardlaw, I.F. 1990. Tansley Review No. 27. The control of carbon partitioning in plants. New Phytol. 116:341-381.

Wareing, P.F., M.M. Khalifa, and K.J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature 220:453-457.

Zabadal, T.J. 1997. Vineyard establishment II. Planting and Early Care of Vineyards. Extension Bulletin E-2645. Michigan State University Extension, East Lansing, MI.