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Phenophase Dependent Tolerance to  
Foliar Herbivory in Grape Vines,  
Vitis labrusca (L.) var. 'Niagara'

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**Phenophase-Dependent Tolerance to Foliar Herbivory in  
Grape Vines, *Vitis labrusca* var. 'Niagara' (L.)**

**By**

**Rodrigo J. Mercader**

**A THESIS**

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## **ABSTRACT**

### **PHENOPHASE-DEPENDENT TOLERANCE TO FOLIAR HERBIVORY IN GRAPE VINES, *VITIS LABRUSCA* VAR. 'NIAGARA'**

**By**

**Rodrigo J. Mercader**

This study measured the response of fruitless *Vitis labrusca* (L.) var. 'Niagara' grapevines to defoliation during bloom and véraison, to determine how carbon source to sink relations alter tolerance to herbivory. In these studies mechanical damage was applied with hole punchers and beetle damage using adult *Macrodactylus subspinosus* Fabricius (rose chafer) during bloom, and adult *Popillia japonica* Newman (Japanese beetle) during véraison. The first set of experiments measured the seasonal growth and single leaf and whole vine photosynthesis of potted vines damaged mechanically or by beetles during bloom and/or during véraison. Also, the relative impact of mechanical and beetle damage during bloom or véraison on carbon assimilation was measured. Tolerance to foliar damage was higher during véraison than during bloom in these studies, and beetle damage at véraison was found to have a more detrimental impact on carbon assimilation than mechanical damage. A second set of experiments in a young vineyard using mechanical defoliation also indicated that damage during bloom had a more detrimental impact on vine growth than damage at véraison. Mechanical defoliation in both of these studies was made on a percentage basis, so the results are not a reflection of the higher leaf area present during véraison, but can be attributed to the relative carbon sink activity in relation to the available source. Comparisons of different levels of mechanical and beetle damage indicated a high level of tolerance to foliar herbivory.

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# Chapter 1

## Project Introduction

Plant responses to herbivory may be modulated by their physiological state of development (phenophase) and the demands placed upon them by their developing tissues at these times. When foliar herbivores remove photosynthetic area, plants can become source-limited, and in source-limited plants the distribution of resources is dependent on the strength of sink demands (Trumble et al. 1993). The relative strength of sink demands can potentially impact a plant's response to herbivory, ranging from no response to overcompensation, depending on the availability of resources at the time of damage.

This project focused on the relationship between phenologically-based carbon source to sink ratios and the compensatory responses of grapevines to damage by foliar herbivores. This phenomenon was addressed using young juice grape vines (*Vitis labrusca* var. Niagara), the rose chafer, *Macrodactylus subspinosus*, and the Japanese beetle, *Popillia japonica*. This study tested the effects of source-sink relationships and damage timing on plant compensatory response. Key attributes of the system studied included a well-documented phenology and strength of relative sink demands in the vine, and two economically important foliar herbivores that feed at two significantly different physiological stages; rose chafer adults feed during bloom and Japanese beetle adults feed during veraison.

A primary goal of the work presented here was to gather information on vine response to foliar damage, as part of a larger effort aimed at the future development of damage thresholds for foliar damage in grapevines.

## **Literature Review**

### **Brief Overview of Compensation to Herbivory**

During their annual growth cycle, plants are often subjected to leaf area loss to herbivores, potentially limiting resources for vegetative and reproductive growth. In the 1960's and 1970's the logical notion of a linear relationship between plant growth and leaf area dominated much of the literature (reviewed by Trumble et al. 1993). However, since then the detrimental effects of foliar herbivory have been shown to be attenuated by plant compensatory responses to foliar damage (reviewed by Trumble et al. 1993, Rosenthal and Kotanen 1994, Strauss and Agrawal 1999), and in some cases have been shown to induce increased growth and productivity (e.g. McNaughton 1979, Owen 1980, Paige and Witham 1987, Paige 1992, Vail 1992, Hjalten et al. 1993, Paige 1994; but see Bergelson and Crawley 1992). There are several potential reasons why plants may have evolved not to be maximally efficient, where any loss of leaf area could lead to a cost. These include tradeoffs between selective pressures (e.g. competition, herbivory, soil interactions) and physiological constraints (e.g. sink limitation, nutrient balance, growth patterns).

The phenomenon of compensation has been attributed as an evolutionary response to both herbivore damage and competition. Compensation may have evolved from

selective pressures from competition, because competition for light has led to strong apical dominance in plants (Aarssen and Irwin 1991, Hjalten et al. 1993, Irwin and Aarssen 1996). Therefore, when apical dominance is removed due to damage to the apical meristem, secondary growth occurs leading to higher productivity under conditions where intense competition for light is not present. An alternate hypothesis that compensation has evolved due to herbivore selection pressure arises from the idea that intensive and predictable herbivory could select for plants with restrained growth of primary shoots (Crawley 1987, van der Meijden 1990, Vail 1992, Tuomi et al. 1994). There is increasing theoretical and empirical evidence that plant tolerance is an adaptation to herbivory (e.g. Dyer et al 1991, Järemo et al. 1996, Nilsson et al. 1996, Naber and Aarssen 1998, Simons and Johnston 1999, Strauss and Agrawal 1999). However, as pointed out by Rosenthal and Kotanen (1994) other selective pressures that damage plants (such as drought and fire) can lead to the evolution of compensatory mechanisms, and can be misconstrued as adaptations to herbivory.

Whatever the selective pressures leading to compensatory mechanisms, their existence has been clearly documented (reviewed by Trumble et al. 1993, Rosenthal and Kotanen 1994, Strauss and Agrawal 1999). Maschinski and Whitham (1989) demonstrated how extrinsic factors (plant association, water, nutrients, and timing of damage) interact to affect compensation in *Ipomopsis arizonica*. That study indicated that depending on conditions affecting the physiological state of the plant, a continuum of compensatory responses to damage existed. Other studies corroborate the importance of extrinsic factors in determining a plants ability to compensate (reviewed by Trumble et al. 1993; Hjalten et al. 1993, Shabel and Peart 1994, Weltzin et al. 1998), although the

effect of the extrinsic factor may be debated, such as the negative relationship reported between nutrients and compensatory capacity (e.g. Ovaska et al. 1992, Gertz and Bach 1994, Mutikainen and Walls 1995, Irwin and Aarssen 1996).

In addition to extrinsic factors, several intrinsic factors affecting compensatory mechanisms have been identified such as regrowth patterns, photosynthetic activity, senescence, leaf morphology, and canopy architecture (reviewed by Trumble et al. 1993). These intrinsic factors have been classified by Strauss and Agrawal (1999) into five primary mechanisms involved in increased tolerance to herbivory: 1) increased net photosynthetic rate after damage, 2) high relative growth rates, 3) increased branching or tillering after release of apical dominance, 4) pre-existing high levels of carbon storage in roots for allocation to above ground reproduction, and 5) ability to shunt carbon stores from roots to shoots after damage. The ability to utilize these mechanisms is potentially tied to carbon source: sink relations, since the relationship between sink and source strength have been shown to be important in the regulation of photosynthesis (reviewed by Flore and Lakso 1989, Wardlaw 1990) and growth (reviewed by Wardlaw 1990). Under conditions in which extrinsic factors are not limiting, such as many agricultural situations, carbon source: sink ratios are potentially a major factor influencing plant tolerance to foliar damage.

This study was designed to understand the impact of phenological shifts in carbon source: sink ratios on tolerance to foliar damage in grapevines. Timing of damage is often considered an extrinsic factor (e.g. Maschinski and Whitham 1989, Trumble et al. 1993, Strauss and Agrawal 1999), as the external environment (the herbivores) regulates it. However, in this study I consider timing of damage to be an intrinsic factor, due to its

relation to source: sink ratios in plants. Source: sink ratios in plants change through time depending on the strength of sinks (e.g. meristems, fruits, actively growing tissue, storage tissues) and available sources (e.g. leaves, storage tissues), particularly in perennial plants where the changes are seasonal as well as on a year-to-year basis.

## **Growth and Photosynthesis (Source: Sink relationships)**

*“partitioning is clearly influenced by both the supply and demand for photosynthate and is moderated by vascular connections and the storage capacity of the leaves and pathway tissues” (Wardlaw 1990).*

The preceding quote summarizes the importance of carbon source: sink relations to plant growth, but for a current review of sink regulation of photosynthesis see Paul and Foyer (2001). As carbon is the major source of energy and dry weight, carbon assimilation and partitioning have a central position in a plants ability to compensate for foliar damage. For example, carbon balance was identified by Francesconi et al. (1996b) as the primary force explaining the high tolerance to damage by European red mite, *Panonychus ulmi* (Koch), in lightly cropped apples compared to normally cropped apples. Furthermore, in the same study, whole canopy net CO<sub>2</sub> exchange rates (which were negatively affected by mite damage) had a higher explanatory power for final fruit weight, return bloom, and return fruiting than cumulative mite days.

Upregulation of photosynthesis is considered to be a potential compensatory mechanism (reviewed by Trumble et al. 1993, Strauss and Agrawal 1999) and several studies have reported increased carbon assimilation on leaves of damaged plants (e.g. Kliewer 1982, Chapman et al. 1991, Anten and Ackerly 2001). The ability to upregulate

photosynthetic rates has been suggested to be due to a reduction in the source: sink ratio causing a release of feedback inhibition (Neales and Incoll 1968, Flore and Lakso 1989, Layne and Flore 1995) or due to alleviated competition between leaves (Wareing et al. 1968, Aarssen and Irwin 1991, Ovaska et al. 1992, Irwin and Aarsen 1996). The reduction in interleaf competition is mainly in the form of more available root produced cytokinins, light, water, and nutrients (Wareing 1968, Ovaska et al. 1992, Irwin and Aarssen 1996).

In addition to differences in photosynthetic rates, altered source: sink ratios can drastically affect carbon allocation patterns. Various studies have indicated defoliation can cause a shift in carbon allocation and translocation away from storage tissues and towards shoot growth, leaf growth, and reproductive structures (e.g. Evans 1991, Candolfi-Vasconcelos and Koblet 1990, Koblet et al. 1992, Candolfi-Vasconcelos et al. 1994, Tschaplinski and Blake 1995). These shifts in carbon allocation are in accordance with studies on sink hierarchy, which generally indicate storage tissues are a lower priority than vegetative and reproductive tissues (reviewed by Wardlaw 1990). Dry matter partitioning in grapevines in relation to sink strength has been particularly well studied for vines with varying crop loads. In a series of studies, Edson et al. (1993, 1995 a,b) documented the dry matter partitioning of ‘Seyval’ grapevines, *Vitis vinifera* (L.), with a range of crop loads. Those studies found no differences in whole vine carbon assimilation rates on vines with different crop loads. However, a marked difference was observed in allocation of dry matter away from vegetative growth and towards reproductive structures. Furthermore, Candolfi-Vasconcelos et al. (1994a) reported a strong retranslocation of carbon reserves to support fruit maturation in defoliated vines, while no retranslocation was observed in non-defoliated vines. These studies further

illustrate the importance of source: sink relations in determining carbon allocation patterns in grapevines.

## **Tolerance to Damage in Grapevines**

High levels of tolerance to defoliation by removal of whole leaves in grapevines have been well documented (Boucher and Pfeiffer 1989, Candolfi-Vasconcelos and Koblet 1990, 1991, Candolfi-Vasconcelos et al. 1994b). Tolerance to high levels of arthropod foliar damage has also been documented in grapevines (Laing et al. 1972, Jubb et al. 1983, Boucher and Pfeiffer 1989, Welter et al. 1991, Candolfi et al. 1993; but see Flaherty and Huffaker 1970, Welter et al. 1989a). One important consideration is that, unlike annual plants, woody perennials rely upon their stored reserves for growth the following season. Early in the season a relatively small number of leaves are present, and most carbohydrates used for shoot growth are derived from storage tissues. Indeed, until the 6-leaf stage in grapevines, shoot development is dependent upon re-translocation from storage tissues, and not until bloom is the vine able to rely upon assimilates produced during the current year (Yang and Hori 1979). This is an important consideration when evaluating the degree of tolerance to foliar damage, as impacts may only be seen in storage tissues or growth the following season or seasons. For example, Welter et al. (1991) found that the complete recovery of 'Zinfandel' grapevines to Williamette spider mite, *Eotetranychus williametti* (Mcgreggor), required two damage-free years.

## **Growth and Phenophases in Grapevines in Terms of Source-Sink Relations**

After centuries of grape production, a sizeable amount of information on vine growth and development has been gathered. Not surprisingly, several books and reviews have been written detailing the annual growth cycle of grapevines (e.g. Bush et al. 1895, Winkler et al. 1974, Mullins et al. 1992). Here I will limit my discussion of the growth cycle to the identification of the primary sinks and sources in non-bearing vines at different points in the season.

### **Sources**

Leaves and shoots: Leaves are the primary source of photosynthate in grapevines. However, several studies have indicated that single leaf measurements do not adequately represent whole vine photosynthetic capacity (Edson et al. 1993, Edson et al. 1995 b, Miller 1996, Miller et al. 1997). This is because single leaf measurements can be influenced by leaf age (Kriedmann et al. 1970, Poni et al. 1994), source: sink interaction (Höfacker 1978, Edson et al. 1995b, Petrie et al. 2000a), and the contribution of other photosynthetic organs such as shoots (Kriedmann and Buttrose 1971).

Roots, Canes, and Trunks: As described above the initial flush of growth in grapevines is derived from the photosynthate accumulated the previous season. In Delaware grapevines, Yang et al. (1980a) reported that early shoot development prior to the six-leaf stage is entirely dependent upon retranslocated assimilates, and after this point the retranslocation of assimilates gradually decreased until it stopped by the flowering stage. In addition to providing the necessary assimilates during the initial growth period,

retranslocation can take place during times of sink limitation. Candolfi-Vasconcelos et al. (1994a) demonstrated that defoliation stress can alter natural translocation patterns, directing carbon stored in storage tissues towards the fruit.

## **Sinks**

Shoots and leaves: Three to four weeks after buds break dormancy the season's period of most rapid growth begins and continues until approximately bloom when rapid shoot elongation slows, initially at a rapid rate and then trailing at a continuously slower rate (Winkler et al. 1974). After shoot elongation has slowed, carbohydrates begin to accumulate in the shoots, the accumulation being slow at first and then rapidly accelerating, except for a possible slow down in fruiting vines during the ripening period (Winkler et al. 1974). Newly developing leaves in Delaware grapevines act as sinks until reaching approximately 80% of their full size (Yang et al 1980b).

Roots, Canes, and Trunks: Yang et al. (1980a) recorded the translocation of  $^{14}\text{C}$  fed to leaves at different times of the season to shoots, cane and trunks, and roots. Prior to fruit set, most of the labeled carbon recovered 24 hours after feeding was recovered from the shoots (100% and 86% on the two days measured prior to flower set). However, by the flowering stage the majority of the recovered labeled carbon was in the canes, trunks, and particularly the roots. By midseason when xylem tissue began to become lignified, the accumulation of labeled carbon became more pronounced in the roots than the canes and trunks.

Data from field studies on vine root growth appear to indicate that root growth occurs only when other sinks in the vine are not using large amounts of photosynthate

(Williams and Matthews 1990). In addition, Miller et al. (1996b) reported an increase in root weight in the period between veraison and harvest in uncropped vines and no increase in root growth in cropped vines.

### **Source and Sink Relations During Bloom and Veraison**

**Bloom:** As mentioned above, bloom is the point at which the vine shifts from reliance on retranslocation of assimilates from storage tissues and becomes reliant upon photosynthate produced during the current season. Bloom is also the point at which the rapid rate of shoot production begins to decline. This situation leads to the presence of a strong vegetative sink, a lowered quantity of stored assimilates, and relatively small number of leaves present. For these reasons, at this point in the season the vine is liable to have a lower source to sink ratio than during the remainder of the season in non-fruiting vines.

Circumstantial evidence for the potential source limitation at this time of the season exists from viticultural practices used during bloom to increase or reduce fruit set. For example, reducing vegetative sinks by shoot tipping at bloom (removing competition between vegetative growth and the relatively weak sink of grape inflorescences) increases fruit set (Coombe 1959, Coombe 1962, Skene 1969), while leaf removal during bloom (Candolfi-Vasconcelos and Koblet 1990) reduces fruit cluster set. The effects of these practices indicate that vines at bloom are potentially source limited at bloom.

**Veraison:** During veraison, non-bearing vines lack the strong sink typically present at this time of the season. Several studies found lowered photosynthetic rate per leaf area in cropped vines during veraison compared to uncropped vines. Downton et al. (1987)

reported that the onset of the diurnal decline of photosynthesis occurred earlier in the day for vines without fruit. Studies on potted ‘Seyval’ vines reported lower carbon assimilation rate per leaf area in uncropped vines when compared to cropped vines (Edson et al. 1993, Edson et al. 1995a). In addition, higher dry matter accumulation has been reported per leaf area in cropped vines compared to uncropped vines (Miller et al. 1996b, Petrie et al. 2000a). The results of these studies indicate that sink limitations can occur during veráison in uncropped vines.

## Study System

The rose chafer, *Macrodactylus subspinosus*, and the Japanese beetle, *Popillia japonica*, are two foliar pests considered to be of economic importance in juice grape growing regions of Eastern North America. These insects are both highly polyphagous scarab beetles, which as adults are leaf skeletonizers (Mcleod and Williams 1990, Potter and Held 2002). Adult emergence is temporally separated, the rose chafer emerging during bloom and the Japanese beetle during veráison. Both of these insects aggregate while feeding and, depending on population size and vine susceptibility, can entirely defoliate grapevines.

### ***Vitis labrusca* var. ‘Niagara’ (L.)**

*Vitis labrusca* (L.) is native to North America, growing from New England to Illinois, Ohio, and Indiana to the west and south to Georgia (Vines 1960). In it’s natural habitat it is found in a variety of microenvironments including dry and moist areas, and sun and shade areas (Van Dersal 1938). However, it is most commonly found in well-

drained alluvial soils (Van Dersal 1938). The vine is reported to grow slowly in its first year and quite vigorously once established (Van Dersal 1938), often found climbing or trailing up to 40 ft (Vines 1960).

**Origin of the Niagara Variety.** The ‘Niagara’ variety was first produced by C. L. Hoag and B. W. Clark in Lockport New York in 1868, by fertilizing *Vitis labrusca* (L.) var. ‘Concord’ flowers with *V. labrusca* (L.) var. ‘Cassady’(Hedrick 1919). The Concord variety originated from plantings of seeds of a wild grape in 1843 by E. W. Bull in Concord, Massachusetts one of the seedlings was named Concord (Hedrick 1919). The Cassady variety originated in the yard of H. P. Cassady in Philadelphia as a chance seedling (Bush 1895). Bush (1895) reported that the proprietors of the Niagara variety kept a close guard on it’s planting in hopes of increasing its reputation in order to sell it a higher price. Bush (1895) also reported that it had acquired an assured position as the leading white market grape and that he had tasted a very fine white wine made from it.

**Cultivation.** The Niagara variety is primarily used as a juice grape, and in Michigan is the most actively planted variety, with 1145 acres planted between 1996 and 2000 (Kleweno and Matthews 2001). In 2000, 19,100 tons of ‘Niagara’ grapes were processed (Kleweno and Matthews 2001).

**Attributes.** The Niagara grape variety is considered to be hardy (Edson and Howell 1989). However, it is not as hardy as *V. Labrusca* var. ‘Concord’, which may tolerate temperatures of –20 degrees Farenheit (Howell and Wolpert 1978).

### **Rose chafer, *Macrodactylus subspinosus* (Fabre)**

The adult rose chafer *Macrodactylus subspinosus* (Fabre) is a tan scarab beetle approximately 13 mm long with long, spiny, reddish-brown legs that gradually become darker near the tip (McLeod and Williams 1990). The eggs are oval, white, shiny and are laid in sandy soils at approximately four to six inches in depth. The C-shaped grubs feed on roots of grasses, weeds, grains, and other plants (McLeod and Williams 1990). This beetle is distributed across much of North America east of The Rockies (Chittenden 1916, McLeod and Williams 1990). In areas where it occurs, regions with light sandy soils are preferred as breeding grounds, and crops grown in clay soils are seldom affected by rose chafer damage unless they are near sandy soils (Chittenden 1916). Chittenden (1916) reports that after the rose chafer was first noticed it “confined its ravages to the blossoms of the rose”, but also reports a record indicating it had been destructive to grapes as early as 1810. By at least the late 1800’s the rose chafer was considered a major pest of grapes in areas where it occurred (Bush et al. 1895, Chittenden 1916).

Rose chafers emerge in late May to early June in Michigan, approximately coinciding with bloom in grapevines. The larvae feed on the roots of grasses, having a particularly preference foxtail, timothy, and bluegrass (Hendrick 1919). Adults live for about 4 to 6 weeks, and during this time eggs are laid about 15 cm deep in sandy or grassland soil in groups of 6 to 40 (but each egg is deposited in a separate cavity). Eggs hatch in 1 to 3 weeks, and the larvae feed on the roots of their hosts. Larvae overwinter deep in the soil, and in early spring the grubs migrate upward and pupate in early May in earthen cells (Anonymous 1997).

The rose chafer adult is highly polyphagous, feeding on a variety of ornamentals, cultivated trees and shrubs, along with a variety of fruit crops including grapes (reviewed by Potter and Held 2002). The major economic damage caused by the rose chafer to grapevines is from feeding upon developing flowers and newly set berries. If not controlled, heavy infestation can result in little or no grape production (McLeod and Williams 1990). In addition to feeding on developing clusters these beetles feed on the foliage, in some cases almost defoliating thin-leaved cultivars (Williams 1979, McLeod and Williams 1990). The foliar damage caused by the rose chafer can be visually alarming due to the gregarious nature of the beetle skeletonizing individual leaves. This can create the perception of a significant problem even under low infestation levels.

### **Japanese beetle, *Popillia japonica* Newman**

The Japanese beetle, *Popillia japonica* Newman, is a scarab beetle native to Japan where it is considered a pest of minor importance. Prior to its introduction into the United States, *P. japonica*'s range was limited to the main islands of the Japanese archipelago, where it is common in Kyushu, Shikoku, Honshu, and Hokkaido (Fleming 1972). Within this distribution it is most abundant in Northern Honshu and all of Hokkaido where grasslands occur (Fleming 1972). The beetle was first observed in the United States in southern New Jersey in 1916 (Fleming 1972). Since then the population has expanded over much of the Northeastern United States, where it has become a pest on turf grass and a multitude of ornamental and horticultural crops. *P. japonica* has infested all states east of the 85<sup>th</sup> meridian and north of the 35<sup>th</sup> parallel as well as Illinois and Indiana, and has partially infested Michigan, Wisconsin, Minnesota, Nebraska, Iowa, Missouri,

Alabama, Georgia, and South Carolina (Allsopp 1996, Anonymous 2000). In Canada the beetle has become established in the Niagara peninsula of Ontario, and in Bellevue and Gananoque on the northern edge of Lake Ontario (Waithe 1991). In addition, *P. japonica* was found on the Terceira island of Azores in 1974, and has since become established in half of the island (Martins et al. 1988).

In the majority of its range, *P. japonica* has a one-year life cycle. The egg, three larval instars, and pupal stages all occur underground and comprise approximately 80% of the beetle's lifespan. The beetle has a dormancy period, in which the larva forms an earthen cell and remains in a state of arrested development throughout the winter, where it can survive temperatures as low as  $-9.4^{\circ}\text{C}$  (Fleming 1972). The cycle from egg to adult is generally completed within one year; although in the coldest limits of its range the larval stage is extended and the life cycle is completed in two years (Clausen et al. 1927). The adult stage lasts for approximately 1 to 3 months, depending upon local conditions. The availability of grassland or prairies is considered to be one of the main indicators of the suitability of habitat for *P. japonica*. This notion is supported from the observation that in its native Japan it occurs in areas where grasslands are abundant (Clausen et al. 1927, Fleming 1972), and that in the United States the same pattern is observed. The larvae are able to feed on decaying organic matter, but their growth is significantly affected by the absence of living roots (Smith and Hadley 1926). The larvae feed on the roots of a wide variety of grasses, and occasionally feed on the roots of fruit, vegetable, or ornamental plants. Fleming (1972) reports that larvae do not thrive in plantings of certain clover species (*Trifolium* spp. and *Melilotus indica*), soybeans (*Glycine max*), buckwheat (*Fagopyrum esculentum*), and orchardgrass (*Dactylis glomerata*).

Soil moisture appears to be the most important limiting factor affecting oviposition and survival of all the immature stages. The eggs have no mechanisms to retain water, and the absorption of water is necessary as a prelude to and during embryonic development (Ludwig 1932). Ludwig and Landsman (1937) also found fairly high water requirements for the developing larvae, pre-pupa and pupa. In general, *P. japonica* is found in areas where the annual rainfall is uniformly distributed and averages at least 250 mm during the summer (Fleming 1972). Oviposition usually occurs in the closest suitable site to the plant on which the female was feeding, with a strong preference for pasture lands (Fleming 1972). However, during droughts when soils are fairly dry the female beetle will search for a more suitable site, usually selecting low poorly drained ground, fields and turf under irrigation, and cultivated and fallow fields where the soil is loose and moist (Fleming 1972).

Topography has a very strong effect on dispersal, particularly on dispersal through appetitive flight. The spread of *P. japonica* is facilitated by the presence of nearly level or gently rolling country (Fleming 1972), as found in the areas of infestation in the United States. Mountainous regions and large forests significantly reduce the spread of *P. japonica*, by providing ill suited habitat for development of the immature stages (Fleming 1972). In the absence of strong winds adults can sustain flight for approximately 5 miles (Fleming 1972), enough to infest vineyards located within five miles of grasslands or pastures as is the case in the majority of commercial vineyards in Michigan.

*P. japonica* is a highly polyphagous species, feeding on the roots of a wide variety of plants during its immature stages, and on the foliage and fruit of a wide variety of

plants as adults. The adults feed on approximately 300 plant species in 139 plant families (Fleming 1972). Resistance to *P. japonica* adult feeding has been found in several plants closely related to favored hosts (e.g. Fulcher et al. 1998). Even plants that are generally considered to be non-hosts for the adults can induce feeding and subsequent growth (Ladd 1989). In addition, adult Japanese beetles appear to be able to detoxify a large number of plant toxins, as shown by feeding assays on plants known to cause paralysis in the Japanese beetle. Adult *P. japonica* that previously fed on geranium, *Pelargonium domesticum*, consumed seven times more geranium and had lower incidence of paralysis than naïve beetles (Potter & Held 1999). This study in a plant known to be toxic to *P. japonica* indicates the strength and inducibility of detoxification systems within this species.

Loughrin et al. (1996, 1997) have demonstrated that *P. japonica* utilizes feeding-induced plant volatiles to locate appropriate host plants within a mosaic of host and non-host plants. This ability to utilize feeding-induced plant volatiles is not restricted to feeding by other *P. japonica*, but includes feeding by other herbivores such as the fall webworm, *Hyphantria cunea* (Loughrin et al. 1997). This mechanism of host location potentially allows *P. japonica* to locate suitable host plants that it has never encountered before. In addition, this host-location mechanism also serves to create aggregations of *P. japonica* on host plants. This results in the ability to rapidly locate mates, and high levels of damage on individual plants.

## **Control Methods for the Rose Chafer and Japanese Beetle**

Methods of controlling the rose chafer have evolved through time, beginning with hand removal or shaking the beetles onto sheets as the sole recommended forms of control (Bush et al. 1895). Later control methods, included cultivation to kill the pupae and sweetened arsenical sprays to kill the adults (Hedrick 1919). The methods of cultivation described by Hedrick (1919) were cultivating crops to disrupt the grasses on which the larvae feed on and cultivating during the pupating stage to break the cells and crush the pupae. Currently several insecticides are recommended for use against the rose chafer in Michigan vineyards; Guthion, Imidan, Lannate, Sevin, Danitol, and Surround (Gut et al. 2002). Control of the Japanese beetle is primarily accomplished through chemicals. Chemicals recommended for its control are almost identical to those registered for the rose chafer (Gut et al. 2002).

## CHAPTER 2

### **Phenophase-Dependent Effects of Foliar Damage on the Growth and Photosynthetic Capacity of Non-Bearing Juice Grape Vines, *Vitis labrusca* (Linnaeus) var. 'Niagara'**

#### **Introduction**

Leaf area loss due to damage by phytophagous insects presents an instantaneous source of plant stress. The rapid loss of photosynthetic machinery can have a drastic impact on the carbon economy of the plant, and can cause a direct shift in the carbon source to sink ratio. A source-limited plant can incur significant loss in terms of growth and reproductive potential, as shown by the abundant examples of yield loss due to arthropod foliar damage in crop plants (e.g. Welter et al. 1989a, Graf et al. 1992, Francesconi et al. 1996a,b, Martinson et al. 1997, Norris 1997, Burkness and Hutchison 1998, Muro et al. 2001). However, the loss of photosynthetic machinery may not have significant effects at the whole plant level due to compensatory mechanisms that have been found in various plants (reviewed by Trumble et al. 1993, Strauss and Agrawal 1999). The degree to which plants can tolerate foliar damage can depend on the environmental conditions (Maschinski and Whitham 1989, Trumble et al. 1993, Hjalten et al. 1993, Shabel and Peart 1994, Weltzin et al. 1998, Strauss and Agrawal 1999), and on the physiological state of the plant (Trumble et al. 1993, Rosenthal and Kotanen 1994, Strauss and Agrawal 1999). Strauss and Agrawal (1999) identified the five primary mechanisms reported to increase tolerance: 1) increased net photosynthetic rate after damage, 2) high relative growth rates, 3) increased branching or tillering after release of apical dominance, 4) pre-existing high levels of carbon storage in roots for allocation to

aboveground reproduction, and 5) the ability to shunt carbon stores from roots to shoots after damage. A common thread amongst these mechanisms is that, as with most major factors affecting plant growth and differentiation, they can be heavily affected by carbon source to sink ratios.

The importance of source to sink ratios in determining a plant's ability to compensate for foliar damage can be seen in the various studies that have demonstrated altered carbon assimilation rates and allocation patterns due to shifts in the source to sink ratios (e.g. Flore and Lakso 1989, Layne and Flore 1995, Miller et al. 1996a,b Cruz-Aguado et al. 1999). Edson et al. (1993, 1995a,b) illustrated the impact of increased sink strength on grapevine carbon allocation patterns by manipulating the number of clusters per vine. Those studies indicated that total vine carbon may remain identical for vines over a range of cluster numbers, but the allocation of resources drastically shifts according to the size of the fruit sink. In addition, Candolfi-Vasconcelos et al. (1994a) demonstrated that defoliation during the ripening period alters carbon translocation patterns, moving carbon from lower tissues (storage sites) to the fruits.

Varying source to sink ratios can also significantly affect a vine's ability to tolerate foliar damage by directly affecting the size and the likelihood of causing a source limitation due to herbivory. For example, carbon balance has been identified as the primary force explaining the high tolerance of 'Starkimson Delicious' apples, *Malus domestica* Borkh to damage by European red mite, *Panonychus ulmi* (Koch), in lightly cropped trees compared to normally cropped trees (Lakso et al. 1996, Francesconi et al. 1996a,b).

An important aspect of carbon source to sink ratios in plants is that they are highly dynamic and change throughout the season as sink strengths and available sources shift. In apples, based on carbon assimilation rates and growth curves, Lakso et al. (1998) were able to estimate that source limitations in apples could take place at two points in the season, 2-3 weeks after bloom and at the end of the season. In grapevines, the relative sink strength of various tissues in grapevines changes drastically throughout the growing season, in accordance to their phenophase (Williams and Mathews 1990). This shift in tissue activity during the growing season presents two important considerations to the understanding of the impacts of foliar damage; 1) tissues will be affected differently depending on the timing of damage, and 2) the impact of damage on a plant may shift depending on the overall sink strength and the available source at the time of damage. This emphasizes the need to consider the impact of source-sink interactions at the time of damage, rather than simply focusing on whole season sink intensity.

The impact of insect foliar damage on plant growth is difficult to assess directly through the use of insects due to the high level of variation in feeding intensity that they may produce, and the difficulty of controlling the quantity of damage produced. However, the importance of understanding the specific effects of insect damage on growth and photosynthetic capacity cannot be ignored. Insect damage simulations, although useful, have been shown to not accurately reflect insect damage (reviewed by Baldwin 1990). In Michigan, the polyphagous leaf skeletonizing scarab beetles, the rose chafer, *Macrodactylus subspinosus* (F.), and the Japanese beetle, *Popillia japonica* (Newman) are considered to be pests of economic importance in vineyards. The

emergence of adults of these two beetles is temporally separated, with the rose chafer emerging during bloom and the Japanese beetle during veraison.

This study examines how source-sink relations at the time of damage impact a grapevine's ability to tolerate foliar damage, using mechanically-simulated damage to achieve accurate damage levels and using beetles to observe the response of leaves to actual herbivory. We predicted that vines would be better able to tolerate foliar damage during periods in the growing season when there is a relatively high source to sink ratio. To test this, the growth and photosynthetic rates of non-bearing 1 yr old *Vitis labrusca* (L.) var. 'Niagara' vines were measured before and after mechanical or beetle damage during bloom and/or veraison. The use of non-bearing plants reduced the variability introduced by crop load and ensured that time for compensatory growth was not a factor explaining our results. Canopy size at bloom is small and the relative activity of vegetative sinks is high early in the season. By veraison, leaf area is relatively high and vegetative sinks are low (Williams and Mathews 1990).

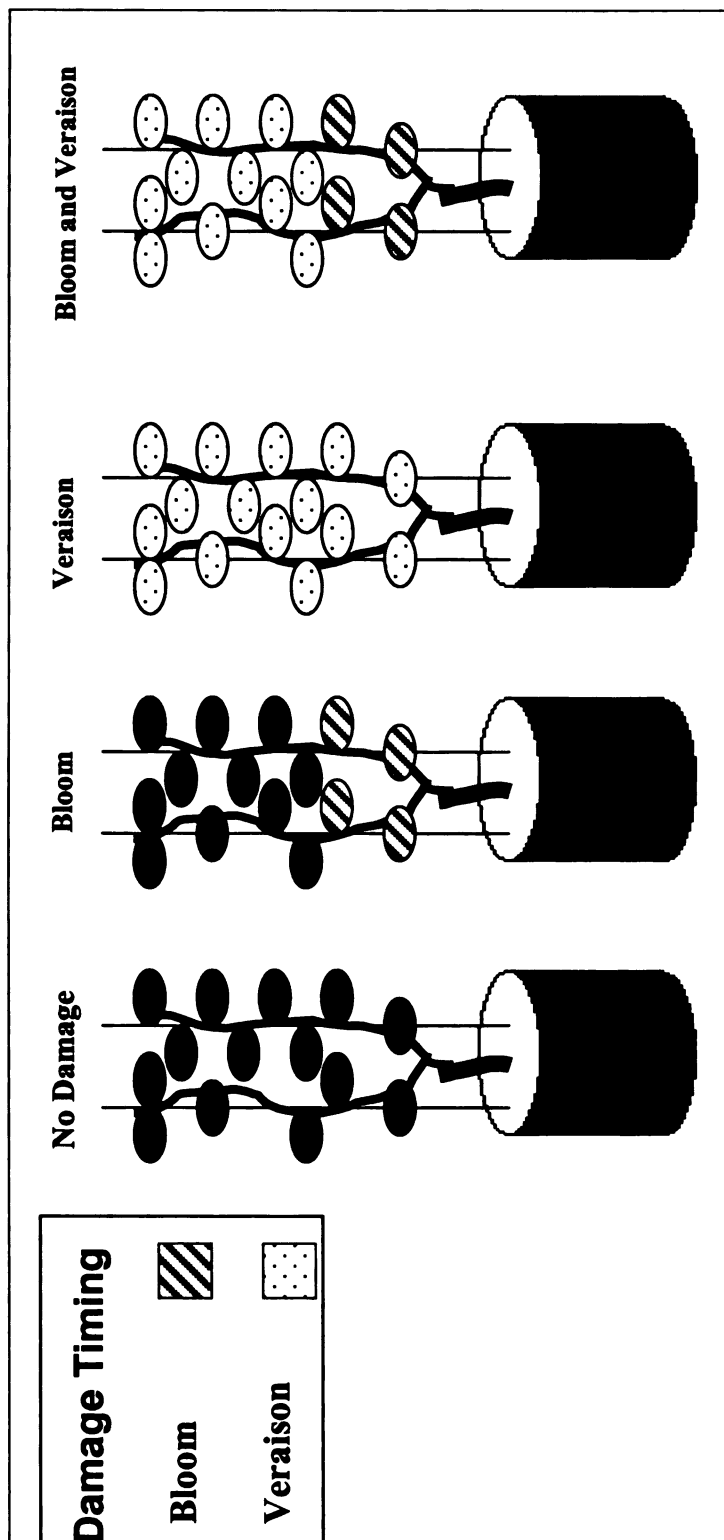
In addition, we compared the impact of mechanical and beetle damage on the photosynthetic rates of damaged and undamaged portions of leaves during bloom and veraison, using the rose chafer during bloom and the Japanese beetle during veraison.

## **Materials and Methods**

**Plant Material.** Eighty 1 yr old, own-rooted *Vitis labrusca* var. 'Niagara' grapevines were weighed and planted in 8 liter pots in loamy soil on 23-24 April 2001. Vines were trained on two 1.5 m stakes per pot and grown in the Michigan State University greenhouse facilities under natural light conditions. Vines were fertilized with an all-

purpose fertilizer (15-30-15, N-P-K) on June 13, July 15, and August 20 2001. Experimental vines did not bear clusters, but six cluster-bearing vines were grown simultaneously under identical conditions to determine the appropriate phenophases.

**Mechanically Damaged Vines.** Vines of similar weights were assigned to two blocks of 12 plants each according to position along a greenhouse bench. Bloom damage or veráison damage treatments were imposed on these vines in a 2 x 2 factorial design. Vines were either damaged at bloom, at veráison, at bloom and veráison, or not damaged. Damage consisted of removing 20% of the interveinal leaf area of each fully expanded leaf using a hole puncher (size of holes = 38.5 mm<sup>2</sup>) to avoid damaging major veins. To allow time for measurements to be taken, damage was applied to each block on consecutive days; bloom damage was applied on 1 June 2001 for block 1 and on 2 June 2001 for block 2, and veráison damage treatments were applied on 13 or 14 August 2001 for block 1 and 2, respectively. Leaves were damaged only once, therefore vines damaged only during veráison had the same level of damage after veráison damage treatments were imposed as vines damaged during bloom and veráison (Figure 2.1).



**Figure 2.1.** Representation of leaves damaged mechanically during bloom or veraison after veraison damage treatment was applied. Black leaves represent undamaged leaves, striped leaves represent leaves damaged during bloom, and spotted leaves represent leaves damaged during veraison.

Whole Vine Carbon Assimilation: Whole vine carbon assimilation was measured using the open gas exchange system outlined by Miller et al. (1996 c), using a CIRAS I infrared gas analyzer (PP-Systems, Hertfordshire, U.K.) to measure CO<sub>2</sub> concentrations. Early in the season, weather conditions made ideal light conditions difficult to obtain, and therefore measurements used were taken at a minimum of 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  photon flux density. By midseason light conditions had significantly improved and measurements were taken at an excess of 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  photon flux density. Vines were allowed to adjust to the chambers for 10 minutes and three measurements were taken per vine with at least 5 minutes between recordings. The average of the three measurements were used in the analysis. Temperature inside the chambers was generally within 0.2 °C of the ambient temperature and never exceeding a 1.5 °C difference, mean ambient temperature when measurements were taken was  $30.33 \pm 0.16$  °C, and ranged between  $26.05 \pm 0.34$  °C on September 29, 2001, and  $34.9 \pm 0.95$  °C on 12 June, 2001.

Whole vine carbon assimilation was recorded on alternate days for vines in blocks 1 and 2 on the following dates: at bloom (29, 30 May 2001), post bloom damage (9, 11 June 2001), midseason (10, 11 July 2001), veráison (12, 13 August 2001), post veráison damage (28, 29 August 2001), and post full berry ripening (28, 29 September 2001). Measurements taken prior to veráison were analyzed as a blocked one-way ANOVA, with bloom damage as the sole treatment and initial vine weight as a covariate. Measurements taken after veráison were analyzed by date as a blocked 2 x 2 factorial analysis with initial vine weight as a covariate, using the SAS System Version 8 statistical package (SAS Institute 1999).

Single leaf carbon assimilation: Single leaf carbon assimilation was recorded using a CIRAS I unit with a PL6U broad leaf cuvette (PP-Systems, Hertfordshire U.K) with a 2.5 cm<sup>2</sup> chamber and a light unit attached to the cuvette set at 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  photon flux density. Carbon assimilation values were adjusted for damaged leaves by subtracting the leaf area missing (holes were 38.5 mm<sup>2</sup>), and using adjusted leaf area in the calculations. Carbon assimilation calculations were made using a Microsoft Excel spreadsheet developed by Parsons et al. (1998).

Single leaf carbon assimilation was recorded on leaves from a single shoot on each vine. Data were taken from the basal leaf, a leaf at the third or fourth node position, the most recently fully expanded (MRFE) leaf at bloom, the MRFE leaf 10 days after bloom damage, the MRFE leaf at veraison, and the most recently fully expanded leaf 10 days after veraison damage. Recordings were taken on the leaves present 1 day prior to damage treatments and once a week for 4 wks after damage treatments were imposed. In addition, leaves were measured once a week for 3 wks during midseason (7-8, 14-15, 21-22 July, 2001).

Measurements taken prior to veraison were analyzed as a blocked repeated measure analysis of variance with bloom damage as the sole treatment, and initial vine weight as a covariate. Measurements taken after veraison were analyzed as a blocked two-factor factorial repeated measures analysis of variance, using SAS System Version 8 statistical package (SAS Institute 1999).

Vine Growth: Trunk diameter was measured directly below the main branching point using Vernier calipers on 11 May, 14 June, 17 July, 16 August, and 13 September, 2001.

Total shoot length was measured keeping individual shoots and their laterals separate on 25 May, 13 June, 13 July, 16 August, and 13 September, 2001.

Leaf area was measured non-destructively using a linear correlation between the length of the midvein (measured from the tip of the petiolar vein to the tip of the midvein) and leaf area, as used by Edson et al. (1993) and Smithyman et al. (1998). To determine this relationship all fully expanded leaves were removed from six vines grown under the same conditions, and for each leaf the midvein length was recorded. The leaf area of each leaf was determined using a HP ScanJet 6300c scanner and Scion Image-Release Beta 4.0.2 software (Scioncorp). There was a strong relationship between midrib and leaf area ( $r^2=0.86$ ,  $P<0.001$ ) using the equation [Leaf Area= $1.7243 \times \text{Midvein length}^{1.7471}$ ]. The midvein length of every fully expanded leaf on each vine was then recorded throughout the season, and the total leaf area estimated using this relationship.

At the end of the growing season (once basal leaves had senesced), the vines were destructively partitioned into leaves, shoots, trunks, and roots (5 and 10 October 2001) and maintained in a freezer (below 0 °C) until they could be dried. The individual components were then oven dried at 80 °C until no further weight loss was observed. On 3 September, 2001 the senescent leaves were counted and collected as they fell and kept frozen to dry along with all other leaves from the same vine.

Measurements taken prior to veraison were analyzed as a blocked one-way ANOVA, with bloom damage as the sole treatment and initial vine weight as a covariate. Where F-values for the blocking factor and initial weight were below 1, the analysis was performed without using the block and initial weight as factors. Measurements taken after veraison were analyzed by date as a blocked 2 x 2 factorial analysis with initial vine

weight as a covariate, using the SAS System V8 statistical package (SAS Institute 1999). The effect of treatments on senescent leaves per vine was analyzed for bloom damage within veraison damage and veraison damage within bloom damage with the non-parametric Median test (reviewed by Zar 1999). This was due to data not being normally distributed.

**Beetle-Damaged Vines.** Twenty vines of similar weights were assigned to two blocks as described for the mechanically damaged vines, with eight plants in block 1 and 12 plants in block 2. As with mechanically damaged vines, two treatments were imposed on these vines, early season damage (2 wks post bloom) and late season damage (at veraison), in a 2 x 2 factorial design. Early season damage was induced with adult rose chafer, *Macrodactylus subspinosus*, and late season damage with adult Japanese beetles, *Popillia japonica*. Rose chafer beetles used in this study were collected with traps (Great Lakes IPM, Vestaburg, Michigan) from fields with sandy soils surrounding peach orchards in Oceana County Michigan on 20 June 2001. Japanese beetles were collected with traps (Trécé Inc., Salinas, California) at the Trevor Nichols Research Complex in Allegan County Michigan on 10 August 2001. In both of these cases, traps were emptied the night before beetles were collected in order to ensure beetles used in this study had spent no more than 1 d in traps. Vines were damaged by exposing each vine to 36 hours of feeding by 120 beetles.

Damage levels on these vines were estimated by scoring the approximate percent damage of each leaf, using the visual system used by Boucher and Pfeiffer (1989), and estimating the leaf area of the damaged leaves in relation to the leaf area of the whole

vine, using the previously mentioned relationship between midrib length and leaf area. During both of these damage periods, all vines were caged in highly porous Bridal illusion fine mesh (Fabric Gallery, Williamston, MI) draped over supporting stakes and fastened to the pot. These cages did not restrict plant growth and cages were only placed twice for no more than 40 hours.

Measurements taken: Vine growth parameters, whole vine carbon assimilation, and single-leaf carbon assimilation were recorded using the same protocol and analyzed in the same manner as for the mechanical damaged vines. Single leaf carbon assimilation measurements were all taken on undamaged portions of leaves.

**Comparisons of Mechanical and Beetle Damage on Single Leaves.** To compare the impact of simulated and insect herbivory on carbon assimilation, twenty-four vines were divided into two groups of 12 vines each. One of these groups was designated for damage during bloom and the other for damage during veraison. Within the two groups one leaf at the third or fourth node was selected from each vine and randomly assigned to one of the following treatments: beetle feeding, mechanical damage, or no damage. The three treatments were blocked into one group, whereby the mechanically damaged leaves received approximately the same percentage of leaf area loss as the beetle damaged leaves in the same group. Beetle feeding was applied by placing 10 beetles on each leaf enclosed in a single cage made of white plastic mesh (mechanically damaged leaves and no damage leaves were also caged for the same period of time). Treatments were applied during bloom using rose chafers and during veraison using Japanese beetles. Mechanical damage was applied using a hole-puncher (size of holes =  $38.5 \text{ mm}^2$ ) at the same time.

CO<sub>2</sub> assimilation rates were measured on damaged and undamaged sections of the leaves and on the leaf apical to the damaged leaf using the same CIRAS unit and cuvette system described above. Measurements on these leaves were taken 1, 3, 8, and 16 d after damage for the group damaged at bloom and 1, 3, 10, and 17 d after damage for the group damaged during véraison.

The effect of damage on carbon assimilation rates were analyzed by date as a blocked one-way ANOVA. Means separation was performed using the Student Newman Keuls method, using the SAS System Version 8 (SAS Institute 1999) statistical package.

## **Results**

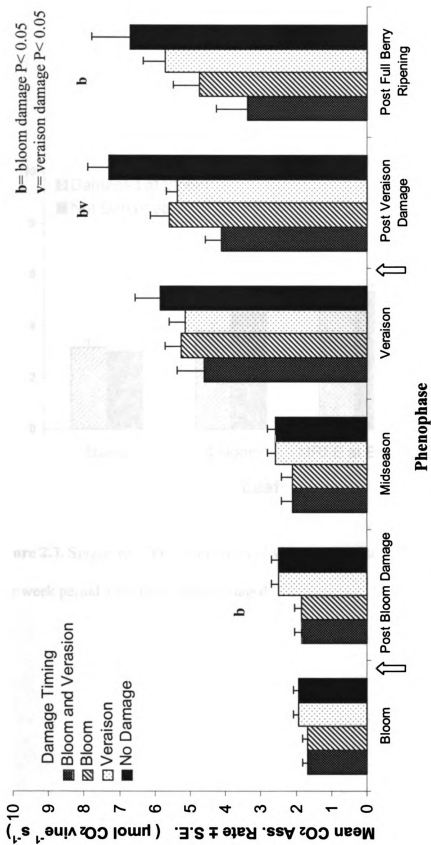
### **Mechanically Damaged Vines.**

Carbon assimilation: There were no significant interactions in whole-vine carbon assimilation between bloom damage and véraison damage treatments, so main effects were analyzed separately. Ten days after bloom damage was imposed there was a significant reduction in whole vine carbon assimilation ( $F_{1,13}=5.95$ ,  $P=0.03$ ). This difference was not significant by midseason, and by véraison, no effect of damage was apparent (Figure 2.2). Ten days after véraison damage treatments were imposed there was a significant reduction induced by both bloom and véraison damage on whole vine carbon assimilation ( $F_{1,16}=9.19$ ,  $P=0.008$  and  $F_{1,16}=12.01$ ,  $P=0.003$ , respectively). However, by the post-harvest samples only bloom damage had a significant negative effect on whole vine carbon assimilation rate ( $F_{1,20}=6.36$ ,  $P=0.02$  and  $F_{1,20}=1.91$ ,  $P=0.182$ , respectively).

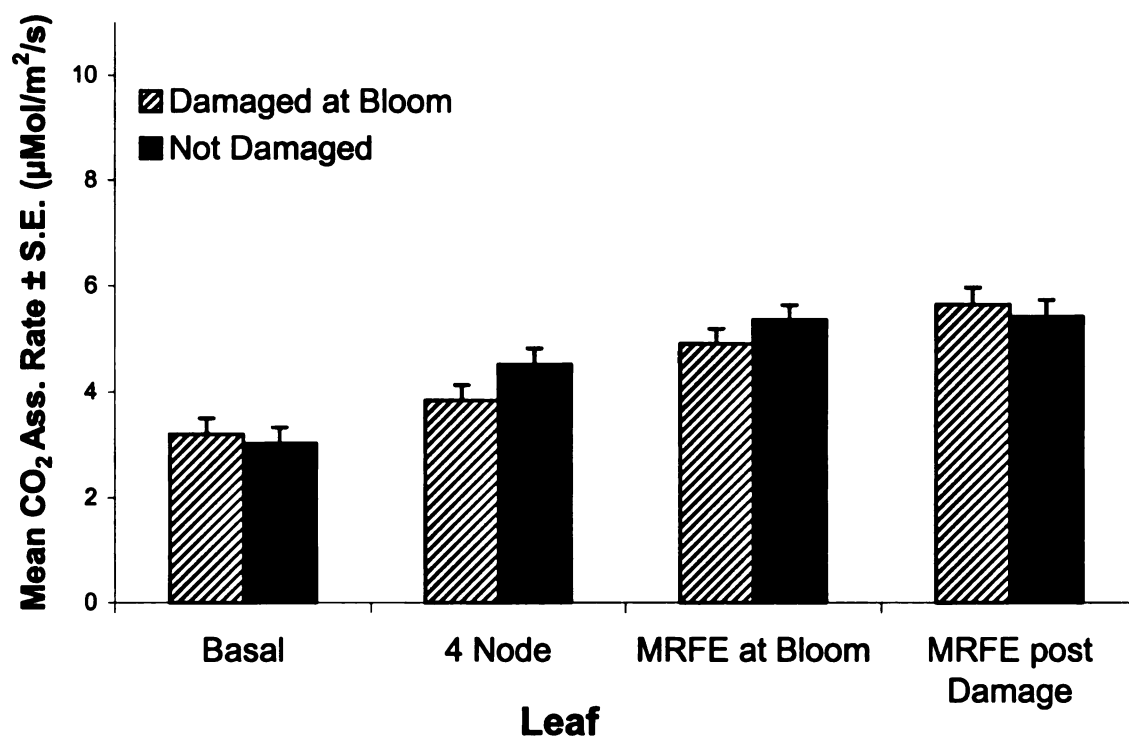
Prior to veráison there were no significant effects of bloom damage on single leaf carbon assimilation rate (Figure 2.3). However, there was a significant negative effect of bloom damage on carbon assimilation rates of basal and third to fourth node leaves during veráison ( $F_{1,19}=4.52$ ,  $P=0.046$  and  $F_{1,19}=6.62$ ,  $P=0.018$  respectively). These negative effects of bloom damage on photosynthesis later in the season (Figure 2.4) appear to indicate an early senescence of vines damaged at bloom.

Vine growth parameters: Mechanical damage had no significant effect on trunk diameters or shoot length were found throughout the season. However, there was a significant effect on leaf area growth early in the season after bloom damage was imposed (Figure 2.5). This effect was present 10 days, 1 month, and 2 months after bloom damage had been imposed ( $F_{1,22}=14.66$   $P=0.001$ ,  $F_{1,22}=10.11$   $P=0.005$  and  $F_{1,22}=4.89$ ,  $P=0.039$  respectively). Post-harvest, no effect of either bloom damage or veráison damage on leaf area was observed.

Veráison and bloom damage both had significant impact on the number of senescent leaves. Within vines damaged at veráison, bloom damage had no significant impact ( $\chi^2=0.41$ ,  $P=0.52$ ), but within vines not damaged at veráison, bloom damage significantly increased the number of senescent leaves ( $\chi^2=4.9$ ,  $P=0.027$ ). In contrast veráison damage significantly decreased the number of senescent leaves on vines damaged at bloom ( $\chi^2=4.9$ ,  $P=0.027$ ), and no impact on vines not damaged at bloom ( $\chi^2=1.37$ ,  $P=0.24$ ).



**Figure 2.2.** Whole vine carbon assimilation of mechanically damaged vines at different phenophases. Arrows represent points at which damage was applied. Significant effects ( $P < 0.05$ ) of bloom damage treatment are denoted as b and of veraison damage treatment as v.



**Figure 2.3.** Single leaf CO<sub>2</sub> assimilation of vines mechanically damaged at bloom, for the four week period after vines were damaged.

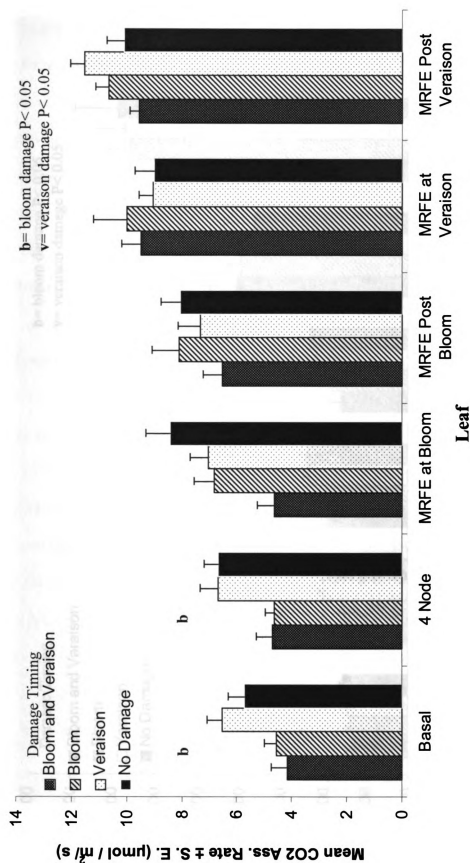
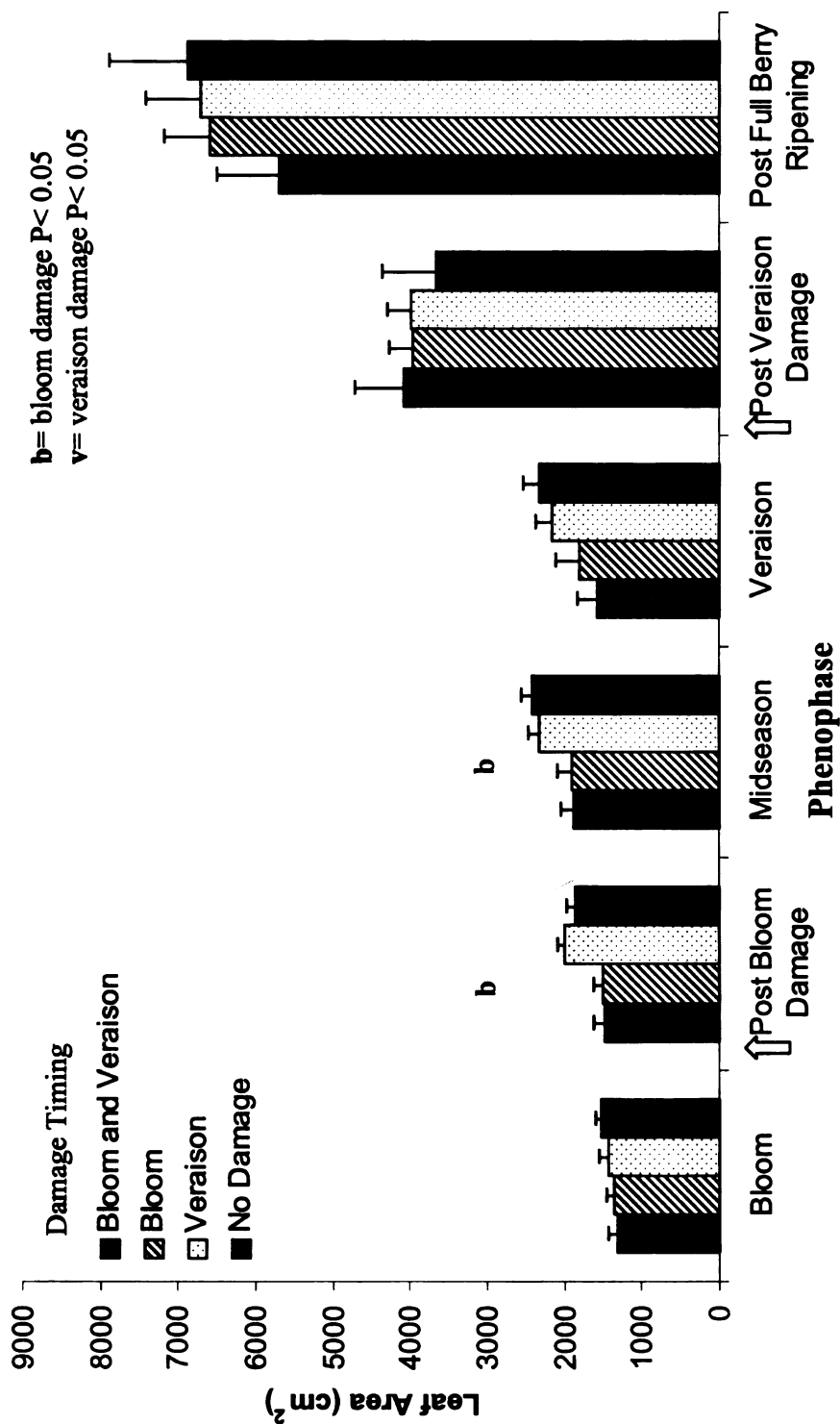


Figure 2.4. Average single leaf CO<sub>2</sub> assimilation rates of vines mechanically damaged at bloom and/or veraison, for the four-week period after vines were damaged at veraison. Significant effects ( $P < 0.05$ ) of bloom damage treatment are denoted as b. No significant effects of veraison damage were found.



**Figure 2.5.** Mean leaf area of mechanically damaged vines separated by the phenophase at which the measurements were taken.

Arrows represent points at which damage was applied. Significant effects ( $P < 0.05$ ) of bloom damage treatment are denoted as b. No

Significant effect of veraison damage was found.

Weights: There was no significant effect of mechanical damage at either bloom or veraison on dry weights of leaves, shoots, or two-year old wood. However, there was a significant negative effect of both bloom damage ( $F_{1,18}=23.7$ ,  $P<0.001$ ) and veraison damage treatments ( $F_{1,18}=6.25$ ,  $P=0.022$ ) on dry root weight. Bloom damage had a significant negative effect on whole vine dry weight ( $F_{1,18}=22.19$ ,  $P=0.0087$ ) whereas veraison damage did not ( $F_{1,18}=3.12$ ,  $P=0.0945$ ) (Table 2.1).

### **Beetle-Damaged Vines**

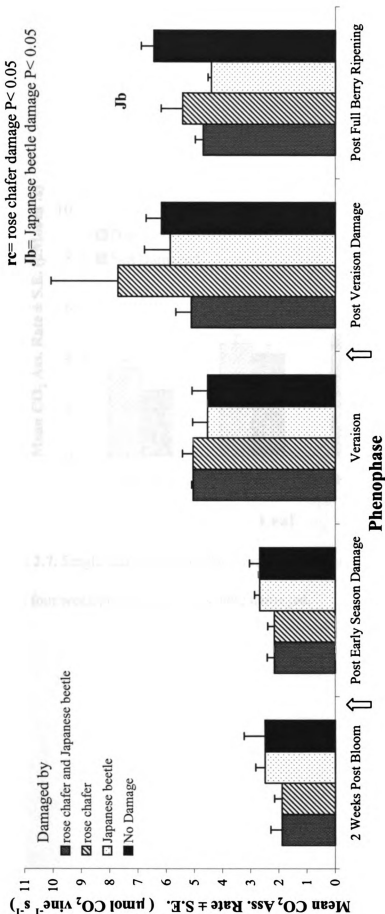
Defoliation levels induced by beetle damage were lower than those caused by mechanical damage and therefore comparisons between beetle damage and mechanical damage need to be made with caution. The mean defoliation caused by rose chafers was  $8.0 \pm 1.1\%$ , and the mean defoliation caused by Japanese beetles was  $17.1 \pm 2.4\%$  of the total leaf area.

Carbon assimilation: As with mechanically damaged vines, there were no significant interactions between bloom damage and veraison damage treatments in whole carbon assimilation measurements, so main effects were analyzed separately (Figure 2.6). Feeding by rose chafers or Japanese beetles did not impact carbon assimilation from the beginning of the season through veraison. However, measurements taken post-harvest indicated a significant negative impact of Japanese beetle damage ( $F_{1,15}=10.12$ ,  $P=0.006$ ).

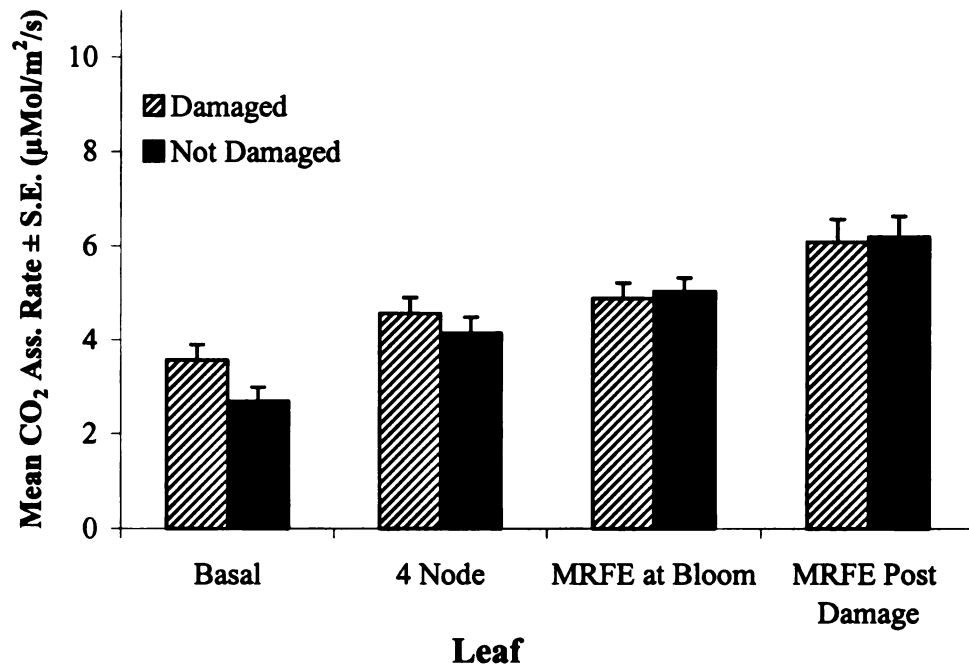
No significant effects of rose chafer or Japanese beetle damage on single leaf carbon assimilation rates were found (Figures 2.7 and 2.8).

**Table 2.1.** End of season dry weight (g) of tissues on vines subjected to mechanical damage treatments. Numbers within the same column followed by the same letter are not significantly different ( $P<0.05$ ).

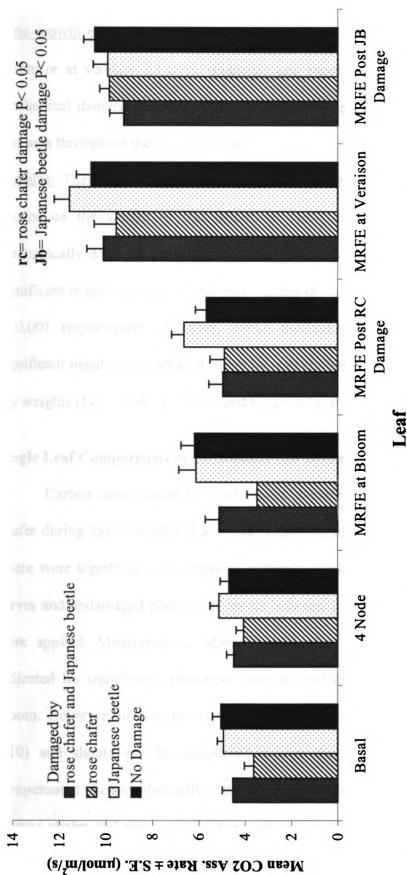
| Damage Timing      | Leaves       | Shoots       | Trunk        | Roots          | Total          |
|--------------------|--------------|--------------|--------------|----------------|----------------|
| Bloom and Veraison | 33.0 ± 4.7 a | 25.7 ± 4.4 a | 11.5 ± 0.7 a | 65.6 ± 2.6 a   | 135.9 ± 11.7 a |
| Bloom              | 37.4 ± 3.5 a | 29.1 ± 3.6 a | 10.3 ± 0.5 a | 75.8 ± 6.11 ab | 152.6 ± 11.2 a |
| Veraison           | 37.3 ± 3.0 a | 30.5 ± 2.9 a | 12.2 ± 0.9 a | 86.7 ± 5.2 bc  | 166.7 ± 9.0 ab |
| No Damage          | 40.0 ± 4.6 a | 33.0 ± 4.3 a | 12.0 ± 0.8 a | 99.8 ± 5.4 c   | 184.7 ± 10.5 b |



**Figure 2.6.** Whole vine carbon assimilation of vines damaged by beetles at the phenophases indicate by the arrows, separated by the phenophase at which measurements were taken. Significant effects ( $P < 0.05$ ) of Japanese beetle damage treatment are denoted as Jb. No significant effects of rose chafer damage were found.



**Figure 2.7.** Single leaf CO<sub>2</sub> assimilation rates of vines mechanically damaged at bloom, for the four week period after vines were damaged.



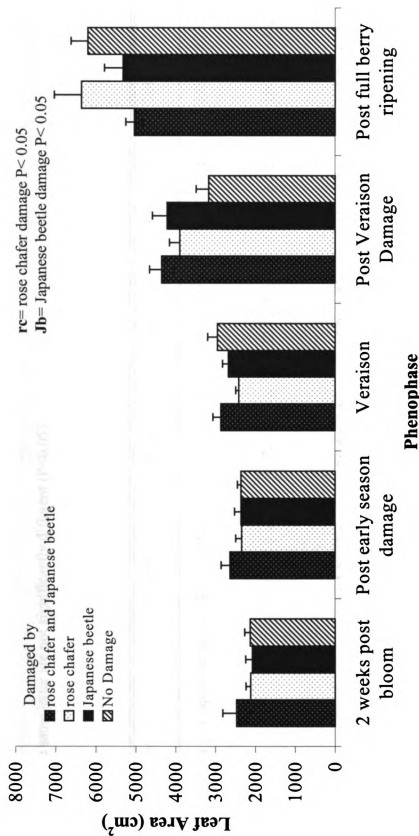
**Figure 2.8.** Average of single leaf CO<sub>2</sub> assimilation of beetle damaged vines, for the four-week period after vines were damaged at veraison with the Japanese beetle. No significant effects ( $P < 0.05$ ) of rose chafer damage or Japanese beetle damage treatments were found.

Vine growth parameters: There was no significant impact of damage two weeks after bloom or at veraison on trunk diameters and shoot length. In contrast to the effect of mechanical damage during bloom, there was no significant effect of beetle feeding on leaf area throughout the season (Figure 2.9).

Weights: There was no significant effect of feeding by either rose chafers or Japanese beetles on the weight of leaf, shoot, or two-year old wood (Table 2.2). As with mechanically damaged vines, foliar damage by rose chafers and Japanese beetles had a significant negative impact on dry root weights ( $F_{1,14} = 26.78$ ,  $P < 0.001$  and  $F_{1,14} = 16.26$ ,  $P = 0.001$  respectively). However, unlike mechanically damaged vines, there was a significant negative impact of damage by rose chafers and Japanese beetles on total vine dry weights ( $F_{1,14} = 9.86$ ,  $P = 0.007$  and  $F_{1,14} = 8.75$ ,  $P = 0.01$  respectively) (Table 2.2).

### **Single Leaf Comparisons of Mechanical and Beetle Damage**

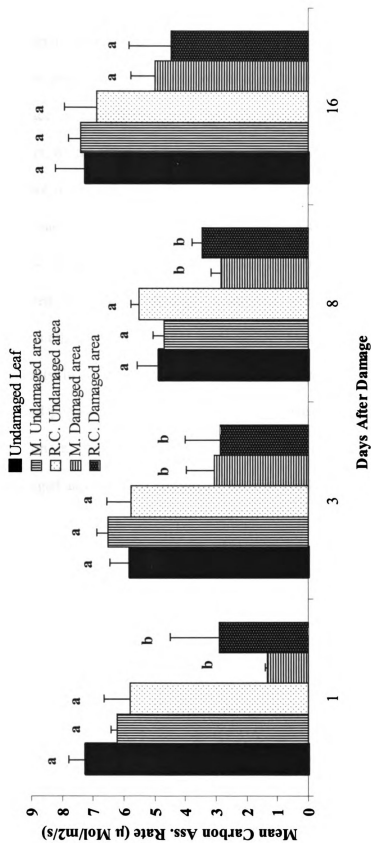
Carbon assimilation rates of leaves damaged mechanically and with the rose chafer during bloom exhibited a consistent pattern of response to damage (Figure 2.10). There were significant differences in carbon assimilation between damaged portions of leaves and undamaged portions of leaves between 1 and 8 days after damage treatments were applied. Measurements taken 16 days after damage treatments were imposed indicated no significant differences between undamaged vines and vines damaged at bloom. However, measurements taken during this period were highly variable (Figure 2.10) and should not be considered a sign that damaged portions of leaves had compensated photosynthetically at the tissue level. Measurements of undamaged portions of rose chafer and mechanically damaged leaves did not detect a significant difference from the undamaged controls.



**Figure 2.9.** Mean leaf area of beetle damaged vines separated by the phenophase at which the measurements were taken. Arrows represent points at which damage was applied. No significant effects ( $P < 0.05$ ) of rose chafer damage or Japanese beetle damage treatments were found.

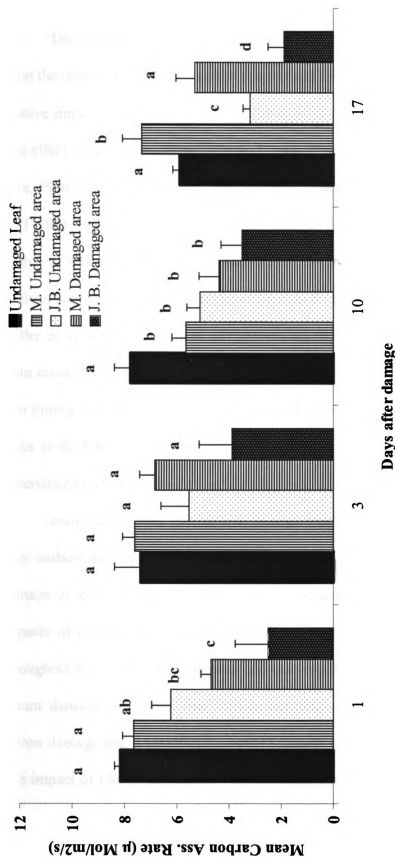
**Table 2.2.** End of season dry weight (g) of tissues on vines subjected to beetle damage treatments. Numbers within the same column followed by the same letter are not significantly different ( $P<0.05$ ).

| Damaged by                      | Leaves       | Shoots       | Trunk        | Roots        | Total         |
|---------------------------------|--------------|--------------|--------------|--------------|---------------|
| Rose chafer and Japanese beetle | 42.7 ± 2.9 a | 33.2 ± 2.4 a | 14.8 ± 1.9 a | 83.0 ± 3.1 a | 173.7 ± 4.7 a |
| Rose Chafer                     | 48.6 ± 2.5 a | 37.8 ± 2.5 a | 12.9 ± 1.0 a | 86.8 ± 3.5 a | 186.2 ± 6.8 a |
| Japanese beetle                 | 44.1 ± 2.7 a | 36.4 ± 2.5 a | 15.9 ± 1.5 a | 91.3 ± 2.0 a | 187.7 ± 6.4 a |
| No Damage                       | 47.4 ± 2.3 a | 34.6 ± 1.7 a | 15.9 ± 1.1 a | 118.3 ± 5.5b | 216.2 ± 8.7 b |



**Figure 2.10.** Single leaf carbon assimilation rates of leaves damaged mechanically, leaves damaged with rose chafers, and undamaged leaves. All leaves initiated at the fourth node and all measurements were taken at bloom. Measurements taken on damaged portions of leaves include 25% leaf area removed in the cuvette. Means with different letter indicate significance ( $P < 0.05$ ) by day. Means separation was performed using the Student Newman Keuls Method.

Measurements taken from leaves damaged during veraison indicated a significant reduction in carbon assimilation rate 1 day after damage treatments were imposed in damaged portions of leaves compared to undamaged portions. There was no significant difference in assimilation rates between undamaged portions of leaves (Figure 2.11). However, by the third day after damage treatments were imposed, the earlier differences could not be detected. Ten days after damage treatments were imposed, the undamaged control had a significantly higher carbon assimilation rate than damaged and undamaged portions of leaves damaged mechanically or by the Japanese beetle (Figure 2.11). Seventeen days after damage treatments were applied, undamaged portions of mechanically damaged leaves had higher carbon assimilation rates than all other treatments. In addition, no significant differences between the undamaged control and the damaged portion of mechanically damaged leaves were found. In contrast, a significant reduction in carbon assimilation rate between the undamaged control and both the undamaged and damaged portion of Japanese beetle damaged leaves was found.



**Figure 2.11.** Single leaf carbon assimilation rates of leaves damaged mechanically, leaves damaged with Japanese beetle, and undamaged leaves. All leaves initiated at the fourth node and all measurements were taken at veraison. Measurements taken on damaged portions of leaves include 25% leaf area removed in the cuvette. Means with different letter indicate significance ( $P < 0.05$ ) by day. Means separation was performed using the Student Newman Keuls Method.

## Discussion

This study indicated that the ability of vines to tolerate foliar damage is dependent upon the relative strengths of carbon sources and sinks at the time of damage, and that the relative impacts of different modes of damage are dependent upon the timing of damage. The effect of sink strength, as crop load, on tolerance to foliar damage the European red mite, *Panonychus ulmi* (Koch), has been demonstrated previously in apples by Lakso et al. (1996) and Francesconi et al. (1996a,b). In grapevines, the importance of carbon source to sink relations has been stressed by researchers working on the effects of crop load on carbon assimilation and dry matter partitioning (e.g. Edson et al. 1993, 1995a,b Miller et al. 1996a,b, Petrie et al. 2000). This study builds on the knowledge gathered from research on crop load, by using the principal of source-sink dynamics and applying it to timing of damage. This study illustrates that the relation between carbon sources and sinks at the time of damage has a stronger impact on growth than the level of damage experienced by the vine.

Immediately after mechanical damage treatments at bloom and véraison, whole vine carbon assimilation rates were reduced by both damage, indicating that foliar damage at both of phenophases induced a source limitation. However, the negative impacts of damage at bloom persisted throughout the season, but were not consistent throughout the season. At midseason and early véraison there was no significant effect of bloom damage on whole vine carbon assimilation, but at véraison and post-harvest, bloom damage had a significant negative impact upon whole vine carbon assimilation. The impact of bloom damage on whole vine carbon assimilation late in the season may have been due to increased senescence of leaf tissue at this time, see below, or due to a

smaller root system caused by damage at bloom creating a smaller sink size. We did not look directly at carbohydrate movement or root growth throughout the season and it is therefore difficult to speculate as to the causes of this reduction in whole vine photosynthesis late in the season in terms of the source to sink relation in the vines.

Although no impact of bloom damage on whole vine carbon assimilation was observed by midseason (Figure 2.2), impact upon growth was evident in the leaf area present up to 2 months after damage was imposed (Figure 2.5). This lasting impact on leaf area, but not on whole vine carbon assimilation could be explained by an increased photosynthetic efficiency of the vines on a per leaf basis. Several studies have indicated increased levels of photosynthesis in the remaining leaves of grapevines after partial defoliation through whole leaf removal (Hofäcker 1978, Kliewer 1982, Candolfi-Vasconcelos and Koblet 1991). However, we failed to detect any significant differences in single leaf carbon assimilation rates prior to veraison at any leaf position (Figure 2.4). Our single leaf results agree with studies in which damage was caused without removing the whole leaf by either herbivores or mechanical simulations (Boucher et al. 1987, Welter et al. 1989b, Candolfi et al. 1993). In these studies no increase or decrease in carbon assimilation rates was observed on damaged leaves. The lack of any differences detected upon whole vine carbon assimilation may be due either to the presence of a small difference in carbon assimilation rate undetected by our set up, or within-canopy interactions such as lower self-shading, greater air movement, and leaf angle. Other studies comparing whole vine and single leaf assimilation rates in grapevines have also indicated large discrepancies between whole vine and single leaf carbon assimilation measurements (e. g. Edson et al. 1993, Edson et al. 1995b, Miller et al. 1997).

The significantly lower exact leaf area carbon assimilation measurements on the basal and 3-4 node leaves on vines damaged at bloom (Figure 2.2), are indicative of early senescence. These two leaves were the oldest leaves measured and a lower carbon assimilation rate is associated with leaf age and senescence (Kriedmann 1968, Flore and Lakso 1989). In addition, leaves on vines damaged at bloom were observed to senesce earlier. Accelerated leaf senescence has been observed as a plant compensatory response to various stresses including drought, excess water, minerals, temperature, pathogens (reviewed by Smart 1994), and O<sub>3</sub> (reviewed by Pell et al. 1994). Edson (1993) observed increased senescence on the basal leaves of vines with high crop loads compared to those with medium, low, or no crop present. This indicates that carbohydrate-induced stresses may also be a factor influencing leaf senescence. In addition, in a study comparing shoot number and dry matter accumulation and partitioning in non-bearing grape vines, Miller et al. (1996a) found no differences in whole vine dry weight or dry weight partitioning between budburst and veraison, but a significant reduction in dry weight accumulation between veraison and harvest. The similarity between these results appears to indicate a potential for reduced dry matter accumulation late in the season caused by high stress levels early in the season. However, a mechanism for such a relationship is unknown, and further investigation of early season stress levels on late season dry matter assimilation is needed.

Despite the difference in leaf area observed early in the season, by post-harvest there was no significant difference in leaf area detected between any of the damage treatments and undamaged control vines (Figure 2.5). The similar leaf and shoot dry weights indicate that this was not due to thinner leaves or shoots being produced. No

increase in carbon assimilation was detected at any point throughout the season. Rather, only reductions in whole vine carbon assimilation were detected, indicating that the absence of differences between any of the damage treatments was not due to a compensatory photosynthetic response.

The lack of difference in above ground growth despite the absence of higher carbon assimilation rates can be understood in terms of carbon allocation patterns. During the period between bloom and *veraison*, shoot and leaf growth are the primary sinks and therefore a source limitation is most likely to be observed in the storage tissues. In addition, Candolfi-Vasconcelos et al. (1994) demonstrated that stress levels induced by defoliation can induce re-translocation of assimilates from the roots. Through a shift in allocation patterns, the difference in leaf area produced before *veraison* could have been mitigated by the time of harvest. Miller et al. (1996b) found an increase in leaf dry weight in the period between *veraison* and harvest in non-bearing vines, but at a rate much slower than between bud-burst and *veraison*, suggesting that the relative sink strengths of leaves and storage tissues had changed. They found that in non-bearing vines, roots accumulated dry weight faster than any other organ in the period between *veraison* and harvest. In this study damage at bloom had a significant negative impact on root weight, and bloom-damaged vines exhibited a greater allocation towards the current seasons growth and away from the roots (Table 2.1). However, we also found that damage at bloom caused a reduction in whole vine carbon assimilation rates during *veraison* and post harvest, which may have caused significant reductions in root weight at this time.

Because damage was applied on a percentage basis and only on previously undamaged leaves, vines damaged only during *veraison* and those damaged during bloom

and véraison had the same level of damage imposed upon them (Figure 1). The finding that vines damaged during bloom and véraison had lower dry root weights than vines damaged only during bloom or only during véraison (Table 2.1), indicates that bloom damage compromised the vines ability to compensate for damage during véraison. Véraison damage also led to a reduction in root weight. However, unlike bloom damage there was no significant difference observed in total vine weight when compared to the undamaged control. This indicates that damage at véraison may have induced a source limitation, but it did not affect vines as severely as bloom damage did. During véraison non-bearing vines lack the strong sink typically present at this time of the season. Previous studies have indicated lowered photosynthetic rate per leaf area in cropped vines during véraison compared to uncropped vines. For example, Downton et al. (1987) reported that the onset of the diurnal decline of photosynthesis occurred earlier in the day for vines without fruit. As a result those vines fixed 22% less carbon than fruiting vines, an indication that fruitless vines at véraison are sink limited. In addition, using potted ‘Seyval’ vines Edson et al. (1993, 1995a) showed a lower carbon assimilation rate per leaf area in uncropped vines when compared to cropped vines. Further evidence comes from reports of higher dry matter accumulation per leaf area in cropped than in uncropped vines (Edson et al. 1993, Miller et al. 1996, Petrie et al. 2000).

Prior to qualitative comparisons between mechanically damaged vines and beetle damaged vines, two major differences in treatment application need to be recognized; early season rose chafer herbivory was applied two weeks after bloom and only removed an average 8% of the leaf area compared to 20% in mechanical damage treatments. The difference in timing of damage is highly important, as Candolfi-Vasconcelos et al.

(1994b) found no effect of whole leaf removal treatments starting at pea size berry on single leaf photosynthesis, while Candolfi-Vasconcelos and Koblet (1991) found a significant increase in single leaf photosynthesis in vines defoliated by whole leaf removal starting around bloom. Damage induced by the Japanese beetle during *veraison* was more similar to mechanical damage treatments at 17% mean defoliation, applied within 3 days of mechanical damage. The small level of defoliation caused by the rose chafer probably explains the lack of major effects upon season long growth parameters and photosynthetic efficiency. However, as with mechanical damage at bloom, there was a significant negative impact upon root and whole vine dry weight (Table 2.2), illustrating that despite the low level of damage, herbivory early in the season can still have a strong impact upon vine growth and allocation patterns.

The response of vines to Japanese beetle herbivory suggests a greater impact of beetle damage than mechanical damage at *veraison*. Whole vine carbon assimilation at post-harvest was significantly reduced by Japanese beetle damage (Figure 2.6). In addition, unlike in mechanically damaged vines, a negative effect on whole vine dry weight was observed (Table 2.2). Mechanical simulations of herbivore damage rarely reflect feeding damage accurately, because factors such as the time required to perform damage, the tissues damaged, the amount of cellular shearing, and/ or the presence of frass and saliva (Baldwin 1990) may be required for the full response. In apples, Hall and Ferree (1976) found that the amount of cut surface had a higher impact on photosynthetic rate than the amount of leaf area removed. Damage by these leaf-skeletonizing beetles can create a larger proportional level of cut surface to leaf area removed than can mechanical damage induced with hole punchers. In addition, the instantaneous removal

of leaf tissue by hole-punchers is markedly different from the slower tissue removal caused by insect mandibles.

The comparisons of carbon assimilation rates between similar levels of damage to single leaves by mechanical and beetle damage during bloom and veraison illustrate some of these differences. In these experiments only a single leaf was damaged and therefore the source to sink relation at the whole vine level is unlikely to have been affected. Although the rose chafer and Japanese beetles are both polyphagous leaf skeletonizers producing visually similar types of damage, the results indicate a differential response of vines to these two beetles as compared to undamaged and mechanically damaged leaves (Figures 2.10 and 2.11). The differences found between these two damage timings are most likely a reflection of responses to damage influenced by leaf age and activity at the time of damage. Leaves damaged mechanically or by rose chafers during bloom maintained a similar pattern of response, whereby undamaged portions of leaves had similar carbon assimilation rates as the undamaged controls while damaged portions had a reduced assimilation rate. In contrast, in leaves damaged during veraison mechanical damage had a lesser negative effect than beetle damage 17 days after damage (Figure 2.11). The difference was found on both damaged and undamaged portions of the leaf indicating that the difference in assimilation rates was not simply due to the amount of damaged area, but likely a systemic reaction at the leaf level.

In a study measuring the effect of different densities of hole punches on carbon assimilation, Boucher et al. (1987) found that on leaves with low levels of damage there was a greater depression of assimilation rate 12 days after damage was inflicted. That result is similar to our results for 10 day after damage (Figure 2.11). However, in this

study 17 days after damage treatments were imposed undamaged portions of mechanically damaged leaves had a significantly higher carbon assimilation rate than the undamaged control, and no significant differences were found between damaged portions of mechanically damaged leaves and the undamaged control. The release of feedback inhibition or the creation of a new sink due to the mechanical damage is unlikely due to the delay in response. In addition, an induction of higher root produced cytokinin levels reducing leaf senescence is unlikely, as there was no reduction in competition between leaves. This increase in photosynthetic rate in mechanically damaged leaves, and reduction in photosynthetic rate of Japanese beetle damaged leaves, illustrates that leaf age and type of damage have a potentially strong interaction.

In conclusion, the results presented in this study demonstrate the importance of vine phenology when considering response to damage. Source-sink interactions are a critical component of plant physiology that has been used to understand the effects of crop load on vine growth (e.g. Edson et al. 1993, 1995a,b). The results in this study demonstrate the importance of source-sink interactions at the time of damage on vine tolerance to foliar damage. The application of mechanical damage treatments on a percentage basis in this study removed intensity of damage and whole season sink size as factors explaining the increased tolerance to damage at veraison when the source to sink ratio was highest. In addition, the results from this study illustrate the importance of timing of damage and plant physiology on the adequacy of mechanical simulations of herbivory. This study stresses the importance of studying herbivory within the physiological context of the plant.

## CHAPTER 3

### Phenophase-Dependent Growth Responses to Foliar Damage in Establishing Juice Grape Vines, *Vitis labrusca* (Linnaeus) var. 'Niagara'

#### Introduction

In Michigan, *Vitis labrusca* var. 'Niagara' grapevines have been planted at a faster rate than any other grape variety in the past 20 years (Kleweno and Matthews 2001). The establishment period of grapevines is a highly important period as a poor start can hinder vineyard productivity for several years (Zabadal 1997). The smaller size and lower levels of carbohydrates generally found in the storage organs of young vines can significantly reduce the compensatory abilities of young vines to foliar damage compared to those of mature vines. However, in their first years of establishment, vines bear very little or no fruit, and the fruit that is produced are generally removed. 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 studies using potted grapevines have indicated sink limitations in fruitless vines during veraison (Miller et al. 1996b, Petrie et al. 2000a). The potential for a sink limitation during veraison indicates that in non-bearing vines a high level of tolerance to foliar damage may be present at this time.

The lack of fruits in young vines changes the plant protection strategies employed, as there is no need to control fruit damaging pests (such as the grape berry moth, *Endopiza viteana*). Insecticides used are generally broad spectrum in nature, and therefore also control foliar pests such as the rose chafer, *Macrodactylus subspinosus*, and the Japanese beetle, *Popillia japonica*. For this reason it is important to understand

how young vines react to damage, as they may be vulnerable to foliar damage at this time and control methods would be targeted mainly at these indirect pests. In addition, the potential for high levels of tolerance to foliar damage late in the season may allow for a reduction in the use of insecticides even under high infestations in young *V. labrusca* vines.

This study examines the relative ability of young *V. labrusca* (L.) var. 'Niagara' vines to tolerate foliar damage during bloom and veraison. In particular this study tested whether non-bearing grapevines are capable of higher tolerance to damage during veraison than bloom, as would be expected by the higher source to sink ratio at this time. This was tested by a study in 2000 where similar absolute levels of damage were performed during bloom and/or veraison, and in the 2001 by damaging vines on a percentage of their total leaf area at bloom and/or veraison.

### **Materials and Methods**

**Plant material.** This study was undertaken in a *V. labrusca* (L.) var. 'Niagara' vineyard established in 1999, at the Trevor Nichols Research Complex in Fennville, Michigan. Two shoots from two canes (total of four shoots) of each vine were trained onto a 1.37 meter high bilateral cordon Hudson River Umbrella trellis system. There were seven vines per row, with 1.8 meters in between vines and 3 meters between rows. Vines were maintained using 45.5 kg of Urea fertilizer (46% Nitrogen) per acre, applied on 16 March 2000 and 102.3 kg of Urea on 25 March 2001, and standard plant protection program (Gut et al. 2002), except on rows where vines were caged with beetles. On these rows, no insecticides were applied at least one month prior to beetles being caged on vines and

insecticide and fungicide applications were postponed until cages were removed. Treatments were initiated in spring 2000.

**2000 Experiment.** Sixteen vines with cane height between 0.5m and 1.0m were selected to receive mechanical damage treatments during bloom and/or during veraison. Treatments were imposed in a 2 x 2 factorial design; vines were either damaged at bloom, at veraison, at bloom and veraison, or not damaged. Leaf area was removed using hole punchers (size of holes = 38.5 mm<sup>2</sup>). This was done to avoid all major veins in order to imitate beetle feeding and to avoid the differential impacts on photosynthetic capacity caused by interveinal damage when compared to whole leaf removal or treatments including midrib and main lateral vein damage (Hall and Ferree 1976, Boucher et al. 1987). Damage at bloom consisted of removing 30% of the total leaf area of every fully expanded leaf during bloom between the 19-21 June 2000. Damage during veraison (15-16 August 2000) 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 shoot first reached the trellis. To ensure appropriate damage levels were applied, visual aids were made for use while damaging leaves.

During the 2000 growing season, vegetative growth parameters were measured at trace bloom (13-14 June), at veraison (6 August), and after leaf senescence (21 October) on vines damaged at bloom and veraison. In addition, the number of mature nodes and the total shoot length were measured after leaf loss (10-11 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 Stren digital scale (Stren, Madison, N.C.) in the field. Prior to bloom the following season (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 prior to veráison damage were analyzed as a one-way ANOVA, with bloom damage as the sole treatment and cane diameter at trace bloom as a covariate. Measurements taken after veráison damage were analyzed by date as a 2 x 2 factorial analysis with cane diameter at trace bloom as a covariate, using the SAS statistical package (Version 8, SAS Institute 1999). The analysis of pruning weight data indicated a significant bloom damage by veráison damage interaction, therefore bloom damage was analyzed within veráison damage and veráison damage within bloom damage. This was performed using the “LSmeans Slice” function of ProcGLM (Version 8, SAS Institute 1999).

**2001 Experiment.** On 20 February, 2001, 40 vines were pruned to 15 nodes on each of two canes and the pruning weights recorded as described above. The number of shoots on these vines were adjusted to four per cane on 8 May, 2001. Due to strong winds between 5 June 2001 and 11 June 2001, vines lost shoots and only 28 vines were retained for the experiment. Vines were assigned to three blocks according to shoot number; there were 12 vines with 5 shoots, 12 vines with 6 shoots, and 4 vines with 7 shoots. These vines were mechanically damaged during bloom and/or veráison as a 2 x 2 factorial design within each block. Bloom damage consisted of removing 20% of the total leaf area of all fully expanded leaves between 18 June and 19 June 2001, and veráison damage consisted

of removing 20% of the total leaf area of all fully expanded leaves between 21 August 2001 and 24 August 2001. Because leaves were damaged only once, vines damaged only during veraison had the same level of damage as vines damaged during bloom and veraison.

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

Statistical Analysis. Measurements taken prior to veraison damage were analyzed as a blocked one-way ANOVA with bloom damage as the sole treatment and the pruning weights as covariates. Measurements taken after veraison damage were analyzed by date as a blocked 2 x 2 factorial analysis with pruning weights as covariates, using the SAS System V8 statistical package (SAS Institute 1999). Where F-values for the blocking factor were below 1 they were considered to be ineffective (Kuehl 2000), and the analysis was performed without the blocking factor.

## **Results**

**2000 Experiment.** Damage at bloom did not cause any reduction cane diameter, or node

number when vines were measured at veráison ( $F_{1,12}=1.71$ ,  $P=0.30$  or  $F_{1,12}=0.25$ ,  $P=0.63$  respectively). No significant interactions between bloom and veráison damage were observed in the growth parameters measured after leaf senescence. These measurements indicated that damage at bloom had no significant effect of damage on cane diameters ( $F_{1,10}=0.02$ ,  $P=0.88$ ), total node number ( $F_{1,10}=2.66$ ,  $P=0.13$ ), and mature node number ( $F_{1,10}=1.99$ ,  $P=0.19$ ). Damage at veráison also had no significant impact on the above ground growth parameters (cane diameters:  $F_{1,10}=0.19$ ,  $P=0.67$ ; total node number:  $F_{1,10}=0.24$ ,  $P=0.64$ ; mature node number:  $F_{1,10}=0.66$ ,  $P=0.44$ ). However, damage at bloom did have a significant negative impact upon shoot length ( $F_{1,10}=6.64$ ,  $P=0.03$ ), while damage at veráison did not ( $F_{1,10}=0.45$ ,  $P=0.52$ ). This difference in shoot length due to bloom damage was not found in our means comparisons (Table 3.1).

Damage at both bloom and veraison significantly affected pruning weights. In this case there was a significant interaction between the damage timings. Within vines that were not damaged at bloom, veráison damage caused a significant increase in pruning weights ( $F_{1,10}=10.77$ ,  $P=0.01$ ). However, among vines damaged during bloom, damage at veráison caused a significant reduction in pruning weights ( $F_{1,10}=5.79$ ,  $P=0.04$ ). Within vines damaged at veráison, bloom damage had a significant negative impact on pruning weights ( $F_{1,10}=41.2$ ,  $P<0.01$ ), and within vines not damaged at veráison bloom damage had no significant impact on pruning weights ( $F_{1,10}=0.61$ ,  $P=0.45$ ) (Table 3.1).

**Table 3.1.** Growth parameters taken at leaf loss and dormancy on vines damaged during the 2000 growing season. Treatments with the same letters are not significantly different from each other at the  $P < 0.05$  level. Means separation performed by least squares difference using the Tukey-Kramer adjustment method to control for experimentwise error.

| Damage             | Mature Node #         | Total Node #          | Total Shoot Length (m) | Pruning Weight (g)    |
|--------------------|-----------------------|-----------------------|------------------------|-----------------------|
| No Damage          | 96.8 $\pm$ 8.7    a   | 116.0 $\pm$ 8.7    a  | 14.91 $\pm$ 1.6    a   | 637 $\pm$ 92.9    b   |
| Bloom              | 86.0 $\pm$ 2.4    a   | 102.4 $\pm$ 5.0    a  | 12.31 $\pm$ 1.2    a   | 598 $\pm$ 129.7    ab |
| Veráison           | 109.5 $\pm$ 10.6    a | 134.3 $\pm$ 14.6    a | 17.13 $\pm$ 1.5    a   | 987 $\pm$ 64.0    c   |
| Bloom and Veráison | 92.3 $\pm$ 21.1    a  | 107.8 $\pm$ 27.4    a | 11.73 $\pm$ 3.4    a   | 342 $\pm$ 142.0    a  |

Cane diameters measured prior to bloom in the 2001 growing season were significantly impacted by damage at bloom during the previous season ( $F_{1,10}=6.5$ ,  $P=0.03$ ), but no significant difference in cane diameters was found in vines damaged at veraison ( $F_{1,10}=0.51$ ,  $P=0.49$ ). No significant effects of either bloom ( $F_{1,10}=0.37$ ,  $P=0.56$ ) or veraison ( $F_{1,10}=0.05$ ,  $P=0.82$ ) damage were observed in the number of nodes remaining dormant after the 16 inch shoot growth stage.

**2001 Experiment.** At midseason no significant impact of bloom damage was observed on 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, bloom damage had a significant negative impact upon the 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 shoot length ( $F_{1,23}=5.59$ ,  $P=0.03$ ). No significant impact of bloom damage 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 at post-harvest still indicated a significant negative impact of bloom damage on the total number of nodes ( $F_{1,22}=10.56$ ,  $P=0.004$ ) and number of nodes on lateral shoots ( $F_{1,22}=11.18$ ,  $P=0.003$ ), but not on shoot length ( $F_{1,23}=2.84$ ,  $P=0.11$ ). As found during veraison, no significant impact of bloom damage 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 damage at veraison damage was observed on total node number ( $F_{1,22}=0.10$ ,  $P=0.75$ ), lateral shoot node number ( $F_{1,22}=0.39$ ,  $P=0.54$ ), shoot length ( $F_{1,23}=1.21$ ,  $P=0.28$ ), main shoot node number ( $F_{1,22}=0.66$ ,  $P=0.43$ ), or cane diameter

( $F_{1,21}=0.02$ ,  $P=0.89$ ).

Bloom damage had a significant negative effect on mature node number ( $F_{1,21}=13.68$ ,  $P=0.001$ ) and pruning weights ( $F_{1,21}=11.26$ ,  $P=0.003$ ). In contrast, veráison damage treatments did not have a significant impact on either one ( $F_{1,21}=0.05$ ,  $P=0.82$  and  $F_{1,21}=1.0$ ,  $P=0.33$  respectively) (Table 3.2).

### **Discussion**

The results presented here indicate that non-bearing young *V. labrusca* vines are better able to tolerate foliar damage during veráison than during bloom. In both 2000 and 2001, bloom damage had significant negative impacts upon several of the growth parameters measured, while veráison damage did not affect any of the growth parameters measured. The negative impact of bloom damage during the 2000 growing season was observed the following season in reduced cane diameters. However, in other research performing similar damage treatments in the same vineyard in the same year, we did not find a negative impact of bloom damage on cane diameters the following season (see Chapter 4).

**Table 3.2.** Growth parameters taken leaf loss and dormancy on vines damaged during the 2001 growing season. Treatments with the same letters are not significantly different from each other at the  $P < 0.05$  level. Means separation performed by least squares difference using the Tukey-Kramer adjustment method to control for experimentwise error.

| Damage             | Mature Node #       | Total Node #        | Total Shoot Length (m) | Pruning Weight (g) |
|--------------------|---------------------|---------------------|------------------------|--------------------|
| No Damage          | 271.7 $\pm$ 14.5 ab | 725.0 $\pm$ 54.0 ab | 23.17 $\pm$ 1.76 a     | 1035 $\pm$ 142 b   |
| Bloom              | 218.7 $\pm$ 23.0 ab | 635.1 $\pm$ 42.9 ab | 20.36 $\pm$ 1.42 a     | 617 $\pm$ 65 a     |
| Veráison           | 277.3 $\pm$ 16.3 b  | 831.3 $\pm$ 78.0 b  | 21.2 $\pm$ 2.16 a      | 862 $\pm$ 105 ab   |
| Bloom and Veráison | 201.9 $\pm$ 13.5 a  | 561.7 $\pm$ 19.8 a  | 19.15 $\pm$ 1.17 a     | 559 $\pm$ 65 a     |

Vines damaged solely at veraison in 2000 had significantly higher pruning weights than all other vines. This indicates that a certain level of foliar damage can potentially induce an increase in above ground growth late in the season. This increase in above ground growth may have been caused by a reallocation of resources or an increase in sink activity induced by damage. Candolfi-Vasconcelos et al. (1994 a) have demonstrated that defoliation-stressed vines can re-translocate carbohydrates stored in storage tissues to fruit. In addition, studies on potted *V. labrusca* var. 'Niagara' vines have shown that root weight is significantly impacted by damage at veraison while no differences in above ground damage were observed (see Chapter 2). Increases in individual leaf carbon assimilation rates have been reported in vines where defoliation has been induced 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 (e.g. McNaughton 1979, Owen 1980, Paige and Witham 1987, Paige 1992, Vail 1992, Hjalten et al. 1993, Paige 1994; but see Bergelson and Crawley 1992). However, in these cases the damage released apical dominance increasing branching patterns, and reduced competition for cytokinins and other root-produced resources between leaves. These changes 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 Aarsen 1996). The type of mechanical damage in this study is unlikely to have caused a release of apical dominance or reduced competition between leaves. Whether the difference observed here is due to an increase in sink activity or a reallocation of resources is an important consideration, as a reallocation of resources towards above ground growth may cause a reduction in

carbohydrates stored in roots and other tissues, potentially compromising future growth and yield.

When vines that had been damaged during bloom were damaged at veraison in 2000, they did not exhibit an increase in above ground growth. Indeed, these vines had significantly lower pruning weights than did the control vines. The reversal in vine response to veraison damage indicates that bloom damage compromised the vines ability to respond to damage at veraison. Various types of stresses, from pollution to plant association, have been shown to reduce plant compensatory abilities (e.g. Maschinski and Whitham 1989, Hjalten et al. 1993, Shabel and Peart 1994, Irwin and Aarssen 1996, Weltzin et al. 1998, Zvereva and Kozlov 2001; but see Coughenour et al. 1990). In addition, various studies have found plants unable to tolerate several episodes of damage (e. g. Hare 1980, Crawley 1983, Cartwright and Kok 1990). This response to damage suggests that the increase in pruning weights exhibited in vines damaged solely at veraison is probably due to a reallocation of resources towards above ground growth.

Damage 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 vines damaged 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 post harvest indicated no significant difference in main shoot node number between bloom damaged vines and controls. This indicates that bloom damage treatments primarily affected the production of lateral shoots in these vines. A similar response has been reported in *V. vinifera* var. 'Pinot Noir' and var. 'Riesling' vines subjected to water stress, in which lateral shoot growth was

significantly reduced by water stress (Reynolds and Naylor 1994).

In contrast to results from vines damaged in 2000, vines damaged solely at veráison in 2001 did not have a significant increase in pruning weights compared to undamaged controls. This difference between 2000 and 2001 indicates that the level of damage can potentially affect the vines response to damage. Damage applied at veráison in 2001 was applied on all fully expanded leaves while veráison damage in 2000 was only applied on 1.5 m of the shoot (average shoot length in 2000 = 3.62 m). The application of damage at veráison in 2001 reduced 20% of the available source at the time of damage at both bloom and veraison. Because of the vine growth between bloom and veráison, the total amount of damaged leaves at veráison was approximately three times more than what was damaged at bloom. This enabled a direct comparison of bloom damage and veráison damage in terms of the vine source to sink ratio at the time of damage. The comparison between bloom and veráison damage in 2001 suggests that the stronger effect of bloom damage is not due to the presence of a higher source (leaves) at veráison, but due to a lower relative sink at veráison in these fruitless vines.

In conclusion, these results are consistent with the notion that source to sink ratios at the time of damage have a strong impact on a vines ability to tolerate damage. This effect translates to a higher risk of injury due to foliar damage early in the growing season than late in the growing season in non-bearing *V. labrusca* vines.

## CHAPTER 4

### Grapevine tolerance to foliar damage by two temporally-separated scarab beetles and by mechanical damage during bloom or veraison

#### Introduction

The rose chafer, *Macrodactylus subspinosus* (Fabricius) (Scarabaeidae: Macrodactylini), and the Japanese beetle, *Popillia japonica* Newman (Scarabaeidae: Anomalini), are two leaf skeletonizing scarab beetles considered to be pests of economic importance in vineyards in eastern North America. Emergence of adult rose chafers coincides with grape bloom in most of the beetle's geographic range, while Japanese beetle adults coincide with veraison (berry ripening). Grapevines have been shown to tolerate significant levels of foliar damage (Petrie et al. 2000a,b, Candolfi-Vasconcelos et al. 1994, Boucher & Pfeiffer 1989), and insecticide applications may not be necessary if foliar damage by these insects is below levels that impact vine growth and productivity. The relationship between the level of herbivory and the impact on *Vitis labrusca* (Linnaeus) growth and production is not well understood, particularly in young establishing vineyards that typically do not have a crop. However, in bearing vines, Boucher and Pfeiffer (1989) found that natural infestations of Japanese beetle in Virginia failed to have any significant impacts upon fruit quality, quantity, or growth of *Vitis vinifera* (Linnaeus) var. 'Seyval Blanc'. This indicates a high level of tolerance in grapevines to foliar damage by leaf skeletonizers.

The detrimental effects of foliar herbivory are often attenuated by plant compensatory responses to foliar damage (Trumble et al. 1993). Reduction in leaf area by beetle feeding can alter the carbon source to sink balance, potentially causing a source

limitation. This in turn may drastically affect the distribution of carbon resources, because their allocation is dependent on the strength of sink demands in resource-limited plants (Wardlaw 1990, Trumble et al. 1993).

The relative sink strength of various tissues in grapevines changes significantly throughout the growing season, in accordance to their physiological stage of development (phenophase) (Williams & Matthews 1990). Plant responses to foliar damage may be affected by the seasonal change in demands placed upon the available sources by developing tissues and reproductive sinks. Studies of tolerance and compensation in perennial crops have focused on mature plants, in which vegetative growth tends to be the major carbon sink early in the season, while fruit production dominates carbohydrate distribution late in the season (Williams & Matthews 1990). In contrast, young woody plants, including grapes, produce relatively few fruits. Indeed, viticultural recommendations include cluster removal in the first years of growth to ensure that energy is directed toward vine establishment (Zabadal 1997). The lack of fruits as carbohydrate sinks may create a differential response to foliar herbivory late in the season in young plants when compared to mature, fruiting plants. While vineyards are being established, the photosynthetic and storage tissues act as the main sources of carbon, while actively growing tissues and damaged tissues act as the main sinks. During and prior to bloom, vegetative growth in grapevines is highly active, but by veraison shoot and leaf growth slows considerably (van Zyl 1984, Williams 1987). This translates into a situation with a low carbon source and high carbon sink during bloom and a high source and low sink during veraison. This difference in source to sink ratio is expected to pose a greater risk of source limitation during bloom than veraison, potentially affecting the

vines ability to tolerate damage early in the year.

This study examined the tolerance of young (1 yr after planting) grape vines, *Vitis labrusca* L. var. 'Niagara', to beetle and mechanical defoliation during bloom and veraison. The goals were to quantify the level of feeding by *M. subspinosus* and *P. japonica* on young *V. labrusca* vines, and to determine the response of young grapevines to different levels of mechanical and beetle damage during the different phenophases.

### **Materials and methods**

**Plant material.** This study was undertaken in a *V. labrusca* (L.) var. 'Niagara' vineyard established in 1999, at the Trevor Nichols Research Complex in Fennville, Michigan. Two shoots from two canes (total of four shoots) of each vine were trained onto a 1.37 meter high bilateral cordon Hudson River Umbrella trellis system. There were seven vines per row, with 1.8 meters in between vines and 3 meters between rows. Vines were maintained using 45.5 Kg of Urea fertilizer (46% Nitrogen) per acre applied on 16 March 2000 and 102.3 Kg of Urea per acre on 25 March 2001, and standard plant protection program (Gut et al. 2002), except on rows where vines were caged with beetles. On these rows, no insecticides were applied at least one month prior to beetles being caged on vines and insecticide and fungicide applications were postponed until cages were removed. Treatments were initiated in spring 2000.

**Beetle Damage.** Four densities of rose chafer or Japanese beetles were maintained inside caged vines during bloom or veraison respectively. Four vines in a row of seven vines were selected with a cane size between 0.5 m and 1 m. Selected vines within a row had 0,

10, 20, or 40 beetles caged onto them for two weeks during bloom or veraison, arranged as two randomized complete block designs (one for bloom and one for veraison) with ten replicates each. During bloom, vines were infested using adult rose chafers collected from traps (Great Lakes IPM, Vestaburg, Michigan) in Oceana County, Michigan. During veraison, Japanese beetles were collected from traps (Trécé Inc., Salinas, California) in Allegan County, Michigan. For both beetles, traps were emptied the day before beetles were collected, so that recently caught beetles were used. To ensure beetle densities remained constant in cages, beetles were counted every other day and any dead beetles replaced with live ones. Cages consisted of a highly porous bridal illusion plastic mesh (Fabric Gallery, Williamston, Michigan) draped over the trellis and suspended from a 0.3 m radius wire ring taped onto the trellis. Mesh was fastened to the base of the vine with garden wire and the side of the cage was sealed with binder clips. This created a cone-shaped cage that encased all of the above-ground vine tissues, and allowed for plant growth and beetle movement.

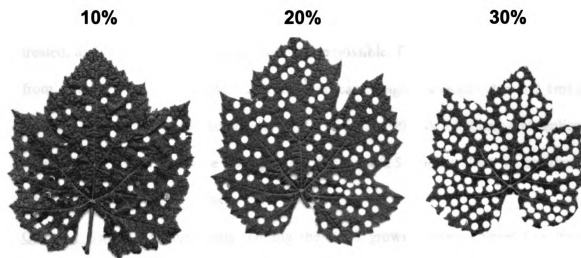
Growing Season Measurements. Adult rose chafers were placed on vines on 20 June, 2000 and removed on 4 July, 2000. The level of defoliation was determined using visual aids adapted from Boucher & Pfeiffer (1989). Cane and trunk diameters were measured using Vernier calipers at bloom (19 June), veraison (30 August), and leaf senescence (29 October), and prior to bloom the following season (9 May, 2001). The number of mature nodes was determined after leaf loss (11 November).

Adult Japanese beetles were placed on separate vines on 3 August, 2000 and removed 17 August, 2000, and the level of defoliation determined. On these vines, cane diameters were measured just prior to veraison (26 July) and at leaf senescence (29

October). The number of mature nodes was determined after leaf loss (11 November).

Post-Growing Season Measurements. Vines damaged by beetles in 2000 were pruned to 15 nodes per cane (30 total) between 26 January and 6 February 2001. For each vine, the weight of mature cane prunings (pruning weights) was determined by bundling and weighing them with a digital scale in the field. To determine the possible impacts of beetle feeding on vine storage, growth parameters were measured prior to bloom the season after caging. We recorded the diameters of canes and trunks (9 and 14 May, 2001, respectively), and the number of nodes remaining dormant after the 16-inch shoot growth stage had been reached (22 May, 2001).

**Mechanical Damage Treatments.** To determine the effect of leaf area loss during bloom and veraison on vine development, vines were subjected to mechanical damage during each of these phenophases. Either 0, 10, 20, or 30% of the total leaf area was removed from every fully expanded leaf during bloom or veraison (Figure 4.1). Leaf area was removed using hole punchers, avoiding all major veins in order to imitate beetle feeding and to avoid the differential impacts on photosynthetic capacity caused by interveinal damage when compared to whole leaf removal or treatments including midrib and main lateral vein damage (Hall and Ferree 1976, Boucher et al. 1987). To ensure appropriate damage levels were applied, visual aids were made for use while damaging leaves.



**Figure 4.1.** Leaves of 'Niagara' grapevines after using a hole-puncher to apply mechanical damage treatments of either 10, 20, or 30% interveinal leaf area removal.

For vine defoliation applications during bloom, thirty-two vines with cane height between 0.5 m and 1 m were separated into two blocks of 16 plants each. Within each block, selected vines were randomly assigned to one of the four damage levels, creating eight replicates of each treatment. These vines were damaged at bloom to the appropriate level between the 15 and 23 June 2000.

Larger canopy size during veraison restricted the number of vines that could be treated, and therefore only four replicates were possible. For these treatments four vines from a row of seven were selected (vines with cane height between 0.5m and 1m) and assigned to one of the four damage levels (0, 10, 20, or 30% defoliation), and replicated four times. These vines were damaged on the 14 and 15 August, 2000 in an identical fashion to bloom damaged vines.

Growing Season Measurements. During the 2000 growing season vegetative growth parameters were measured at trace bloom (13-14 June), at veraison (6 -11 August), and at leaf senescence (21 October) on vines damaged at bloom and veraison. On each vine, the node number of every shoot and cane diameters were measured. In addition, the number of mature nodes and the total shoot length were measured after leaf loss (10-11 November).

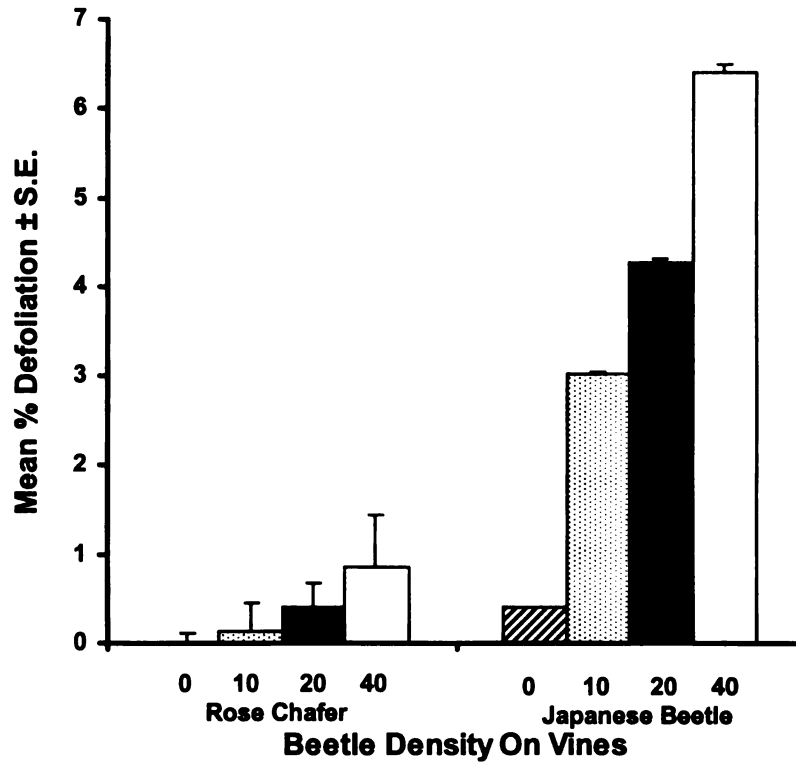
Post-Growing Season Measurements. On 16 and 26 January, 2001, all vines were pruned to 15 nodes per shoot and the pruning weights recorded as above. Prior to bloom the following season (2001) the diameter of canes and trunks (9 May) and the number of nodes remaining dormant after the 16 inch shoot growth stage had been reached (22 May) were recorded on all vines.

**Statistical Analysis.** Data were analyzed by one way ANOVA using cane diameters measured prior to applying treatments as covariates and blocking where appropriate (PROC GLM, SAS Institute, 1999). Cane diameters were used as covariates in order to reduce variance introduced by differences in vine size. Means separation was performed where appropriate using the Student Newman-Keuls method.

## **Results**

**Beetle Damage.** Defoliation by the rose chafer was minimal even at the highest beetle density, with less than one percent of the leaf area removed. Defoliation by the Japanese beetle was much greater, approaching 7% at the highest beetle density (Figure 4.2). This difference in defoliation intensity was even greater when the relative canopy size present during veraison is considered (approximately 2-3 times larger during veraison than during bloom). However, even at the highest beetle density, neither beetle species had any significant effect upon any of the growth parameters measured. The diameter of canes on rose chafer damaged vines was not significantly affected by beetle foliar damage, when measurements were taken at the end of veraison or at leaf senescence ( $F_{3,26}=0.75$ ,  $P=0.53$ , and  $F_{3,26}=0.52$ ,  $P=0.67$ , respectively). In addition, there was no significant effect of foliar herbivory on above-ground growth in the year of damage, whether measured as the number of mature nodes after leaf loss ( $F_{3,26}=0.31$ ,  $P=0.82$ ) or pruning weights ( $F_{3,26}=1.09$ ,  $P=0.37$ ). Growth parameters taken prior to bloom the following season (2001) also indicated no impact of rose chafer damage; cane diameters and number of shootless nodes were not impacted by the treatments imposed ( $F_{3,26}=0.64$ ,

$P=0.60$  and  $F_{3,26}=0.42$ ,  $P=0.74$  respectively).

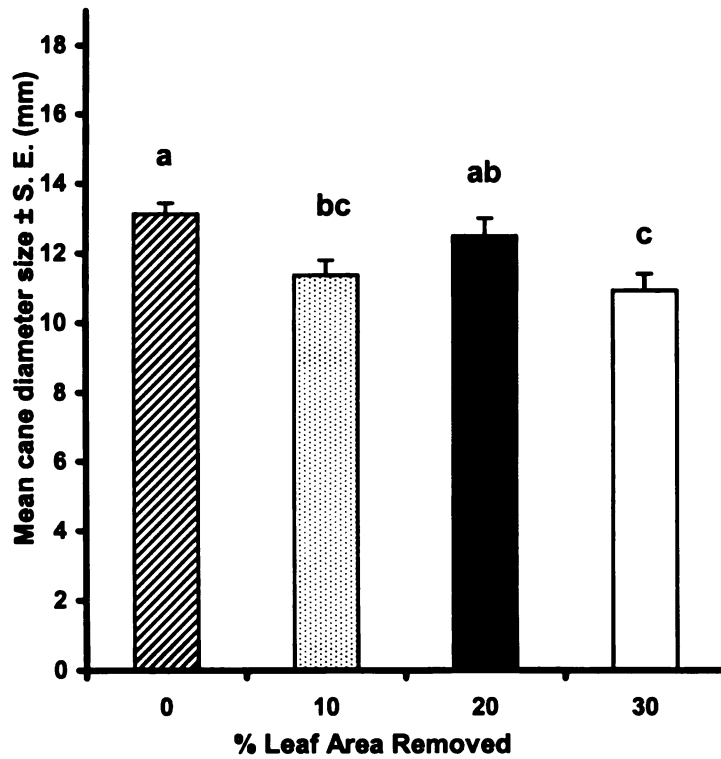


**Figure 4.2.** Percent defoliation of total vine canopy area caused by two weeks of different densities of adult rose chafer and Japanese beetle.

On vines subjected to Japanese beetle feeding, a similar result was found; cane diameters measured at leaf senescence ( $F_{3,26}=1.06$ ,  $P=0.38$ ), mature node numbers measured at leaf loss ( $F_{3,26}=1.26$ ,  $P=0.31$ ), and pruning weights ( $F_{3,26}=0.55$ ,  $P=0.65$ ) were not affected by Japanese beetle damage. Growth parameters taken prior to bloom the following season (2001) also indicated no impact of Japanese beetle damage; cane diameters and number of shootless nodes for Japanese beetle damaged vines were not

impacted by the treatments imposed ( $F_{3, 26}=0.81$ ,  $P = 0.50$  and  $F_{3, 26}=0.87$ ,  $P=0.85$  respectively).

**Mechanical Damage.** Mechanical damage during bloom did not affect vegetative growth of the vines measured as the number of nodes at veraison ( $F_{3,25}=1.12$ ,  $P=0.67$ ). However, a reduction in cane diameter ( $F_{3,25}=5.3$ ,  $P=0.006$ ) was observed on bloom damaged plants, when measured at veraison (Figure 4.3). Although the 20 % leaf area removal treatment was not significantly different from the control, the overall pattern indicates that early season foliar damage induced a source limitation, reducing the amount of resources allocated to cane growth. When these vines were measured at leaf senescence, there were no significant differences between treatments in the number of nodes ( $F_{3,25}=0.21$ ,  $P=0.89$ ) or cane diameters ( $F_{3,25}=2.22$ ,  $P=0.11$ ). In addition, total shoot length ( $F_{3,25}=0.39$ ,  $P=0.76$ ) and mature node number at leaf loss ( $F_{3,25}=0.86$ ,  $P=0.48$ ) was not impacted by early season defoliation. The total weight of new shoots produced, measured as pruning weights, was not affected by defoliation at bloom ( $F_{3,25}=1.19$ ,  $P=0.33$ ). Finally, the diameter of canes ( $F_{3,25}=1.39$ ,  $P=0.27$ ) and number of shootless nodes ( $F_{3,25}=1.33$ ,  $P=0.29$ ) recorded the following season (2001) were not impacted by bloom damage treatments ( $F_{3, 25}=0.71$ ,  $P=0.56$ ).



**Figure 4.3.** Cane diameter of vines damaged at bloom to different levels of defoliation, measured at veraison. Means separation by Student Newman Keuls method. Treatments with different letters are significantly different at  $P < 0.05$ .

Mechanical damage during veraison had no significant effect upon any of the vine growth parameters measured after leaf senescence. Cane diameters ( $F_{3,8}=0.73$ ,  $P=0.56$ ), number of nodes ( $F_{3,8}=0.97$ ,  $P=0.45$ ), shoot length ( $F_{3,8}=1.49$ ,  $P=0.29$ ), and mature node numbers ( $F_{3,8}=0.97$ ,  $P=0.45$ ) were not significantly different between the different damage levels. In addition, pruning weights were not significantly impacted by the defoliation treatments during veraison ( $F_{3,8}=0.24$ ,  $P=0.86$ ). Growth measurements taken early the following season also indicated no significant impacts of damage at veraison on subsequent vine growth (cane diameters  $F_{3,8}=0.5$ ,  $P=0.69$  and shootless nodes  $F_{3,8}=0.97$ ,  $P=0.45$ ).

### **Discussion**

This study demonstrated that two of the primary scarab beetle pests of vineyards in eastern North America remove a very small proportion of the leaf area on *V. labrusca* vines. This small level of herbivory caused no significant impact on the above ground vegetative growth of young vines, even when 40 beetles were allowed to feed for two weeks. In addition, mechanical removal of leaf area at levels much higher than seen in our caging study showed that vines were negatively impacted by damage early in the season, but no significant impacts were found in above-ground tissues by the season's end and at the beginning of the following season.

Vine growth between bloom and veraison resulted in approximately two to three times the leaf area being present at veraison, compared to that at bloom. Due to mechanical damage treatments being applied on a percentage basis, the total amount of

leaf area removed during veraison far exceeded that removed during bloom. Despite the greater leaf area removed during veraison, no impact of this damage was observed in above ground tissues. The relative ratio of carbon source to sink during bloom and veraison provides a framework for understanding this result. Early in the season a relatively small number of leaves are present, and most carbohydrates used for shoot growth are derived from storage tissues. Indeed, until the 6-leaf stage, shoot development is dependent upon re-translocation from storage tissues, and not until bloom is the vine able to rely upon assimilates produced during the current year (Yang et al. 1980a). At bloom and prior to bloom there is also a relatively high activity of growth in all vegetative tissues (van Zyl 1984, Williams 1987). In contrast, during veraison a full canopy is present and vegetative sinks have been shown to be relatively inactive in irrigated *V. vinifera* vines (van Zyl 1984, Williams 1987). In non-irrigated *V. labrusca* vines grown under rainy conditions root activity is considered to remain active (G. S. Howell, personal communication), making roots a potentially strong sink during veraison. However, increased root activity is unlikely to cause a source limitation at this period, as potted vine studies (Miller et al. 1996b, Petrie et al. 2000a) have indicated sink limitations at veraison in uncropped vines when compared to cropped vines.

Mechanical damage at bloom had a significant impact on storage tissues, measured as cane diameters, but no impact upon shoot growth, measured as node number, when measured at veraison. This preferential allocation to growth over storage is in accordance with studies on sink hierarchy (Wardlaw 1990), indicating that defoliation during bloom in young vines can induce a source limitation. However, no impact upon above ground storage tissues was detected by the time of leaf loss in the study reported

here, and vegetative growth parameters measured the following season did not differ between damage treatments. These findings indicate that young *V. labrusca* vines were able to compensate for high levels of defoliation during bloom by the end of the season, despite the initial source limitation experienced after damage was applied at bloom. However, results from a study performed in the same vineyard in the same year using similar damage treatments did indicate a significant reduction in growth parameters measured the following year (see Chapter 3). The main difference between the two studies lies in the experimental design; the study reported in chapter 3 used a factorial design comparing damage during bloom and veraison with only one level of damage. The design of that study may have added more power to the statistical test. These contrasting results indicate the limitation of using cane diameter as an estimate of impacts on storage. Root growth has been shown to be the lowest sink priority and impacts on storage tissues would most likely be detected here.

Whether foliar herbivory leads to changes in allocation to below-ground tissues was not studied here, and is experimentally challenging in vineyard studies. However, given the low level of defoliation caused from these scarab beetles and the lack of significant impacts on aboveground vegetative growth during the year following damage, the potential for high levels of tolerance is likely. This is may be particularly true during veraison when the source to sink ratio is particularly high. During bloom the higher sink activity is a potential source of concern, but the low level of defoliation caused by the rose chafer (Figure 4.2) leads one to believe that unless exceptionally high numbers of beetles are present the impact on the vine should be minimal.

The lack of effect of mechanical damage during veraison on cane diameter or

shoot growth indicates that at this point of the season, when sink demands are low in non-fruiting vines, the creation of a source limitation is extremely difficult. Although replication was low due to vine canopy size, the highest damage treatments were extreme (Figure 3.1). Despite the severe intensity of damage applied during this period, vines with 30% leaf area removed were able to produce enough photosynthate to mature the same number of nodes as the undamaged vines. Furthermore, no impacts on initial growth parameters were observed the following season, suggesting a high level of tolerance.

We propose that mechanical damage during veraison did not affect vine growth because non-bearing vines have relatively few sinks and a full vegetative canopy, making them sink-limited. Other authors working on grapevines have found similar results. For example, using potted vines with and without fruit, Petrie et al. (2000) found that despite a higher leaf area in non-bearing vines compared to bearing vines, no significant differences in total dry weight were found. Furthermore, Layne & Flore (1995) have demonstrated the impact of end-product inhibition in sour cherry, *Prunus cerasus* (L.), as a mechanism for sink limitations at a whole plant level. These studies illustrate the importance of source to sink ratios in understanding a plant's ability to assimilate carbon, and therefore their ability to respond to leaf area loss.

In light of the high levels of mechanical defoliation and the lack of significant differences in above ground growth by the end of the season, it is not surprising that the level of herbivory caused by beetles did not impact their growth. This study illustrates the low level of defoliation that *M. subspinosus* and *P. japonica* are capable of causing on *V. labrusca* var. 'Niagara' vines. Based on these findings we expect defoliation in establishing 'Niagara' vineyards with less than 40 beetles per vine to be below levels

likely to affect vine establishment, particularly after the initial vegetative growth has taken place.

Due to the large canopies present at veraison, the proportion of leaf area damaged by Japanese beetle in established *V. labrusca* vineyards ought to be minimal, but further studies are required to test this prediction. Boucher & Pfeiffer (1989) found no effect of natural infestations of Japanese beetle (6.5% defoliation) on fruit quality and quantity or vine growth in *V. vinifera* 'Seyval blanc' vines, even though these vines had fruit as an active sink for carbon. Due to the relatively small level of defoliation by 40 adult Japanese beetle in our study (6.4% mean defoliation, and mean leaf number at veraison =187), we expect lower defoliation levels in established *V. labrusca* vineyards than were found by Boucher & Pfeiffer (1989) on *V. vinifera*. However, viticulture in cool climates such as Michigan requires consideration of climatic conditions that are near the limits of commercial grape production (Howell 2001). Shorter growing seasons reduce the post-harvest carbon assimilation period, limiting the available time to recover and sequester enough carbohydrates to tolerate cold temperatures. Cropping level is expected to be an important factor that will impact tolerance to grapevine foliar herbivory. Further studies should include various cropping levels in order to develop economic injury thresholds for these or any other foliar pests on fruiting grapevines.

While the impact of foliar herbivory by rose chafers has been shown here to be negligible, future studies should concentrate on their impacts upon flower clusters. This insect is still likely to be a potential source of concern in fruiting vineyards due to feeding on flower clusters during bloom (Chittenden 1916, R.J. Mercader unpublished data).

It is apparent from these studies that young *V. labrusca* vines have a significant

ability to tolerate foliar damage, in particular after the initial vegetative growth has occurred. This tolerance was seen in above ground growth at levels of leaf area loss far beyond the defoliation potential of 40 rose chafers or Japanese beetles per vine. This indicates that even under intense infestations of these two pests, the damage caused may not warrant chemical control unless other forms of stress such as disease or drought have critically stressed the vines. Sustainable grape production, as defined by Howell (2001), refers to maintaining the highest yields of ripe fruit per unit area without reducing vegetative growth and doing so over a period of years at costs which return a net profit. Within this framework, it is important to consider the unique characteristics of the initial years of vineyard establishment in which no crop is produced, and vines therefore have fewer carbohydrate sinks.

## CHAPTER 5

### Conclusion

This study has yielded three primary results 1) agreement with the notion that source to sink ratios at the time of damage are a major factor in grape vines ability to tolerate damage, 2) vine photosynthetic response to damage is dependent upon the timing of damage and the type of damage, and 3) two of the primary foliar herbivores in Eastern U.S. vineyards consume relatively small amounts of foliage compared to the size of the vine canopy.

In young *Vitis labrusca* (L.) vines, foliar damage early in the season presents a greater risk to young vines than damage late in the season. The application of mechanical damage treatments on a percentage basis removed intensity of damage and whole season sink size as factors explaining the increased tolerance to damage at veraison when the source to sink ratio was highest. Despite the apparent compensation to damage at bloom, there was a significant impact of bloom damage on photosynthetic rate late in the season. This effect appeared to be due to an early senescence in bloom damaged vines, a further indication that stress induced by defoliation can have similar impacts as stress induced by high crop loads (Edson et al. 1993).

The work presented in Chapter 2 illustrates the importance of timing of damage and plant physiology on the adequacy of mechanical simulations of herbivory. The differences in carbon assimilation found between Japanese beetle and mechanical damage at veraison illustrated that the physiological stage of the plant needs to be taken into account when considering the accuracy of simulations of herbivore damage. This

research stresses the importance of studying herbivory within the physiological context of the plant.

Finally, these studies also indicated that young *V. labrusca* vines have a significant ability to compensate for foliar damage, in particular after the initial vegetative growth has occurred. Compensation in above ground growth was seen at levels of leaf area loss far beyond the defoliation potential of forty rose chafers or Japanese beetles per vine. This indicates that even under high infestations of these two pests, the damage caused may not warrant chemical control in *V. labrusca* vineyards unless other forms of stress such as disease or drought have compromised the vines ability to tolerate defoliation.

## **APPENDIX I**

## Appendix 1

### Record of Deposition of Voucher Specimens\*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2002-04

Title of thesis or dissertation (or other research projects):

Phenophase dependent tolerance to foliar herbivory in grape vines, *Vitis labrusca* (L.) var. 'Niagara'

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name(s) (typed)

Rodrigo J. Mercader

\_\_\_\_\_  
\_\_\_\_\_

Date 16/08/2002

\*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.  
Museum(s) files.  
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

# Appendix 1.1

## Voucher Specimen Data

Page 1 of 1 Pages

| Species or other taxon                     | Label data for specimens collected or used and deposited | Number of: |        |        |       |        |        |       |                        |
|--------------------------------------------|----------------------------------------------------------|------------|--------|--------|-------|--------|--------|-------|------------------------|
|                                            |                                                          | Eggs       | Larvae | Nymphs | Pupae | Adults | Adults | Other | Museum where deposited |
| <i>Macroductylus subspinosus</i> Fabricius | MI, Oceana Co., Shelby June 2001                         |            |        |        |       | 10     | 10     |       | MSU                    |
| <i>Popillia japonica</i> Newman            | MI, Allegan Co., Fennville August 2001                   |            |        |        |       | 10     | 10     |       | MSU                    |

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Rodrigo J. Mercader

Date Aug. 16 2002

Voucher No. 2002-04

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

*[Signature]* Date 20 Aug 2002  
Curator

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