

Reduction of Tomato Leaflet Photosynthesis Rates by Mining Activity of *Liriomyza sativae* (Diptera: Agromyzidae)¹

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ABSTRACT Effects of mining activities of *Liriomyza sativae* Blanchard on leaf conductance and photosynthesis rates of tomato leaflets were examined in the field. Photosynthesis rates in mined tissues were reduced 62% compared with rates in unmined leaflets. A negative linear correlation was found between the percentage of mining in a leaflet and photosynthesis and stomatal conductance rates in the unmined tissues. Effects of *L. sativae* mining upon leaflet photosynthesis were not isolated to mined areas alone, and low levels of mining activity greatly reduced leaflet photosynthesis.

The vegetable leafminer, *Liriomyza sativae* Blanchard, is a secondary pest of fresh-market tomatoes in southern California. Use of scheduled broad-spectrum insecticide treatments for control of lepidopterous pests such as *Heliothis zea* Boddie and *Keiferia lycopersciella* (Walsingham) often produces high densities of *L. sativae* by destruction of the agromyzid's effective natural enemies (Johnson et al. 1980 a, b). Lack of consistent results has made establishment of density treatment levels for control of leafminers on tomatoes difficult. Levins et al. (1975) and Wolfenbarger and Wolfenbarger (1966) attempted to correlate reductions in tomato yield with leafminer damage, but their data appear inconclusive. Schuster et al. (1976) obtained reduced tomato yields in control plots compared with oxamyl-treated plots; they noted that yield was affected by season and variety of tomato. Quantification of fruit yields, resulting from mechanical defoliation of plants at various foliage levels and periods during the season, indicated that control of *L. sativae* after bloom may not be necessary until defoliation levels reach ca. 50% (Keularts 1980).

Presently, no data are available on the relationship between *L. sativae* mining injury and resultant effects on tomato leaflet photosynthesis. Attempts to quantify leafminer induced injury and subsequent tomato yields have not included an analysis of *L. sativae* mining on tomato plant physiology. Sances et al. (1979) suggested that an understanding of a plant's physiological capacity to withstand feeding injury by an arthropod was necessary before accurate density treatment levels could be established.

The work reported here was done to determine the effects of various levels of *L. sativae* injury on stomatal and mesophyll conductance and photosynthesis rates of mature leaflets in the field.

Materials and Methods

Field studies were conducted at the University of Cal-

ifornia's South Coast Field Station, Irvine, in 1982. Physiological measurements were conducted on a planting of trellised fresh-market tomatoes, Hybrid 6718 VF (Peto Seed Co., Saticoy, Calif.) established on 4 May 1982. Plants were grown using local, commercial practices. Before measurements, methomyl (1.0 kg of AI/ha) was applied on 13 and 27 August to increase *L. sativae* densities by suppression of its natural enemies. Insecticide treatments were applied by a tractor-mounted boom sprayer (10 nozzles per row) operated at a pressure of 58.6 kg/cm², delivering 420 liters of water per ha.

On 20 September 1982, 10 mature main leaflets (Luckwill 1943), each of about the same age and size, were selected which had 0, 1, 2, 3, 4, 5, 6, or 8 *L. sativae* mines per leaflet (80 leaflets total). Ten additional leaflets were selected which had large mined areas (ca. 1.5 cm²) of leaf tissue as viewed from the upper leaf surface. Leaflets were located on the secondary and tertiary lateral branches of each plant sampled (Johnson 1979). Samples were limited to 10 adjacent tomato plants. Stomatal and mesophyll conductance and photosynthesis rates were measured on each attached leaflet by using a dual isotope porometer by the techniques of Sances et al. (1979) and Johnson et al. (1979). Selected leaflets were sampled in random order. Physiological measurements were taken from unmined areas of leaflets selected with reference to individual *L. sativae* mine densities. On leaflets exhibiting large areas of mining, physiological measurements were taken from within the circumference of mined areas to determine effects due to mining alone. After physiological measurements, leaflets were taken to the laboratory, where all except the latter-described group were individually placed between two panes of glass and illuminated from behind with one 500-W tungsten light. Leaflets were photographed with Kodak high-speed Ektachrome transparency film (tungsten type, ASA 200) with a Minolta SRT-101 SLR camera equipped with 100-mm focal length lens and extension tubes. The glass surface closest to the camera was inscribed with a 1-cm² area to permit area calibration. Projection of developed transparencies permitted determination of total leaflet areas and corresponding areas of mined tissue by summation of projected leaflet images on a grid background which was divided into 0.25-cm² squares (1 cm² projected = 400 squares).

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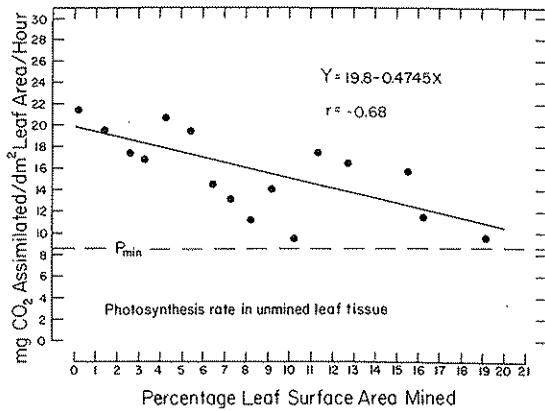


FIG. 1. Photosynthesis rates from unmined tissues in tomato leaflets with various percentages of *L. sativae* mining damage, where P_{min} represents the mean photosynthesis rate in mined tissues.

Data were analyzed with a *t* test and regression analysis.

Results and Discussion

Areas mined by *L. sativae* larvae ranged from a mean of 0.25 cm² at a density of 1 mine per leaflet to 2.09 cm² at 8 mines per leaflet. Because leaflet areas varied, ratios of mined tissue to total leaflet areas varied greatly within mine density categories. For example, mined areas in leaflets with five mines ranged from 1.16 to 2.68 cm², whereas the total leaflet areas ranged from 12.56 to 26.6 cm². This produced percentages of mined tissues which ranged from 4.7 to 12.9% per leaflet. To reduce variation, means were calculated for percentages of mining injury which fell within 1% intervals ranging from 0 to 20% and their relative corresponding physiological parameters.

Photosynthesis rates from unmined leaflets ranged from 16.86 to 32.20 mg CO₂ assimilated per dm² per h, with a mean of 22.8 mg of CO₂ assimilated per dm² per h. Rates from totally mined surface areas ranged from 2.92 to 13.37 mg of CO₂ assimilated per dm² per h, with a mean of 8.51 mg of CO₂ assimilated per dm² per h (P_{min}). Thus, photosynthesis rates in mined tissues were significantly reduced ca. 62% ($P < 0.01$). A significant linear correlation was found between the percent mining within a leaflet and reductions in photosynthesis rates in adjacent unmined tissues (Fig. 1). Mean stomatal and mesophyll conductance values in unmined tomato leaflets were 0.128 and 0.179 cm/sec, respectively, compared with values of 0.046 (C_{min}) and 0.064 cm/sec in tissues mined totally. Diffusion of water vapor and CO₂ is primarily a function of the degree of stomatal opening. This function is positively correlated with stomatal conductance and is used as a measure of stomatal opening. Mesophyll conductance which is a measure of the degree of diffusion and transport of CO₂ after entering the leaf, also includes biochemical processes associated with CO₂ assimilation. Reductions in stomatal conductance are thus interpreted as decreases in stomatal opening, whereas

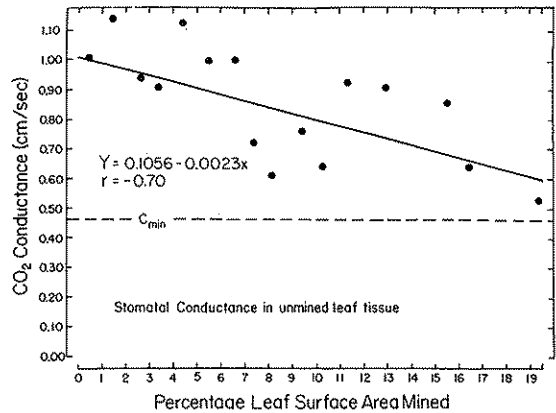


FIG. 2. Stomatal conductance rates from unmined tissues in tomato leaflets with various percentages of *L. sativae* mining damage, where C_{min} represents the mean conductance rate in mined tissues.

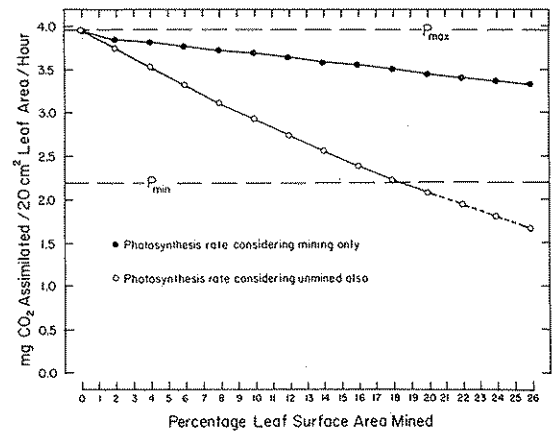


FIG. 3. Theoretical photosynthesis rates in a 20-cm² tomato leaflet, where *L. sativae* mining injury is considered only to directly mined tissues and in combination with the effects on adjacent unmined tissues where P_{max} and P_{min} represent photosynthesis rates in unmined and totally mined 20-cm² leaflets, respectively.

decreases in mesophyll conductance indicate internal damage expressed as decreased movement of CO₂ and fixation within the leaf (Sances et al. 1982).

Regression analysis of the stomatal and mesophyll conductance values in unmined tissues with respect to increases in percentages of mining injury revealed a significant negative correlation associated with stomatal conductance ($P < 0.01$) (Fig. 2). Decreases in mesophyll conductance in unmined tissues with respect to increases in mining injury were weakly correlated ($r^2 = 0.25$). Thus, mining injury primarily affected gas exchange by reducing stomatal conductance in adjacent unmined tissues. Although mesophyll conductance was reduced in mined tissues, only a weak correlation was found in unmined tissues. We do not know how leaf damage, in general, affected our measurements of stomatal conductance. However, we do expect that leaf

injury resulting from mining would cause water imbalance and subsequent stomatal closure.

Total photosynthesis rates for a 20-cm² leaflet were calculated in relation to the effects of *L. sativae* mining only and in combination with effects on the surrounding tissues as the percentage of mining injury increased (Fig. 3). Considering only the effect of mining on directly injured tissues, a 10% reduction in leaflet photosynthesis occurred when ca. 18% of the leaf was mined. Inclusion of the effects of mining on adjacent unmined tissues indicated that a 10% reduction in photosynthesis occurred when only 4% of the leaflet was mined. In addition, 18% mining injury reduced the tomato leaflet's photosynthesis rate to the equivalent to a totally mined leaflet (as viewed from the upper leaflet surface) when the effects on adjacent unmined tissues were considered. Thus, the effects on leaflet photosynthesis rates were not isolated only to the mined areas, and small levels of mining activity can reduce leaflet photosynthesis greatly.

Although these results show that small percentages of *L. sativae* mining injury may greatly reduce photosynthesis rates, the exact relationship between decreases in photosynthesis rates due to leafminer-induced injury and subsequent tomato fruit yields is unknown. Tanaka et al. (1974b) reported that photosynthesis rates in tomatoes remain relatively stable, even during the rapid growth of fruit. The photosynthetic potential of the whole tomato plant usually exceeds the current demand for assimilates for both growth of vegetative organs and development of fruits (Tanaka et al. 1974a, c). In addition, Tanaka et al. (1974b) postulated that the tomato leaf is the main sink for the assimilates it produces. Thus, leafminer damage may not reduce total photosynthesis to a level which decreases fruit production. Studies of Tanaka and his associates provide some insight into the reasons for inconsistent results in the analysis of the quantitative relationships between leafminer injury and fruit yields. The findings presented here emphasize the need to further understand the relationship between agromyzid leafminer injury, photosynthesis, carbon sources and sinks, and fruit production physiology in tomatoes. Fixed-effect experiments, with well-defined *L. sativae* densities, are essential to determine accurate density treatment levels for this agromyzid.

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