JAPANESE BEETLE *POPILLIA JAPONICA* NEWMAN: FOLIAR FEEDING ON WINE GRAPES IN VIRGINIA

by

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(ABSTRACT)

The natural infestation level for 1985 of the Japanese beetle, *Popillia japonica* Newman, in the Shenandoah Valley of Virginia failed to reduce berry quality, yield or shoot growth in a commercial vineyard. Intensive postvéraison foliage feeding by Japanese beetle resulted in fruit with lower soluble solids and higher total titratable acidity at harvest, but did not affect pH, sugar per berry, berry weight, yield, leaves per vine or shoot length. Intensive prevéraison feeding also resulted in fruit with higher total titratable acidity. All other parameters were unaffected.

In a separate experiment with 0, 10, 20, and 33% leaf removal, no relationship was shown between leaf area loss and soluble solids, total titratable acidity or pH. Data from one season of damage by the beetle indicate that control measures may not be warranted in some years.

In a third experiment, grape leaves on potted vines were

artificially damaged by removing leaf disks with a paper punch. The leaves showed an increased loss of efficiency (measured in net photosynthesis, P_n) for the remaining tissue as leaf area loss (LAL) increased. This loss of efficiency in the remaining leaf area at low levels of damage was more pronounced after 12 days than after either 1 or 5 days. The additive effect on P_n of both LAL and lowered efficiency predicted the total shutdown of Pn at 60% damage at 1 and 5 days after treatment, but not at 12 days.

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INTRODUCTION

Evolution of the Industry

Grape is commercially the most important fruit grown. It comprises approximately 43% of the world's total fruit crop and accounts for the largest proportion of fruit in the human diet (Amerine and Singleton 1977). There are over 25 million acres of grapes grown worldwide. Ninety percent of these grapes are varieties of a single species, *Vitis vinifera* L., prized throughout the ages for its superior qualities in wine production. Other varieties used in wine production stem from crosses of various American species (e.g. *Vitis labrusca* L. 'Concord') or crosses between *Vitis vinifera* and American species termed either French hybrids or French-American hybrids (Weaver 1976).

The U.S. currently ranks sixth in wine production behind France, Italy, Spain, the U.S.S.R. and Argentina (Weaver 1976). California vineyards account for 88% of the grape production in this country, which is worth more than one billion dollars in annual cash receipts. Most of the remaining acreage in the U.S. is in New York, Ohio, Michigan, Pennsylvania and Washington.

Attempts to establish a viable grape industry in Virginia date back to the settlement of Jamestown. Early viticulturists did not have the benefit of grafted rootstocks to prevent root damage to the vines by grape phylloxera [*Daktulosphaira vitifoliae* (Fitch)] or the advantages provided by modern fungicides in Virginia's humid climate. However, many of the benefits of modern pesticides can be negated if they are used inappropriately (Stern 1973).

In recent years both Virginia and out-of-state investors have shown an interest in the Virginia grape and wine industry. In 1973 there were only 24 hectares of commercial vineyards in Virginia. By 1982 the industry had grown to 306 hectares of grapes and by 1985 expanded to 575 hectares and 30 farm wineries (Phillips 1985)

Severity of the Japanese Beetle Problem

Grape is a preferred host of adult Japanese beetles (*Popillia japonica* Newman) (Langford and Cory 1948, Fleming 1972a), which have a broad host range including more than 300 species of plants in eastern North America. The adult beetle is an indirect grape pest (i.e. feeding on non-harvested parts of the plant); Japanese beetle feeds almost exclusively on the foliage of the plant unless the berries have been previously damaged (Fleming 1972a, Pfeiffer and Schultz 1986). Many Virginia vineyards fit the description given by Regniere et al. (1983) of an "intensive production site" for the Japanese beetle, possessing preferred adult food and being adjacent to pastures which support high larval densities. McGiffen and Neunzig (1985) found that in North Carolina the Japanese beetle was more numerous and produced more severe damage in vineyards closer to Virginia than in vineyards farther south.

Growers at the 10th Annual Grape Growers Short Course (17 March 1984) in Charlottesville, Virginia indicated that the Japanese beetle was the most consistent insect pest on grape in Virginia. They reported that in years of high adult population densities, insecticide applications were administered at 7-14 day intervals from June until harvest in early September.

Despite a vast amount of data compiled about the beetle since its introduction in 1916, there seems to be no information available that quantifies economic losses due to beetle infestations. Therefore, commercial spray schedules have traditionally recommended treating infested vines with carbaryl at 3.6 kg AI per hectare from the time beetles first become a problem until harvest (Pfeiffer et al. 1985, Steiner et al. 1985)

Cost of control

At 1983 prices (carbaryl $22.74/hectare, labor $4.94/hectare, tractor and sprayer $6.62/hectare), each grower spends approximately $34.30/hectare to administer an application of carbaryl (Vaden and Phillips 1983, O'Dell 1983). Depending on weather conditions, from 3-7 fungicide applications are usually necessary during the adult beetle season, which effectively eliminate labor and machinery costs for many Japanese beetle sprays. However, if Virginia's 1985 vineyard acreage (575 hectares) were treated every two weeks of the adult Japanese beetle season (six applications), the annual cost for insecticide alone would exceed $78,000.

Along with immediate expenses, there may be additional costs associated with the use of carbaryl for Japanese beetle control. Pfeiffer et al. (1983) found that populations of European red mite [*Panonychus ulmi* (Koch)] increased on peach when applications of carbaryl were used to control the Japanese beetle. A variety of mite predators [e.g. *Leptothrips mali* (Fitch), *Stethorus punctum* LeConte, and *Amblyseius fallacis* Garman] help control mite populations in eastern vineyards. Excessive insecticide applications may cause *P. ulmi* and other spider mites to escape from natural biological control agents and so attain pest status in Virginia vineyards, as they have in Pennsylvania and California vineyards (Stern 1973, Jubb 1974, Jubb et al. 1981, Flaherty et al. 1982).

Other biological control systems could also be disrupted by excessive pesticide use in the vineyards. The wasp *Anagrus epos* Girault, parasitizes eggs of grape leafhoppers (*Erythroneura* spp.) and can provide substantial control (Doutt and Nakata 1973). This parasite also attacks eggs of white apple leafhopper (*Typhlocyba pomaria* McAtee) (Mulla 1956), a pest in Virginia apple orchards.

Carbaryl is recommended for Japanese beetle control because of its low mammalian toxicity, rapid kill of the insect and low cost when compared to other insecticides. Lawrence et al. (1973) tested 25 chemicals for beetle toxicity and failed to find any as effective as carbaryl. Unfortunately, this chemical has a short residual period (7-14 days) necessitating repeated applications (Fleming 1976).

Development of resistance is hastened by repeated exposure to a single insecticide (Croft and Hoyt 1978). The Japanese beetle has already demonstrated its ability to develop resistance to several insecticides including endosulfan, which is registered for use on grape (Tashiro et al. 1975). The cost of registering new chemicals and the lack of a suitable substitute for carbaryl (Fleming 1976) make it desirable to prolong the effectiveness of currently labelled products by reducing frequency of application.

Grape tolerance to damage

The grape is a vigorously growing vine that can tolerate more foliar damage than is allowed under present spray programs. Jubb et al. (1983) showed that 'Concord' grapevines can withstand much higher levels of foliar feeding than was previously believed economical. Studies where parts of shoots or whole leaves were removed have shown that grapevines can withstand substantial leaf or shoot removal before manifesting a drop in berry quantity or quality (Kliewer and Antcliff 1970, Peterson and Smart 1975, Jensen et al. 1976).

A critical problem that Virginia's grape producers face today is competition from out-of-state regions where grape production may be less costly (Phillips unpublished data 1985, Winkler et al. 1974). The success of Virginia's expanding grape industry depends on the use of efficient management practices (e.g. an integrated pest management program) to help reduce production costs (Phillips 1984). Elimination of excessive insecticide treatments aimed at the Japanese beetle would save growers money (Jubb et al. 1978).

Goals and Objectives

The development of economic injury levels (that population level where cost of damage justifies cost of control) and action thresholds (that population level at which control measures should be taken to prevent the pest from reaching the economic injury level) are basic requirements which must be developed before an IPM program can be initiated. Before these goals can be realized, preliminary investigations quantifying the effects of Japanese beetle damage to grape are essential.

Our objectives in this study were to: (1) quantify the effects of Japanese beetle damage on fruit quality and yield at various times during berry maturation, (2) develop a rapid means of assessing Japanese beetle damage, (3)examine the effects of various levels of defoliation on fruit quality, (4) quantify the effects of various levels of simulated feeding injury on the photosynthetic activity of a damaged leaf and evaluate its effect on the remaining tissue of the leaf, and (5) provide suggestions for future investigations involving alternative management strategies.

LITERATURE REVIEW

History and Life Cycle

The Japanese beetle was introduced from Japan into New Jersey around 1912 and was first identified in 1916 (Dickerson and Weiss 1918, Fleming 1972a). Due to favorable climatic conditions, a lack of natural enemies, and the beetle's ability to sustain flight for as far as 8 km, many attempts to eradicate or contain the spread of the Japanese beetle in the first five years after its introduction failed. The beetle soon spread to all surrounding states.

Popillia japonica was first found in Virginia in 1928, and by 1952 had been reported in almost every county. It is thought that the semi-arid climate west of the 100th meridian will stop the spread of the beetle westward, except possibly to the irrigated farmland in the Great Basin and central California (Fleming 1972b).

The Japanese beetle will adapt to areas where the summer mean soil temperature is between 17.5 ^{o}C and 27.5 ^{o}C and the winter soil temperature is consistently above -9.4 ^{o}C. A minimum of 25 cm of precipitation during June, July and August is necessary for egg hatch and larval development. Japanese beetle eggs, like other scarab eggs, cannot retain moisture and thus rely on a constant supply from the surrounding soil. In summers with less than 25 cm of rainfall, a high egg mortality occurs. The beetle is therefore more adapted to areas with uniform precipitation throughout the year (Fleming 1972b, 1976).

Popillia japonica has one generation per year. The average life span of the adult beetle is 30-45 days, and the larva generally completes development in one year except in extreme northern parts of its range, where two years may be required for a small fraction of the population. Mating and oviposition occur in mid-summer. Fleming (1972b) listed pastures as the most frequent oviposition sites for *P. japonica*, although egg deposition is also heavy in the vicinity of preferred adult foods (Regniere et al. 1983).

The larvae feed on roots of grass and weeds in the top 10 cm of the soil in late summer then migrate to a depth of 10-20 cm where they enter diapause to pass the winter months. The larvae return to within 10 cm of the surface in the spring to continue feeding and to pupate.

In central Virginia, where the majority of the state's commercial vineyards are located (Phillips unpublished data), the adults first emerge during late June and peak during August (French et al. 1949, Fleming 1963, Pfeiffer and Schultz 1986). Adult beetle populations then decline steadily until mid-September.

The Japanese beetle forms aggregations on grapevines and other hosts while feeding. Iwabuchi and Takahashi (1983) found that a beetle of either sex would attract males to form clusters of beetles on the vines. Ladd (1970) showed the existence of a sex pheromone which causes males to aggregate around females on the ground. Apparently, different factors are involved in causing the aggregation on the plants.

The rate of feeding is affected by environmental conditions and sex of beetles. The Japanese beetle tends to feed in direct sunlight beginning at the top of a plant when temperatures range from 29-35 °C and the relative humidity is above 60% (Fleming 1972b). When the relative humidity falls below 60%, it induces a flight response in the beetle. Although female beetles spend less time on the host plant than males do, they feed more often in a given time period. Fleming (1972b) showed that in a six-hour period, females spent approximately twice the time feeding on grape or apple foliage as did males.

Feeding is also affected by host preference and morphological characteristics within a plant species. The host range of the Japanese beetle includes almost 300 species of plants, but many of these species are rarely or only slightly damaged by feeding even in years of high population density. There may also be considerable variation between cultivars of a species in degree of resistance to damage (Langford and Cory 1948, Stevenson 1970). Langford and Cory (1948) categorized many varieties of wine grape depending on the degree of damage incurred by beetle feeding. Unfortunately, many popular varieties of *Vitis vinifera*, French hybrids and American hybrids were listed as preferred hosts and are subject to severe injury or complete defoliation.

Japanese Beetle Control

The most successful limitation on the population growth of the beetle, at least at high densities, has been a soil-borne bacterial disease (Milky disease) caused by *Bacillus popilliae* Dutky (Dutky 1940, Fleming 1976, Dunbar and Beard 1975). The bacteria was first produced commercially in the 1930's and was used to inoculate 132,000 sites in 14 eastern states to accelerate the spread of the pathogen (Fleming 1976). It then became established throughout most of the area and spread through natural dispersion (Dutky 1940, Fleming 1972a and 1976, Hutton and Burbutis 1973, Dunbar and Beard 1975).

Initially, *B. popilliae* produced high larval mortality and substantially reduced the beetle population. However, studies in areas where the beetle population has made a recent resurgence have revealed that the bacteria has lost much of its virilence.

Other attempts to contain or limit dense populations of the beetles include: large-scale insecticide applications, collection of the beetles by hand, colonization and release of insect parasites, liming of the soil, mass trapping, crop rotation, releasing sterile males and quarantines (Langford and Cory 1940, Fleming 1976). At best, these practices resulted in a temporary delay in the spread of the beetle or a temporary suppression of the population density (Fleming 1972a, 1976).

Recent attempts to limit crop destruction on a local level using pheromone or feeding attractant beetle traps is impractical (Fleming 1976). Gordon and Potter (1985) found that grapevines adjacent to beetle traps usually experience greater defoliation than vines with no traps present. Timely and thorough insecticide applications were recommended by Fleming (1976) to protect crops and ornamentals from Japanese beetle damage.

Grape Berry and Vine Growth

The CO_2 fixed by the chloroplasts in a plant's foliage during photosynthesis is used to produce carbohydrates, and thus has a substantial effect on the quantity and quality of the fruit. Leaves have a finite capacity to absorb and utilize CO_2. The amount of leaf surface area of a plant directly affects the amount of CO_2 fixed, and thus determines the potential carbohydrate production under a given set of environmental conditions. Trellis systems which expose greater leaf surface area to higher levels of light (e.g. Geneva double curtain) can produce greater yield and fruit with higher sugar levels because of increased CO_2 fixation (Shaulis et al. 1966, Cawthon and Morris 1977).

These carbohydrates (photosynthates) are the building blocks of plants and are channeled to whichever part of the plant has the highest requirement (e.g. shoot and root growth, leaf expansion or fruit production). Leaves where the carbohydrates are produced are regarded as the "sources" of photosynthates, while actively-growing portions or parts to which carbohydrates move are known as "sinks" (Kliewer 1982).

Hale and Weaver (1962) exposed leaves on different areas of the shoots and at different times during the season to radio-labeled (C^{14}) CO_2 to determine photosynthate movement to sinks. They found that leaves did not begin to export photosynthates until 50% of their full size was reached. Before véraison (the point at which berries begin to color, soften, accumulate sugars rapidly, and lose acids) newly-expanded leaves near the shoot tip would export photosynthates to the shoot tip. Leaves four to five nodes from the shoot tip would export photosynthates to the clusters and the trunk and roots. Leaves below the clusters translocated carbohydrates almost exclusively to the trunk and roots.

After véraison, shoot expansion slows and all leaves apical to the fruit clusters translocate photosynthates mainly to the fruit. Leaves basal to the clusters translocate ^{14}C both to the fruit and towards the plant trunk after veraison. Hale and Weaver (1962) also found that fruit clusters could draw photosynthates from any shoot on the vine at this time, and that totally defoliated shoots were stronger sinks than shoots with leaves. Kriedemann et al. (1970) showed that both carbon assimilation and net photosynthesis (mg CO_2 hr^{-2} dm^{-1}) of a leaf peaked approximately 40 days after a new leaf unfolded and declined slowly thereafter due to senescence.

Harris et al. (1968) found that berry growth (whether measured by volume, dry weight, fresh weight or by a length times breadth ratio) consisted of two phases: (Phase one) before véraison, and (Phase two) after véraison. A lag phase in the growth pattern was observed at veraison. In growth Phase one both cell division and cell enlargement occurred, while during the second growth phase only cell enlargement occurred.

Hrazdina et al. (1984) determined that fruit undergo a rapid rise in sugar, pH, K^+, and anthocyanins starting at véraison. Tartaric acid declined throughout berry development, while malic acid and the total acid concentration increased early in berry development and decreased rapidly thereafter. Most divalent cations (Ca^{++}, Cu^{++}, Mg^{++} and Mn^{++}) decline rapidly during berry expansion before stabilizing at low levels around harvest. Metabolic processes associated with berry maturity continue to advance until eight weeks after véraison and then almost level off under New York conditions.

Sugar is transported through the phloem of the vine in the form of sucrose. Sucrose is converted in the fruit to glucose and fructose by the enzyme invertase (Hawker 1969). These two sugars comprise more than 99% of the total sugar in the berry which usually ranges between 12-27% of the berry's total weight. The concentration of the sugar in the juice of the grape is normally measured in °Brix (percent soluble solids) (Winkler et al. 1974).

Boulton (1980b) stated that "pH is perhaps the most important measure of juice and wine acidity. It has a controlling influence on the incidence of the malo-lactic fermentation ... and on the susceptibility to microbial contamination ... It plays an important role in the sourness of taste, in the stability of soluble grape proteins ..., in the extent of potassium bitartrate precipitation ... and in color stability of red table wines

... The titratable acidity, while of some importance in sourness of taste, plays no role in any kind of wine stability and is a poor indicator of organic acid content."

Total titratable acidity (TTA) represents only about 74% of the total acidity in the wine or juice (Boulton 1980a). TTA is still widely used by growers as a harvest parameter (Winkler et al. 1974). The major constituents measured as TTA in juice include tartaric, malic and, to a lesser extent, citric acid. Tartaric acid is a stronger acid and is not lost as rapidly at high temperatures as is malic acid. Therefore, at any quantity of TTA, the pH can change due to a change in the ratio of tartaric to malic acid (Winkler 1974). Potassium and sodium acid salts are not accounted for by titration. However, K$^+$ and Na$^+$ ions do produce a higher pH (Boulton 1980b, 1980c). It is therefore possible that the pH can rise or remain the same as monovalent cations increase in concentration, while the TTA drops due to acid respiration and volatilization (Boulton 1980b).

Economic Injury Levels on Grape

There has been limited research on economic injury levels (EIL) for indirect pests on grape. Dutcher and All (1972) established an EIL for the grape root borer (*Vitacea polistiformis* Harris) on 'Concord' grape in Georgia by correlating yield reductions with larval root feeding. In

California, an action threshold (AT) for the leafhopper *Erythroneura comes* Say, was set at 20% leaves lost after defoliation experiments showed that vines could tolerate this loss if it occurred at least one month after fruit set (Flaherty et al. 1982). Jubb et al. (1983) after four years of exposing 'Concord' vines to caged *E. comes* found that their initial AT of 15% leaf injury was too low. Laing et al. (1972) attempted to find an EIL for the Pacific spider mite (*Tetranychus pacificus* McGregor), using densities of 2.1 to 225 mites per leaf for a three-week period. They were unable to show any reduction in yield or fruit quality when correlating mite densities with fruit weight or sugar content. Despite these reports of EIL research on sucking insects and root feeders there has been no attempt to quantify effects of damage by the wide variety of chewing insects that attack grape foliage [e.g. the redbanded leafroller *Argyrotaenia velutinana* (Walker), the grape flea beetle *Altica chalybea* Illiger, or the Japanese beetle] (Jubb et al. 1978, McGiffen and Neunzig 1985, Pfeiffer and Schultz 1986). Investigations where photosynthetic analyses has been used to evaluate leaf damage indicate that chewing damage may differ from other forms of foliar damage (Hall and Ferree 1976).

INFLUENCE OF JAPANESE BEETLE (COLEOPTERA: SCARABAEIDAE) FOLIAR FEEDING ON 'SEYVAL BLANC' GRAPEVINES IN VIRGINIA

INTRODUCTION

Japanese beetle, *Popillia japonica* Newman, is common throughout most of the eastern United States and is abundant in Virginia where climatic conditions and both larval and adult food supplies favor large populations. The adult beetles feed voraciously on the leaves of most cultivars of *Vitis vinifera* and hybrid crosses of *Vitis* species used in wine production (Langford and Cory 1948), producing irregularly shaped holes which reduce the total leaf area of the vine (Figure 1). The abundance and feeding habits of this insect can produce extensive leaf area loss (LAL) which has consistently made the Japanese beetle the pest for which the most insecticide applications are made on wine grapes in Virginia.

Reduced leaf area on grapevines delays ripening and reduces yield, berry quality, shoot growth, and hardiness (May et al. 1969, Kliewer 1970, and Kliewer and Antcliff 1970, Mansfield and Howell 1981). Kliewer and Antcliff (1970) demonstrated that both the time of defoliation and the position of leaf damage on the shoot have a great effect on berry quality and yield. Kliewer (1970) showed that

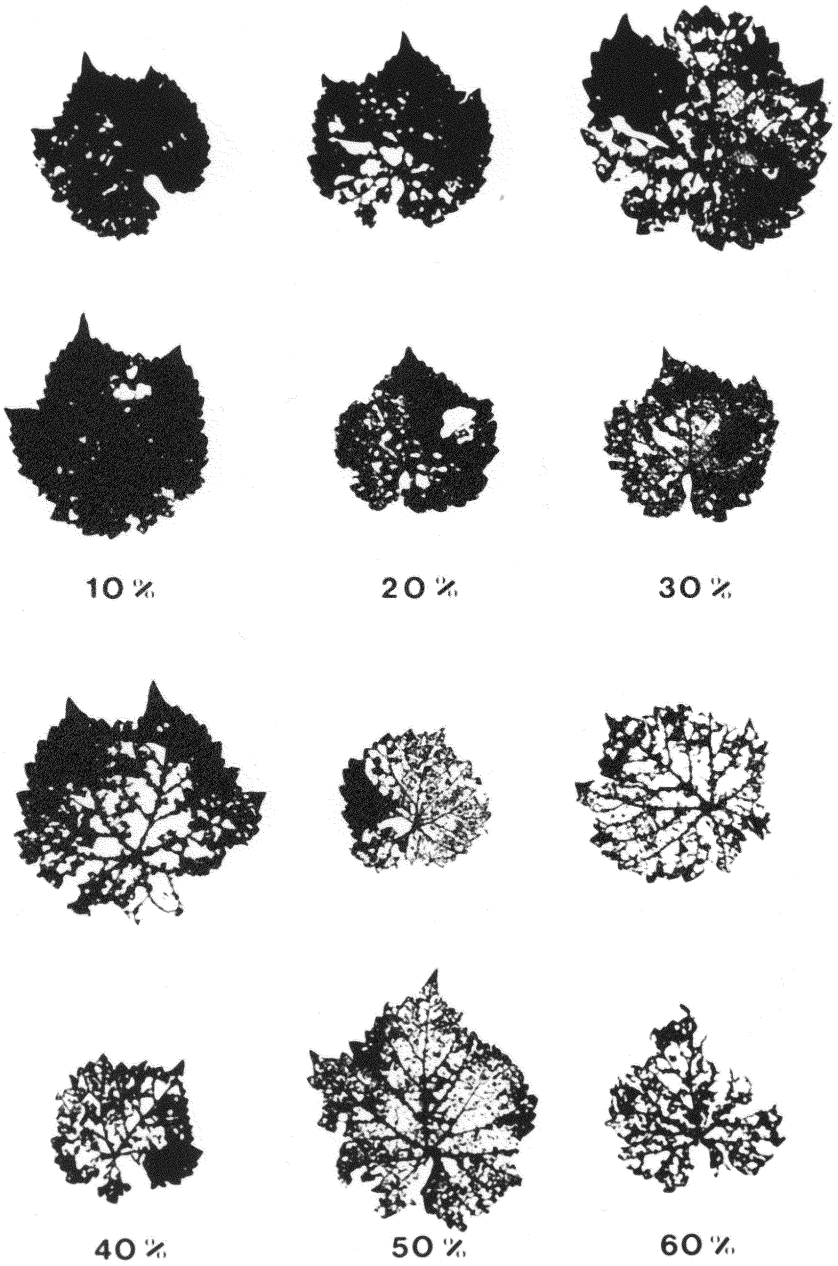

Fig. 1. Visual leaf damage index showing the percent leaf area loss for six levels of damage.

early season defoliation could actually increase soluble solids (SS) concentration in the berries while later defoliation caused a drop in SS concentration. He also found that the earlier and the greater the severity of defoliation "the greater the reduction in berry weight and sugar per berry".

Most of the above studies where loss of berry quality has been demonstrated involve defoliation in excess of 25%. In contrast, several studies involving other indirect pests of grape have dealt with less severe damage and have often failed to show a reduction in grape berry quality (Flaherty and Huffaker 1970, Laing et al. 1972, Kinn et al. 1974, Jubb et al. 1983).

Since the grapevine can tolerate certain levels of indirect damage, the potential exists to reduce control costs and insecticide applications by establishing an economic injury level (EIL) and action threshold (AT) for this insect on grape. The first study described herein was undertaken to determine if natural or high population densities affect grape berry quality or yield, and to determine if there is a differential effect due to the timing of Japanese beetle damage. A second study was undertaken to quantify the effects of various degrees of LAL on berry quality.

MATERIALS AND METHODS

The studies were conducted in a three-year old vineyard in Rockbridge County, Virginia, on the French hybrid *Vitis rupestris* X *vinifera* 'Seyval Blanc' trained to a bilateral cordon system. The first experiment utilized four adjacent vineyard rows, with at least one vine between each test vine. A randomized block design was utilized with 14 single-vine replicates each for four treatments (thereby comprising 54 total plants).

Standard viticultural practices were employed in the maintenance of the vines, except that there was no application of herbicides during the year of the study. Weeds were controlled by mowing between and under vineyard rows. Vines were spur-pruned during dormancy to 20-25 buds per cordon. The vines were not balance-pruned but were selected for uniformity of size.

Adult beetles were caged onto vines for 2300 beetle-days, (one beetle-day is equivalent to one Japanese beetle on the vine for one 24-hour period) both prior to and after véraison to measure the effects of damage at different periods during berry maturation. These treatments coincided with the first and second growth phases of berry development, respectively (Harris et al. 1968). Véraison occurred between 25 and 28 July, while peak bloom occurred on approximately 31 May. Grapes were harvested on 3

September.

Vines were caged in the prevéraison treatment from 8 July to 26 July beginning 39 days after bloom, and in the postvéraison treatment from 28 July through 20 August. At the start of each treatment, 100 beetles were added to each cage. This population density was maintained by replacing the dead or moribund beetles on the bottom of each cage every two or three days. An additional 100 beetles were added to each cage of the prevéraison treatment on 21 July to assure an adequate degree of damage before véraison.

Control vines were sprayed weekly with carbaryl (1.80 kg AI per hectare) from 7 July until a week prior to harvest. Vines in the pre- and postvéraison treatments were also sprayed when cages were not in place except that vines in the postvéraison treatment were not sprayed during the two weeks prior to véraison. Cage removal coincided with an application of carbaryl. A fourth treatment was left unprotected throughout the season to determine the effects of damage by the naturally occurring Japanese beetle population for the area in 1985.

Cages were constructed of 5.5 X 5.5 m squares of nylon netting, draped loosely over an entire vine. The material was secured at the edges and bottom by folding loose edges together several times and fastening them with common clothespins. The nylon had 9.5 hexagonal holes per cm^2, and produced approximately 8% shading, as measured with a photometer (Licor^{TM} model Li-185).

At harvest, the basal fruit cluster of the first two fruitful shoots beyond the first fruitful spur from the trunk were removed from each arm of the cordon. Fruit clusters (hereafter referred to as clusters) from basal buds of each spur were not used. The four clusters were weighed and ten berries from the periphery of each cluster were removed and combined to determine cluster weight and berry weight, respectively. The remainder of the primary clusters were harvested and weighed to determine yield per vine. The shoots bearing the clusters were tagged and measured for cane length on 18 November. The number of leaves per vine was estimated by counting the leaves on one cordon and doubling the count.

The forty-berry samples were ground in a blender and then strained with cheesecloth. The clear juice was then analyzed for SS using a temperature-compensated refractometer, and for pH with a LiCor^{TM} pH meter. NaOH (0.1M) was used to titrate 20 ml of berry juice to pH 8.2 to determine the total titratable acids (TTA). The sugar per berry was estimated by multiplying the SS concentration by the mean berry weight (Kliewer and Antcliff 1970).

A visual leaf damage index was constructed by making an acetate photocopy of the damaged leaf and darkening the damage on the copy with a black felt tip marker. The area of the photocopy was used as the total surface area of the leaf. The area of both the copy and the original leaf with the damage were determined using a Licor™ (model Li-3000) leaf area analyzer. The percent LAL was then calculated from the difference between the two measurements.

Leaf area loss per vine was determined by comparing leaves to the visual damage index and ranking them into one of seven categories: 0-5, 6-15, 16-25, 26-35, 36-45, 46-55, or 100% LAL (Figure 1). Leaves with an estimated LAL of over 55% were lumped into the 100% category because such leaves usually became totally necrotic within a few days and abscised. Every fifth leaf on every shoot on one of the two cordons was rated for damage. The cordon that was rated was systematically determined by alternating between the left and right cordon of the vines. Personnel that rated the leaves were first trained in the lab by ranking photocopies of leaves with predetermined damage levels. With practice, each person was able to rate the leaves to within 1.5% of the mean LAL of 60 leaves.

Adult Japanese beetles were monitored over the season by trapping adults in a standard trap (Ellisco™) baited with 2-phenylethyl propionate (6%) and eugenol (2.6%). Trap contents were removed and counted every 2-3 days and fresh bait was added weekly. The weekly relative abundance of adult beetles was calculated by dividing the weekly catch by the total catch for 1985 (Figure 2). Beetle abundance was monitored at the Shenandoah Valley Research Station 4 km north of the vineyard. Data were analyzed using Fisher's least significant difference (LSD) test at the 5% level of significance (Goodnight et al. 1982). Data were also analyzed by row to examine any border effects caused by the woods along the southwest boundary of the vineyard.

In the second experiment, vines were subjected to different levels of defoliation to study the effects on fruit quality. On 29 and 30 June vines were artificially defoliated to four different levels: 0, 10, 20, and 33%. This consisted of removing no leaves, or every tenth, fifth or third leaf, respectively, from every shoot of the vine. Leaves on new shoot growth were removed according to treatment on 28 July. All vines, including the control, were protected from further damage by weekly applications of carbaryl. All vines were located in a single vineyard row in a randomized block design, replicated nine times. Data were analyzed by analysis of variance and linear regression (Goodnight et al. 1982).

RESULTS

The natural beetle population failed to produce significant reductions in any of the parameters tested: SS,

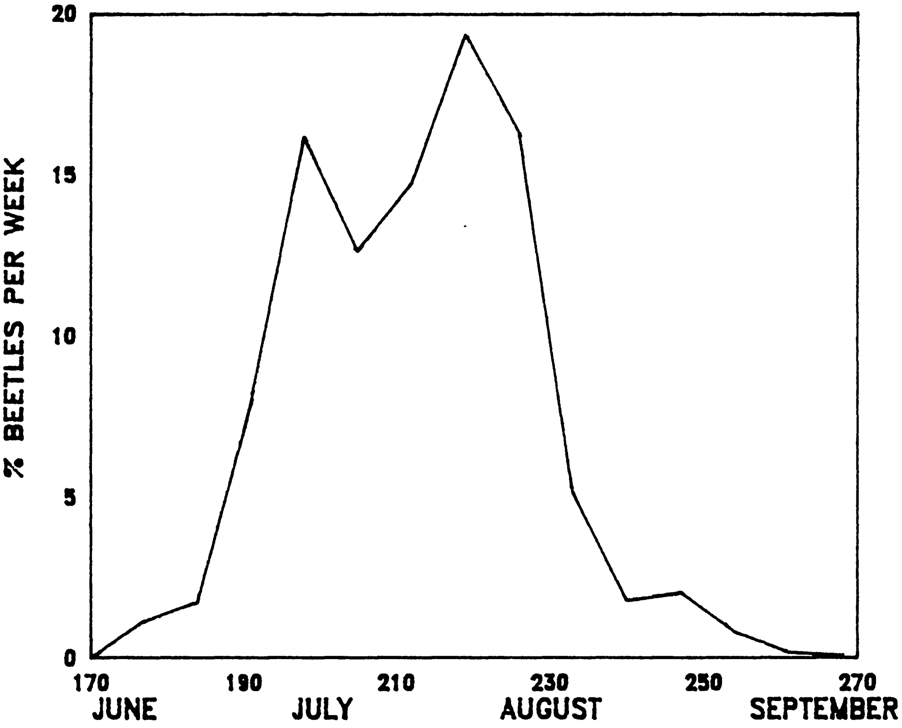

Fig. 2. 1985 Proportion of adult beetles caught per week at Steeles Tavern, Virginia.

TTA, pH, sugar per berry, cluster weight, berry weight, leaves per vine or shoot length. At harvest, both pre- and postvéraison treatments had significantly lower cluster weights and higher TTA than the control. Postvéraison feeding also lowered the soluble solid concentration in the berries. No significant differences were shown in shoot length, leaves per vine, berry weight, yield, sugar per berry, or pH when the time of damage was varied (Table 1).

Each treatment had significantly greater foliar damage than the control. Postvéraison feeding produced the highest amount of damage (11% LAL), followed by prevéraison feeding (9% LAL), the natural level of feeding (6.5% LAL), and the control (3% LAL).

In general, there was a positive relationship between berry maturity and an increased distance from the woodland along the southwest boundary of the vineyard (Table 2). Rows farther from the edge of the vineyard (approaching 37 m), had a significantly higher SS concentration and a lower TTA than rows closer to the edge.

In the second experiment, linear regression analysis failed to show any relationship between SS, pH, or TTA, and the percent of artificial defoliation (Figures 3-5). The regression line ($Y=20.46 - .0051X$) and coefficient of determination ($R^2=.090$) for SS plotted against LAL reveal a general lack of relationship between these variables.

Table 1. Effects of Japanese Beetle Feeding on 'Seyval Blanc' Grapevines using Artificially High Beetle Populations.

	Treatments			
	Control	Natural Infestation	Pre-veraison	Post-veraison
Shoot length (cm)	155	158	160	178
Leaves per vine	1355	1112	1175	1207
Yield (kg per vine)	5.1	5.3	4.0	4.3
Mean cluster wt. (g)[a]	316a	295ab	255b	261b
Mean berry wt. (g)	2.2	2.3	2.4	2.3
Sugar per berry (mg)	438	454	454	437
Soluble solids[ab]	19.5ab	19.8a	19.1cb	18.7c
TTA[abc]	0.89b	0.88b	0.94a	0.98a
pH	3.27	3.28	3.26	3.28
% leaf area loss[ab]	3.0d	6.5c	9.0b	11.0a

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[a] Means within a row followed by the same letter are not significantly different at the 5% level using Fisher's Least Significant Difference (LSD) Test.

[b] Percentage data were transformed using the arcsin.

[c] TTA = grams of tartaric acid per 100 ml of juice.

Table 2. Analysis of Berry Soluble Solids and Total Titratable Acidity by Rows.

Distance From Woods	Mean Soluble Solids[a]	Total Titratable Acidity[ab]
37 m	19.9a	0.89b
33 m	19.5ab	0.94ab
30 m	19.0bc	0.92ab
27 m	18.7c	0.96a

[a] Means within a column followed by the same letter are not significantly different at the 5% level using Fisher's Least Significant Difference Test. Percentage data were transformed by the arcsin.

[b] Total titratable acidity = grams of tartaric acid per 100 ml of juice.

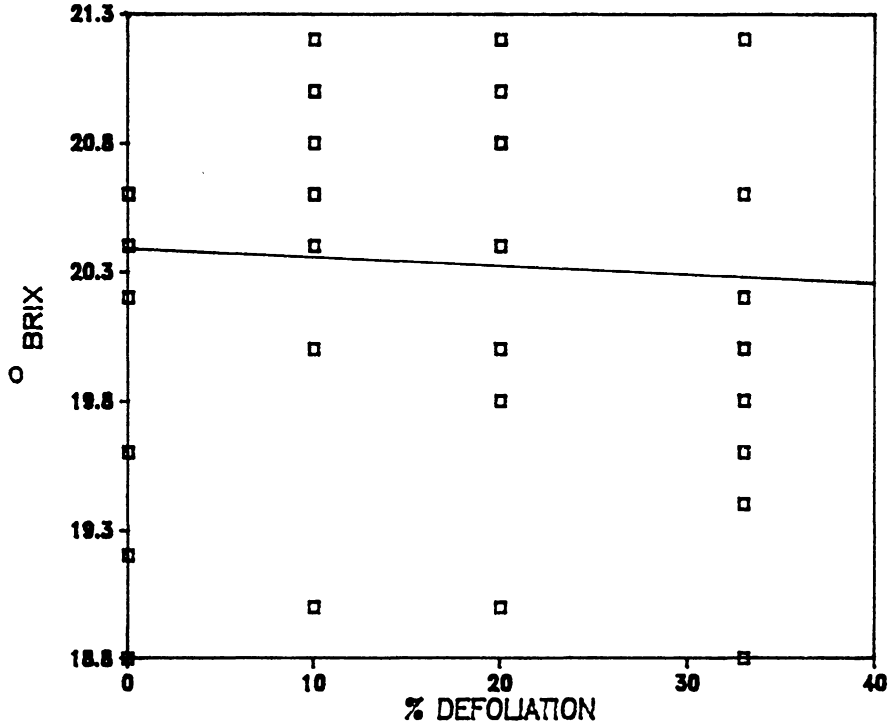

Fig. 3. Relationship between varying degrees of vine defoliation and berry (□) °Brix (soluble solids).

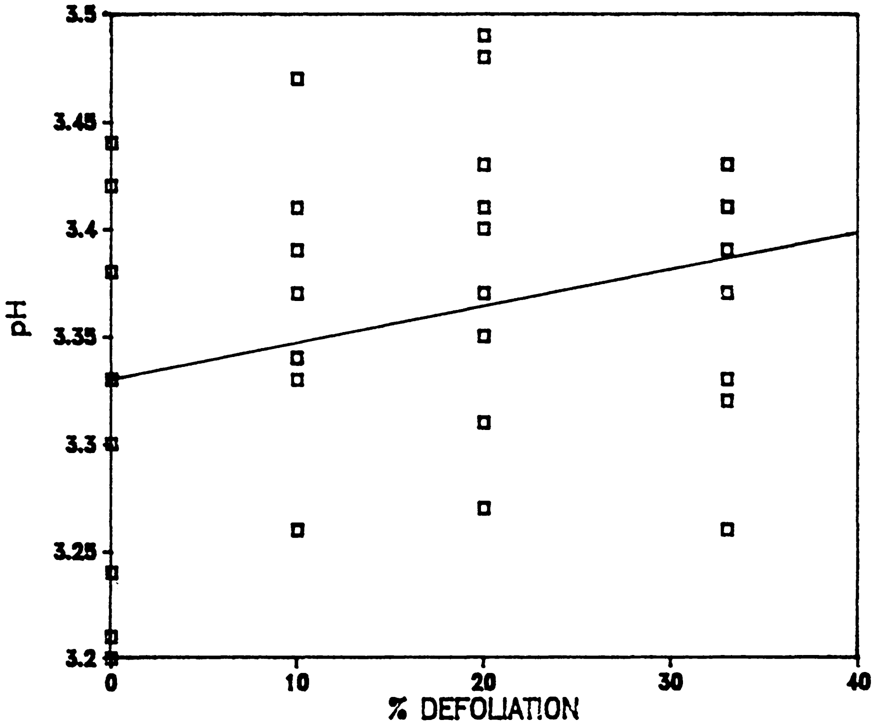

Fig. 4. Relationship between varying degrees of vine defoliation and berry (□) pH.

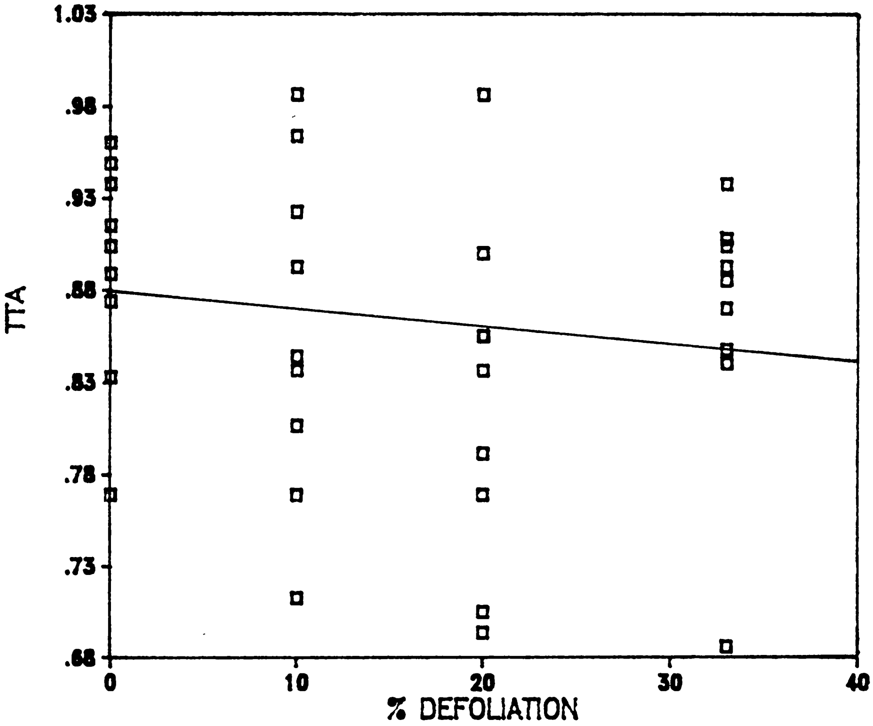

Fig. 5. Relationship between varying degrees of vine defoliation and berry (□) total titratable acidity (TTA).

Similar statistics for pH ($Y=3.33+.0017X$, $R^2=.087$) and TTA ($Y=.88-.001X$, $R^2=.023$) fail to show any influence of LAL at the rates applied in this experiment.

DISCUSSION

Natural infestations of the Japanese beetle failed to produce a reduction in fruit quality, quantity or shoot growth. A preliminary experiment in 1984 in a different vineyard where exclusion cages were used instead of inclusion cages, also indicated that beetles were not present on the vines in sufficient numbers to cause a loss in berry quality. Population densities in 1984 were greatly reduced because of a drought in 1983; such droughts have been shown to reduce Japanese beetle populations in subsequent years (Fleming 1972a). Although _P. japonica_ damage was more severe in 1985 than in 1984, it is unknown whether the population had recovered to its predrought levels.

Intensive Japanese beetle feeding after véraison significantly lowered the SS of the fruit. Kliewer and Antcliff (1970) found that partial defoliation occurring approximately one month after bloom was more detrimental to berry weight than to the increase of fruit sugar, but that "complete defoliation at véraison reduced berry sugar concentration much more than the berry weight". Reducing leaf area and thus photosynthate production may retard sugar accumulation in the berries, the major sink at this time (Kliewer 1982). Prevéraison damage would not have the same effect on sugar accumulation because at this time the fruit cluster is competing with other major carbohydrate sinks (Kliewer 1982). Kliewer (1970) partially defoliated vines at three different periods (12, 35 and 58 days after bloom) and determined that later defoliation had progressively less effect on berry size. He attributed this decreasing effect on berry size in part to the possible interruption of hormone production or translocation from leaves and the dual effect on cell division and elongation during growth stage one, as opposed to an effect on elongation alone in the lag and second growth phases of berry development.

Buttrose (1966) observed in potted vines a progressive delay in the onset of sugar accumulation with decreasing leaf area. This delay would serve to lower sugar levels in both pre- and postvéraison treatments. He also found that defoliation delayed the decline of TTA. Both pre- and post véraison treatments resulted in TTA levels significantly higher than the control. This is consistent with findings by Buttrose (1966). Winkler et al. (1974) discussed the inverse relationship between malic acid (one of the main constituents measured as TTA) and SS. Ribereau-Gayon (1966) also found that organic acids (malic and tartaric) could be converted to SS, though this accounts for a minor portion of the SS.

No difference was found in berry weight or yield per vine. Some investigators have observed a loss in berry weight associated with early defoliation which contributed to a corresponding decrease in cluster weight or yield (Buttrose 1966, May et al. 1969, Kliewer 1970). In these studies, defoliation was induced prior to 30 days after bloom and exceeded 30% damage (earlier and more severe than in the present study). Treatments usually consisted of removal of leaves or portions of shoots. A combination of later, slower, and less severe damage may account for the lack of difference in berry weight and yield per vine in this study. Jubb et al. (1983) failed to detect a reduction in yield per vine or fruit quality during most years when investigating leafhopper (Erythroneura comes Say) damage on 'Concord' grapes ranging from 0-25% leaf injury. Flaherty et al. (1982) found that wine grapes in California could tolerate 20% manual defoliation without a detrimental effect on yield or quality, provided damage followed fruit set by 30 days. Laing et al. (1972) found that gradual leaf injury caused by the Pacific spider mite (Tetranychus pacificus McGregor) did not reduce yield or fruit quality of 'Thompson Seedless' vines.

The first row of the vineyard was planted 21.3 m from the adjacent woodland (approximately the height of the trees).

This has become common practice in Virginia. Although rows 3-6 were used in the first experiment (27.4-36.6 m from the woodline), analysis by row indicates that the vines may have been affected differently by shading or by direct competition with extensive tree roots. Rows closest to the vineyard's southwest margin were consistently shaded for longer periods during sunset. This may have contributed to the progressive increase in SS as the distance from the trees increased within the experiment. Shaulis et al. (1966) showed that differences in exposure to solar radiation due to shading within the canopy leads to variability in fruit maturity at harvest.

When artificial defoliation was used to reduce canopy size, linear regression failed to show any relationship between fruit maturity parameters and varying levels of damage up to 33% defoliation. Several studies have demonstrated a loss in berry quality by removing approximately 25% of the leaves from vines (May et al. 1969, Kliewer 1970). Increased leaf efficiency and increased exposure of clusters to direct sunlight may compensate for LAL. Kliewer and Lider (1968) showed that exposure of clusters to direct sunlight could cause lower TTA and Kliewer and Antcliff (1970) found that covered clusters produced higher soluble solids than uncovered clusters.

Many studies involving the removal of whole leaves or partial shoots have shown that only 5-17 cm^2 of leaf area are required to mature each gram of fruit (Winkler 1930, Buttrose 1966, Amberg and Shaulis 1966, May et al. 1969, Kliewer and Antcliff 1970, Kliewer and Weaver 1971). In experiment I, where 2300 beetle-days produced approximately 11% LAL after véraison, vines were estimated to possess approximately 24 cm^2 of leaf area per gram of fruit yet there was a drop in fruit quality compared to the control. Unfortunately, no data on the weight of the secondary clusters were gathered because they are not commercially important and usually represent a small percentage of the total yield. This phenomenon warrants further investigation, using beetle damage to establish the difference between whole leaf removal and removal of a portion of the interveinal area.

It was concluded that artificially defoliating grapes by removing whole leaves may not adequately simulate beetle damage because 10% LAL induced by beetles lowered fruit quality while 33% whole leaf removal did not. These tests indicate that varying caged beetle densities in a manner that simulates the relative beetle abundance through the season (Figure 2) may be a more accurate alternative.

Additional information on long-term effects of Japanese beetle feeding is necessary. The finding of no significant effect on fruit quality or shoot length by naturally occurring populations is important because although Japanese beetle has been the target of repeated insecticide sprays, at least in some years *P. japonica* may not be an economic problem.

EFFECTS OF SIMULATED INSECT DAMAGE ON PHOTOSYNTHESIS OF POTTED GRAPEVINES

INTRODUCTION

In viticultural studies, investigations utilizing artificial defoliation have usually consisted of removing whole leaves or portions of shoots (Buttrose 1966, May et al. 1969, Kliewer 1970, Mansfield and Howell 1981). While this type of simulated injury has been useful in determining the effects of foliar loss resulting from mechanical harvesting or disease on yield and berry maturity, research in other crops has indicated that it may not be adequate to simulate certain insect injury (Poston et al. 1976, Hall and Ferree 1976).

Hall and Ferree (1976) and Ferree and Hall (1981) studied the effects of simulated insect injury on net photosynthesis (P_n) in apple and determined that "the amount of cut surface exposed by injury was more important than the amount of leaf area removed." In addition, Hall and Ferree (1976) and Poston et al. (1976) found that it is important to avoid cutting the midrib or the main lateral veins of the leaf to simulate damage by insects that feed on interveinal area.

Kliewer (1982) demonstrated an increase in P_n by the remaining leaves on potted grapevines following removal of whole leaves. If a similar drop in efficiency occurs in grape leaves from such insect damage (e.g. Japanese beetle *Popillia japonica* Newman), this could serve to increase the leaf area required to mature the fruit. However, the effects on the remaining leaf area when an insect removes a portion of many leaves has not yet been investigated on grape. Furthermore, in working with apple leaves, Hall and Ferree (1976) found that a "secondary reaction" which further reduced P_n occurred when over 20% of the leaf area was removed.

Information gained in this area will be helpful in determining economic injury levels (EIL) for certain insect pests. Poston et al. (1976) studied effects of simulated insect damage on soybean P_n and found that certain artificial injury techniques (e.g. paper punch) adequately simulated damage by certain defoliators. This study was initiated to determine if a drop in efficiency occurs in grape, and if so, at what level of interveinal leaf area loss (LAL) it occurs. Another objective of this study was to show the total effects of both the loss of efficiency and loss of leaf area on the P_n of the leaf.

MATERIALS AND METHODS

Five grafted 'Meurier/Elvira'(*Vitis* spp.) grapevines were grown in 15-cm pots containing Promix™ in an open-ended greenhouse from 1 March through July, 1984. The vines were fertilized at a rate of 200 ppm N weekly, beginning in April using a solution of 20N-8.6P-16.6K. Plants were transported to the laboratory approximately two hours prior to determining P_n to allow time for adjustment to laboratory lighting. The plants were returned to the greenhouse each day after measurements were completed.

On 1 August, four adjacent leaves near the midlength of the shoots (approximately 10-13 nodes from the shoot apex) were selected and P_n was determined using a Beckman™ model 865 infrared gas analyzer. P_n was again determined 24 hours after treatments and five and twelve days later. P_n was determined using methods similar to Schaffer et al. (1986) with attached leaves.

P_n is based on the amount of CO_2 the plant uses during photosynthesis and is determined by measuring the concentration of CO_2 entering and leaving the leaf chamber (P_n=mg CO_2 dm^{-2} hr^{-1}). The air flow rate into the leaf chamber was five liters per minute with chamber temperature maintained at $28^o \pm 2^o$C and the level of photosynthetically active radiation maintained at 850 uEm^{-2} s^{-1}. The leaves were randomly assigned to one of four treatments (approximately 0, 10, 20, or 40% LAL) based on leaf size as estimated by length times width measurement. Leaf disks

(6.5 mm diameter) were removed from the interveinal area using a common paper punch.

The outline of each leaf was traced and cut out at the conclusion of the experiment, and both the tracings and the damaged leaves were measured with a LiCor^{TM} model 3000 leaf *area meter. The percent LAL was determined from the* difference between the two measurements, and ranged from 9-12% (10% treatment), from 20-28% (20% treatment) and from 42-52% (40% treatment).

Net photosynthesis was first calculated on the basis of the remaining leaf area after treatments to determine the photosynthetic capability of the remaining leaf tissue (Hall and Ferree 1976). P_n was again calculated using the area of the tracings to represent the original leaf area. Hall and Ferree (1976) reported that P_n based on the original leaf area indicates a "reduction in photosynthetic potential" for the entire leaf due to the compounded effects of leaf area loss and a drop in the efficiency of the remaining tissue.

Posttreatment P_n rates are presented as a percent of the pretreatment rates. A general linear model procedure and multiple regression analysis were used to analyze the data (Goodnight et al. 1982).

RESULTS

Leaves showed a similar change in P_n due to defoliation one and five days after treatment (Figures 6 and 7). There was a greater depression of P_n among leaves with low levels of LAL (0-12% LAL) 12 days after damage was inflicted than after one and five days (Figure 8). As the degree of LAL increased, the efficiency of the remaining leaf area decreased (Figures 6-8). This decline started between 20-30% LAL one and five days after treatment and between 0-12% LAL 12 days posttreatment.

The compounded effects of LAL and decreased efficiency produced a 10% drop in P_n between 10-15% LAL for the first five days posttreatment (Figures 6 and 7) and between 5-10% LAL after 12 days (Figure 8). The regression equations for this additive effect predicted the total shutdown of photosynthesis at approximately 60% LAL one and five days after damage. Reduction in P_n at high levels of LAL (43-53% LAL) were not as extreme 12 days after treatment (Figure 8).

There was a drop in the P_n of undamaged leaves (0% treatment) throughout the 14 days of the study. The mean P_n values for the undamaged leaves on days 0, 1, 5 and 12 were 16, 13, 13 and 12 respectively. This gradual decline in P_n may have been due to both the handling of the leaves during measurements (Detling et al. 1979, Ferree and Hall 1981) and to leaf aging (Kriedemann et al. 1970). It was assumed that P_n values below that of the control vines (0% treatment)

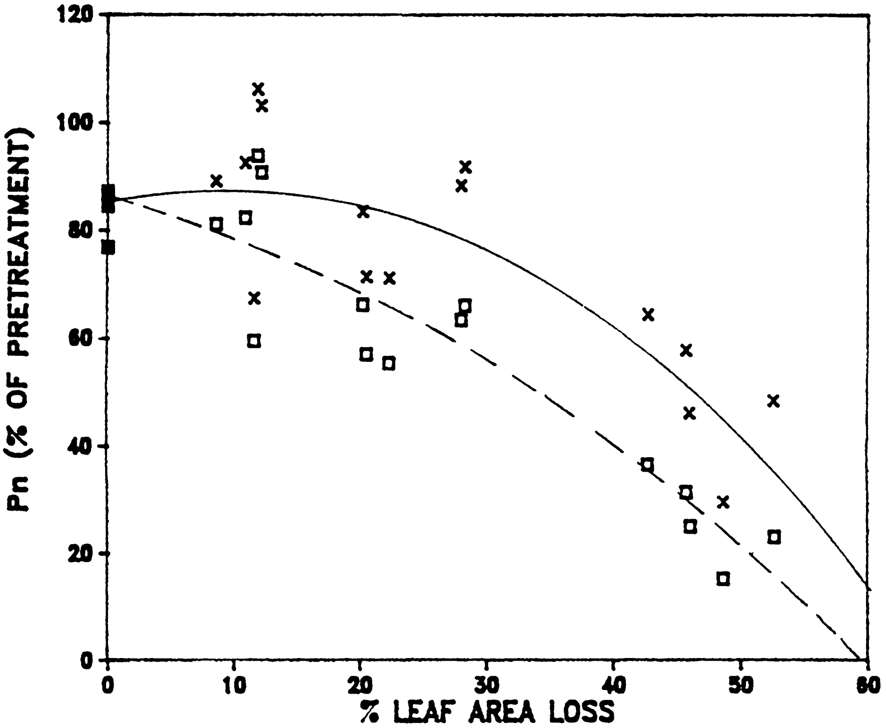

Fig. 6. Net photosynthesis one day after simulated insect damage. Top line (x) ($Y = 84.62 + .6698X - .0297X^2$, $R^2 = 0.70$, $P < .0001$) is P_n based on remaining leaf area. Bottom line (□) ($Y = 85.08 - .5105X - .0154X^2$, $R^2 = 0.88$, $P < .0001$) is P_n based on pretreatment leaf area.

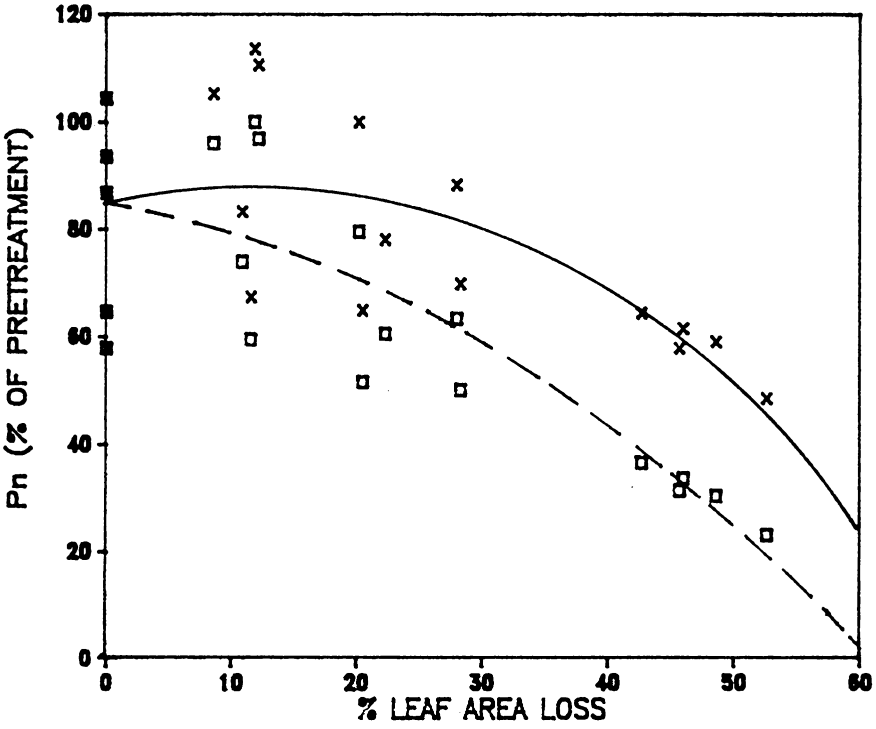

Fig. 7. Net photosynthesis five days after simulated insect damage. Top line (x) ($Y = 84.46+.6670X-.0261X^2$, $R^2 = 0.43$, $P<.01$) is P_n based on remaining leaf area. Bottom line (□) ($Y=84.50-.4166X-.0154X^2$, $R^2 =0.71$, $P<.0001$) is P_n based on pretreatment leaf area.

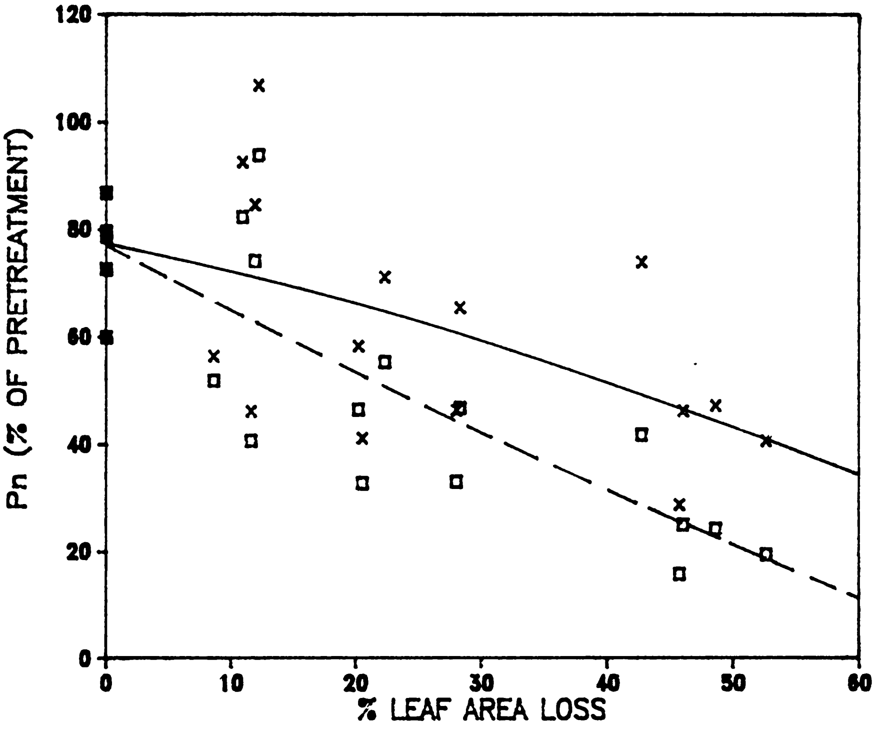

Fig. 8. Net photosynthesis 12 days after simulated insect damage. Top line (x) ($Y = 76.71-.4821X-.0037X^2$, $R^2 = 0.35$, $P<.03$) is P_n based on remaining leaf area. Bottom line (□) ($Y=76.67-1.2817X+.0035X^2$, $R^2=0.69$, $P<.0001$) is P_n based on pretreatment leaf area.

represented treatment effects and were interpreted in that manner.

DISCUSSION

It appears that there was a "secondary response" to LAL similar to that encountered by Hall and Ferree (1976) in apple, which produced a drop in the efficiency of the remaining tissue of the damaged leaf. This response, when coupled with the drop in P_n resulting from the loss of leaf area, could cause a complete shutdown in photosynthesis by 60% LAL (Figures 6 and 7).

A leaf with this degree of damage may fail to recover (Boucher and Pfeiffer unpublished data) resulting in the loss of the leaf and the premature loss of productivity from the remaining 40% of the leaf. Leaves damaged in excess of 20% should be considered separately from lower levels of leaf damage when developing EIL for defoliating insects, as they may be affected more than indicated by the loss of tissue alone (Figure 6-7). This may also be the case for leaves with less than 20% damage more than five days after damage (Figure 8). Detling et al. (1979) showed the beginnings of a decline in efficiency using Pn for the remaining leaf area of damaged wheatgrass leaves on the sixth day posttreatment (25% damage). Hall and Ferree (1976) observed a significant drop in the efficiency of P_n

for the remaining apple leaf tissue at three and seven days after the removal of 15% of the leaf.

Specific information on the productivity of damaged leaves would become more important to developing EIL and ET as the severity and percent of leaves damaged increased, especially on less vigorous vines with trellis systems that do not maximize light exposure. Shaulis et al. (1966) showed that the amount of leaf area exposed to direct solar radiation plays an important role in determining the quality and quantity of the yield. Further investigations are necessary to determine the physiological factors involved in the drop in P_n efficiency of damaged leaves. In addition, it is important to ascertain if adjacent leaves can compensate for partial tissue loss on several leaves and how much they compensate at various levels of LAL. Such information will be valuable in producing the advanced types of ET and EIL.

SUMMARY

This series of experiments was designed to evaluate the host-pest relationship between the Japanese beetle, *Popillia japonica* Newman, and Virginia's wine grape varieties. This investigation was meant to provide information that will help determine an economic injury level (EIL) for the Japanese beetle on grape, alleviate the problem of calendar spraying for this pest and thus facilitate the development of an integrated pest management program for grape.

Japanese beetles were caged onto field-grown vines both before and after véraison to determine the effects of beetle feeding on the fruit yield, quality and vine growth at different phenological stages of berry development. Another set of vines was left unprotected throughout the season to measure the effects of the natural infestation density of beetles in the vineyard. Pre- and postvéraison treatments were exposed to 2300 beetle days and lost approximately 10% of their leaf area during their respective periods of exposure, while the natural infestation treatment lost 6.5% spread over the entire Japanese beetle season. Effects of beetle feeding on fruit quality were evaluated by determining SS, TTA, pH and total sugar per berry. Effects on crop load and vine growth were evaluated by determining yield, cluster weight, berry weight, shoot length and leaves per vine.

In 1985, there were no significant differences between the unprotected vines and vines protected with weekly insecticide sprays (control) for any of the parameters tested. This is important because it shows that in some years Japanese beetle infestations are not economically important and therefore do not warrant control measures.

Vines with intensive postvéraison leaf feeding produced fruit with lower SS and higher TTA than the control vines but pH, total sugar per berry, berry weight, yield, shoot length or leaves per vine were not affected. Intensive prevéraison feeding had a similar effect on TTA but not on SS, and produced no significant effect on pH, total sugar per berry, berry weight, yield, leaves per vine and shoot length. Postvéraison feeding had a more severe effect on berry quality than did prevéraison feeding.

In the second experiment 0, 10, 20, and 33% of the leaves were removed from field-grown vines to determine the effects of various levels of leaf loss on fruit quality. Linear regression analyses failed to reveal any relationship between SS, pH, or TTA and the percent of foliage removed. Removing whole leaves proved inadequate in determining an EIL for the Japanese beetle on grape.

In a laboratory study, four adjacent leaves on potted grapevines were randomly assigned one of four levels of simulated insect damage (0, 10, 20, 40% leaf area loss, LAL) which were administered with a common paper punch. Net photosynthesis (P_n) was determined for each leaf prior to treatment and 1, 5, and 12 days after treatment. Regression analysis revealed that the drop in P_n was not adequately accounted for by the loss of leaf area alone. This secondary effect on the remaining leaf area was described as a drop in photosynthetic efficiency.

Leaves with more than 20% LAL showed a loss of efficiency 1 and 5 days after treatment, but 12 days after treatment there was a loss of efficiency with less than 12% LAL. Regression analysis predicted a total shutdown in P_n at 60% LAL due to the combined effect of LAL and lower efficiency in the remaining leaf area.

These three experiments showed that there is a substantial difference between removing whole leaves and the type of injury caused by the Japanese beetle. There were no significant differences in experiment II with up to 33% defoliation while both experiments I and III showed that removal of interveinal area could produce detrimental effects with between 10 to 20% LAL. To determine an EIL for the Japanese beetle on wine grapes the second study should be repeated using several levels of *P. japonica* (e.g. 2300, 4600, 6900 beetle-days) feeding for the entire season. Several important wine grape varieties and trellis systems should be incorporated in the study to produce a more universal EIL. It will also be necessary to continue this experiment for a second and third growing season to ascertain long-term effects of beetle damage on yield.

This research has also shown that further investigations are needed to determine a safe planting distance between vines and adjacent woodlands, especially along the southwest boundary of a vineyard. This could be easily accomplished by determining fruit SS and distances for vines at increasing intervals from woodland and recording differences in exposure to solar radiation.

Finally, the results of this investigation indicate that there are several possible management strategies which may offer an immediate alternative to calendar spraying. These include: 1) applying carbaryl for Japanese beetle control only after véraison, 2) applying carbaryl only after a period of heavy precipitation, since trap catch data indicates an increase in beetle activity following such periods (Appendix 1).

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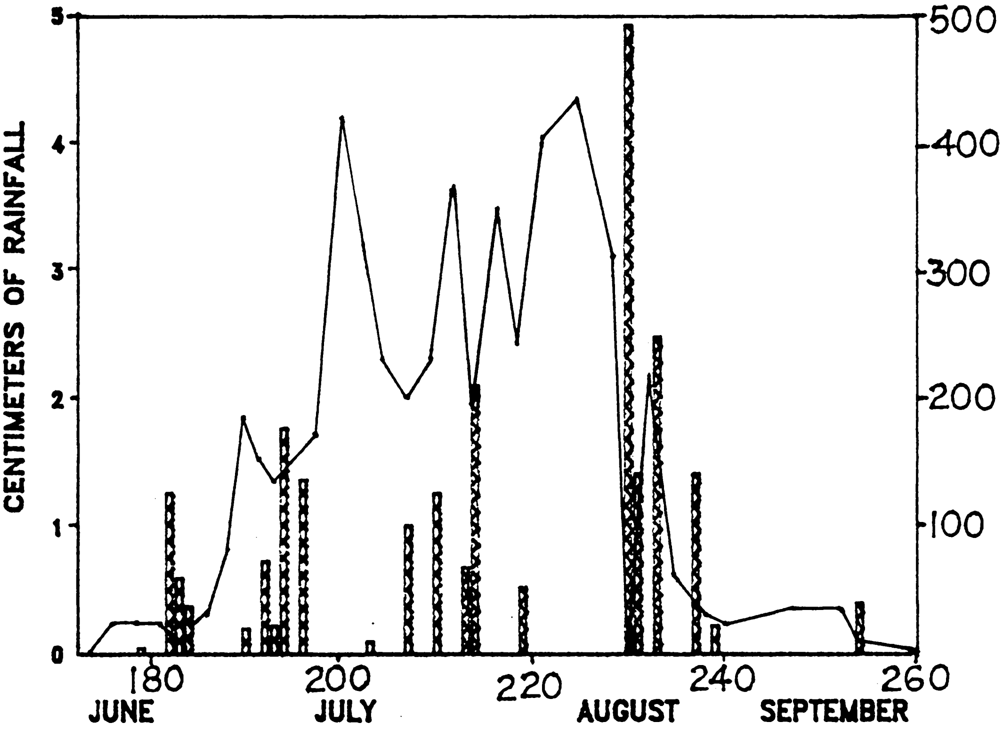
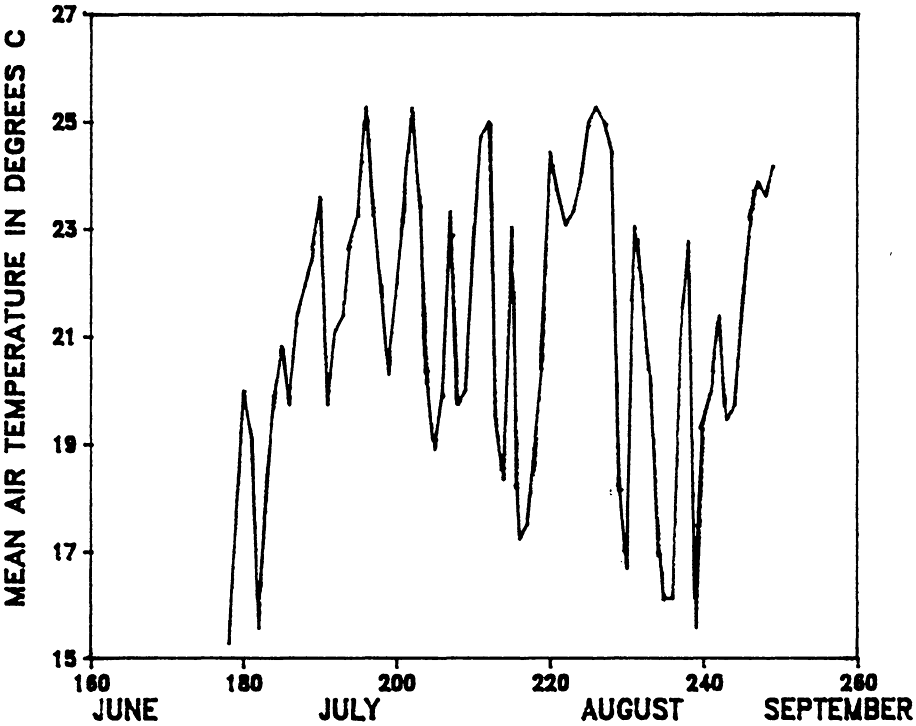
APPENDICES



Appendix 1. Adult beetles caught per day (—) and summer rainfall (▨) for 1985 showing sharp increases in the beetle population following periods of substantial precipitation.



Appendix 2. Means of summer maximum + minimum daily temperatures for 1985 at Steeles Tavern, Virginia.