DAMAGE THRESHOLDS FOR SIMULATED TRUNK AND LEAF INJURY IN 'MONTMORENCY' SOUR CHERRY

By

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ABSTRACT

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Trunk and leaf injury to sour cherry (Prunus cerasus L. 'Montmorency') trees resulting from stresses such as mechanical harvest and insect or disease infestation can reduce tree vigor, productivity and orchard life.

Simulated trunk injury by bark removal or bark crushing of up to 50% around the trunk circumference of young, fruiting trees had a minimal effect on tree vigor, productivity or mortality. Differentiated phloem produced in wound callus of trees with bark removed completely around the trunk, coupled with tree survival after two years, suggested that vascular reconnection across some wounds had occurred.

Simulated leaf injury by holepunching did not significantly reduce net carbon dioxide assimilation (A) when up to 20% of the leaf area was removed. Photosynthetic compensation to leaf injury was observed 4 days following leaf area removal (L.A.R.) and maintained for at least 3 weeks. Removal of 20% of the leaf area of the whole plant did not significantly reduce dry weight accumulation.

To my family

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Guidance Committee:

The journal paper format was chosen for this thesis in accordance with departmental and university regulations. The thesis is divided into three sections. Section one is an overall literature review and sections two and three are intended for publication in The Journal of the American Society for Horticultural Science.

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LIST OF ABBREVIATIONS

A	net carbon dioxide assimilation (molar units)
6-BA	6-benzyladenine
CHES	Clarksville horticultural experiment station
C_i	intercellular CO_2
E	transpiration
GA	gibberellic acid
g_s	stomatal conductance
HRC	horticultural research center
IAA	indole-3-acetic acid
LAL	leaf area loss
LAR	leaf area removal
LSD	least significant difference
PAR	photosynthetically active radiation
Pn	net photosynthesis (mass units)
PPFD	photosynthetic photon flux density
PP-333	paclobutrazol
ppm	parts per million
PRD	peach rosette and decline disease
r	correlation coefficient
r^2	coefficient of determination
RuBP	ribulose 1,5-bisphosphate
Rubisco	ribulose bisphosphate carboxylase/oxygenase
SLW	specific leaf weight
TCA	trunk cross-sectional area
T_{50}	temperature required to kill 50% of samples
TRC	tree research center
VPD	vapor pressure deficit
VPG	vapor pressure gradient
WUE	water use efficiency

SECTION I

REVIEW OF LITERATURE

INTRODUCTION

Two major types of above-ground injury to the non-reproductive portions of fruit trees in the genus Prunus (including peaches, cherries, apricots and plums) are important to the grower: 1) damage to the bark and 2) damage to the foliage. Damage to the photosynthetic manufacturing capacity or the vascular transport system could reduce vigor and may result in tree mortality. A damage threshold is defined as the degree of damage, above which there is a negative effect on growth and health of the tree. Values for damage thresholds are available for some crops but have not been determined for members of the genus Prunus. Damage to fruit trees can be caused by many factors. The severity, timing and duration of damage will determine whether or not there is a negative effect on the growth and health of the tree.

Damage to the bark and cambium of the trunk and or main scaffold branches of the tree is detrimental to tree health. Injury to the trunk and branches is commonly caused by mechanical damage during harvesting or from careless use of implements in the orchard. Other types of damage such as freezing injury, feeding injury from various orchard inhabiting animals (deer, rabbits, mice), feeding or boring by insects and invasion by diseases can also have a negative effect on tree health and productivity.

Damage to the foliage is commonly caused by insect feeding, disease (fungal, bacterial, or viral) infection, environmental stress (frost, lack of water and or nutrients, pollution, etc.) pesticide toxicity, herbicide drift and even damage from severe winds or hail. Since leaves contain the photosynthetic apparutus whereby trees photosynthesize, any injury could reduce the production of carbohydrates. The carbohydrate produced during photosynthesis is transported to different parts of the tree, accumulating in the fruit, bark and roots. Reduced carbohydrate levels adversely affect tree productivity and overwinter survivability.

Damage thresholds for trunk or leaf injury are not currently available for members of the genus _Prunus_. This review will examine the literature relative to fruit tree injury. First, the physiological responses of the whole tree to various types of injury will be examined. Second, damage to the bark and cambium and its effects will be considered. Finally, damage to the foliage and its effects will be examined. Since little of the literature specifically relates to _Prunus_, other tree fruits will be considered. Some reports on non-tree fruit crops will also be reviewed because they pertain to the subject of damage thresholds.

WHOLE PLANT EFFECTS

Since fruit trees are cultivated to provide a harvestable crop, their health and vigor are extremely important. A tree in poor health may produce a reasonable crop in a given season, but as it ages, vigor and productivity will likely decrease. Eventually, if the tree is excessively stressed, it will be more susceptible to injury and subsequent decline. The ability of the tree to survive the winter and to slow pathogen attack may be greatly reduced.

Kenworthy (1974) demonstrated for sour cherry that fruit quality is related to tree vigor (as measured by terminal shoot growth). He suggested that practices that promote vigor (fertilization, irrigation, pruning, pest control) and result in up to 18 inches of terminal growth should give the best fruit quality and the highest yield. Low tree vigor resulting from inadequate cultural practices may increase the risk of trees to adverse conditions.

Pest injury to the foliage from insects and mites is an important source of damage to the tree. Rather than reducing the marketability of the fruit, the leaf damage can reduce the vigor or carbohydrate content of the tree. Briggs and Avery (1968) demonstrated that shoot extension and tissue dry weights of fruit trees ('Brompton' plum, 'Malling IV' and 'Crab C' apple rootstocks) infested with red spider mite (Panonychus ulmi (Koch)) were reduced when compared with noninfested trees. Apple trees had reduced bud initiation and fruit development the year following heavy mite infestation (Lienck et al. 1956).

Defoliation has many significant effects on fruit trees. For example, Lloyd and Couvillon (1974) examined the effects of date of defoliation on flower and leaf bud development of peaches in Georgia. Single shoots and entire trees were manually defoliated from mid July to late September at 2 week intervals. Terminal buds had set and were subsequently removed at the time of treatment. The number of flower buds per tree increased as defoliation was delayed. Vegetative bud break decreased with each successive defoliation. This same result was reported again in a subsequent experiment by Couvillon and Lloyd (1978) for peach.

Defoliation of fruit trees also affects their winter hardiness. Kennard (1949) manually defoliated sour cherry trees and observed an increased susceptibility to low temperature injury followed by delayed blossoming the following spring. Similarly, Howell and Stackhouse (1973) observed that early defoliation of sour cherry trees by hand or by pathogens caused the tissues to be more susceptible to low temperature injury. They also noted that early defoliation resulted in fewer viable flowers per tree. Hennerty and Forshey (1971) observed that flowering of 'Golden Delicious' apple trees that had been defoliated and defruited one year was reduced the following year. Howell and Stackhouse (1973) noted that leaves should be maintained until the first frost would remove them naturally. Maintaining foliage can improve the ability of the tree to survive harsh winters and ensure subsequent productivity the following season. However, active growth at the end of the season is undesirable due to its inability to acclimate adequately prior to the onset of freezing temperatures.

Simulation of insect injury has been an effective means to evaluate the effects of leaf injury on whole plant productivity. Holes punched in leaves of apple trees, to simulate damage by the spotted tentiform leaf miner (Phyllonorycter blancardella), reduced the trunk growth, fruit number and yield in the year of injury (Kappel, 1986). Kappel (1986) further demonstrated that simulated injury reduced growth of the rootstock portion of the tree and also reduced bloom and fruitset the year following defoliation. Bassman et al. (1982) artificially damaged nursery grown poplars and showed that by removing 75 to 80 percent of the leaf area, growth was reduced by only up to 20 percent. Stacey (1983) demonstrated that when 75 percent of the leaf area of tomato was removed it caused a 40 percent reduction in yield. By removing all spur leaves on 'Golden Delicious' apple trees, Ferree and Palmer (1982) observed an 80 percent reduction in fruit yield. Leaf area removal of any kind, depending on the level of severity, can markedly effect yield and growth.

Apparently, the plant can compensate for certain levels of injury.

BARK AND CAMBIUM DAMAGE

The mature tree trunk is composed of the following layers from the outside: periderm (phellem, phellogen and phelloderm), cortex, phloem, vascular cambium, xylem and pith (Esau 1977). Depending on the age of the tree, both primary and secondary xylem and phloem may be present.

Bark Strength

Injury to the bark or cambium can take many forms. In Michigan, sour cherries are usually mechanically harvested. The mechanical harvester clamps on to the trunk at the base of the tree and then the trunk is repeatedly displaced by the force of the machine. The fruit are dislodged and fall to a catching apron below. This vigorous trunk displacement stresses the tree and, depending on the skill of the machine operator, trunk damage can occur.

Bark strength of fruit trees is lowest when the cambium activity is high (rapid cell division and high moisture content). Maximum damage to the bark may occur during this period of high activity, commonly known as bark slipping (Cargill et al. 1982; Fridley et al. 1970; Brown et al. 1984). Damage to the trunk may cause the bark to separate from the wood, thereby, resulting in an interrupted flow of sap in the trunk (Cargill et al.

1982). Damaged bark provides a favorable environment for pathogens (especially borers) to enter the tree (Fridley et al. 1970; Cargill et al. 1980). As cambial activity decreases in the fall, cambial cells shrink and bark strength increases (Fridley et al. 1970).

Diener et al. (1968) investigated cherry, apple and peach bark to compare directional strength properties. They noted that in the vertical direction, apple bark was twice as strong as peach or cherry. In the horizontal direction, however, peach bark was 50 percent stronger than cherry or apple. In the 45 degree plane, peach strength was only half that of apple or cherry bark. Clearly, the plane or direction in which the stress is imposed can affect the bark damage to a given tree. Trunk displacement by mechanical harvesters may occur in a straight back and forth or slightly elliptical shaking pattern, depending on the position of the clamping attachment (Kirk and Booster 1979).

Brown et al. (1984) outlined a series of recommendations to reduce bark damage to cherry trees during mechanical harvesting. They suggested: 1) properly training operators; 2) properly maintaining equipment; 3) limiting the clamping force; 4) clamping perpendicularly to the trunk; 5) lubricating the clamp between the sling and the flap to minimize the shear force on the bark; and 6) using single, short shaking periods instead of multiple or long shaking periods. Cargill et al. (1982) also suggested havesting the fruit at proper maturity because immature fruit require extra harvest force which increases the potential for trunk damage. Ethephon is now currently used to promote uniform fruit ripening and loosening for sour cherries and this has reduced the haverst force needed.

Temperature

The temperature of the air and the light incident on the tree trunk can have a dramatic effect on the temperature of the cambium. Jensen et al. (1970) noted that extreme temperature variations could occur in the cambium of peach and result in extensive injury. On a bright, sunny day, the temperature of the cambium can be significantly higher than the air temperature (as much as 27^{o}C higher). At night, the cambium temperature will be similar to that of the air. Because of this temperature stress, Jensen et al. (1970) observed vessel plugging in peach that resulted in decreased water flow from the roots. This caused an increased demand for water in the leaves and, if the stress was great enough, the trees would wilt and die.

Daniell and Crosby (1968) observed similar occlusion of xylem elements in peaches that had been artificially frozen in a bioclimatic chamber. Tissues of these trees were sampled the year following the freeze and xylem tissues were substantially plugged. In some cases, tyloses were so prevalent that some of the larger xylem elements were completely plugged. This experiment did not attempt to kill the trees, and the authors noted that injury of this type (to simulate winter damage) may limit the growth and yield of peach trees.

Ashworth et al. (1983) exposed apricot and peaches to differential thermal analysis where tissue samples were cooled at a rate of 20 °C per hour. Both apricots and peaches exhibited a strong correlation between exotherm temperature and xylem injury. Xylem tissue injury was caused by the freezing of supercooled water within the tissue. This occurred at temperatures corresponding to the low temperature exotherm.

Cain and Anderson (1979) observed that cultivar injury in cold stressed peaches is correlated to twig moisture content. They pointed out that much of the adsorbed water in twigs may be contained in large xylem vessels where it may cause little damage. In a subsequent experiment, Cain et al. (1980) observed that on the same cultivars of peach, xylem water froze more quickly than bark because it was less closely associated with the living protoplast. Xylem injury did not begin in acclimated peach twigs until -28.9 to -31.7 °C, and complete death did not occur until -37.2 °C. Cain et al. (1980) and Ashworth et al. (1983) noted that living xylem ray cells of peach undergo deep supercooling, which is an inherent mechanism for the tree to protect itself in extremely cold weather.

Wounding Responses

Carlson and Yu (1969) examined the effects of banding and scoring on one-year-old potted cherry trees. The trees were banded by fastening an aluminum strip around the trunk or scored (girdled) 5 centimeters above the graft union. They observed a swelling as an overgrowth above the scoring. When tissues above and below the wound were analyzed for starch content, there was no significant difference between trees that were banded or scored.

Heinicke (1932) ringed the stems of apple trees by removing a 5 millimeter wide strip around the bark. He noted that where the ring healed over, recovery of photosynthetic activity was apparent, but where healing did not occur, the photosynthetic efficiency of the shoot remained low and the leaves dropped.

Soe (1959) scored limbs of apple and pear trees and examined bark regeneration over time. Six to 9 days following scoring, new vascular cambium was regenreated and after 20 days the plants showed normal and regular development of xylem and phloem elements in the wound zone. The author suggested that callus formation was contributed by living cells of the vascular rays in the proximity of the cut.

Callus formation in Hibiscus rosa-sinensis where strips of bark had been removed took place in five distinct stages according to Sharples and Gunnery (1933):

1) extension of the outermost cells of the vascular rays after 2-3 days; 2) cell divisions near the ray ends, leading to the covering of the wound surface by a palisade-like layer of large globular cells; 3) further cell division and compaction at the seat of the callus; 4) establishment of a phellogen beneath the surface of the callus; and 5) after about 20 days, the differentiation of a new vascular cambium through the middle of the callus. They contended that the bark/wood callus developed mostly from medullary ray elements.

Noel (1968) cut 25 cm^2 bark sections from trunks of Trema orientalis Bl. These wound areas were either left alone or the borders were scraped to isolate the debarked area from the surrounding tissue. The new vascular tissue produced in the wound zone became continuous with the xylem and phloem above and below the debarked area when it was left alone but no connection resulted when the wound was scraped. The author noted that the vascular cambium differentiated in the middle of the callus and that healing occurred by extension of mounds of callus tissue by cell division in all directions. He suggested that vascular rays played a more important role than the vascular cambium in callus tissue formation and differentiation.

Biggs (1986a), used a cork borer to damage the bark tissue of scaffold limbs on peach trees. The wounds were then excised through the cambium using a larger cork borer. Microscopic examination revealed two types of tissue changes: 1) cell hypertrophy, lignification and suberization giving rise to an impervious boundary of non-living cells; and 2) subsequent differentiation of new phellogen beneath the boundary zone. Biggs (1986b) performed a similar experiment comparing wound responses of peach, apple and sweet cherry. He observed that wound responses were related to the degree days accumulated after wounding. The lignification in wounded tissues was fastest for apple, then sweet cherry and slowest for peach.

Mullick (1977) noted three non-specific autonomous responses to wounding for woody plants which included: 1) phellogen regeneration; followed by 2) vascular cambium regeneration; and finally 3) blocking of sapwood conductive tissues.

Martin and Snydor (1987) evaluated the rate of wound closure to the rate of twig growth and vigor in 12 tree species. They observed a poor correlation between wound closure rate and twig extension and suggested that twig extension was a poor parameter for predicting wound closure. In fact, wound closure rates were more closely related to species than twig extension or trunk caliper increase.

Wound Treatment

The use of different compounds to treat tree wounds has been well documented although one 'cure-all' compound has yet to be found. A brief history is described here to note the progress in this field. Shear (1936) used lanolin to treat wounds of apple trees. Because this material was non-toxic to plants and prevented wound desiccation, it provided great utility. When 5000 ppm indole - acetic acid was incorporated into a lanolin paste it stimulated callus proliferation from the cut surface of apple cuttings but not for pruning wounds.

Chadwick and Nank (1949) examined the effects of certain pruning practices and wound dressings on callusing of English elm wounds. Smaller wounds and wounds on limbs closest to 90 degrees angle to the trunk healed the most rapidly, especially for trees of high vigor. They noted that orange shellac was especially effective in stimulating callus growth of small wounds.

In an elaborate study for the Camouflage Branch of the U.S. Army, McQuilkin (1950) examined the effects of tree vigor, season of wounding, timing and type of wound treatment on wound healing in a number of native trees. After three years of data collection on 13,560 different wounds the author noted that no wound treatment significantly increased the rate of healing in any tree species tested. He did observe that wounds in the spring to vigorous trees healed faster than wounds occurring in other seasons. He suggested that lanolin provided an effective antidessicant for wounds.

Crowdy (1953) wounded apple trees with a 1 inch drill bit and then treated the wounds with a number of compounds in lanolin paste (4-chloro-3:5-dimethylphenoxyacetic acid, 2:4-dichlorophenoxyacetic acid and indolyl-3-butyric acid). An initial stimulation in the rate of callusing was observed, but soon thereafter, nontreated and treated wounds callused similarly.

Neeley (1970) wounded 10 year-old white ash, honey locust and pin oak trees and studied wound healing responses over three years. He noted that wounds in the spring healed better than any other time of the year. Wound dressings including shellac, latex house paint, petrolatum, asphalt emulsion and asphalt aerosol did not provide any appreciable benefit in increasing the amount or rate of wound healing.

Shigo and Wilson (1977) examined the effectiveness of different wound dressings on red maple and American elm trees. Orange shellac, polyurethane or an asphalt emulsion had no stimulatory effect on wound healing nor did they have better success in shielding pathogen attack than the untreated control. The authors went further to note that the asphalt dressing (most commonly used) was the worst and of no value because it kept moisture in the wound and actually promoted development of wood inhabiting microbes especially in the wound margin.

In light of the limited success or failure of many attempts to aid injured trees, it seems that wound treatment might provide little if any benefit.

PHOTOSYNTHETIC CHARACTERISTICS OF FRUIT TREES

Net photosynthesis (Pn - based on mass units) also referred to as CO_2 assimilation (A - based on molar units) plays a crucial role in fruit tree metabolism. The environmental and physiological regulation of photosynthesis in fruit crops has recently been reviewed by Flore and Lakso (1989). Photosynthesis in most fruit trees follows a diurnal pattern. Lakso and Seeley (1978) observed the maximum A rate for apples in the morning followed by a decrease in the afternoon. Crews et al. (1975) and Chalmers et al. (1975) noted a peak A rate for peach in the early hours of illumination, followed by a decline later in the day. Sams and Flore (1983) found a similar pattern for the A rate of sour cherry. The decline in A observed in the afternoon may be due to accumulation of carbohydrates which could affect stomata (Azcon-Bieto 1983). Although light intensity and relative humidity may remain the same during the late morning and early afternoon, the leaf temperature increases. This results in an increased vapor pressure gradient (VPG) between the leaf and the air which may affect stomatal conductance (Flore and Lakso 1989).

Crews et al. (1975) noted that the A rate of peaches increased throughout the season, to a maximum at harvest and then declined postharvest. Chalmers et al. (1975) hypothesized that A rate for peach may be partly controlled by the physiological needs of the tree. Fruit harvest reduced the sink for photosynthate, hence the photosynthate demand of the tree decreased and the A rate was reduced (Crews et al. 1975). Sams and Flore (1983) observed a gradual decrease in A rate of cherry towards the end of the growing season, and attributed this, in part, to leaf senescence. While working with peach, DeJong and Doyle (1985) noted that the seasonal changes between leaf N content (photosynthetic capacity) and light exposure corresponded to seasonal patterns of canopy development.

Early growth in the spring occurred at the expense of carbohydrate reserves accumulated during the previous growing season for apples (Hennerty and Forshey, 1971). They further observed that the photosynthetic production of apple leaves did not equal utilization until about six weeks after growth had begun.

FACTORS INFLUENCING PHOTOSYNTHESIS

The maximum A rate attained by a given leaf or tree occurs when all environmental conditions are above threshold levels. Many factors affect this environment. The abiotic factors that will be examined include the available light, carbon dioxide and temperature. The biotic factors that will be considered include diseases, insects and mites, simulated injury, fruit effects and cultural factors.

Light

In fruit trees, A rate is greatly influenced by the photosynthetic photon flux density (PPFD) reaching the foliage. Sams and Flore (1982) observed that the A rate of sour cherry increased hyperbolically with increasing PPFD. This same response has been observed for peach (Crews et al. 1975), apple (Watson et al. 1978), birch (Koike and Sakagami 1985) and poplar (Ceulemans and Impens 1980) to note just a few deciduous woody trees. Powles (1984) reported that at high PPFD's, beyond that needed for saturation, inhihition of A may result; he termed this photoinhibition. Flore and Lakso (1989) noted that the three most important points on the light response curve were the light compensation point, saturation point and maximum A rate. They also pointed out that photochemical efficiency (moles of CO_2 fixed per mole of photons absorbed) could be calculated from the linear portion of the curve when CO_2 is not limiting.

Light intensities vary during the day and during the season, but they also vary throughout the canopy of the tree. DeJong and Doyle (1985) and Chalmers et al. (1975) found that the photosynthetic capacity of peach was not uniformly distributed over the tree canopy. They showed that this capacity was directly related to the microenvironment surrounding the leaf. As shoot extension in peaches continued throughout the season, penetration of photosynthetically active radiation (PAR) generally decreased (Kappel and Flore 1983; Marini and Marini 1983). Marini and Marini (1983) also observed that PAR decreased from the periphery to the interior of the tree as well as from upper to lower levels within the tree canopy.

Crews et al. (1975) demonstrated that the total leaf area increased from the bottom to the top of the canopy of peach trees. Similarly, Marini and Marini (1983) observed that specific leaf weight and A rate increased from the inside to the periphery of the tree. Barden (1978) and Marini and Marini (1983) found that specific leaf weight and A rate were linearly related. Barden (1971) defined specific leaf weight as the dry weight of the leaf in milligrams divided by the leaf area in square centimeters (now referred to as specific leaf density).

The exterior leaves of apple trees are convoluted in shape, while the interior leaves are relatively flat providing an effective means of enhancing light penetration through the canopy of the tree (Lakso and Seeley, 1978). DeJong and Doyle (1985) defined shade leaves in peaches as those leaves that experience longer periods of shade than other leaves more exposed to the light. Marini and Marini (1983) observed that shaded interior leaves had a greater chlorophyll content and lower specific leaf weight than leaves at the periphery. This corresponded with data from Kappel and Flore (1983) on shading of peach. Kappel and Flore (1983) also observed that as shading increased, stem diameter of shoots decreased and leaves became more horizontal in orientation. If the light intensity at the periphery of the tree is optimal, shaded interior leaves will have a lower A rate because of inadequate light exposure.

Carbon Dioxide

If CO_2 is limited, A rate may be reduced. A direct curvilinear relationship between A rate and CO_2 concentration exists for sour cherries (Sams and Flore 1982), apple (Lakso and Seeley 1978, Watson et al. 1978), highbush blueberry (Moon et al. 1987) and bigtooth aspen (Jurik et al. 1984). Atmospheric carbon dioxide enrichment greatly stimulated seedling growth in apple (Lakso and Seeley 1978) and lodgepole pine (Higginbotham et al. 1985). The CO_2 compensation point is the CO_2 concentration at which gross photosynthesis equals photorespiration, hence net photosynthesis is zero. The CO_2 compensation point is approximately 69 ppm CO_2 for peach (Smith and Neales 1977) and 80 ppm for sour cherry (Sams and Flore 1982).

Temperature

Photosynthetic temperature response curves follow a parabolic pattern between 20 and 30^{o}C for many plants. Sams and Flore (1983) found that under light saturated conditions, sour cherries had the highest A rate at 25 ^{o}C. Under similar light conditions, Crews et al. (1975) observed that maximum A rate in peach occurred at 30 ^{o}C.

Lakso and Seeley (1978) found a range of optimal temperatures for apple leaf assimilation of 20 to 30 ^{o}C while Watson et al. (1978) found this range to be 16 to 26 ^{o}C . Avery (1977) tried to explain the range of values for apple leaf A rate by noting that poor airflow in the instrument measuring photosyntheisis could increase the leaf temperature above optimum, causing an increase in respiration and decrease in photosynthesis. The leaf-air vapor pressure gradient (VPG) usually increases as temperature increases and this may also affect A rate of some species (Flore and Lakso 1989).

Diseases

The photosynthetic capacity of a leaf can be influenced by diseases. Diseases that infect the leaf may be fungal, bacterial or viral. Smith and Neales (1977) examined the effects of virus infection of peach leaves. They observed a reduction in A rate and leaf growth of young peach leaves infected with the viruses causing peach rosette and decline disease (PRD). Smith and Neales (1977) presented a number of possible theories for the photosynthetic reduction in infected leaves: 1) decreased activity of enzymes associated with carboxylation processes; 2) chloroplast disruption; 3) lower chlorophyll content; and 4) greater retention of carbohydrate assimilates that could possibly inhibit photosynthesis. They concluded that the viruses had the greatest effect on leaf growth.

Spotts and Ferree (1979) found that apple scab infection from the fungus Venturia inaequalis caused a foliar stress in McIntosh leaves because of a lowered the leaf water potential. They observed a significant decrease in A rate of apple leaves 28 days after innoculation, and that the average percent of diseased leaf area exceeded the percent decrease in A. They hypothesized that the remaining healthy tissue of infected leaves may have increased A and partially compensated for the overall decrease in A resulting from scab infection.

Ellis et al. (1981) studied the effects of another fungus, Podospharea leucotricha, the causal agent of powdery mildew, on apple leaf A. This fungus had the greatest effect on A of young leaves, but all infected leaves had lower A and transpiration (E) rates plus a reduced carbohydrate content when compared with the noninfected control. They also found that if leaves were infected early in their development, they would never attain full photosynthetic capacity unless the fungus was eradicated. Smith and Neales (1977) noted that diseases reduce the amount of light penetrating the leaf and also permanently damage the leaf. However, low levels of infection of grape leaves with powdery mildew Unincula necator actually increased A (Lakso et al. 1982).

Insects and Mites

Insects and mites can have dramatic effects on the A rate of leaves because, in most cases, they feed directly on the leaves or they may introduce toxins to the tissue. In addition, some insects are also known to vector diseases from one plant to another.

Mites typically feed on the foliage and may reduce tree vigor. Hall and Ferree (1975) investigated the effects of two-spotted spider mite infestations on A of 'Franklin' apple trees. Nine days following infestation of 15, 30 and 60 mites per leaf, they observed reductions of A by 26, 30 and 43 percent, respectively, when compared to an noninfested control.

Spotted tentiform leaf miner (Phyllonorycter blancardella) is an important foliage feeding pest of apple trees. The larvae feed inside the leaf on the mesophyll and can substantially reduce the effective photosynthetic leaf area. Proctor et al. (1982) looked at five levels of injury (0,3,7,10 and 20 mines per leaf) caused by the spotted tentiform leafminer for the effects on net A rates of apple leaves. The lowest A rate occurred at the 3 mines per leaf treatment. This indicated that damage beyond this point was somehow compensated for by the leaf. Leaves injured by 20 mines per leaf, which corresponded to a 32.9 percent reduction in leaf area, had a photosynthetic reduction of only 23.2 percent. This ability of leaves to compensate for damage was also observed by Spotts and Ferree (1979) and Flore and Irwin (1983).

Childers et al. (1941b) caged 100 leafhoppers per leaf over a 'Stayman Winesap' apple whip for three days and observed a 23.2 percent reduction in A rate. They also noted that leafhopper injury, which typically occurs to apple early in the season, is permanent.

Simulated Leaf Injury

Several researchers have simulated insect injury to leaves and studied the effects on A (Poston et al. 1976; Ferree and Hall 1976; Proctor et al. 1982; Flore and Irwin 1983; Boucher et al. 1987). One useful application of insect injury simulation is to establish crop damage-yield relationships without pest populations present (Poston et al., 1976). Li and Proctor (1984) simulated pest injury on apple leaves by cutting the leaf midrib, pricking the lamina and by using a 250 °C iron. They observed the greatest reduction in A rate when the leaf midrib had been cut. Six midrib cuts caused an A reduction equivalent to an infection of 20 spotted tentiform leafminer mines per leaf.

Hall and Ferree (1976) used cork borers to remove a predetermined percentage of leaf area from apple leaves. 7.5, 10 and 20% leaf area loss (L.A.L.) resulted in no reduction, a nonsignificant reduction and a significant reduction in A rate, respectively. In grape (Boucher et al. 1987) and apple (Flore and Irwin 1983), up to 20% leaf area loss did not significantly reduce CO_2 assimilation.

Injury to the leaves in the form of many small holes had a greater impact on leaf A rate than equal leaf area removal from larger holes (Hall and Ferree, 1976; Li and Proctor, 1984). Ferree and Hall (1981) determined that as the number of lamina cuts per leaf in apple increased, so did the reduction of the A rate. They found that 24 cuts to the leaf had the same effect on A rate as 20 percent leaf area removal.

Poston et al. (1976) determined that both cork borer and paper punch defoliations are adequate simulations of insect damage in soybeans, but cuts made across the leaf midrib are not.

Fruit Effects

Both reproductive and vegetative growth are competitive sinks for photosynthates produced by a plant. Fruit has a significant effect on A rate of adjacent leaves; both DeJong (1986) and Chalmers et al. (1975) noted an increase in A of peach leaves during final swell (stage III). In sour cherry, leaves on shoots with fruit had a higher average seasonal A rate than those shoots without fruit (Sams and Flore 1983). Inconsistent or nonexistent fruiting effects have been observed for sour cherry (Gucci 1988) and sweet cherry (Roper et al. 1988) and it is likely that conditions causing source limitation (necessary for a fruiting effect) had not existed at the time of measurement (Flore and Lakso 1989).

Crews et al. (1975) demonstrated with peach that the closer the leaf to a fruit on a branch, the higher the A rate. DeJong (1986), also working on peach, noted that the primary effect of fruit on A was through effects on stomatal regulation of carbon dioxide and water exchange. According to Barden (1978), the A rates of apple leaves close to a fruit were higher than those situated further away from a fruit. In a review on apple by Lakso and Seeley (1978), it was noted that the presence of fruit increased the A rate, translocation and stomatal conductance, while lowering leaf respiration rates, starch levels and specific leaf weight. They further suggested that about 50 percent of the total daily translocation occurred during the photosynthetic period.

The presence of fruit can help to check excessive tree vigor by providing a substantial sink for photosynthates that may otherwise be directed to vegetative growth. Avery (1969), Hansen (1971) and Barden (1978) showed that cropping apple trees produced more total dry matter than noncropping trees. Overcropping may result in insufficient vegetative growth and reduced carbohydrate storage which may reduce hardiness levels and cause poor flowering and fruit set the following year.

Cultural Factors

Ferree (1978) listed several factors known to affect A rate in apples: pesticides (depending on nature of compound); growth regulators; air pollutants; herbicides; mineral nutrition; and shape and size of the tree. Water stress in the orchard also has an effect on A rate in apple (Avery, 1977). Hand et al. (1982) attributed reduced A of water stressed leaves to stomatal closure. When peach seedlings were exposed to a moderate water stress of -3.6 MPa, no permanent damage was observed. The A rate of these seedlings increased upon rewatering but this rate was dependant on the decrease in stomatal resistance.

Water stress caused by flooding can also influence the A rate. Childers et al. (1941a) observed reductions of A from 25 to 95 percent in apple after flooding for 15 and 30 days. These observations applied to trees growing in chambers in the greenhouse. A was reduced in highbush blueberries upon short-term flooding from a decrease in stomatal conductance (Davies and Flore 1986). Longer term flooding resulted in a decreased carboxylation efficiency of these leaves. Beckman et al. (1987) applied xylem exudates of flooded and nonflooded sour cherry plants to leaves of nonstressed plants. They observed an inhibition of A from the exudate of flooded plants suggesting that a photosynthetic inhibitor may be produced by the roots of flooded plants.

The cultivar and rootstock may or may not affect the A rate. Looney (1968) and Ferree and Barden (1971) observed that the A rate of apple leaves from a spur strain was higher than that for a standard strain. Ferree and Barden (1971) also observed a higher A rate in apple trees grown on a seedling rootstock when compared with a semidwarfing rootstock. Brown et al. (1985) did not observe any differences in A between M.9 and MM.111 rootstocks or between 'Red Delicious' and 'Northern Spy'.

Pinching (the removal of the tips of green growing shoots) and ringing (cutting through the bark completely around the shoot) both attempt to check excessive vegetative growth and accelerate fruit bud formation. Pinching and bark ringing, effect photosynthate distribution and A rate in apple (Mika and Antoszewski, 1973). The authors then fed leaves on shoots of apple trees (pinched or ringed) with $^{14}CO_2$ and studied the pattern of photosynthate distribution. They observed an approximate 50 percent reduction in A rate of shoots that had been pinched and ringed. Ringing alone led to an accumulation of photosynthates in the leaves of the ringed shoot which, in turn, caused a decrease in A rate. Pinching did not cause assimilate accumulation because assimilates were quickly utilized by axillary meristems, which were stimulated to grow by pinching. Ferree and Palmer (1982) observed that ringing of apple shoots at petal fall caused a decrease in A rate, but this had no effect later in the season.

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Section II

THE EFFECT OF SIMULATED TRUNK DAMAGE ON VEGETATIVE AND REPRODUCTIVE CAPACITY, TREE MORTALITY AND WOUND HEALING RESPONSE OF YOUNG, FRUITING SOUR CHERRY TREES

ABSTRACT

Trunk injury to sour cherry trees resulting from mechanical harvest, careless orchard implement use, freezing temperatures, animal feeding, boring insects and disease invasion can reduce tree vigor, productivity and orchard life. Simulated injury by bark removal or bark crushing up to 50% around the trunk circumference had little effect on tree vigor, productivity or mortality suggesting that the threshold level for one-time injury is quite high. Differential healing was observed to varying degrees depending on type of injury. Crushed bark that was left intact had the greatest healing. Callus production was rapid when bark was removed with a knife. Differentiated phloem observed in wound callus of trees with 100% bark removal, coupled with tree survival two years following injury, suggested that vascular reconnection occurred across some wounds. Wound treatment with grafting wax, asphalt emulsion, and chemicals including IAA, GA_{4+7}, 6-BA or PP-333 provided no benefit.

INTRODUCTION

Michigan is the largest producer of sour cherries in the U.S. and about ninety to ninety five percent of sour cherries in Michigan are harvested mechanically. However, with the advent of this technology, the average age of trees in orchards has decreased in the last 20 years (Cargill et al. 1982; Brown et al. 1984). Trunk or bark injury resulting from mechanical harvest are one of a number of factors contributing to the more rapid decline of sour cherry orchards observed today (Brown et al. 1984). Bark damage that results from tree shaking can be attributed to operator or mechanical error, high cambial activity (low bark strength) at time of harvest (Fridley et al. 1970) or use of excessive force to remove immature fruit (Cargill et al. 1982). Bark may be ruptured without disturbing the periderm and go unnoticed (Deiner et al. 1968) or bark separation may occur (Cargill et al. 1982) and in either case, vascular flow may be reduced. Trees with damaged bark are more susceptible to pathogens, since the wound provides a favorable environment for fungal or canker development (Fridley et al. 1970; Cargill et al. 1982).

Healing may occur depending on the size or severity of the wound, the time of year at which it occurs and the health and vigor of the tree. For example, wounds incurred in the spring will more likely heal (and more rapidly) than wounds occuring in late summer or fall

(McQuilkin 1950; Crowdy 1953; Wensley 1966; Neeley 1970). High vigor trees will heal wounds more rapidly than those of low vigor (Chadwick and Nank 1949; McQuilkin 1950; Wensley 1966).

Callus tissue develops in the wound zone as healing occurs. The vascular rays in close proximity to the cut surface contribute primarily to this callus proliferation (Sharples and Gunnery 1933; Soe 1959; Noel 1968). In some cases, vascular continuity above and below the wound has been reestablished as a result of vascular differentiation within the new callus tissue (Noel 1968).

Wound treatment with various compounds has had limited success. Grafting wax (Heinicke 1932), lanolin (Shear 1936), orange shellac (Chadwick and Nank 1949), growth regulators (McQuilkin 1950; Crowdy 1953), asphalt emulsion or latex paint (Neeley 1970) and even polyurethane (Shigo and Wilson 1977) provided no improved or accelerated rate of wound healing compared to untreated wounds.

The purpose of this study was: 1) to determine threshold levels of trunk damage that would be detrimental to vegetative and reproductive capacity and tree mortality of young fruiting trees; and 2) to describe the wound healing process in sour cherry.

MATERIALS AND METHODS

Plant material. All trunk damage experiments were conducted on sour cherry trees (*Prunus cerasus* L. cv. 'Montmorency' on Mahaleb rootstock). Three sites were utilized as follows: 1) H.R.C. - the Horticultural Research Center at Michigan State University, East Lansing. Trees were planted in 1983 in a single east-west oriented row at approximate 1 m spacing and soil type was a Miami loam (pH = 5.5-6.0). 2) T.R.C. - the Tree Research Center at Michigan State University, East Lansing. Trees were planted in 1982 in two east-west oriented rows at an approximate spacing of 3.0 x 6.0 m on a Miami loam soil. 3) C.H.E.S. - Clarksville Horticultural Experiment Station, Clarksville, Michigan. Trees were planted in 1982 in north-south oriented rows at two spacings of 3.0 x 6.0 m and 3.0 x 4.5 m on a Bixby sandy loam soil (pH = 5.9-6.1). Pesticides were applied according to commercial recommendations (Mich. Ext. Bul. E-154, Fruit Pesticide Handbook) and pruning, fertilization, and other cultural practices were performed according to standard practices.

Statistical calculations. Unless otherwise indicated, a randomized complete block design was used for all studies and trees were blocked for size by trunk cross-sectional area (Westwood and Roberts 1970). The number of replicate trees per treatment for each experiment are listed in table 1. All data were subjected to analysis of variance and treatment means were separated using Duncan'a Multiple Range Test. Data analysis was performed using SAS version 6.02 (SAS Institute Inc., Cary, N.C.).

Table 1. Location, date of treatment, tree age at treatment and number of replicate trees for simulated bark damage experiments.

EXPERIMENT	LOCATION	DATE	TREE AGE	REPS
Bark removal	H.R.C.	07/11/86	4	10
Bark compression	C.H.E.S.	07/22/86	5	7
Bark removal	C.H.E.S.	07/08/87	5	6
Type of injury	C.H.E.S.	07/07/87	5	6
Carbohydrate reduction	C.H.E.S.	07/10/87	5	6
Wound treatment	T.R.C.	07/03/87	5	6

Trunk Injury Treatments. Fifty trees were selected at H.R.C. based on vigor and uniformity. Trunk damage was simulated by removing a strip of bark 5 cm in height 0, 25, 50, 75, or 100 percent around the circumference of the trunk at a height of 15 cm from the bud union. All treatments were imposed using a sharp knife to make a defined cut to the cambium and then the bark was peeled off. The underlying tissue was left undisturbed. These same treatments were repeated in 1987 on thirty trees selected at C.H.E.S., except the wounds were imposed at a height of 30 cm from the bud union.

Compression damage was imposed in 1986 to trees at C.H.E.S. in the same orchard using an instrument developed by the Agricultural Engineering Department at M.S.U. which simulated tree shaker injury. This instrument (Brown et al. 1984) applied both clamping pressure and shear stress to a 14.3 mm diameter circular section of bark. A constant pressure of 50 - 55 p.s.i. (pounds per square inch) was maintained in the hydraulic cylinder and the bark and underlying cambium were crushed in a 5 cm long strip at a height of 30 cm from the bud union with damage treatments of 0, 10, 20 and 40% around the circumference of the trunk. The designated wound area was traced on the trunk and then bark compressions were made to completely fill in the wound area. The bark was left intact.

In 1987, two separate experiments were performed on sixteen trees each in this same orchard at C.H.E.S. using the same 30 cm wound height. The first experiment compared different types of injury 50% around the trunk circumference including: bark removal; bark compression (described above) where bark was left intact; or bark compression where bark was immediately excised.

In the second experiment all trees had 50% bark removal and then whole tree carbohydrate reduction was attempted using two techniques: 1) artificial shading to 20% of full sunlight for 7 weeks using shade cloth (as described by Kappel and Flore 1983); or 2) a one time application of 500 ppm Sinbar (a photosynthetic inhibitor) to the foliage on July 21, 1987. The light intensity inside the shade frame was 370 as opposed to 2000 μmol m^{-2} s^{-1} at noon under full light intensity (measured with a LI-COR LI-190S quantum sensor attached to a LI-COR LI1000 datalogger. LI-COR Lincoln, Nebraska). Net photosynthesis was measured for leaves sprayed with Sinbar and untreated leaves one week following application using the portable open gas exchange system equipped with a Parkinson broad leaf chamber (model ADC LCA-2, Analytical development Co., Hoddesdon, England) (see Davies and Flore 1986 for details). Net photosynthesis was measured under the following conditions: light intensity > 1700 μmol m^{-2} s^{-1}, ambient CO_2 of 340 μl l^{-1}, flow rate 0.4 l/min, inlet relative humidity 27% and leaf temperature range of 27 to 30^{o}C.

A third experiment was conducted in 1987 at T.R.C. where different types of wound treatment were applied to the trunks of trees that had had 100% bark removal by peeling. The same wound height of 30 cm above the bud union was used. The following materials were immediately applied to the wound in a one time application: grafting wax (Trowbridge's Grafting Wax, Walter E. Clark and Sons, Orange, Conn.), asphalt emulsion (Wilson Pruning Paste, Wilson Laboratories Inc., Dundas, Ontario, Canada), and one of either of the following growth regulators prepared at 1000 ppm in lanolin paste from the following stock solutions - gibberellic acid (GA_{4+7} - 50 w.p. I.G.I Americas Inc., Goldsboro, N.C.), 6-benzyladenine (6-BA - 2% w/w, Abbott Laboratories, Chicago, Ill.), indole acetic acid (IAA - 2% w/w, Abbott Laboratories, Chicago, Ill.) or paclobutrazol (PP-333 - 2% w/w, Abbott Laboratories, Chicago, Ill.).

Non structural carbohydrates. Bark tissue was collected on Nov. 17, 1987 from trees at H.R.C. using a 16 mm cork borer by sampling to the xylem. Only the 100% and 0% bark removal treatments were sampled. Five disks were collected above and 5 below the wound for the 100% bark removal treatment and 5 at the approximate wound height on the 0% bark removal trees. Five replicate trees representing each of the TCA size categories were sampled for each treatment. The protocol as described by Gucci (1988) was used. Briefly, samples were immediately transported to the laboratory and freeze dried for 72 hours in a Virtis 10-010 freeze drier (Virtis Inc., Gardiner, New York). Tissue was then removed and samples were ground in a Wiley mill, passed through first a 20 mesh and then a 40 mesh screen. Four 100 mg subsamples of each sample were weighed out on an analytical balance (Mettler AE 163 Mettler Instruments AG, Griefensee, Switzerland), and extracted 4 times each for 20 minutes in 2 ml of 80% ethanol. The homogenates were centrifuged at 1500 rpm (Glc, Sorvall, Connecticut) for 5 minutes after each extraction. The supernatant was used for soluble sugars and the pellet for starch determination.

For determination of soluble sugars (sorbitol, fructose, glucose, inositol and sucrose) the supernatants were transfered into 100 ml round bottom flasks, evaporated to dryness using a rotary vacuum evaporator in a water bath at 40°C, and the residuestored overnight in a dessicator. The samples were converted into oximes (Roper et al. 1988) and derivatized to tri-methylsilyl ethers (Sweeley et al. 1963). Standards for sorbitol, fructose, glucose, sucrose, and inositol were prepared by dissolving 0.25 g of the first four compounds in 50 ml of 80% ethanol and 0.1 g of inositol in 25 ml of 50% ethanol, then combining the two solutions and drying 0.5 ml aliquots in a stream of nitrogen at room temperature. Standards were derivatized in the same way as the samples. Analyses were performed using a dual column, temperature programmed Varian 3700 gas chromatograph (Varian Associates, Inc., Sunnyvale, California) with a flame ionization detector and 3% OV-17 on 80/100 mesh chromsorb WHP in 2 mm x 2 m glass column. Temperature was programmed from 150°C to 250 °C at a rate of 5°C per minute. Quantity was calculated by peak area using the internal standards with a Spectra Physics SP4100 integrator (Spectra Physics, San Jose, California). Two separate 1 μl injections were made for each sample and results were averaged. Soluble sugars were expressed as mg/100 mg dry tissue.

Starch was measured in the pellet remaining after extraction with 80% ethanol using the method of Roper et al. (1988) modified as follows. Samples resulting from incubation at 55°C for 16 hr with amyloglucosidase were diluted with distilled water to 15 ml and three 0.25 ml aliquots from each sample were assayed colorimetrically using glucose oxidase (Sigma Tech. Bull. 510; EC 1.1.3.4). Absorbance at 440 nm was read with a Shimadzu UV-Vis 260 spectrophotometer (Shimadzu Corporation, Kyoto, Japan).

Cold hardiness. Deep winter hardiness was evaluated for current season shoots from trees at H.R.C. that were sampled Feb. 8, 1987 and evaluated according to methods of Bittenbender and Howell (1974). Four shoots were randomly selected from each of 20 trees representing all treatments. Shoots were cut into two inch sections and then subjected to a controlled temperature reduction in a freezing chamber. Samples were exposed to temperatures ranging from -20 to -40°C and then visually evaluated for xylem browning. T_{50} values, or the temperature (°C) required to kill half of the samples, were determined for each treatment.

Anatomical examination. Bark tissue was sampled on March 24, 1987 as a 7 x 0.5 cm strip of bark (to the xylem) starting immediately above, then passing completely through the wound callus, and finally into the bark below the wound. Five trees were sampled where callus had completely filled in the wound area during the season of injury. The plant material was fixed in FAA (formalin acetic acid), imbedded in paraffin according to Johansen (1968), serially sectioned to 13 um using a Spencer 820 microtome (American Optical Company, Instrument Division, Buffalo, New York) and then stained with safranin and fast green. Sections were examined with a Zeiss Photomicroscope II at 250X magnification and photographs were taken using Kodak Panatomic X (32 ASA) film.

Reproductive and vegetative growth determinations. Wound healing was rated in the fall of 1986, 1987, and 1988 when terminal growth had ceased. The amount of callus tissue present was visually determined as a percent of the total wound surface (eg. a wound half filled in with callus tissue was rated 50% healed).

Trunk cross-sectional area (TCA) was calculated from the average of two perpendicular trunk diameters measured by a vernier caliper, for all trees wounded in 1986 (see above) both at the time of injury (July 11-22, 1986) and in late fall (Nov. 15-17, 1986) immediately above and below the wound. Change in TCA, or trunk growth, was calculated for all trees for the year of injury.

Current season shoot growth was measured for eight shoots per tree (Oct. 26,1986) for all trees at H.R.C. and average shoot growth was determined. For all trees that were wounded in 1987 at C.H.E.S. and T.R.C. shoot growth of 10 shoots per tree was measured and average shoot growth determined on July 14, 1988, after terminal buds had set.

Fruit set was determined as the number of fruit per cm^2 area at the base of two branches on opposite sides of each tree the season following injury (May 21 - June 2, 1987) for all trees wounded in 1986. On July 6, 1987, 25 fruits per tree for the 0 and 100% bark removal treatments at H.R.C. were measured for fruit retention force (using a pull force guage which measures the amount of force in grams to separate the fruit from the pedicel). Average fruit weight per tree was also calculated. Percent soluble solids were determined for each fruit using a portable refractometer (Carl Zeiss, model 1808).

Copious wound gumming and watersprouts (or suckers) developed below the wound in trees with chemical treatments (at T.R.C.) and they were scored on a scale of 1 (none) to 5 (copious) on Aug. 20, 1987. Tree mortality was determined for each treatment on Aug. 2, 1988 as the number of dead trees per treatment expressed as a percent.

All trees wounded in 1987 at C.H.E.S. were harvested the following summer on July 6, 1988. Fruit yield was based on the average fruit weight (kg) per tree. Data were not collected for trees at T.R.C. because fruit dropped prematurely or they were eaten by birds.

RESULTS

H.R.C. bark removal experiment (1986). Bark removal level had no significant effect on wound healing in the year of injury (1986) or in the two subsequent years of evaluation (Table 2). The highest healing percentage was consistently observed in the trees with 100% bark removal. Healing progression for one tree with 100% bark removal is shown in Figure 1. Deep winter cold hardiness and shoot growth the season following injury was only reduced in those trees with 100% bark removal (Table 2). Fruit set the season following injury was not affected by any level of bark removal. Change in TCA above the wound from trees with 100% bark removal was significantly greater than below the wound (Table 3). Both sorbitol and starch significantly accumulated in the bark tissue above the wound for trees with 100% bark removal. Glucose, fructose or inositol content of these tissues was not affected. No significant differences existed between the 0 and 100% treatments for fruit retention force (mean value 55 g) or fruit weight (mean value 3.5 g). Percent soluble solids were slightly higher in the uninjured trees (16%) than those with 100% bark removal (14.7%). Phloem sieve tube cells were found in callus tissue that closely resembled those in bark tissue (Figure 2). It is also interesting to note that there was no tree mortality after two years for this experiment (data not shown).

C.H.E.S. bark compression experiment (1986). No significant swelling was observed above the wound in these trees at the end of the season of injury (Table 4). Fruit

Table 2. The effect of bark removal on healing, cold hardiness, shoot growth, and fruit set of sour cherry trees at H.R.C.

Bark removal (%)	Healing 1986 (%)	Healing '86-'87 (%)	Healing '86-'88 (%)	Cold hardiness (T_{50}) 1987	Shoot growth (cm) 1987	Fruit set ($\#/cm^2$) 1987
0	-	-	-	-29.0 a	25.5 a	0.75
25	48.5	71.5	76.4	-29.4 a	25.1 a	0.96
50	58.5	69.0	74.0	-28.9 a	23.6 ab	0.88
75	53.0	72.0	74.4	-28.1 a	24.9 a	0.93
100	71.3	79.0	83.5	-25.6 b	19.3 b	0.93

Means followed by different letters, within columns, are significantly different (P = 0.05) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Wound healing was rated as the % of the wound area filled in with callus tissue by September (for each year noted) when growth had ceased. Current season shoot growth was sampled and evaluated for cold hardiness on Feb. 8, 1987. Shoot growth was measured for eight shoots per tree on Oct. 26, 1987 after terminal bud set. Fruit set was determined from the number of fruit per cm^2 area of two branches per tree on May 21, 1987. Each value is the mean based on 10 replicate trees per treatment.

Table 3. The effect of 100% bark removal on trunk bark characteristics of sour cherry trees at H.R.C.

Bark removal (%)	Change in TCA (mm^2)	Sorbitol content (mg/100 mg)	Starch content (mg/100 mg)
0 - Control	462 b	0.74 b	1.03 ab
100 - Above Wound	761 a	1.18 a	1.21 a
100 - Below Wound	383 b	0.84 b	0.77 b

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Change in trunk cross-sectional area (TCA) was determined from the difference in area (mm^2) from harvest date (July 11, 1986) to Nov. 11, 1986. Sorbitol and starch content was based on 100 mg tissue samples. TCA values are means of 10 replications while sorbitol and starch values are means of 5 replications.

Figure 1. Wound healing progression of a tree with 100% bark removal at H.R.C. Photographs were taken on: (a) July 11, 1986 (date of treatment); (b) July 28, 1986; (c) Sept. 16, 1986; and (d) a year later on Sept. 16, 1987.

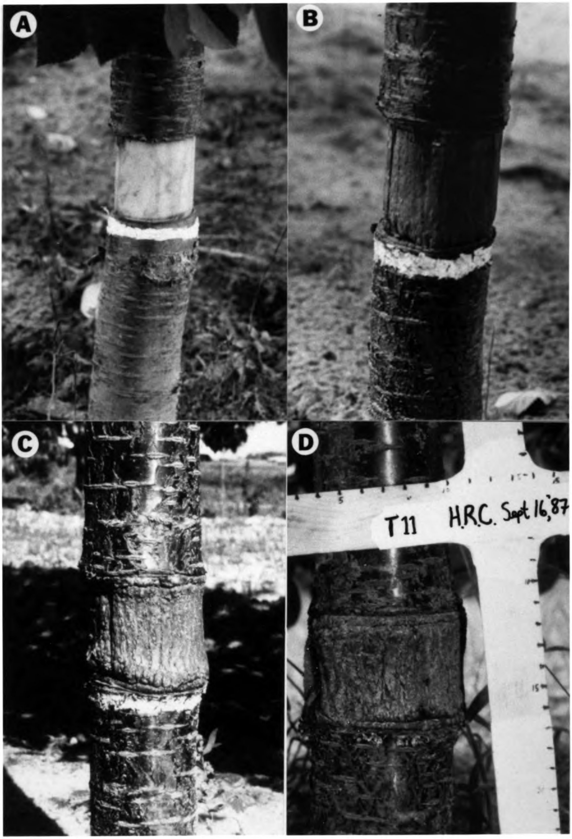

A
B
C
D
T11
H.R.C. Sept 16,'87
5
10
15

Figure 2. Cross - sections through sour cherry (a) noninjured bark and (b) callus tissue illustrating presence of sieve plate and pores of phloem sieve tube cells (magnified 250X).

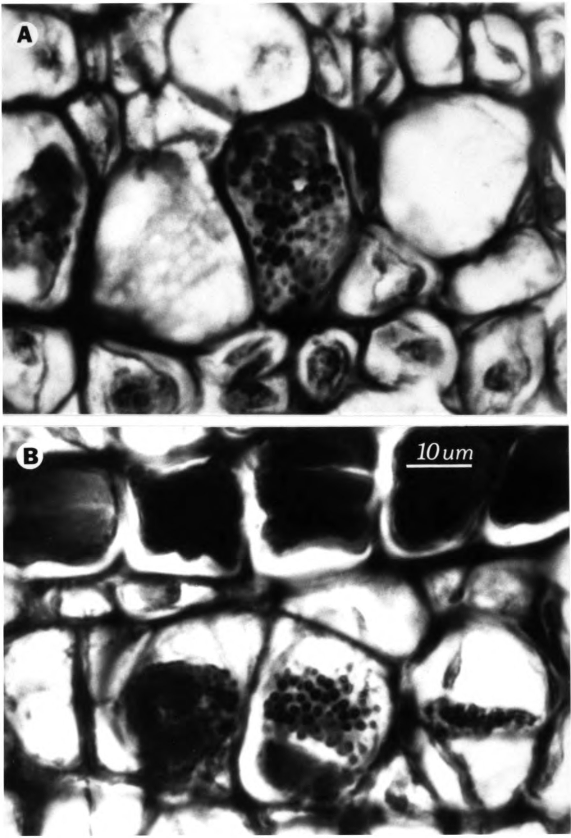
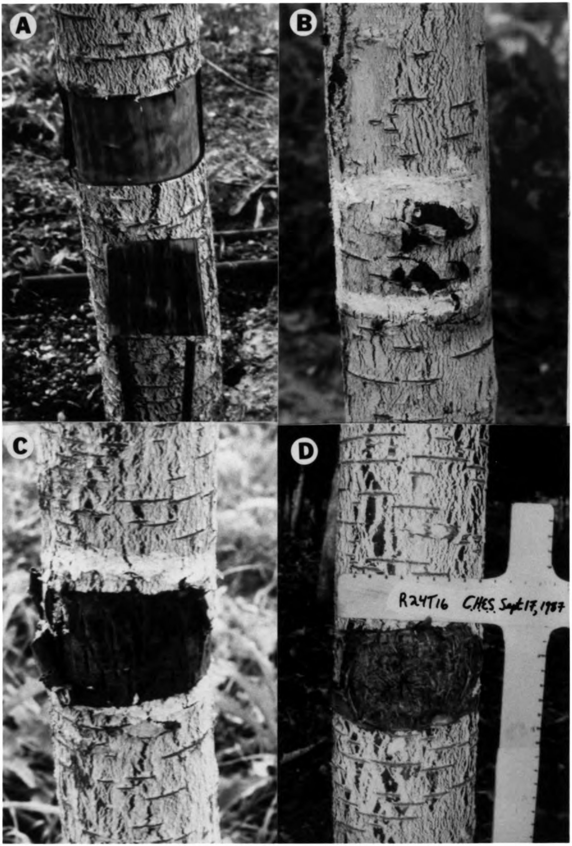

A
B
10 um

Figure 3. The bark compression instrument developed by the Ag. Engineering Department at M.S.U. attached to a cherry tree trunk with the plunger compressing bark at 55 p.s.i.

Figure 4. Photographs of injury from bark compression instrument: (a) immediately after bark compression 50% around the trunk circumference when bark was excised (note browning of exposed wood and peeled off bark below); (b) immediately following bark compression 40% around the trunk circumference on July 22, 1986; (c) tree in (b) on Aug. 5, 1986; (d) tree in (b) on Sept. 17, 1987 (note that periderm and outer bark have fallen off wound at this time).


A
B
C
D
R24T16 C.H.E.S. Sept 17, 1987

set the season following injury was not significantly affected by bark damage treatment at these levels. Bark was peeled back from wounds at the end of the summer in 1987 and all wounds were completely healed. The bark compression instrument is shown in Figure 3. Photographs of one tree with 40% bark compression, taken at different dates following injury are presented in Figure 4.

C.H.E.S. bark removal experiment (1987). Wound healing was not affected by tree size or bark removal level in the season of injury or the year following injury (Table 5). Average shoot growth was significantly reduced by bark removal level. In fact, shoot growth was reduced at all levels of injury. For trees with 100% bark removal, shoot growth was reduced by over 470% when compared to the uninjured trees. Fruit yield significantly increased in trees with 75% bark removal. No significant differences in yield were observed between the 0, 25, 50 or 100% bark removal treatments. By the end of the season following injury, half of the trees at the 100% bark removal level were dead (Table 5).

C.H.E.S. type of injury experiment (1987) Wound healing was dramatically affected by the type of bark damage during the season of injury (Table 6). Bark compression followed by immediate excision produced essentially no wound callus. One tree with this treatment in shown in Figure 4a immediately following treatment. By leaving the

Table 4. The effect of bark compression (percent around the trunk circumference) on TCA of the trunk and fruit set of sour cherry trees at C.H.E.S.

Bark compression (%)	TCA Change above wound (mm^2)	TCA Change below wound (mm^2)	Fruit set ($\#/cm^2$) 1987
0	29.4	29.4	0.90
10	25.9	25.7	0.93
20	23.9	25.3	0.98
40	24.0	25.6	0.80

Means followed by different letters, within columns, are significantly different (P = 0.05) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Change in trunk cross sectional area (TCA) was determined from the difference in area (mm^2) from date of compression (July 22, 1986) to Nov. 15, 1986. Fruit set was determined from the number of fruit per cm^2 area of two branches per tree on June 2, 1987. Each value is the mean based on 7 replicate trees per treatment.

Table 5. The effect of bark removal on healing, shoot growth, yield and tree mortality of sour cherry trees at C.H.E.S.

Bark removal (%)	Healing 1987 (%)	Healing '87-'88 (%)	Shoot growth (cm) 1988	Fruit yield (kg/tree) 1988	Tree Mortality (%) 1988
0	-	-	31.0 a	9.1 bc	0 a
25	28.3	39.2	25.3 b	9.1 bc	0 a
50	15.0	32.5	26.1 b	8.7 bc	0 a
75	10.0	20.0	17.3 c	13.6 a	0 a
100	29.1	31.7	6.6 d	5.9 c	50 b

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Wound healing was rated as the % of the wound area filled in with callus tissue by September (for each year noted) when growth had ceased. Shoot growth was measured for 10 shoots per tree on July 14, 1988 after terminal bud set. Yield was based on the average fruit weight (kg) per tree on July 6, 1988. Each value is the mean of 6 replicate trees per treatment.

bark intact after crushing, over 83% of the wound zone had filled in with callus tissue. Bark removal resulted in healing of only half of the wound zone on average. Wound healing the season following injury increased slightly for all trees primarily due to callus swelling. Average shoot growth was higher the season following injury in trees that had demonstrated the poorest healing response. Regression analysis of 1988 shoot growth versus 1987 wound healing demonstrated no significant relationship between these two factors ($r^2 = -.36$). Fruit yield the season following injury was not significantly affected by the different types of damage.

C.H.E.S. carbohydrate reduction experiment (1987). Wound healing was not significantly affected by method of carbohydrate reduction in the season of injury or the next year (Table 7). All trees healed poorly. Net photosynthesis was not significantly reduced in leaves that were treated with 500 ppm Sinbar one week following treatment. This may in part be due to a heavy mite infestation. Interveinal browning was observed on these leaves though suggesting that some damage had resulted. Carbohydrate levels of these trees were not measured so it is not possible to verify if treatments affected these levels. The average shoot growth the season following injury was not affected. There was no significant relationship between wound healing in 1987 and avg. shoot growth in 1988 ($r^2 = -.08$). Yield was significantly

<u>Table 6.</u> The effect of different types of bark injury on healing, shoot growth, and yield of sour cherry trees at C.H.E.S.

Injury treatment	Healing 1987 (%)	Healing '87-'88 (%)	Shoot growth (cm) 1988	Fruit yield (kg/tree) 1988
50% Bark Removal	45.0 b	66.7 a	16.2 b	5.1
50% Bark Compression	83.8 a	91.7 a	14.4 b	5.0
50% Bark Compression + Excision	5.8 c	22.5 b	19.4 a	4.4

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Wound healing was rated as the % of the wound area filled in with callus tissue by September (for each year noted) when growth had ceased. Shoot growth was measured for 10 shoots per tree on July 14, 1988 after terminal bud set. Yield was based on the average fruit weight (kg) per tree on July 6, 1988. Each value is the mean of 6 replicate trees per treatment.

Table 7. The effect of tree shading and Sinbar application on healing, shoot growth and yield of sour cherry trees at C.H.E.S.

Treatment	Healing 1987 (%)	Healing '87-'88 (%)	Shoot growth (cm) 1988	Fruit yield (kg/tree) 1988
None	16.7	31.7	26.3	6.6 b
Shading (20% full sun 7 weeks)	21.7	34.1	25.1	11.1 a
500 ppm Sinbar	3.3	21.7	27.6	6.6 b

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Wound healing was rated as the % of the wound area filled in with callus tissue by September (for each year noted) when growth had ceased. Shoot growth was measured for 10 shoots per tree on July 14, 1988 after terminal bud set. Yield was based on the average fruit weight (kg) per tree on July 6, 1988. Each value is the mean of 6 replicate trees per treatment. Note that a heavy mite infestation occurred in these trees shortly after bark removal.

higher the season following injury in trees that had been shaded.

T.R.C. wound treatment experiment (1987) Percent wound healing was not significantly affected by wound treatment in the season of injury (1987) or the following year. Since no new callus was produced in 1988, only the wound healing data were presented for 1988 (Table 8). All trees were rated for wound gumming and suckering (from just below the wound). The greatest wound gumming resulted with the IAA treatment whereas the greatest suckering for the 6-BA treatment. There was essentially no shoot growth the year following injury. Tree mortality was lowest for nontreated trees and highest for those trees treated with IAA, 6-BA and grafting wax. Premature fruit drop prevented harvest data collection the season following injury. This may have been the result of bird damage.

DISCUSSION

All bark injury treatments coincided with the approximate time of commercial harvest. Bark 'slip' was observed at all sites because bark easily separated from the xylem tissue underneath. It is possible that the high cambial activity resulted in a low bark strength at wounding date (Cargill et al. 1982).

The reader is advised that trees used in these experiments were young, fruiting trees from 4 to 5 years old at treatment date. Older commercial trees were not

Table 8. The effect of wound treatment on healing, gumming, suckering, shoot growth and mortality of sour cherry trees at T.R.C.

Wound Treatment	Healing 1988 (%)	Wound Gumming 1987	Suckering 1987	Shoot growth (cm) 1988	Tree mortality (%) 1988
none	19.2	2.5 cd	2.0 b	0.33	33 b
1000 ppm IAA	6.7	4.5 a	2.0 b	0.50	100 a
1000 ppm GA_{4+7}	0.8	2.2 d	1.7 b	0.90	67 ab
1000 ppm 6-BA	1.7	3.7 ab	3.8 a	0	100 a
1000 ppm PP-333	15.8	2.5 cd	2.5 ab	0	67 ab
Asphalt Emulsion	22.5	4.2 ab	3.2 ab	1.88	67 ab
Grafting Wax	0	3.3 bc	3.3 ab	0	100 a

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Wound healing was rated as the % of the wound area filled in with callus tissue by Aug. 2, 1988. Wound gumming and suckering were rated on Aug. 20, 1987 on a visual scale from 1 (none) to 5 (copious). Shoot growth was measured for 10 shoots per tree on July 14, 1988 after terminal bud set. Mortality was expressed as the number of dead trees per treatment on Aug. 2, 1988. Each value is the mean of 6 replicate trees per treatment.

evaluated in this study.

Since the wounding response in the trees from the bark removal experiment at H.R.C. (1986) was so dramatic, it was decided to repeat the experiment at a different site - C.H.E.S. (1987). It should be noted that the trees at the two sites were very different. The trees at H.R.C. were planted in one row, received no irrigation or fertilization and were low in vigor as measured by TCA and shoot growth. Trees at C.H.E.S. were one year older, much larger, planted at commercial density, fertilized, irrigated, sprayed for pests and pruned regularly. The latter were typical of young, fruiting commercial sour cherry trees in Michigan. Although trees at H.R.C. were under considerably more stress than those at C.H.E.S., they healed wounds to a much greater extent. At the end of the season of injury, the average wound healing percentage of the trees at H.R.C. was 58% but only 21% for those at C.H.E.S. (Tables 2 and 5). Two years after treatment, all trees at H.R.C. remained alive while only one year after treatment at C.H.E.S., half of the trees at the 100% bark removal level were dead (Table 5). Remarkably though, at both sites, up to 75% bark removal did not kill any trees through the 1988 growing season, indicating a tremendous threshold to one-time simulated injury. Greater wound repair in trees at H.R.C. may have resulted from greater available carbohydrate. Fruit load was much less than in trees at C.H.E.S. so competition between wound repair and reproductive efforts may have been less.

Differentiated vascular tissue (phloem sieve tube cells) was observed in callus tissue from wounded trees at H.R.C. (Figure 2b) and because all trees are still alive today, it is likely that vascular continuity across the wound was reestablished (Noel 1968). The greatly reduced callus production at C.H.E.S. likely resulted in a reduced regain of vascular capacity compared to trees at H.R.C.

At both sites, as TCA increased for trees of the same age, wound healing increased. This is supported by work of Chadwick and Nank (1949), McQuilkin (1950) and Wensley (1966) who all observed an enhanced wound healing response in trees with higher vigor.

Shoot growth is an indicator of vigor for sour cherry trees (Kenworthy 1974). Comparing shoot growth at the two sites the season following injury (Tables 2 and 5), it appeared that the trees were of similar vigor. The effect of bark removal on shoot growth was much more pronounced at C.H.E.S. than at H.R.C. Trees at C.H.E.S. produced less callus so the available vascular tissue for transport was reduced and they also had a much heavier crop than trees at H.R.C. the year of injury. These two factors may have further contributed to the observed differences.

Although deep winter hardiness was slightly reduced for shoots of trees at H.R.C. where 100% bark removal had been performed (Table 2), the recovery from wounding stress resulted in little difference in hardiness from uninjured trees. The acclimation or hardening of tissue to low temperature (Flore and Howell 1987) appears to have been unaltered in these trees.

Fruit set was unaffected by bark removal at H.R.C. (Table 2) and at harvest, so was fruit removal force (g) and average fruit weight. This suggests that bark removal had no effect on carbohydrate supply to fruits because fruit ripening was unaffected (Kenworthy, 1974). Flore (1980) noted that reduction in carbohydrate supply by shading at the end of stage I or II of fruit develpoment delayed maturity as indicated by higher fruit retention force in sour cherry. Fruit yield at C.H.E.S. (Table 5) was only significantly affected by 75% bark removal which caused a yield increase of 150% relative to the noninjured trees. The higher yield for these trees likely occurred at the expense of wound healing and shoot growth (table 5). Kenworthy (1974) noted that trees with reduced vegetative growth had more flower buds. These results are also similar to that observed when stems are ringed to check vegetative growth and stimulate flower bud formation (Mika and Antoszewski 1973).

Both starch and sorbitol accumulated significantly above wounds for trees at H.R.C. with 100% bark removal. Translocation to the roots was likely arrested since the phloem had been severed by bark removal. This sorbitol and starch accumulation led to tissue swelling, observed as a significant change in TCA above the wound (Table 3). Sorbitol, a sugar alcohol, is the major transported photosynthetic product in many members of the Rosaceae family including sour cherries (Loescher 1987).

In the future, it would be interesting to compare mature sour cherry trees of the same age and vigor at the same site for wound healing response influenced by one factor (e.g. fertility) where other variables could be controlled as in the study by McQuilkin (1950).

Bark compression at 10, 20 and 40% using the portable tester (Brown et al. 1984) did not effect trunk growth or fruit set the following year for trees at C.H.E.S. (Table 4). These small amounts of injury probably presented very little stress to the vigorous, healthy trees. Bark was left intact in these trees and complete wound repair was observed for all trees the following year.

Trees were compared in 1987 at C.H.E.S. for different types of bark injury at the 50% level. It was hypothesized that the exposure to air of a wound with a defined margin would promote healing. Xylem browning (Figure 4a) and a complete lack of callus production (Table 6) suggested that this was not the case for sour cherry. Wound healing occurred to the greatest extent when injured bark was left intact. Cambial/xylem desiccation may have resulted in these injured trees leading to greatly limited callus production because of vascular ray death (Sharples and Gunnery 1933; Soe 1959;

Noel 1968). Shoot growth was only slightly affected and fruit yield was unaffected the season following injury suggesting that different types of injury halfway around the trunk circumference have similar effects (Table 6).

To examine the effect of tree carbohydrate supply on healing of a standard wound (50% bark removal) trees were shaded (Kappel and Flore 1983: Jackson and Palmer 1977) or sprayed with the herbicide Sinbar. A heavy mite infestation occurred and a reduction in CO_2 assimilation was not observed in Sinbar treated leaves (although visual leaf browning did occur). Mite feeding has been observed to significantly reduce photosynthesis in apple trees (Hall and Ferree 1975) and it is possible that the infestation was severe enough that the Sinbar treatment had no effect. None of the carbohydrate reduction treatments significantly affected wound healing (Table 7). Average shoot growth was not affected the year following injury but fruit yield almost doubled for trees that had been shaded the year before. It is possible that whole tree carbohydrate was not reduced by any of these treatments but this was not verified.

Wound treatment did not stimulate wound healing in sour cherry (Table 8). Grafting wax completely inhibited callus production in cherry but this was not observed for apple shoots which had been ringed by removal of a 5 mm strip of bark (Heinicke 1932). All trees treated with grafting wax died the season following injury. Shigo and

Wilson (1977) and Neeley (1970) observed limited wound healing with asphalt emulsion. Although one asphalt emulsion treated wound healed completely, most produced no callus at all and a year later, 66% of these trees were dead (Table 8). Paclobutrazol (PP-333) has been used as a growth retardant in apple seedlings (Steffens and Wang 1984; Quinlan and Richardson 1984; Williams 1984). The primary mode of action of PP-333 is as a sterol synthesis inhibitor but in this case it was hypothesized to redirect carbohydrate from roots to the wound site rather than shoots. Enhanced wound healing was not observed in the presence of this compound. Shoot growth of these trees the season following injury was completely arrested and two thirds of the trees died. The auxin, gibberellins and cytokinin treatments also offered no significant benefit. Shear (1936) used 5000 ppm of IAA in lanolin to treat apple cuttings and observed stimulated callus proliferation but did not observe this on intact plants nor was it observed in sour cherry here. The lowest mortality the season following injury occurred in trees with wounds that were not treated. Again, the present study confirms work of others (Shear 1936; Chadwick and Nank 1949; McQuilkin 1950; Crowdy 1953; Neeley 1970; Shigo and Wilson 1977) that suggested that wound healing was not stimulated by the use of wound treatment compounds.

The damage level selected for this experiment (100% bark removal) was probably too severe. The decision to use this treatment was based on the dramatic wound healing that was observed in 1986 at H.R.C. Because essentially no wound callus was produced in the season of injury and since the phloem had been severed, carbohydrate translocation to the roots was likely disrupted. These trees may have entered the winter poorly acclimated and suffered winter injury (Flore and Howell 1987) or, in the spring when carbohydrate supply reserves were to be mobilized from the roots for shoot development, the reserve may have been insufficient. One year following injury, 76% of all trees were dead in this wound treatment experiment. Trees may not have had enough reserve carbohydrate to heal wounds and the lack of irrigation at this site coupled with the severe drought conditions of the summer of 1988 in the midwest U.S. resulted the death of many trees.

Until experiments such as these are conducted on older, commercial trees, it is unwise to extrapolate these results to the commercial situation. Mechanical harvest injury which may occur annually in a commercial orchard may not heal as well as the one-time injury to trees in these experiments. Commercial trees have a much larger crop load than occurred in these trees and this may also affect wound healing. However, valuable information has been obtained by this study. Wound healing can occur rapidly and in copious amounts in young trees. Also, vascular continuity may have been reestablished in trees with 100% bark removal. Bark compression or removal halfway around the trunk circumference had no significant effect on vegetative or reproductive capacity or tree mortality of young, fruiting trees. In fact, all trees at C.H.E.S. with 75% bark removal remained alive one year later suggesting that the threshold for one time injury in young, fruiting trees is very high. Removal of injured bark and wound treatment provided no benefit in these trees.

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Section III

THE EFFECT OF SIMULATED PEST INJURY TO LEAVES OF SOUR CHERRY (*Prunus cerasus* L. 'Montmorency') ON PHOTOSYNTHESIS AND DRY MATTER ACCUMULATION

ABSTRACT

Injury to the foliage of sour cherry trees results from a number of stresses including mite and insect feeding, disease invasion, pesticide toxicity, herbicide drift, air pollution, nutrient deficiency, drought and hail or wind damage. Leaf area removal (L.A.R.) by holepunching was used to determine leaf damage thresholds for sour cherry. Thirty percent L.A.R. across lateral veins caused a significant reduction in net carbon dioxide assimilation (A) that was permanent. Removal of up to 20% of the leaf area caused an initial decline in A but recovery and an increased A was observed as early as 4 days following L.A.R. Photosynthetic rate of the uninjured tissue increased and compensated for up to 20% L.A.R. and was maintained for over 3 weeks. Dry weight accumulation of greenhouse grown plants was not significantly reduced by removal of up to 20% of the whole plant leaf area over a 5 month growing period.

INTRODUCTION

Injury of sour cherry foliage may occur as a result of various abiotic and biotic stresses. These include air pollution, wind or hail damage, pesticide toxicity, herbicide drift or mite and insect feeding and invasion by fungi, bacteria or viruses. As a result, parts of a leaf may become nonfunctional, or whole leaves may abscise, which reduces the potential photosynthetic capacity of the tree.

Leaf injury resulting from stress has been well documented for various fruit crops. Flower bud number, trunk girth and yield of 'Cortland' apples were reduced the year following a heavy mite infestation (Lienck et al. 1956). Briggs and Avery (1968) noted reduced shoot extension and tissue dry weights of apple trees following an infestation with red spider mites (Panonychus ulmi Koch.). As few as 15 mites per leaf caused a 26% reduction in net photosynthesis (Pn) on 'Franklin' apple leaves (Hall and Ferree 1975) and a 23% reduction in Pn of 'Stayman Winesap' apple leaves was observed after being caged for 3 days with leafhoppers (100/leaf) (Childers 1941). Proctor et al. (1982) demonstrated that 20 spotted tentiform leaf miner (Phyllonorycter blancardella) larval mines per leaf caused a 23% reduction in Pn of apple leaves.

Early defoliation by cherry leaf spot fungus (Coccomyces hiemalis Higgins) reduced bud and twig winter hardiness and fruit set the following season in sour cherry trees (Howell and Stackhouse 1973). Infection of apple leaves with apple scab (*Venturia inaequalis*) caused a significant reduction of whole leaf Pn after 28 days (Spotts and Ferree 1979) and leaf Pn, transpiration and carbohydrate content was reduced for apple leaves infected with powdery mildew (*Podosphaera leucotricha*) (Ellis et al. 1981).

Artificial reduction in leaf area to simulated pest damage, can have a profound effect on the physiology and growth of the plant. Partial hand defoliation of 'Golden Delicious' apple trees decreased flowering the next season (Hennerty and Forshey 1971) and in another study (Ferree and Palmer 1982) a yield reduction of 80% resulted when all spur leaves were removed. For tomato, removal of 50 or 75% of the leaf area caused yield reductions of 16 and 40% respectively (Stacey 1983).

Many plants can compensate for some level of injury or leaf area loss. Photosynthetic compensation has been observed in wheat and barley (Shaw and Samborski 1956), soybean (Wareing et al. 1968; Poston et al. 1976), lucerne (Hodgkinson 1974), apple (Ferree and Hall 1981; Proctor et al. 1982; Flore and Irwin 1983) and grape (Boucher et al. 1987). Whole plant defoliations of up to 20% in apple (Flore and Irwin 1983), 25% in tomato (Stacey 1983) and 40% in poplar (Bassman et al. 1982) were compensated for based on increased dry weight accumulation, fruit yield and vegetative growth, respectively. The objectives of this study were to: 1) determine if a threshold injury level exists for photosynthetic assimilation (A) by sour cherry leaves; 2) determine if loss of leaf area is compensated for by an increase in A of the remaining effective leaf area; and 3) determine if the damage threshold for A based on gas exchange measurements is confirmed by total dry matter studies with whole trees; and 4) to document the wounding response of sour cherry leaves to leaf area removal by holepunching.

MATERIALS AND METHODS

Plant material. One year-old potted sour cherry trees (*Prunus cerasus* cv. 'Montmorency' on Mahaleb rootstock) were used for all experiments. Dormant trees were potted in 11 liter plastic pots with sterilized greenhouse soil mix (sand, silt and clay), cut back to an active bud on the scion (0 - 10 cm from the graft union) and forced in the greenhouse. Trees were trained to a single shoot from which all lateral shoots were removed as they developed. The greenhouse was maintained at an average day and night temperature of 21 and 16 ^{o}C. A 16-hour photoperiod was provided using supplemental illumination from high pressure sodium lamps. Fertilization, watering and pest control was provided as necessary. Leaf area removal (L.A.R.) treatments were imposed using a 'GEM' paper hole punch (area = 0.33 cm^2). Leaf area was determined for fully expanded leaves by multiplying the length of the blade (from the tip to the beginning of the petiole, not including the petiole) and the width (at the widest point) by the conversion factor 0.671 which was determined for sour cherry by Kappes (1985). L.A.R. treatments were imposed to recently fully expanded leaves and leaf discs were punched randomly throughout the lamina maintaining equal numbers of punches on either side of the midrib. The midrib or leaf margins were not injured during treatment. The number of holepunches needed to establish a certain injury level was calculated by knowing the original leaf area and the area removed by the holepunch. Seven treatments were imposed: 0, 10, 20, or 30% leaf area removal between or across lateral veins. Forty uniform plants were selected for gas exchange studies and L.A.R. treatments were randomly assigned to four of the most recently expanded leaves per tree (each of the four leaves had either 0, 10, 20, or 30% L.A.R. between or across lateral veins) on the same date (day 0). On a given date of measurement, 10 replicate plants were randomly selected.

For the dry weight accumulation experiment, a second population of similar plants were grown under the same conditions. These plants had been budded in the nursery, were cut back to this scion bud and forced to one active growing shoot as above. The difference here was that each individual plant had 0, 10, 20 or 30% L.A.R. imposed to all leaves on that plant. Since this could not all be performed at one date, L.A.R. was only performed on those most recently fully expanded leaves at weekly intervals until a terminal bud had set and leaf growth had ceased (approximately 20 weeks of growth). There were nine replicate plants for each treatment.

A third population of plants was selected to evaluate the wounding response (by ethylene production) in leaves with L.A.R. by holepunching. All conditions were the same as outlined for the gas exchange experiment except that leaves were excised at time of measurement (note procedure that follows).

Gas exchange measurements. All measurements were made in the laboratory using the open system described by Sams and Flore (1982) and Gucci (1988) and modified as follows: a) an ADC 225 MK3 infrared gas analyzer (Analytical Development Company, Hoddesdon, UK) was used to measure differential CO_2 concentration at the inlet and outlet of leaf chambers; b) air flow entering the chambers was regulated with Matheson 8100 series mass flow controllers connected to a Matheson multichannel Dyna-Blender 8219 (Matheson Instruments, Horsham, Pennsylvania). Ambient CO_2 concentration was measured using a portable ADC LCA2 infrared gas analyzer and ambient O_2 concentration was measured with a 0-260 Beckman oxygen analyzer (Beckman Instruments Inc., Irvine, California). CO_2 and O_2 levels in the incoming air were consistently 350 ppm and 20%

respectively. Light intensity of 800 μmol m^{-2} s^{-1} was provided by a combination of fluorescent and incandescent lights present in the Conviron growth chamber (Conviron, Canada). Relative humidity in the chamber was maintained at 50% and air temperature at 25^{o}C. Plant material was brought from the greenhouse to the growth chamber at 8:30 am and allowed to acclimate to the above conditions for one hour. Once acclimated, four of the ten plants were selected and one leaf per plant was inserted into a leaf chamber. Four chambers were used at a time. Leaf temperature and vapor pressure deficit (VPD) were maintained at 25 ^{o}C and 1.0 - 1.2 kPa respectively. Flow rates to the chambers were 3.0 l/min. Measurements were made until four replicate leaves of each treatment had been measured (approximately 3 hr). Gas exchange parameters (A, g_s, E, WUE, and C_i) were calculated as previously described (Moon and Flore 1986). Measurements were made immediately before treatment (day 0) and 1, 4, 7, 14, 22 and 28 days following L.A.R..

Leaf chlorophyll. Chlorophyll content was determined according to the method of Moran (1982). Four leaves per treatment were selected on day 28 of the gas exchange experiment and five discs (0.33 cm^2 each) were punched from each leaf and extracted in 5 ml of N,N-dimethylformamide (0.5-0.6% w/v) and stored overnight in a refrigerator. The next day, absorbances of samples were read at 625, 645 and 664 nm with a Shimadzu UV-Vis 260 spectrophotometer (Shimadzu Corporation, Kyoto, Japan). Chlorophyll content was expressed based on leaf area (cm^2).

Dry weight accumulation experiment. The following data was collected for each tree after 20 weeks of growth: plant height from the graft union to the terminal bud (cm); total leaf number; leaf area for the plant; trunk cross sectional area (TCA) in mm^2 3 cm above the graft union; fresh weight in g for leaves, scion wood and rootstock; and following 5 days in a forced air dryer at 40°C, dry weights in g were determined for leaves, scion wood and rootstock. Average specific leaf weight per plant (total weight of all leaves in mg divided by total leaf area in cm^2) and total fresh and dry weights per plant were calculated.

Wound ethylene measurement. Ethylene determination was performed according to the method of Lounds (1987) and modified as follows: immediately following L.A.R. as described previously, leaves were excised and positioned abaxial side outward with minimum overlap in 25 x 200 mm test tubes containing 2 ml of distilled water. Tubes were immediately sealed with rubber serum stoppers and incubated in a constant temperature (25°C) water bath in the light (115 $\mu mol\ m^{-2}\ s^{-1}$).

Ethylene was determined on a 1 ml headspace sample by gas chromatography (Varian 1440, Varian Associates, Inc., Palo Alto, CA) using a 1.2 m steel column packed with activated alumina and a flame ionization detector. The injection port, column and detector temperatures were 130, 100 and 150°C, respectively. N_2 flow was maintained at 15 ml min^{-1}. Ethylene was sampled 1, 2, 3, 4, 5, 6, 7, 8, 10, 12, 24, 48, and 72 hours following L.A.R. Tubes were flushed with air for 30 sec and resealed following each determination. Data were expressed as rate of ethylene evolution, nl g leaf fresh $weight^{-1}$ hr^{-1}.

RESULTS

Gas exchange characteristics. CO_2 assimilation rate (A) was expressed based on original leaf area before L.A.R. (Table 1) and actual leaf area remaining after L.A.R. in (Table 2). Except for Table 1 and Figure 2b all tables and figures are expressed on an actual leaf area basis.

L.A.R. caused an initial reduction in CO_2 assimilation (A) for all treatments the day following injury (Tables 1 and 2). There was no L.A.R. effect on stomatal conductance (g_s), transpiration (E) or water use efficiency (WUE) at day 1 (Tables 3, 4 and 5). Recovery of A was observed as early as 4 days following L.A.R. when there was up to 20% L.A.R. between lateral veins (Figure 1a). One week following L.A.R., only the most severe treatment (30% across vein L.A.R.) had A or WUE that were significantly less than the noninjured (control) leaves (Tables 2 and 5). At all dates of measurement from day 7, g_s, E and WUE remained unaffected for all other L.A.R. treatments. Leaves with 20 or 30% L.A.R. between veins had higher A rates than uninjured leaves on day 7 (Table 2 and Figure 1a). Recovery of A in leaves with across vien L.A.R. was not observed until 14 days following L.A.R. (Table 2 and Figure 1b). On day 14, the highest A, g_s and E were observed for leaves with 20% L.A.R. across veins (Tables 2, 3 and 4). By day 22, there was no significant effect of any L.A.R. treatment on A, g_s, E or WUE (Tables 2-5). Graphical representation of long term effects of L.A.R. on A of sour cherry are presented in Figure 1.

Since by 7 days following L.A.R. there was some recovery of A from the initial depression, data from days 7 - 22 was used to develop prediction equations for the effect of L.A.R. on A. Raw data was combined across the three dates and regression analysis was performed on between vein or across vein L.A.R. either based on actual leaf area or total leaf area (Figure 2). Compensation of A to L.A.R. was observed for all treatments except 30% L.A.R. across veins when data was based on actual leaf area (Figure 2a). The leaf compensated for up to 20% L.A.R. when data was based on total leaf area (Figure 2b).

<u>Cholrophyll content.</u> 28 days following L.A.R., there were no differences between treatments for chlorophyll a, b or total chlorophyll content (data not shown).

Table 1. The effect of time after leaf area removal (L.A.R.) on net carbon dioxide assimilation (A) of sour cherry leaves, expressed on a whole leaf area basis.

L.A.R. (%)	TIME FOLLOWING LEAF AREA REMOVAL (DAYS) A (μmol CO_2 m^{-2} s^{-1}) 0	1	4	7	14	22
0	10.3	9.0 a	11.3 a	11.5 a	9.2 ab	10.0 ab
10 B	10.0	7.9 ab	11.6 a	10.2 a	8.5 ab	12.4 a
10 A	7.9	4.8 c	7.9 abc	9.7 a	7.5 ab	10.7 a
20 B	10.4	4.8 c	8.9 ab	9.9 a	8.5 ab	9.6 ab
20 A	9.5	5.7 bc	8.1 abc	8.3 a	10.0 a	9.2 ab
30 B	10.8	5.0 c	6.5 bc	8.8 a	6.9 b	8.5 ab
30 A	9.0	3.5 c	4.3 c	4.7 b	6.4 b	5.9 b

Means followed by different letters, within columns, are significantly different (P = 0.05) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Each value is the mean of four leaves. A and B represent L.A.R. treatment across and between lateral veins respectively.

Table 2. The effect of time after leaf area removal (L.A.R.) on net carbon dioxide assimilation (A) of sour cherry leaves, expressed on an actual leaf area basis.

L.A.R.	TIME FOLLOWING LEAF AREA REMOVAL (DAYS)					
	A (μmol CO_2 m^{-2} s^{-1})					
(%)	0	1	4	7	14	22
0	10.3	9.0 a	11.3 a	11.5 a	9.2 ab	10.0
10 B	10.0	8.8 a	12.9 a	11.3 a	9.4 ab	13.5
10 A	7.9	5.4 b	8.8 ab	10.7 a	8.4 b	11.9
20 B	10.4	6.2 ab	11.2 a	12.9 a	11.0 ab	12.0
20 A	9.5	7.0 ab	10.2 ab	10.6 a	12.5 a	11.5
30 B	10.8	7.1 ab	9.3 ab	12.6 a	9.8 ab	12.2
30 A	9.0	4.9 b	6.1 b	6.8 b	9.1 b	8.5

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Each value is the mean of four leaves. A and B represent L.A.R. treatment across and between lateral veins respectively.

Table 3. The effect of time after leaf area removal (L.A.R.) on stomatal conductance (g_s) of sour cherry leaves, expressed on an actual leaf area basis.

L.A.R.	TIME FOLLOWING LEAF AREA REMOVAL (DAYS)					
	g_s (mmol H_2O m^{-2} s^{-1})					
(%)	0	1	4	7	14	22
0	68.8	57.8	69.5	91.8	67.1 ab	48.1
10 B	64.7	59.7	66.8	78.7	49.2 b	55.3
10 A	53.4	30.2	54.3	89.3	60.6 ab	70.1
20 B	75.1	46.2	74.6	99.0	60.3 ab	49.7
20 A	58.7	44.5	59.5	100.0	91.8 a	52.9
30 B	85.2	60.0	67.3	86.8	60.1 ab	68.8
30 A	66.2	30.9	44.2	67.9	63.9 ab	47.4

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Each value is the mean of four leaves. A and B represent L.A.R. treatment across and between lateral veins respectively.

Table 4. The effect of time after leaf area removal (L.A.R.) on transpiration (E) of sour cherry leaves, expressed on an actual leaf area basis.

	TIME FOLLOWING LEAF AREA REMOVAL (DAYS)					
L.A.R.	E (mmol H_2O m^{-2} s^{-1})					
(%)	0	1	4	7	14	22
0	1.18	1.09	1.07	1.36	1.11 ab	0.97
10 B	1.17	1.13	1.05	1.30	1.01 b	1.22
10 A	1.05	0.68	1.07	1.50	1.13 ab	1.32
20 B	1.27	0.90	1.27	1.60	1.20 ab	1.09
20 A	1.14	0.90	1.01	1.67	1.64 a	1.17
30 B	1.40	1.15	1.26	1.59	1.31 ab	1.37
30 A	1.18	0.69	0.79	1.17	1.30 ab	0.98

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Each value is the mean of four leaves. A and B represent L.A.R. treatment across and between lateral veins respectively.

Table 5. The effect of time after leaf area removal (L.A.R.) on water use efficiency (WUE) of sour cherry leaves, expressed on an actual leaf area basis.

L.A.R.	TIME FOLLOWING LEAF AREA REMOVAL (DAYS) WUE (mmol CO_2 mol H_2O^{-1})					
(%)	0	1	4	7	14	22
0	9.06	8.66	10.41	8.75 a	9.09	11.74
10 B	8.76	7.88	12.89	8.75 a	10.00	11.27
10 A	7.76	7.64	9.05	7.19 ab	7.58	9.59
20 B	8.55	7.16	9.29	8.11 a	16.39	11.30
20 A	8.58	8.24	12.06	6.48 ab	7.63	10.12
30 B	7.90	6.60	7.63	8.13 a	7.58	9.05
30 A	7.83	22.14	8.05	5.70 b	7.14	8.58

Means followed by different letters, within columns, are significantly different ($P = 0.05$) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Each value is the mean of four leaves. A and B represent L.A.R. treatment across and between lateral veins respectively.

Figure 1. Changes in CO_2 assimilation of sour cherry leaves over time, when leaf area was removed (A) between or (B) across lateral veins. Data was expressed on an actual leaf area basis as percent of control (noninjured leaves) at each date of measurement. Symbols are means of four leaves. Vertical bars indicate least significant difference ($LSD_{.05}$).

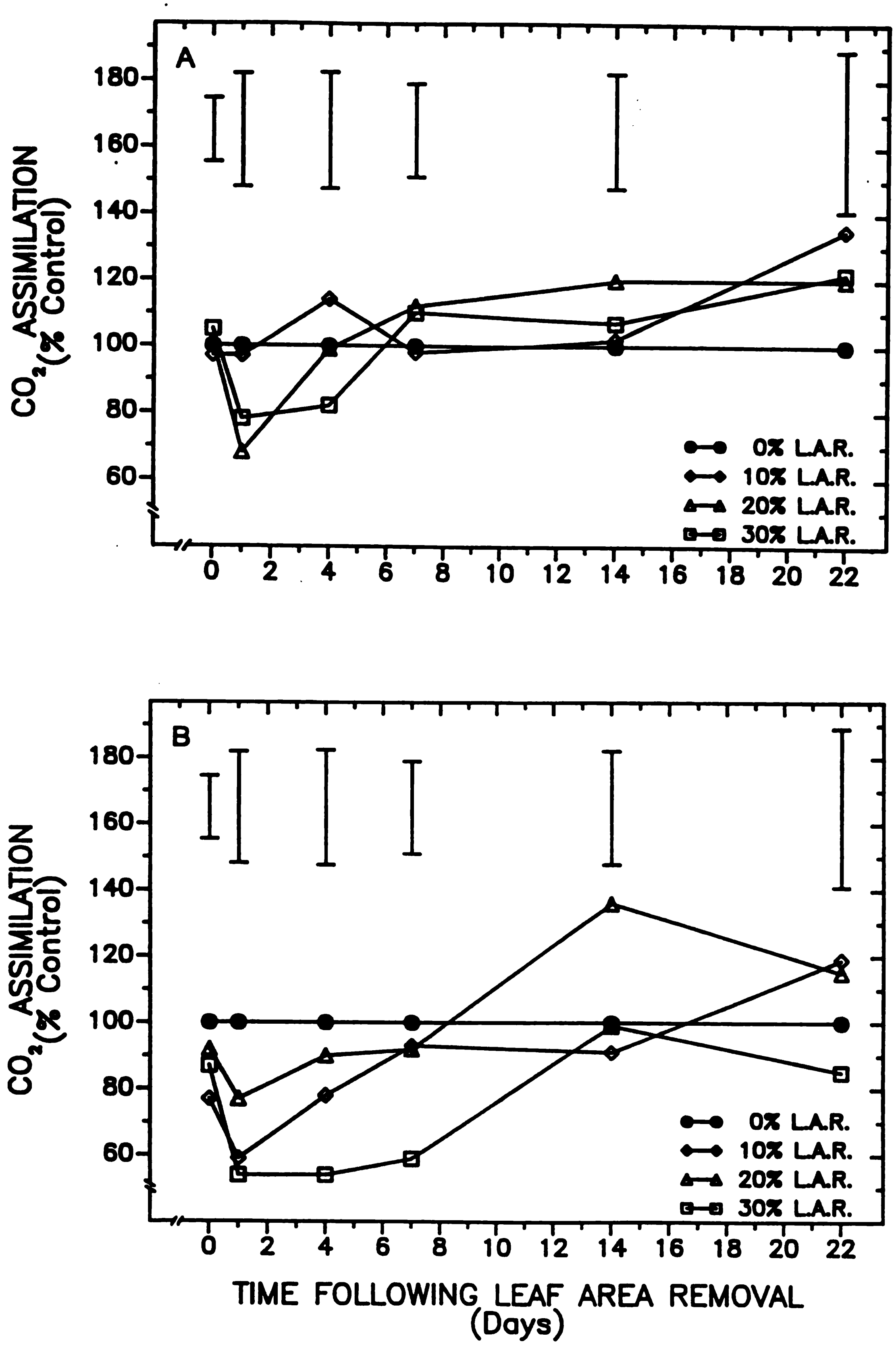
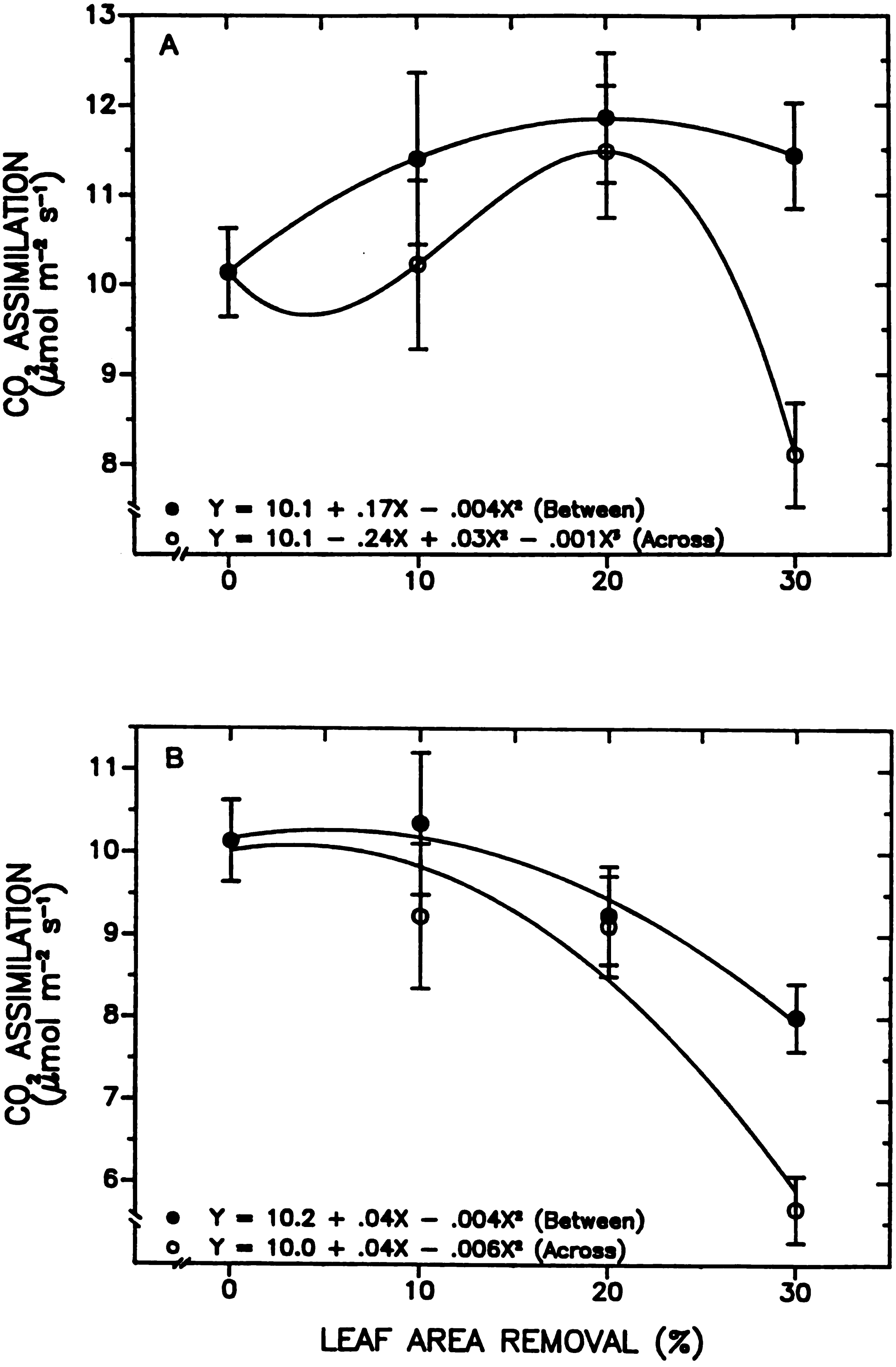

A
B
CO$_2$ ASSIMILATION (% Control)
180
160
140
120
100
80
60
0
2
4
6
8
10
12
14
16
18
20
22
0% L.A.R.
10% L.A.R.
20% L.A.R.
30% L.A.R.
TIME FOLLOWING LEAF AREA REMOVAL (Days)

Figure 2. The effect of leaf area removal between (top curve) or across lateral veins (bottom curve) on CO_2 assimilation of sour cherry leaves. Curves are prediction equations based on regression analysis of raw data. Curves in (A) are based on leaf area remaining following L.A.R. while those in (B) are based on leaf area prior to L.A.R. Symbols are means of four leaves averaged across days 7, 14 and 22 following L.A.R.. Vertical bars indicate standard errors (n = 12).


A
13
12
11
10
9
8
● Y = 10.1 + .17X − .004X² (Between)
○ Y = 10.1 − .24X + .03X² − .001X³ (Across)
B
11
10
9
8
7
6
● Y = 10.2 + .04X − .004X² (Between)
○ Y = 10.0 + .04X − .006X² (Across)
0
10
20
30
CO2 ASSIMILATION (µmol m⁻² s⁻¹)
LEAF AREA REMOVAL (%)

Dry weight accumulation experiment. Control trees had significantly greater shoot elongation, thicker trunks and a higher total fresh weight than those in which leaf area had been reduced (Table 6). Rootstock dry wt. was unaffected by L.A.R. Total plant leaf number and dry weight were not significantly reduced until 30% of the leaf area of the plant was removed. Average specific leaf weight was higher for leaves at all levels of L.A.R. than for leaves in which leaf area had not been reduced.

A linear relationship between scion fresh weight and trunk cross-sectional area (TCA) was determined for these sour cherry trees by regression analysis (Appendix 1).

Wound ethylene experiment. Wound ethylene production was followed over a 72 hour period from the time of wounding. Wound ethylene production peaked between 3 and 4 hours following wounding for all L.A.R. treatments (Figure 3). By 12 hours after wounding, ethylene production was greatly reduced and after 72 hours it was essentially undetectable. The greatest wounding response (nl ethylene produced / g tissue fresh weight / hour) was observed for 20 and 30% L.A.R. across lateral veins (Figure 3b).

DISCUSSION

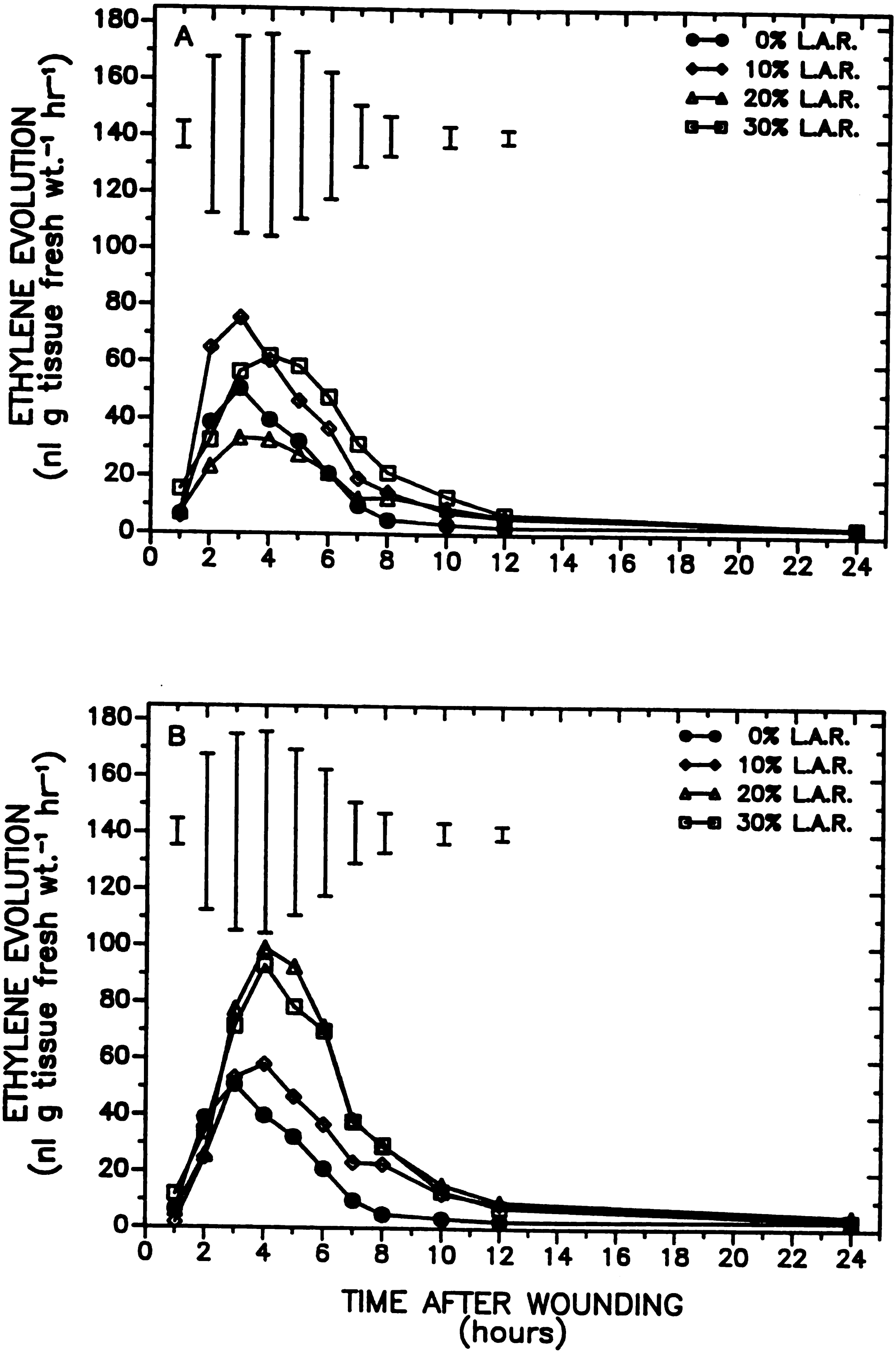
Partial defoliation or leaf injury occurs to most cultivated plants. Many plants have an inherent ability to nullify the negative effect of leaf injury by the mechanism of photosynthetic compensation (Shaw and

Table 6. The effect of leaf area removal (L.A.R.) on various growth parameters in sour cherry.

L.A.R. (%)	GROWTH PARAMETERS Plant Ht. (cm)	Leaf #	Actual L.A. (cm^2)	TCA (mm^2)	Total F.wt. (g)	Total D.wt. (g)	Avg. S.L.W. (mg/cm^2)
0	116 a	44 a	2408 a	146 a	456 a	195 a	0.24 c
10 B	92 b	37 ab	1770 b	111 b	341 bc	166 ab	0.32 ab
10 A	88 b	37 ab	1677 b	107 b	345 b	171 ab	0.31 ab
20 B	88 b	39 ab	1413 bc	99 b	334 bc	156 ab	0.32 ab
20 A	86 b	36 ab	1457 bc	102 b	321 bc	165 ab	0.34 a
30 B	74 b	31 b	1130 c	78 b	251 c	119 b	0.39 a
30 A	80 b	34 b	1068 c	83 b	255 bc	125 b	0.37 a

Plant ht. is the plant height from the bud union to the terminal bud; Leaf # is the number of leaves per plant; Actual L.A. is the total leaf area of the plant less that removed by L.A.R.; TCA is the trunk cross sectional area 3 cm above the bud union; Total F.wt. and D.wt. are the total fresh and dry weight of the plant, respectively; Avg. S.L.W. is the average specific leaf weight per plant. Means followed by different letters, within columns, are significantly different (P = 0.05) by Duncan's Multiple Range Test. Absence of letters within a column indicates a lack of significant differences. Each value is the mean of 9 plants. A and B represent L.A.R. treatment across and between lateral veins respectively.

Figure 3. The effect of leaf area removal (A) between or (B) across lateral veins on wound ethylene evolution over time for sour cherry leaves. Each symbol is the mean of 4 leaves. Data was expressed as nanoliters of ethylene produced per gram of fresh weight per hour (nl/g/h). Vertical bars indicate least significant difference ($LSD_{.05}$).


A
B
0% L.A.R.
10% L.A.R.
20% L.A.R.
30% L.A.R.
ETHYLENE EVOLUTION
(nl g tissue fresh wt.$^{-1}$ hr^{-1})
0
20
40
60
80
100
120
140
160
180
0
2
4
6
8
10
12
14
16
18
20
22
24
TIME AFTER WOUNDING
(hours)

Samborski 1956; Wareing et al. 1968; Hodgkinson 1974; Poston et al. 1976; Ferree and Hall 1981; Proctor et al. 1982; Flore and Irwin 1983; Boucher et al. 1987). In fact, in many of these plants, including sour cherry (Tables 1 and 2; Figure 2) removal of up to 20% of the leaf area did not cause a significant reduction in A (Poston et al. 1976; Ferree and Hall 1981; Proctor et al. 1982; Flore and Irwin 1983; Boucher et al. 1987). An initial decline in A following leaf injury has been observed in apple (Hall and Ferree 1976; Ferree and Hall 1981) and grape (Boucher et al. 1987). The decline in A one day following L.A.R. (Tables 1 and 2; Figure 1) actually may have been less than reported here because mechanical difficulties in the laboratory postponed gas exchange measurements until 1:00 pm and sour cherry does demonstrate a diurnal decline in Pn in the afternoon (Sams and Flore 1983). Nevertheless, the trends presented in Figure 1 should be representative since data was expressed relative to the control rather than in absolute values.

The 'rejuvination' in lucerne A following partial defoliation described by Hodgkinson (1974) was also observed in this study (Tables 1 and 2; Figure 2) and for young expanding apple leaves but not older leaves (Ferree and Hall 1981). However, in grape, Boucher et al. (1987) noted that A reduction following 20% leaf area loss was greater after 12 days than after 1 or 5 days. This was not the case for sour cherry (Table 2). In fact, 22 days following L.A.R., A was higher than the uninjured control in all but the 30% across vein L.A.R. treatment (Table 2; Figure 1b).

In a study by Proctor et al. (1982) on potted apple trees, leaf injury to the extent of 20 mines/leaf by _Phyllonorycter blancardella_ did not have a significant effect on g_s, E, or WUE. L.A.R. by holepunching in sour cherry produced similar results (Tables 3-5). Although A was affected by L.A.R., there was essentially no effect on g_s,E or WUE. Based on data in Figure 2, sour cherry can compensate for a 20% loss in leaf area by increasing its A rate. Perhaps it may be possible that the observed changes in A to compensate for L.A.R. were due to changes in carboxylation efficiency or RUBP regeneration rate (Farquhar and Sharkey 1982; Jones 1985).

Wareing et al. (1968) observed increased ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity in partially defoliated soybeans leaves relative to uninjured leaves. He suggested that partial defoliation increased the demand of the remaining leaves for photosynthates and further noted that uninjured leaves were not operating at their maximum photosynthetic potential. To answer questions regarding the mechanism of photosynthetic compensation in sour cherry, further experiments beyond the scope of this initial study need to be conducted.

Kenworthy (1974) noted that terminal (shoot) growth was a good indicator of vigor for sour cherry trees. Briggs and Avery (1968) observed a significant reduction in shoot growth of 'Brompton' plums infested with mites. L.A.R by holepunching produced similar effects on shoot growth for sour cherry (referred to as plant height in Table 6). Using the criteria of Kenworthy (1974), trees without L.A.R. were significantly more vigorous than trees with L.A.R.

Although plant height (shoot elongation), actual leaf area, TCA and total fresh weight were higher for trees without L.A.R., up to 20% L.A.R. had no significant effect on whole plant dry weight accumulation (Table 6). Flore and Irwin (1983) conducted a similar study in apple and they found that dry weight accumulation was not affected until 20% of the leaf area was removed. For sour cherry though, this occurred at 30% L.A.R. When Stacey (1983) removed 25% of the leaf area of tomato plants there was no significant effect on yield. Since the trees in this experiment were vegetative, dry weight accumulation is synonymous with yield.

Proctor et al. (1982) did observe a significant decrease in leaf chlorophyll content of apple leaves infested with tentiform leafminer. Since the larvae were feeding on the leaf mesophyll for some time, a reduction in leaf chlorophyll may be expected in apple. 28 days following L.A.R. in sour cherry leaf chlorophyll/cm^2 was not reduced by L.A.R. The injury was instantaneous in our study while in his, leaf injury was prolonged due to the feeding nature of the insect.

The average specific leaf weight of the leaves on these sour cherry trees increased as L.A.R. increased (Table 6). Barden (1974) observed reduced specific leaf weight of shaded apple leaves. Shaded peach leaves were larger and thinner (Kappel and Flore 1983). Light was not a limitation to the cherry leaves in this experiment but rather the total leaf area was. Leaves on plants with L.A.R. had reduced leaf area but greater thickness which may have been due to increased production of photosynthetic machinery.

Westwood (1970) observed a linear relationship between the above ground fresh weight of apple trees and their trunk cross-sectional area (TCA). This was also observed here for sour cherries (appendix 1) confirming that TCA is also a good indicator of above ground fresh weight for sour cherry.

By increasing photosynthetic rate and dry weight accumulation, plants can compensate for certain degrees of injury. Apparently, sour cherries can compensate for up to 20% L.A.R. but removal of a greater amount exceeds the compensatory capacity of the leaf. This threshold level is likely to change with crop load, and environmental predisposition, but it represents a large degree of compensation by the plant.

When a tissue such as a leaf is injured, there is usually a fairly rapid wounding response by an increase in ethylene evolution (Yang and Pratt 1978). Ethylene production following wounding has been observed in many plants including pea (Saltveit and Dilley 1978), morning glory (Hanson and Kende 1976), tomato (Jackson and Campbell 1976), tobacco (Nakagaki et al. 1970) and now in sour cherry (Figure 3). Wound ethylene is of metabolic origin, synthesized by the tissue, and not the result of diffusion of ethylene already in the tissue to the wound surface (Yang and Pratt 1978; Saltveit and Dilley 1978). Hyodo et al. (1983) described the sequence of events upon wounding as: first, an increase in synthesis of ACC synthase activity; second, an accelerated production and accumulation of ACC in the wounded tissue; and finally, a high rate of ethylene production is stimulated.

The duration of the wounding response may vary from hours (Saltveit and Dilley 1978) to days (Nakagaki et al. 1970) depending largely on the nature of the wound. Tobacco leaves inocculated with tobacco mosaic virus (TMV) had increased ethylene production as local lesions developed on the leaves for eight days (Nakagaki et al. 1970). In this study, wound ethylene production dropped off approximately 12 hr after wounding (Figure 3). The wounding response of sour cherry leaves was followed for 72 hr but the rate of ethylene evolution was essentially unchanged after 24 hr. Because the wounding event was instantaneous rather than prolonged as in an infection, it seems logical that the wound could heal more rapidly and that the wounding response would be hastened. The intensity of the wounding response (nl/g/hr) was greatest when 20 or 30% of the leaf area was removed across veins (Figure 3). When data was expressed based on cut surface (nl/cm/g/hr), the greatest ethylene production occurred for leaves with 10% L.A.R. It is possible that precursors such as methionine, s-adenosyl methionine (SAM) or even ACC needed for ethylene production were limiting when 20% or more of the leaf area was removed.

Some plants such as soybean, peanut, radish and bean suffer photosyhthetic depression in response to ethylene (Taylor and Gunderson 1986) while others including apple (Dozier and Barden 1971), tomato (Bradford 1983) wheat, corn and pea (Taylor and Gunderson 1986) do not. Although the effects of ethylene on gas exchange of sour cherry were not evaluated in this study, we do not believe that it significantly influenced A. The wounding response had essentially ceased 12 hr following wounding (Figure 3). If ethylene caused a depression in photosynthesis, this may not even have been observed since the first gas exchange measurements were made 24 hours following L.A.R. (Tables 1 and 2). If even very low levels of ethylene produced by wounded leaves could cause photosynthetic depression in those same leaves, then the photosynthetic compensation that occurred should not have been observed. Although no direct evidence exists to state that the photosynthetic depression observed following 30% across vein L.A.R. was not due to ethylene, I would suggest that if ethylene was still being produced at inhibitory levels seven days following L.A.R. that the compensation observed (Table 2) would not have occurred.

Because foliar injury can dramatically affect productivity of cultivated plants, it should be kept to a minimum. Studies such as this are useful in determining damage thresholds for a crop. Although paper holepunch injury does not occur in the field, holepunching has been shown to be an acceptible simulation of insect damage (Poston et al. 1976; Li and Proctor 1984; Kappel 1986). Clearly, many plants can compensate for certain levels of damage or injury. By knowing what these levels are, how to measure them in the field, and by being able to predict possible implications (e.g. reduction in fruit growth, production or quality) the grower may choose to treat or not treat the situation. In circumstances where prophyllactic pest control is always used, knowledge of damage thresholds may reduce the frequency of pesticide application and preserve populations of beneficial insects present in the environment. These two factors alone should provide both direct and indirect monetary incentive for adoption by commercial growers.

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SUMMARY AND CONCLUSIONS

The longevity of sour cherry orchards has significantly decreased in the last 20 years. Damage to the bark or cambial tissue of the trunk or main scaffolds (mechanical harvest, winter injury, animal feeding, insect or disease infestation) and damage to the foliage (insect or disease infestation, or environmental stress) are of significant importance to the fruit grower. Damage thresholds for injury are a necessary input to make intelligent management decisions concerning pest control and tree replacement.

Trunk injury was simulated by bark removal or compression. These types of injury, halfway around the trunk circumference did not significantly reduce vegetative or reproductive capacity nor increase tree mortality. The threshold for one time injury to young, fruiting sour cherry trees appears to be quite high. In some trees, copious wound callus was produced and differentiated vascular tissue was observed in the callus. There are trees still alive today, almost 3 years after a 5 cm long strip of bark was removed completely around the trunk at harvest date. Time of wounding does affect the ability to heal wounds, those occurring in the spring or early summer having the greatest healing rate.

Since a great deal of injury to trunks results from mechanical harvest, it is fortunate that this time of injury permits effective healing. Injury imposed during the winter is much less likely to be repaired. Any practices that can be used to limit trunk injury will be beneficial, especially employing competent and careful mechanical harvest operators.

Leaf injury was simulated by removing known amounts of leaf area with a paper holepunch. From the day of injury, there was an initial decrease in A but this was recovered as early as 4 days following L.A.R. When up to 20% of the leaf area was removed, the leaf compensated by increasing its' A rate. This compensation was observed for at least 3 weeks following leaf injury. Sour cherry leaves have a great capacity to compensate for damage in this way. Carbon assimilation as a result of photosynthesis is observed as an increase in whole plant dry weight. Removal of 20% of the leaf area of potted sour cherry plants from bud break to terminal bud set (20 weeks) did not significantly reduce dry weight accumulation. Based on this study, the threshold for leaf injury by holepunching in one year-old sour cherry trees is 20% L.A.R. Trees in the field should therefore have an inherent defense mechanism for leaf injury. Assessment of injury levels by growers or pest management scouts to determine damage levels could reduce pesticide applications, save the grower money, decrease environmental contamination and preserve beneficial insects in the orchard.

Damage thresholds are not the only consideration for growers making management decisions but they provide a useful tool to aid the process. By considering cultural practices, environmental conditions, costs and benefits of prophyllactic treatment, and the short and long term implications of injury, the grower should be able to make intelligent decisions. It is my hope that this work may provide useful information to sour cherry growers so that the current trend of declining orchard life may be reversed.

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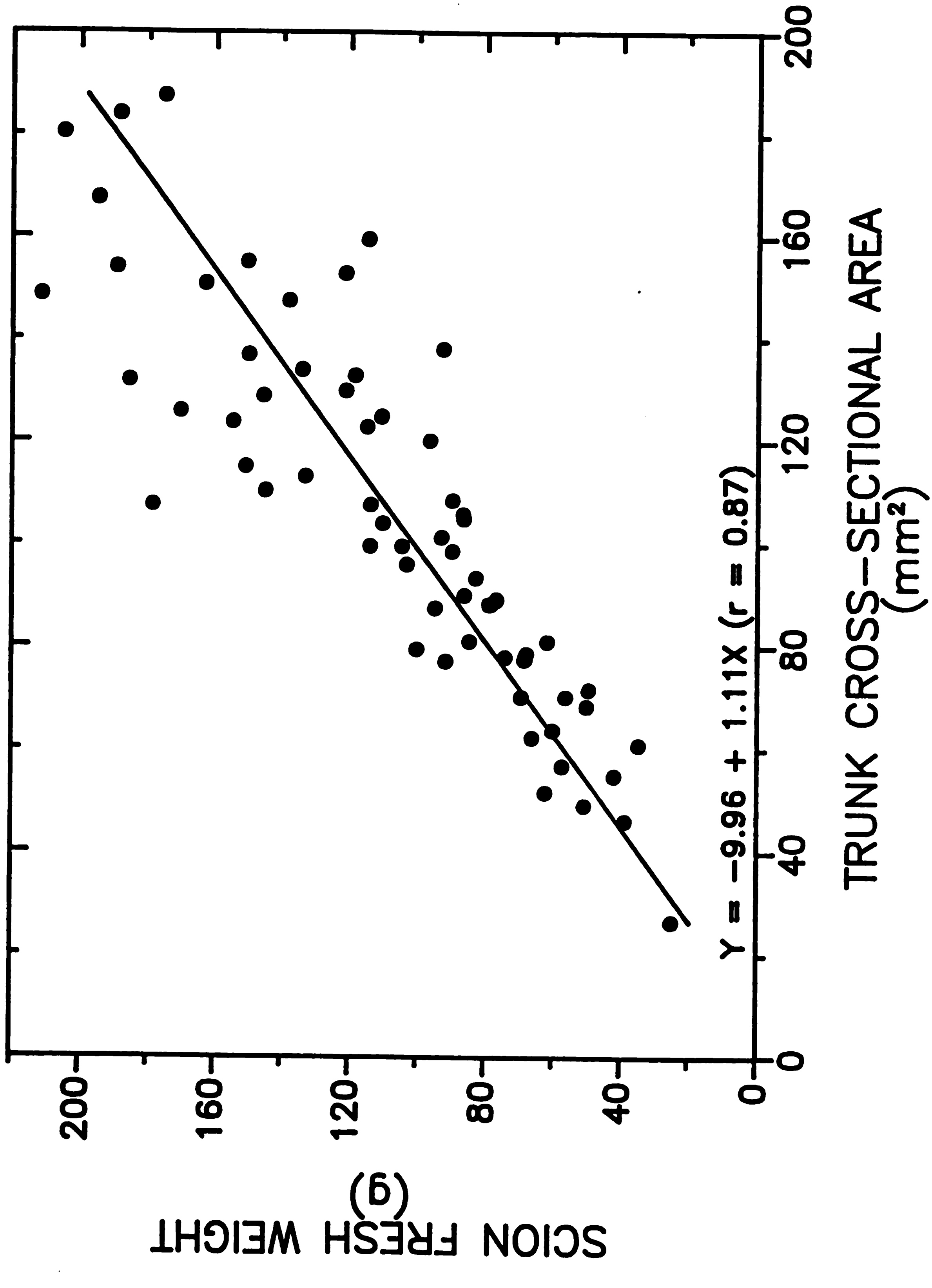
APPENDIX

Figure 1. The relationship between scion fresh weight and trunk cross-sectional area of one year-old potted sour cherry trees after 5 months of active growth in a greenhouse. The line is the linear regression function based on the raw data which occurs about the line ($r = 0.87$).


SCION FRESH WEIGHT
(g)
0
40
80
120
160
200
0
40
80
120
160
200
TRUNK CROSS–SECTIONAL AREA
(mm²)
Y = −9.96 + 1.11X (r = 0.87)