

EFFECT OF THE VEGETABLE LEAFMINER,
Liriomyza sativae BLANCHARD, AND THE ASSOCIATED PLANT
PATHOGENS ON YIELD AND QUALITY OF THE TOMATO,
Lycopersicon esculentum MILL. CV. WALTER

By

JOZEF LEO WILLEM KEULARTS

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Voor mijn ouders, Leo en Maria Keularts,
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JOZEF LEO WILLEM KEULARTS

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In the period from 1977 to 1980 a number of field experiments were carried out at the University of Florida Agricultural Research and Education Center in Homestead to determine the effect of various levels of discrete or repeated, mechanical defoliation of 'Walter' tomato plants on components of marketable yield. Treatments consisted of 100% defoliation and separate 20%, 40%, 60%, and 80% defoliations of the lower or the upper part of the plants.

A differential sensitivity to defoliation in the course of the plants' development was observed. The most sensitive times appeared to be early in the season and at mid-season. In most cases, however, at least 60% of the foliage had to be removed before total marketable fruit yields and yields in the largest, most profitable size categories were significantly reduced when compared to yields from the control plants. Tomato plants exhibited less tolerance of repeated defoliation

with removal of 40% of the total leaf area often resulting in yield loss in the first harvest. However, the total yield of the first two harvests combined was not significantly reduced when compared to yields from nondefoliated plants.

The total marketable yield of the tomato plants at any level of defoliation was significantly correlated with the gross revenue a grower would obtain from the harvested fruit based on different prices for the various size categories.

Major defoliation associated with leafminer damage in commercial production plantings is the result of the adverse effect of pathogens inhabiting the leaf mines. In this study the pathogen most commonly associated with the leaf mines has been identified as Alternaria alternata (Fries) Keissler. It appears to be only weakly parasitic, its detrimental effect depending on the nutrient supply provided in the mine by mesophyll cells lacerated by the leafminer larvae. Additional damage to the leaf can also be done by other pathogens such as Xanthomonas vesicatoria (Doidge) Dows., which may enter mines when bacterial spot disease pressure is high.

The actual damage to the tomato leaf by the leafminer larvae themselves seems to be restricted to the removal of photosynthetically active tissue. The main concern for growers, therefore, should lie in the occurrence of infection of the mines. Infection is probably less likely to occur when the nutrient supply available for the pathogen is too little for it to do harm to the leaf tissue. This is the case when the larvae are killed early in their development so that only a small amount of leaf tissue has been consumed. The most effective way for ensuring their early death and, consequently, low leafminer populations

is effective use of the numerous parasites of the fly. This can best be achieved by applying sound pest management practices. If there are too few parasites to control the leafminer population effectively then insecticide applications specifically to control the leafminer are necessary. If the defoliation level in prebloom plants reaches 30% or in postbloom plants reaches 50%, then insecticide treatments are recommended.

CHAPTER I
INTRODUCTION

The tomato, Lycopersicon esculentum Mill., is one of the most important commercially-grown vegetable crops in the United States. With a market value of \$517,769,000 in 1979, 19.61% of the total value of the principal vegetable crops, it was second only to lettuce. In acreage it was the fourth most important crop with a harvested area of 51,924 hectares, equalling 7.92% of the total commercial vegetable acreage in the United States (Anonymous, 1980a). Florida is the second largest producer of tomatoes in the United States and the country's sole domestic supplier during the months of January, February, and March (Anonymous, 1979; Zepp and Simmons, 1979). The Dade County tomato production area accounts for approximately 25% of the state's total number of harvested acres (Anonymous, 1980b).

For cultivation of tomatoes on the Rockdale soils of South Florida, the investment in land preparation, planting, and cultivation practices, including pesticide applications, was estimated at \$526.75 per cultivated acre for a 842-acre farm in 1973 (Walker and Hunt, 1973). Additional costs for harvesting, processing, and overhead were estimated at \$835.08 per acre. With an investment of this magnitude, it is not surprising that tomato growers, especially in Dade County, Florida, would strive to hold yield losses due to pests to a minimum.

Since the end of World War II when chlorinated hydrocarbons came into widespread use as pesticides, tomato yield has increased from 9.3 metric tons average per hectare for the period 1945-1950 to 17.9 metric tons average per hectare for the period 1965-1970 (Rose, 1973). Although this near doubling of the yield can be attributed to a number of cultural practices, effective control of the large number of insect pests has, undoubtedly, been an important contributing factor.

Leafminers have for the last few decades been considered one of the most serious pests infesting tomatoes (Wene, 1955; Hayslip, 1961; Poe et al., 1978). Serious outbreaks of the vegetable leafminer on tomato occurred for the first time in 1946 and resulted in serious defoliation of the crop (Anonymous, 1947). An increase in leafminer populations has been attributed to the general use of DDT and other chlorinated hydrocarbons as well as organophosphates (Spencer, 1973a). An accentuation of the leafminer problem has been shown to be the result of a reduction of the parasite populations by the use of insecticides (Wene, 1955) as well as a result of the ineffectiveness of the insecticides against the leafminers themselves (Hills and Taylor, 1951; Shorey and Hall, 1963).

The actual damage done by the vegetable leafminer, Liriomyza sativae Blanchard, to the host plant consists of the consumption of the leaf's palisade tissue, which presumably results in a reduction of the photosynthetic activity of the plant. If the mine density is high, this damage alone can trigger leaf abscission, ultimately resulting in serious defoliation of the plant. In some cases defoliation has been reported to have occurred so late in the season that only little damage was done and an actual benefit in advanced maturity has

been suggested (Michelbacher et al., 1949). However, in fields where defoliation occurred early in the season serious fruit loss due to sunburn was observed. Leafminer infestations have been suggested as the cause of yield reduction in tomatoes on occasion (Wolfenbarger and Wolfenbarger, 1966; Schuster et al., 1976), but others report no significant yield decrease despite defoliation by leafminers or increased leafminer density (Levins et al., 1975; Schuster et al., 1976; Schuster and Everett, 1977; Johnson et al., 1980a,b). The possibility of negative effects on tomato yield and quality by leafminer populations larger than those observed was not ruled out, however (Levins et al., 1975).

Even in the case of low mine densities, defoliation may occur. The leafminer flies can be directly or indirectly responsible for any secondary damage occurring as a result of punctures in the leaf epidermis. The exposure of damaged internal leaf tissue to the atmosphere provides opportunities for micro-organisms, including plant pathogens, present on the leaf surface or on the fly's ovipositor to colonize the leaf (Portier, 1930; Baranowski, 1958; Spencer, 1973a). Numerous species of micro-organisms have been found in the phylloplane of healthy plants including tomatoes (Sinha, 1971; Dickinson, 1976) many of which are able to live as parasites (Dickinson, 1976). Secondary damage to mined leaves has been noted on sugarbeet (Landis et al., 1967), alfalfa (Andaloro and Peters, 1977), and grasses (Kamm, 1977).

Discoloration of leaf areas not directly damaged by leafminers has been observed on various plants and was attributed to either effects of the miner itself, its metabolites, or the host tissue (Hering, 1951). Yellowing and necrosis of the mines' vicinity occurs frequently

(Hering, 1951; Kamm, 1977). Leaf injury due to secondary fungal infection has been suggested (Spencer, 1973a) but has been rarely shown (Haddow, 1941). Bacterial diseases associated with leafminer damage have also been shown (Sohi and Sandhu, 1968; Leach, 1927).

Yellowing and necrosis of leaves of vegetables, especially tomato, have been noted frequently. It has been suggested that a pathogen, presumably an Alternaria species, is responsible for this damage (Baranowski, 1958). Research was undertaken during the period 1977-1980 to investigate the effects of the vegetable leafminer and associated pathogen(s) on the yield and fruit quality of the tomato. Specific objectives of this study were to determine:

- (1) the effect of mechanical defoliation of tomato plants in the field, carried out at different levels and times, on the production of fruits,
- (2) the identity of the pathogen(s) and saprophytes, if any, present in the discolored leaf areas adjacent to leaf mines and associated with non-diseased mines, and
- (3) the effect of the presence of leaf mines on the photosynthetic activity of otherwise healthy tomato leaflets.

CHAPTER II

A REVIEW OF THE LITERATURE ON THE IDENTIFICATION AND CONTROL OF THE VEGETABLE LEAFMINER, Liriomyza sativae Blanchard

Introduction

In order to protect a crop efficiently from insects it is best to apply a sound pest management strategy instead of relying for the greater part on insecticides. The successful application of an integrated pest management program for tomatoes has been recently demonstrated (Pohronezny et al., 1978b). The use of insecticides has repeatedly led to a decline in the acreage used for the production of some crops (Metcalf, 1975). A result of the widespread use of insecticides is the selection of secondary pests, formerly controlled by their natural enemies (Metcalf, 1975). The vegetable leafminer, Liriomyza sativae Blanchard, is such a pest (Pohronezny and Waddill, 1978) and it would, therefore, be advisable to control the primary tomato pests by using methods which allow natural enemies to help reduce the leafminer populations below economic thresholds.

The present review summarizes the difficulties encountered in identifying the leafminer and the various methods tried or available for the control of leafminers infesting tomatoes.

Identification of the Vegetable Leafminer

The vegetable leafminer has been given many names. Frost (1924) was the first to record a dipterous leafminer on tomato although the insect was not reared, and, therefore, not identified. Wolfenbarger (1947) reared Liriomyza pusilla (Meigen) from serpentine mines on tomato and a number of other crops. L. pusilla was originally described as Agromyza pusilla by Meigen in 1830 (Frick, 1956). Various workers subsequently reported the serpentine leafminer as occurring on a large number of host plants (Webster and Parks, 1913; Frost, 1924). Frost (1924) describes mines of A. pusilla Meigen as a serpentine type on some hosts and as a blotch type on others. Later Frost (1943) states that larvae of this fly do not produce serpentine mines and concludes that Webster and Parks were working with several species. Spencer (1973a) stated that one of the species involved was undoubtedly Liriomyza sativae Blanchard.

Each leafminer species appears to produce a consistent pattern in the construction of its mine (Spencer and Stegmaier, 1973); so it can be assumed that any report of a leafminer producing mines other than serpentine ones does not refer to the vegetable or serpentine leafminer, L. sativae Blanchard. Furthermore, A. pusilla Meigen, synonymous with L. pusilla (Meigen), is believed to be a European species not occurring in North America (Stegmaier, 1972) and consequently any reference to this species name or its synonyms as listed by Frick (1956) in the United States probably constitutes a misidentification.

Lange (1949) recognized three distinct species, all with a yellow scutellum, infesting tomatoes in California: Agromyza (Liriomyza)

pusilla Meigen, Agromyza (Liriomyza) subpusilla Frost, and a species close to Agromyza (Liriomyza) flaveola Fallen. Frick (1957) describes Liriomyza munda n.sp., L. propepusilla Frost, and L. pictella (Thomson). Various leafminer species reported earlier by Lange and others are classified as belonging to one of these three described species.

Agromyza (Liriomyza) pusilla Meigen was considered a synonym for L. munda Frick; Agromyza (Liriomyza) subpusilla Frost could be synonymous with L. munda Frick, L. propepusilla Frost or L. pictella (Thomson); L. subpusilla (Frost) could be synonymous with L. munda Frick or L. pictella (Thomson). Most of the records of L. pusilla (Meigen) are thought to be on L. munda Frick (Stegmaier, 1972) while all references to L. pictella also include L. munda Frick (Stegmaier, 1966). Spencer (1965) suggested that the name L. pictella (Thomson) should temporarily be restricted to the holotype since all species previously identified as L. pictella proved to be L. munda Frick. Liriomyza munda Frick as well as L. canomarginis Frick, L. guytona Freeman, L. minutiseta Frick, and L. pullata Frick are considered to be synonyms of L. sativae Blanchard by Spencer (1973a). Liriomyza propepusilla Frost is also thought to be synonymous to L. sativae Blanchard (Musgrave et al., 1975).

Spencer (1973a,b) lists ten Agromyzid species occurring on Solanaceous plants. Of these one is a stem miner of the tomato, one a tuber miner of the white potato, and the remainder leafminers on a number of plant species. Of the seven species specifically listed as occurring on tomatoes, only three are reported from the United States: Liriomyza huidobrensis (Blanchard), L. trifolii (Burgess), and L. sativae Blanchard. In South Florida only the latter two have been observed. Liriomyza trifolii (Burgess) may be confused with L. sativae in infestations of crops (Spencer, 1973a).

Many Liriomyza species are morphologically so similar that often only examination of the male genitalia will enable one to make a satisfactory identification (Spencer, 1973a). It is not surprising, therefore, that so many names have been given to the tomato serpentine leafminer when it was discovered with morphological variations different enough from the holotype to make it appear to be a different species.

Control of the Vegetable Leafminer

Control by Parasites

Parasites have been considered capable of keeping leafminer populations below economic levels (Baranowski, 1958; Michelbacher et al., 1951, 1952; Wene, 1955; Getzin, 1960). Musgrave et al. (1975) suggested a pest management strategy in which the leafminer populations are allowed to be controlled by their parasites as much as possible. At least 47 species of Hymenopterous parasites have been reared from L. sativae Blanchard in various locations in the Western hemisphere. A list of these parasites with the reported name of the host from which each one had been reared is given in Table 1.

Of these at least 14 species have been reared from larvae and pupae of L. sativae in Florida (see Table 1). Also reared were unidentified species in the following genera: Opius, Chrysocharis, Achrysocharis, Derostenus, and Diglyphus (Musgrave et al., 1975; Stegmaier, 1966). In addition one species, Diglyphus pulchripes (Crawford) is recorded as occurring in Florida (Stegmaier, 1972) and has been reared from L. sativae elsewhere (Oatman, 1959; McClanahan,

Table 1. Parasites reared from the vegetable leafminer, Liriomyza sativae Blanchard, arranged according to family.

Parasite	Host name ^a	References
BRACONIDAE		
<u>Lysiphlebus</u> sp. ^b	<u>Liriomyza sativae</u> Blanchard	Musgrave et al., 1975
<u>Oenogastra microorhopalae</u> (Ashmead)	<u>L. sativae</u> Blanchard	McClanahan, 1977
<u>Opius aridis</u> Gahan	<u>L. munda</u> Frick	Harding, 1965; Jensen and Koehler, 1970
<u>Opius bruneipes</u> Gahan ^b	<u>L. pictella</u> (Thomson)	Jensen and Koehler, 1970
<u>Opius dimidiatus</u> (Ashmead) ^b	<u>L. munda</u> Frick <u>L. sp.</u> (from tomato)	Harding, 1965 Adlerz, 1961
	<u>L. sativae</u> Blanchard	McClanahan, 1977; Musgrave et al., 1975
	<u>L. munda</u> Frick	Harding, 1965
	<u>L. pusilla</u> (Meigen)	Baranowski, 1959
	<u>L. subpusilla</u> (Frost)	Wene, 1955
	<u>L. sp.</u> (from tomato)	Adlerz, 1961
<u>Opius liriomyzae</u> Fischer	<u>L. subpusilla</u> (Frost)	Krombein and Burks, 1967
<u>Opius nudiscutum</u> Fischer	<u>L. subpusilla</u> (Frost)	Krombein and Burks, 1967
<u>Opius suturalis</u> Gahan	<u>L. munda</u> Frick	Harding, 1965; Jensen and Koehler, 1970

Table 1. Continued

Parasite	Host name ^a	References
<u>Opus suturalis</u> Gahan continued	<u>L. pictella</u> (Thomson) <u>L. subpusilla</u> (Frost)	Jensen and Koehler, 1970; Oatman, 1959 Krombein, 1958
CYNIPIDAE		
<u>Cothonaspis</u> sp.	<u>L. munda</u> Frick	Harding, 1965
<u>Eucoilidea</u> sp.	<u>L. munda</u> Frick	Harding, 1965
<u>Ganaspidium pusillae</u> Weld.	<u>L. munda</u> Frick	Harding, 1965; Wolfenbarger and Getzin, 1963
<u>Ganaspidium</u> sp. ^b	<u>L. sativae</u> Blanchard <u>L. munda</u> Frick	Musgrave et al., 1975 Harding, 1965
<u>Hexacola</u> sp. ^b	<u>L. sativae</u> Blanchard	Musgrave et al., 1975
<u>Pseudeucoila</u> sp.	<u>L. munda</u> Frick	Harding, 1965
ENCYRTIDAE		
<u>Mirini</u> sp.	<u>L. pictella</u> (Thomson)	Oatman, 1959
EULOPHIDAE		
<u>Achrysocharella</u> sp. ^b	<u>L. sativae</u> Blanchard	Muesebeck et al., 1951; Musgrave et al., 1975

Table 1. Continued

Parasite	Host name ^a	References
<u>Achrysocharis</u> sp. ^b	<u>L. sativae</u> Blanchard <u>L. munda</u> Frick	Musgrave et al., 1975 Harding, 1965
<u>Astichus</u> sp.	<u>L. pictella</u> (Thomson)	Oatman, 1959
<u>Chrysocharis ainsliei</u> Crawford	<u>L. sativae</u> Blanchard <u>L. munda</u> Frick	Oatman and Kennedy, 1976; Johnson et al., 1980a,b Harding, 1965; Jensen and Koehler, 1970
	<u>L. pictella</u> (Thomson)	Jensen and Koehler, 1970;
	<u>L. subpusilla</u> (Frost)	Oatman, 1959 Michelbacher et al., 1951
<u>Chrysocharis caribea</u> Boucek	<u>L. sativae</u> Blanchard <u>L. munda</u> Frick	Boucek, 1977 Boucek, 1977
<u>Chrysocharis mallochi</u> Gahan	<u>L. sativae</u> Blanchard	McClanahan, 1977
<u>Chrysocharis parksi</u> Crawford ^b	<u>L. sativae</u> Blanchard	Musgrave et al., 1975; Poe et al., 1978; Johnson et al., 1980a,b
	<u>L. munda</u> Frick	Harding, 1965; Jensen and Koehler, 1970
	<u>L. pictella</u> (Thomson)	Jensen and Koehler, 1970;
	<u>L. pusilla</u> (Meigen)	Oatman, 1959 Baranowski, 1959
<u>Chrysocharis viridis</u> (Provancher)	<u>L. sativae</u> Blanchard	McClanahan, 1977

Table 1. Continued

Parasite	Host name ^a	References
<u>Chrysonotomyia</u> (<u>Achrysocharella</u>) <u>formosa</u> (westwood) ^b	<u>L. sativae</u> Blanchard	Lena and Poe, 1978; Poe et al., 1978
<u>Chrysonotomyia</u> (<u>Achrysocharella</u>) <u>punctiventris</u> (Crawford)	<u>L. sativae</u> Blanchard	Johnson et al., 1980a,b
<u>Chrysonotomyia</u> (Howard)	<u>L. sativae</u> Blanchard	Boucek, 1977
<u>Closterocerus cinctipennis</u> Ashmead ^b	<u>L. munda</u> Frick	Harding, 1965; Stegmaier, 1966
<u>Closterocerus trifasciatus</u> Westwood	<u>L. pictella</u> (Thomson)	Oatman, 1959
<u>Closterocerus utahensis</u> Crawford	<u>L. sativae</u> Blanchard	Oatman and Kennedy, 1976
<u>Derostenus agronyzae</u> Crawford	<u>L. munda</u> Frick	Harding, 1965
<u>Derostenus arizonensis</u> Crawford	<u>L. sativae</u> Blanchard <u>L. munda</u> Frick <u>L. pictella</u> (Thomson)	Oatman and Kennedy, 1976 Harding, 1965 Oatman, 1959
<u>Derostenus diastatae</u> (Howard)	<u>L. munda</u> Frick	Stegmaier, 1972

Table 1. Continued

Parasite	Host name ^a	References
<u>Derostenus followayi</u> Crawford	<u>L. munda</u> Frick	Harding, 1965
<u>Derostenus variipes</u> Crawford ^b	<u>L. sativae</u> Blanchard	Musgrave et al., 1975; Poe et al., 1978
	<u>L. munda</u> Frick	Harding, 1965
	<u>L. pictella</u> (Thomson)	Oatman, 1959
	<u>L. subpusilla</u> (Frost)	Wene, 1955
<u>Diaulinopsis callichroma</u> Crawford ^b	<u>L. pictella</u> (Thomson)	Oatman, 1959
	<u>L. pusilla</u> (Meigen)	Baranowski, 1959
	<u>L. subpusilla</u> (Frost)	Wene, 1955
<u>Diglyphus begini</u> (Ashmead)	<u>L. sativae</u> Blanchard	McClanahan, 1977; Oatman and Kennedy, 1976; Johnson et al., 1980a,b
	<u>L. munda</u> Frick	Jensen and Koehler, 1970
	<u>L. pictella</u> (Thomson)	Oatman, 1959; Jensen and Koehler, 1970
<u>Diglyphus intermedius</u> (Girault) ^b	<u>L. sativae</u> Blanchard	McClanahan, 1977; Musgrave et al., 1975; Oatman and Kennedy, 1976; Johnson et al., 1980a,b; Poe et al., 1978
	<u>L. pusilla</u> (Meigen)	Baranowski, 1959
	<u>L. subpusilla</u> (Frost)	Michebacher et al., 1951
<u>Diglyphus pulchripes</u> (Crawford)	<u>L. sativae</u> Blanchard	McClanahan, 1977
	<u>L. pictella</u> (Thomson)	Oatman, 1959

Table 1. Continued

Parasite	Host name ^a	References
<u>Diglyphus websteri</u> (Crawford)	<u>L. munda</u> Frick <u>L. pictella</u> (Thomson)	Harding, 1965 Oatman, 1959
<u>Phigalio flavipes</u> (Ashmead)	<u>L. sativae</u> Blanchard	McClanahan, 1977
<u>Tetrastichus</u> sp.	<u>L. sativae</u> Blanchard	Oatman and Kennedy, 1976
<u>Zagrammosoma americanus</u> Girault	<u>L. sativae</u> Blanchard	McClanahan, 1977
<u>Zagrammosoma multilineatum</u> (Ashmead)	<u>L. munda</u> Frick	Stegmaier, 1972
<u>Zagrammosoma mirum</u> Girault	<u>L. pictella</u> (Thomson)	Oatman, 1959
MYMARIDAE		
<u>Polynema</u> sp.	<u>L. pictella</u> (Thomson)	Oatman, 1959
PTEROMALIDAE		
<u>Halticoptera aenea</u> (Walker) ^b	<u>L. sativae</u> Blanchard <u>L. munda</u> Frick <u>L. pictella</u> (Thomson)	Musgrave et al., 1975; McClanahan, 1977; Oatman and Kennedy, 1976 Harding, 1965; Jensen and Kochler, 1970; Stegmaier, 1966 Oatman, 1959

Table 1. Continued

Parasite	Host name ^a	References
<u>Halticoptera circulus</u> (Walker) ^b	<u>L. sativae</u> Blanchard	Musgrave et al., 1975
SCELIONIDAE		
<u>Telenomus</u> sp.	<u>L. pictella</u> (Thomson)	Oatman, 1959

^aName given to the vegetable leafminer from which the parasite was reared and since considered synonymous to Liriomyza sativae Blanchard.

^bReared from the vegetable leafminer in Florida.

1977). A Geocoris species has been observed by the author to attack leafminer pupae on plastic mulch underneath the tomato canopy.

Cultural Control

Abandoned tomato fields could be an important factor in contributing to the leafminer problem (Adlerz, 1961). It has been recommended that plants and plant debris remaining in the field after the final harvest be destroyed to eliminate this fly source (Brogdon, 1961; Wolfenbarger, 1961). However, others feel that abandoned fields contribute few vegetable leafminers to the agroecosystem (K. Pohronezny and V.H. Waddill, personal communication, 1980).

Use of various types of mulching has on several occasions been shown to decrease the number of leaf mines of L. sativae in tomato and squash (Wolfenbarger and Moore, 1968; Chalfant et al., 1977). An increase, using plastic coated paper as the mulch, was found also (Price and Poe, 1976).

Staking has been shown to increase the leaf mine density and decrease parasitism of the leafminer by Opius dimidiatus (Price and Poe, 1976).

Control by Host Plant Resistance

Differential response of Liriomyza sativae Blanchard in cantaloups, chrysanthemums, muskmelons, and tomatoes has been found (Keisheimer, 1953; Wolfenbarger, 1966; Webb and Smith, 1969; Webb et al., 1971; Kennedy et al., 1975, 1978; Schuster and Harbaugh, 1979). These differences in resistance in the tomato cultivars were not great although

several accessions of species related to the cultivated tomato were virtually immune or demonstrated a considerable antibiosis (Webb and Smith, 1969; Webb et al., 1971).

A relatively low level of leafminer resistance in tomato may sufficiently reduce leafminer damage to provide adequate control (Webb et al., 1971).

Chemical Control

Since the vegetable leafminer became a major pest on various truck crops in the mid-1940's, many insecticides have been applied to reduce its populations. DDT has been shown ineffective against leafminers and, because of the reduction of their parasite populations, actually caused an increase in the fly population (Hills and Taylor, 1951; Shorey and Hall, 1963). Research on insecticidal control of the leafminer has been intensive (Musgrave et al., 1975). A large number of compounds has been shown to be promising, but the effectiveness of several has decreased over years of use. Chlordane was one of the first insecticides recommended for leafminer control (Wolfenbarger, 1947). Toxaphene, parathion, aldrin, and dieldrin were also effective in the 1940's (Wolfenbarger, 1948, 1958; Michelbacher et al., 1951; Wene, 1953). All these products, however, seemed to be losing their effectiveness (Wolfenbarger, 1958; Baranowski, 1958; Wene, 1955). Toxaphene, parathion, and aldrin were shown to reduce the parasite population without directly affecting the leafminers (Wene, 1955). In the mid-1950's diazinon became the most effective insecticide (Baranowski, 1958; Wolfenbarger, 1958), although it was very toxic to some parasites

(Getzin, 1960). Brogdon (1961) and Adlerz (1961) found that diazinon was no longer effective in 1961 in south Florida but that it still controlled leafminer populations in north and central Florida. Good reduction of the fly population on tomato with diazinon was also obtained in California (Shorey and Hall, 1963). Dimethoate was shown to be very effective in controlling leafminers in the late 1950's (Getzin, 1960; Hayslip, 1961; Wolfenbarger, 1961). Getzin (1960) found that dioxathion gave excellent control; on the other hand, Harris (1962) found it to be ineffective. Harding (1971) noted good control of the vegetable leafminer on tomato with methamidophos, monocrotophos, and dimethoate in Texas. These three compounds were also effective on tomato in south Florida in 1976 (Schuster et al., 1976). However, dimethoate is not considered effective against the leafminer anymore (Pohronezny and Waddill, 1978). Oxamyl gave good control of leafminer on tomato in south Florida in 1974 (Bear, 1975) and in 1975 (Schuster et al., 1975). In 1977, however, control of defoliation of tomatoes by applications of oxamyl was not satisfactory (Schuster and Everett, 1977). Janes and Genung (1977) also found no control of the vegetable leafminer on celery with this insecticide. The use of methomyl for the control of Lepidopterous pests of tomato destroys the parasite population and subsequently increases the leafminer densities (Oatman and Kennedy, 1976; Janes and Genung, 1977; Johnson et al., 1980a,b).

The negative effects of juvenile hormone analogs on biological control agents appear to outweigh the beneficial effects on target pests (Poe, 1974; Lema and Poe, 1978). Synthetic pyrethroids like permethrin seem to give excellent control of leafminer populations (Schuster et al., 1975; Janes and Genung, 1977; Tryon, 1979) and are

relatively non-toxic to some of the parasites (Waddill, 1978). This group of compounds may be a good alternative to the conventional insecticides because of the spectrum of activity and low toxicity to parasites and mammals (Schuster et al., 1975).

Conclusions

It would be reasonable to suggest that the vegetable leafminer, Liriomyza sativae Blanchard, has become resistant to many insecticides since many of these chemicals have been ineffective in reducing the leafminer populations. Before the development of DDT and other chlorinated hydrocarbons, the leafminer had never been considered a problem in tomato production. Apparently its population was kept sufficiently low by natural enemies. The list of Hymenopterous parasites recorded for L. sativae illustrates the large number of natural enemies of this pest species. Since neither host plant resistance nor cultural methods have as yet been capable of reducing leafminer populations effectively, the solution to the problem seems to lie in integration of chemical and biological control.

Allowing the parasite population to build up rapidly as early in the season as possible would be of great value. This may be accomplished by maintaining the parasite population on weeds or crops grown outside the normal growing season. This is applicable to south Florida, especially since year-round cultivation of crops is possible. The application of selective insecticides for control of the Lepidopterous pests only when needed instead of on the basis of a regular application schedule would be very beneficial to the leafminer's natural enemies since it would aid in the buildup of parasite populations.

CHAPTER III

MECHANICAL DEFOLIATION OF THE TOMATO, Lycopersicon esculentum MILL. CV. WALTER, AND ITS EFFECT ON YIELD AND FRUIT QUALITY

Introduction

Several important tomato pests are foliage feeders although many of them inflict damage directly to the fruit as well. Reduction of marketable yield is, therefore, not solely related to the amount of foliage consumed. Damage by the vegetable leafminer, Liriomyza sativae Blanchard, in contrast, is restricted to the leaves and the injury is different from that caused by most foliage feeders. Only the leaves' mesophyll is consumed (even the spongy tissue remains for the most part untouched) leaving both upper and lower epidermis intact. The presence of a large number of leafminer larvae within one leaf may result in such a serious impairment of the functions of this plant organ that leaf death and subsequent abscission occurs. In addition to this type of damage, yellowing and necrosis of the leaf tissues in the mines' vicinity may occur, even if the larval population is small, again possibly resulting in abscission of the entire leaf. It is clear that, in the case of serious leafminer infestations, partial or even complete defoliation of tomato plants may occur.

In recent years the population of the vegetable leafminer has become so large that growers consider this insect as their most serious pest

(Pohronezny et al., 1978b). Because of the clearly visible damage inflicted on tomato plants, a negative effect on the yield is often suspected. However, it has been shown repeatedly that consumption of leaves and other plant tissues by insects does not necessarily reduce plant vigor or reproductive capacity (Harris, 1972). In fact, Harris (1974) suggested that sometimes a certain density of "pest" insects may be required for a crop to attain its maximum yield. Potato yield increase following partial defoliation has been demonstrated (Skuhravý, 1968). Despite many attempts to find a correlation between leafminer damage and tomato yield no consistent results were obtained. Naturally occurring leafminer populations and insecticide-induced populations have been found to have no significant effect on tomato yield (Levins et al., 1975; Schuster and Everett, 1977; Johnson et al., 1980a,b) although in some fields and in some years yield reduction was found (Wolfenbarger and Wolfenbarger, 1966; Schuster et al., 1976).

Many references have been made to serious leafminer damage of cultivated plants (Spencer, 1973a; Spencer and Stegmaier, 1973) but only on a few occasions has an indirect reduction of yield of a crop plant been demonstrated. A loss in cash value of plants which are grown for their foliage is obvious. These crops include foliage ornamentals, celery (Musgrave et al., 1976), cabbage, lettuce (Musgrave et al., 1975), and alfalfa (Jensen and Koehler, 1970).

The greatest damage by leafminers is often considered to be done to seedlings or young plants which, as a result of weakening, may die or become stunted (McGregor, 1914; Elmore and Ranney, 1954; Adlerz, 1961). Severe damage by leafminers to cantaloups, resulting in complete crop

loss (Hills and Taylor, 1951), and to honeydew melon, resulting in reduction in yield and fruit quality (Michelbacher et al., 1951), have been reported.

Defoliation by means other than insect injury has also been found to have varying effects on fruit production in tomato. The various levels of defoliation caused by Alternaria blight controlled to varying degrees with fungicides, appeared not to be correlated with tomato yield (Richards, 1947). Defoliation by Xanthomonas vesicatoria (Doidge) Dows. resulted in significant reduction of fruit size (Pohronezny et al., 1978a). One commercial variety of tomato could withstand considerable foliar damage due to ozone exposure for a long period of time (Oshima et al., 1975) without significant reduction in fruit size, weight or number, even though the fresh weight of stems and leaves was lowered by 27%. Even a decrease in fresh weight of 62% seemed to have minimal effects on yield.

Mechanical defoliation of tomato plants to study its effect on yield has been performed several times. Wiebe (1970) found a significant yield reduction in greenhouse tomatoes, when all except the top 2 feet of leaves were removed, when compared to plants with only the senescent leaves taken off. Selective removal of overlapping leaves had no effect on yield. A yield reduction, especially in the largest fruit size categories was found as a result of repeated defoliation at high levels (60% or more) in staked tomato plants (Jones, 1980).

The effects of mechanical defoliation on yield and fruit quality of unstaked tomatoes, as they are grown commercially in Dade County, Florida, have not previously been studied.

Actual damage to tomato plants by the leafminer-disease complex occurs gradually, sometimes over a considerable period of time. Exact duplication of this damage is virtually impossible so that simulation by mechanical defoliation may not show the effect of natural defoliation completely (Capinera and Roltsch, 1980).

The study presented here was undertaken to determine:

- (1) the times at which unstaked tomato plants are most sensitive to defoliation,
- (2) the damage threshold at which unstaked tomato plants will show significant loss in yield and fruit quality when
 - (a) defoliated only once, and
 - (b) defoliated repeatedly.

Materials and Methods

General

Tomatoes, cv. Walter, were planted in 1977 and 1978 at the University of Florida Agricultural Research and Education Center in Homestead, Dade County, Florida. After metribuzin was incorporated into the soil at a rate of 0.84 kg ai/ha, seedbeds were prepared in groups of seven with their midlines 182 cm apart. Irrigation pipes with frost protection nozzles were set on the middle bed. The other beds were fertilized with 7-14-14 at a rate of 2242 kg/ha placed in two bands 30 cm apart. For the spring crop of 1978 and the spring crop of 1979 the beds were fumigated with Dowfume MC33[®] at a rate of 314 kg/ha; for the fall crop of 1978 the rate was 247 kg/ha.

Immediately after the fumigation, the beds were covered with plastic mulch, and, simultaneously, drip tubing for irrigation was placed approximately 15 cm in the soil below the plastic. Tomato seeds were planted with a seed drill 30 cm apart in the rows. One to two weeks after emerging the seedlings were thinned to one plant per hill.

The foliage was removed by cutting the leaves off at the distal end of the petiole with scissors. The fresh leaf weight was consistently found to be highly correlated to the total leaf area (Romshe, 1939). For the one-time defoliations the fresh weight of the foliage removed from the completely defoliated plants was used as a reference for removal of the correct amount from the other plants to be defoliated.

From all but the outer two plants of each plot all mature green and colored fruit was harvested three times except for the spring crop of 1979 which was harvested only twice because of poor fruit set. The first harvest was initiated when approximately 5% of all fruit present showed color. The fruit was then graded into USDA grade 1 or 2 after all culled fruit had been removed. These were then sized as extra large, large, medium, small, and very small according to the measurements given in Table 2. The culled fruit was subdivided into several types: misshapen, blemished, sunscalded, decayed, damaged by insects or slugs, and showing gray wall.

One-Time Defoliation

The defoliation experiments were conducted utilizing a split-plot randomized complete-block design. Rows were assigned at random within each of the 4 blocks for defoliation at one particular time. Defoliation levels were assigned at random to the subplots within each

Table 2. Size ranges and mean weights of the size categories of 'Walter' tomatoes.

Size category	Size range in mm	Mean weight in grams
very small	48 - 54	67
small	54 - 58	99
medium	58 - 64	142
large	64 - 73	174
extra large	73	213

Source: Marlowe (1978).

whole plot (row). Each subplot consisted of 12 plants in the spring crop of 1978, of 22 plants in the fall crop of 1978 and of 17 plants in the spring crop of 1979. Each subplot of plants except for the control group was defoliated only once, and those in each row in a block on a different date. Defoliation levels investigated were total (= 100%), 20%, 40%, 60%, and 80% starting from the top of the plant (= 20% upper or 20U; 40% upper or 40U; etc.), or 20%, 40%, 60%, and 80% starting from ground level (= 20% lower or 20L; 40% lower or 40L; etc.).

Yield data were analyzed and comparisons with the control were made as a two-sided test using the Dunnett's procedure (Steel and Torrie, 1960).

Experiment 1. Spring crop 1978. The tomato seeds were planted on November 3, 1977. Beginning November 10, 1977, pesticides were applied twice weekly by a high volume, low concentrate boom sprayer. The insecticide permethrin (FMC 33297) was used at alternate rates of .056 kg ai/ha and .112 kg ai/ha. The fungicide applied simultaneously with the insecticide was either chlorothalonil (Bravo[®]) at a rate of 1.58 kg ai/ha or mancozeb (Dithane M45[®]) at a rate of 1.34 kg ai/ha. Form-a-Turf[®] was applied at a rate of 7.02 l/ha when bacterial diseases threatened (Pohronezny et al., 1979).

The times of defoliation were: 30 days after planting, 40 days after planting and so on with 10 days intervals up to and including 100 days after planting. The levels of defoliation were: 100%, 80% upper, 80% lower, 60% upper, 60% lower, 40% upper, 40% lower, 20% upper, and 20% lower.

Harvesting was done between February 14, 1978, and March 23, 1978.

Experiment 2. Fall crop 1978. The tomato seeds were planted on September 13, 1978. A mixture of permethrin (Ambush[®]) at a rate of .112 kg ai/ha and either chlorothalonil at 1.68 kg ai/ha or mancozeb at 1.34 kg ai/ha was applied weekly, and Form-a-Turf[®] on demand as in Experiment 1.

The times of defoliation were: 30 days after planting, 40 days after planting and so on with 10 day intervals up to and including 80 days after planting. The levels of defoliation were 100%, 80% upper, 80% lower, and 60% upper.

Fruit was harvested between December 8, 1978, and December 28, 1978.

Experiment 3. Spring crop 1979. The tomato seeds were planted on December 28, 1978. Pesticide applications were made at the same schedule and rates as in Experiment 2. Due to the very poor stand of the crop only a limited area of the field could be used. The number of defoliations, therefore, had to be limited. The times of defoliation were: 70 days after planting, 80 days after planting, and 90 days after planting. The levels of defoliation were: 100%, 80% lower, 60% lower, and 40% lower.

Fruit was harvested between April 23, 1979, and May 2, 1979.

Repeated Defoliation

The defoliation experiments were conducted on the fall crop of 1978 using a randomized complete-block design. Defoliation levels were assigned at random within each of the 3 blocks. Plants were treated on several days by removing the required percentage of the foliage present on the day of defoliation from the appropriate part of the plants. Each

plot consisted of 22 plants. One plot in each block was not mechanically defoliated and functioned as the control.

The tomato seeds were planted on September 13, 1978. Pesticide applications were made as described in Experiment 2.

Fruit was harvested between December 8, 1978, and December 28, 1978.

Experiment 4. Tomato plants were partially defoliated at 30, 50, and 70 days after planting. The levels of defoliation were 60% lower, 40% upper, 40% lower, and 20% upper.

Experiment 5. Tomato plants were partially defoliated every 10 days, for the first time at 30 days after planting and for the last time at 80 days after planting. The levels of defoliation were 40% upper, 40% lower, and 20% upper.

Gross Revenue Computation

The computation of the gross income per hectare was based on the total amount of marketable fruit harvested in the first two pickings in the sizes extra large, large, medium, and small. The prices used for each size are listed in Table 3, and are based on market prices in the season 1978-79 for Dade County, Florida.

Results

Experiment 1

Defoliation from mid-season on had a striking effect on the fruit set if the defoliation levels were 60% upper, 80% or 100%. In nearly

Table 3. Prices in dollars per 13.6 kg box of tomato fruit of the four main size categories and two grades.

Grade	Size category	Low price	Medium price	High price
USDA 1	small	3.00	4.50	8.50
	medium	4.00	6.50	12.50
	large	5.00	9.00	15.00
	extra large	6.00	10.00	16.00
USDA 2	small	3.00	4.00	6.50
	medium	4.00	6.00	9.50
	large	4.50	7.00	12.50
	extra large	6.00	8.00	12.50

Source: H. H. Bryan, personal communication, 1980.

all these cases fruit set was significantly reduced to below that of the control ($P < 0.05$). The most severe reduction was at the 100% level at the beginning of the last third of the growing season (Table 4). Early defoliation had no significant effect on fruit set.

The analyses of all the extra large fruit harvested in both first and second pickings (Tables 5 and 6) and of the large fruit harvested in the second picking only (Table 9), showed that very few treatments resulted in significant yield reductions in these size categories. The variation among the usually small number of fruit in these sizes was large. Combining the yields of the two largest fruit categories also did not reveal any significant reductions (Table 12). Whenever defoliation took place the yield of the large fruit and the combination of the two largest fruit classes showed significant reduction in many of the highest levels of defoliation in the first harvest (Tables 8 and 11). The plants were especially sensitive to leaf removal early in the first half (30 days after planting) and early in the second half (60 to 80 days after planting) of the season. The amount of medium size fruit, especially in the first picking, was affected by defoliation at any level during the last few weeks before harvesting (Table 14). Generally speaking defoliation earlier in the season, of 60% or higher led to serious yield reduction in both first and second pickings (Tables 14 and 15).

Plants defoliated 30 days after planting at the three highest levels still showed lush growth at the time of the harvests while leaves of the other plants were senescent to varying degrees. Analysis of variance of the fresh weight of all above ground parts of the plants most severely defoliated at 30, 60 and 100 days after planting, after

all fruit had been removed, showed a significantly higher value for the plants defoliated early in the season than for the plants in the control (Table 17). No significant difference was found in any of the other times or levels of defoliation tested.

The analysis of the gross revenue per hectare (Tables 18 and 19) illustrate the detrimental effect of high levels of defoliation (60% or more) carried out at any time during the season. In the first harvest losses can also be expected to occur if the foliage loss takes place late in the season even at lower levels.

The average weight of all marketable fruit was significantly reduced only in the first harvest for the 80% upper and 100% defoliations 30 days after planting. The total weight of all marketable fruit showed a reduction pattern very similar to that of the gross revenue pattern, the latter based on different prices for the various size categories (compare Tables 18 and 20, and Tables 19 and 21). For both first and second harvests and for all price ranges a highly significant correlation exists between the two variables, total weight and gross revenue.

No treatment resulted in significant increases or decreases in the weight of the culled fruit in the first two harvests or in any particular cull category. Only in the third picking there were significantly more misshapen fruit present on plants defoliated at the 80% and 100% levels early in the season (30 and 40 days after planting).

In many cases where defoliation significantly reduced the fruit weight, this reduction was more noticeable in the USDA grade 1 fruit than in the USDA grade 2 fruit, especially in the two largest fruit categories (Tables 5, 8 and 11).

If the data from the first two harvests are combined (Tables 7, 10, 13 and 16) the impact of mechanical defoliation on the grower's yield can be summarized. It shows that the effect is most pronounced in the plants at first harvest. However, increases in the second harvest tend to compensate for the loss in yield in the first.

Experiment 2

In the first harvest the weight of both the extra large (Table 22) and the large fruit (Table 24) was significantly reduced by defoliation in the first month of the season at all levels investigated and in the second month of the season only at the 100% level. No effect at all was noted for defoliation in the last month of the season except a possible yield increase. In the second harvest no significant yield reduction in the extra large fruit was observed (Table 23) while the weight of the large fruit was reduced significantly (Table 25) especially in the very high levels of defoliation (80% or more) in the last two months of the season. The 60% upper defoliation had a significant effect on the USDA grade 1 fruit only, the most severe reduction occurring from defoliation at 50 days after planting.

Analysis of the combination of the two largest fruit sizes (Tables 26 and 27) summarize the differences in effects of defoliation in the first two harvests.

A reduction in the weight of the medium sized fruit as a result of foliage removal occurred only in the second harvest (Tables 28 and 29). The reduction pattern was very similar to that of the large fruit.

Analysis of both the total weight of all marketable fruit and of the gross revenue per hectare show significant reductions at defoliation

levels and times at which the weight of the extra large and large fruit was also reduced (Tables 30 and 31; Figures 1 and 2). As in Experiment 1 a very close correlation existed between the total fruit weight and the gross revenue based on different prices for different size categories.

From combining the total yields of the first two harvests (Figure 3) it appears that the only significant reduction due to 50% defoliation occurred in plants defoliated 50 days after planting.

The average weight of all marketable fruit was significantly reduced only in the first harvest by 100% defoliation of the tomato plants 50 days after planting. In the second harvest no significant reductions were found.

The weight of all culled fruit together in any of the treatments showed no significant difference from the control in any of the harvests. However, more sunscalded and decaying fruit were present on plants defoliated 15 days before the first harvest at the 80% and 100% levels. Defoliation at 80 days after planting also resulted in more decaying fruit when 80% or more of the foliage was removed from the plants.

Experiment 3

Since only late-season defoliations could be examined for effects on yield and fruit quality, differences in reduction patterns as found in the first two experiments could not be verified. In fact, analysis of the weight of the various fruit sizes, total weight, and gross revenue revealed only very few significant reductions when compared to the control.

No significant differences in the weight of the extra large fruit was detected (Figure 4). No extra large fruit was harvested in the second picking.

The weight of the large fruit was only reduced significantly by defoliating plants 80 days after planting at the 100% level in the first picking, while in the second picking the reduction was only significant when the plants were completely defoliated 90 days after planting (Figure 5). The latter was also the case for the weight of the medium size fruit in the second harvest (Figure 6).

Combining the weight of all extra large and large fruit for analysis showed a reduction by complete defoliation 70 days or 80 days after planting (Figure 7).

Both the weight of all marketable fruit (Figures 8 and 9) and the gross revenue per hectare (Tables 32 and 33) were significantly reduced by 100% defoliation at 80 or 90 days after planting.

Total weight of the culled fruit was not significantly different between any of the treatments and the control. The weight of the culled fruit as a percentage of the total marketable fruit plus culls was significantly higher only in the second harvest if the tomato plants were completely defoliated 80 or 90 days after planting. Significantly more sunscalded fruit occurred on plants defoliated 90 days after planting at the 60% and higher levels of defoliation. Weight of the decaying fruit was significantly greater than the control in plants completely defoliated 70 or 90 days after planting in the first picking.

Experiment 4

When tomato plants were defoliated three times during the growing season, the threshold for reduction in fruit weight per plant in several size categories was lower than that found in one-time defoliation experiments.

Analysis of all extra large fruit in the first harvest showed that the repeated removal of 40% from the upper part and 60% from the lower part of the foliage of the tomato plants had the same effect on yield in this fruit size. Removal of 40% of the foliage starting at soil level also reduced the yield, but not as severely (Figure 10).

In the second harvest significant differences in the yield of extra large fruit also occurred (Figure 10) but because of the low total yield in this size category its effect on the overall fruit yield in this harvest was negligible (Figure 14).

The yield of large fruit in the first harvest was also significantly reduced at some defoliation levels (Figure 11) but not as severely as that of the extra large fruit. The effect of defoliation on the yield in the two largest size categories is summarized in Figure 12.

Reduction in the weight of the medium size fruit in the first (Figure 13) had only a minimal effect on the total yield (Figure 14). In the second picking the increase in the weight of medium size fruit and large fruit accounted for the significant increase of the total yield.

The total yield of the first two harvests was not significantly reduced by defoliation at any level (Figure 15) while the combined weight of all extra large and large fruit was significantly reduced only at the 60% defoliation level.

Experiment 5

Frequent defoliation of tomato plants resulted in a reduction of the yield of extra large fruit at all levels tested (Figure 16) and of the large fruit at the 40% level (Figure 17) in the first harvest only. Reduction was evident in all defoliation levels when the two largest size categories were combined for analysis (Figure 18).

The yield of the medium size fruit was only significantly reduced as a result of removal of 40% of the foliage from the upper part of the plants (Figure 19).

In no size category was a yield reduction observed in the second harvest.

The total yield loss as a result of repeated defoliation (Figure 20) was mainly caused by the fewer extra large and large fruit harvested and although in the second harvest no significant differences were observed, the larger fruit weight removed from the plants at that time compensated for the lesser weight harvested in the first, since combining the yield of the first and the second harvests showed no significant differences (Figure 21).

Discussion

Defoliation of unstaked tomato plants revealed a changing sensitivity to this type of damage in the course of their development as was demonstrated for potato by Skuhravý (1968) and sugarbeet by Capinera (1979).

Damage early in the development, before or at anthesis, when most of the metabolic activity of the plant is directed at vegetative

Table 4. Influence of defoliation of 'Walter' tomato plants on fruit set.

Defoliation level ^b	Mean number of fruit per 10 plants ^a									
	Time of defoliation (in days after planting)									
	30	40	50	60	70	80	90	100		
20% lower	437	399	437	397	378	368	392	376		
20% upper	468	404	388	415	346	372	318*	413		
40% lower	456	487	425	382	338	415	364	358		
40% upper	409	396	415	344	347	358	325	334		
60% lower	436	402	411	424	338	327	354	346		
60% upper	463	394	320*	314*	230**	315*	338	313*		
80% lower	415	409	372	278**	281**	310*	319*	328		
80% upper	376	419	351	294**	268**	269**	294**	296**		
100%	434	490	297**	259**	212**	225**	259**	274**		

^aA significant difference from the control (418 fruits) is indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^bFor an explanation of the defoliation level codes see page 26.

Table 5. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large fruit in the first harvest of the spring crop of 1978.

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}									
		30	40	50	60	70	80	90	100		
20% lower	1	73.10	124.15	77.31	128.53	158.86	140.66	18.62*	46.07		
	2	156.96	128.70	103.48	135.83	97.39	117.83	109.13	91.30		
	1+2	107.35	126.00	87.99	131.51	133.75	131.33	55.60	64.55		
20% upper	1	92.79	123.72	52.08	101.33	98.80	95.80	48.95	31.06		
	2	76.09	131.30	32.35	147.83	87.57	126.70	85.65	92.61		
	1+2	85.97	126.82	44.05	120.32	94.21	108.42	63.94	56.20		
40% lower	1	85.41	78.38	141.26	95.33	61.99	97.58	22.52*	77.01		
	2	144.09	71.48	117.57	123.65	120.17	152.17	106.52	119.57		
	1+2	109.41	75.56	131.62	106.93	85.79	119.89	56.84	94.39		
40% upper	1	55.86	148.17	68.17	73.71	98.50	89.32	65.47	42.94		
	2	92.61	87.83	119.13	81.30	74.35	64.35	87.13	114.09		
	1+2	70.87	123.52	88.99	76.80	88.63	79.11	74.32	72.01		
60% lower	1	86.19	91.29	92.01	89.03	17.72*	67.09	91.72	138.56		
	2	144.78	56.70	130.43	113.04	77.13	131.04	61.48	78.87		
	1+2	110.12	77.16	107.71	98.83	41.99	93.25	79.40	114.21		
60% upper	1	30.63	104.02	113.81	96.70	70.40	57.06	67.87	75.50		
	2	51.04	88.00	78.70	30.00	101.30	69.74	77.13	110.61		
	1+2	38.97	97.51	99.47	69.45	83.02	62.24	71.65	89.99		

Table 5. Continued

		Mean yield per treatment as a percentage of the mean yield of the controls ^{a,b}								
Defoliation level ^c	Fruit ^d grade	Time of defoliation (in days after planting)								
		30	40	50	60	70	80	90	100	
80% lower	1	46.38	101.26	123.42	35.74	15.45*	28.95	19.35*	87.09	
	2	44.35	70.87	154.35	42.17	39.57	104.96	47.57	70.17	
	1+2	45.54	89.06	136.06	38.37	25.29*	60.04	30.91*	80.18	
80% upper	1	10.21*	47.60	54.49	42.04	56.58	31.96	47.15	50.45	
	2	33.91	62.18	99.57	27.13	72.78	50.43	61.91	84.52	
	1+2	19.89*	53.53	72.90	35.95	63.23	39.50	53.18	64.37	
100%	1	3.30**	42.18	37.97	19.52*	10.51*	36.16	56.76	42.95	
	2	5.39*	14.52	101.30	5.65*	38.43	40.87	27.39	79.30	
	1+2	4.16**	30.91*	63.30	13.85**	21.92*	38.08	44.76	57.80	

^aMean yield per plant for the control: USDA grade 1, 166.5 g; USDA grade 2, 115.0 g.

^bYield is significantly different from the control if indicated by * for P < 0.05 or by ** for P < 0.01.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 6. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large fruit in the second harvest of the spring crop of 1978.

Defoliation level _C	Fruit _D grade	Mean yield per treatment as a percentage of the mean yield of the control _{A,B}								
		30	40	50	60	70	80	90	100	
20% lower	1	150.25	109.45	125.38	89.55	149.25	237.56	228.86	212.69	
	2	0	0	113.31	0	71.94	167.27	161.87	192.09	
	1+2	88.97	64.71	120.59	52.94	117.65	208.82	201.47	204.41	
20% upper	1	83.08	114.43	28.60	169.15	130.60	0	174.13	297.26	
	2	0	0	0	95.32	35.97	215.83	165.47	276.98	
	1+2	49.26	67.65	16.91	138.97	91.91	88.24	170.59	288.97	
40% lower	1	141.79	87.06	185.31	205.22	161.69	419.15*	318.41	160.45	
	2	71.94	41.37	127.70	0	113.30	343.53*	39.57	39.57	
	1+2	113.24	68.38	161.76	121.32	141.91	388.24*	204.41	111.03	
40% upper	1	112.94	105.47	155.47	85.82	164.93	143.78	109.45	181.59	
	2	0	37.77	0	0	158.27	0	23.38	80.94	
	1+2	66.76	77.94	91.91	50.74	221.32	144.12	74.26	140.44	
60% lower	1	131.84	26.12	131.84	140.55	557.21*	24.88	60.95	57.21	
	2	41.37	188.85	55.76	0	95.32	86.33	75.54	93.53	
	1+2	94.85	92.65	100.74	83.09	368.38*	50.00	66.91	72.06	
60% upper	1	24.88	115.42	109.45	251.24	85.82	251.24	202.74	52.24	
	2	0	0	37.77	142.09	100.72	107.91	70.14	118.71	
	1+2	14.71	68.38	80.15	206.62	91.91	192.65	148.53	79.41	

Table 6. Continued

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	26.12	29.85	263.68	212.69	94.53	154.23	0	31.09	
	2	0	0	7.19	44.96	163.67	39.57	120.14	215.83	
	1+2	15.44	17.65	158.82	144.12	122.79	107.35	49.26	106.62	
80% upper	1	28.36	110.45	26.12	162.94	0	82.09	103.23	77.11	
	2	0	34.17	46.76	221.22	39.57	39.57	0	104.32	
	1+2	16.91	79.41	34.56	186.76	16.18	64.71	61.03	88.24	
100%	1	28.36	88.06	29.85	0	24.88	113.18	64.68	123.13	
	2	35.97	0	43.17	0	152.88	124.10	41.37	79.14	
	1+2	31.62	52.21	35.29	0	77.21	117.65	55.15	105.15	

^aMean yield per plant for the control: USDA grade 1, 20.1 g; USDA grade 2, 13.9 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 7. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large fruit in the first two harvests of the spring crop of 1978.

Defoliation level _C	Fruit _D grade	Mean yield per treatment as a percentage of the mean yield of the control _{A,B}								
		30	40	50	60	70	80	90	100	
20% lower	1	81.46	122.56	82.53	124.33	157.82	151.13	41.26	64.04	
	2	140.03	114.82	104.50	121.18	94.65	123.13	114.82	102.17	
	1+2	105.35	119.36	91.48	123.00	131.97	139.64	71.29	79.59	
20% upper	1	91.75	122.72	49.57	108.63	102.20	85.48	62.43	59.75	
	2	67.88	117.15	28.86	142.13	82.00	136.31	94.26	112.49	
	1+2	81.97	120.41	41.10	122.31	93.95	106.21	75.41	81.27	
40% lower	1	91.48	79.31	146.03	107.18	72.72	132.21	54.39	86.01	
	2	136.31	68.27	118.70	110.32	119.47	172.77	99.30	110.94	
	1+2	109.79	74.78	134.82	108.43	91.79	148.76	72.72	96.17	
40% upper	1	62.00	143.62	77.55	75.03	116.40	105.95	70.20	57.88	
	2	82.62	82.39	106.28	72.54	83.40	57.41	80.29	110.55	
	1+2	70.41	118.58	89.26	73.99	102.88	86.09	74.30	79.37	
60% lower	1	91.10	84.24	96.30	94.59	75.83	62.54	88.42	129.80	
	2	133.59	70.99	122.34	100.85	79.13	126.22	62.99	80.45	
	1+2	108.43	78.80	106.94	97.12	77.15	88.56	78.01	109.63	
60% upper	1	30.01	105.31	113.34	113.34	72.08	77.97	82.37	72.99	
	2	45.54	78.51	74.24	42.05	101.24	73.86	76.42	111.48	
	1+2	36.34	94.33	97.34	84.19	93.97	76.27	79.91	88.72	

Table 7. Continued

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	44.21	93.89	138.53	54.77	23.95*	42.44	17.26*	81.03	
	2	39.57	63.23	138.48	42.44	52.91	97.91	55.47	85.88	
	1+2	42.30	81.34	138.47	49.75	35.80	65.11	32.86	83.02	
80% upper	1	12.17*	54.39	51.45	55.04	50.48	37.35	53.16	53.32	
	2	30.26	59.12	93.87	48.10	69.20	49.26	55.24	86.66	
	1+2	19.55*	56.31	68.76	52.19	58.14	42.21	54.02	66.92	
100%	1	6.03**	47.16	36.28	17.42*	12.06*	44.48	57.61	51.55	
	2	8.69*	12.69	95.03	5.04*	50.81	49.81	28.86	79.29	
	1+2	7.13**	33.17	60.27	12.36*	27.88	46.64	45.85	62.90	

^aMean yield per plant for the control: USDA grade 1, 186.6 g; USDA grade 2, 128.9 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 8. Influence of defoliation of 'Walter' tomato plants on the mean yield of all large fruit in the first harvest of the spring crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the controls ^{a,b}								
		30	40	50	60	70	80	90	100	
20% lower	1	125.00	77.30	122.26	100.57	91.01	78.44	22.64**	29.47*	
	2	135.00	77.36	63.88	53.58	35.63	100.78	46.13	84.46	
	1+2	129.68	77.30	94.59	78.31	64.81	88.99	33.75**	55.47	
20% upper	1	76.66	78.57	96.11	92.16	74.30	131.51	46.88	36.80*	
	2	99.89	54.29	57.98	82.79	63.17	91.55	65.44	70.76	
	1+2	87.64	67.06	78.07	90.06	69.01	112.56	55.65	52.89*	
40% lower	1	62.31	80.17	107.46	88.01	88.65	49.43	29.02*	36.03*	
	2	84.10	75.73	99.36	78.07	85.17	95.25	63.52	79.84	
	1+2	72.60	78.07	103.59	83.28	86.97	71.09	45.33*	56.75	
40% upper	1	96.75	109.82	87.05	108.10	111.42	57.08	35.52*	47.83	
	2	57.13	41.16	39.74	36.34*	24.27*	42.02	40.45	45.07	
	1+2	77.97	77.30	64.64	74.11	70.18	49.93*	37.84**	46.51*	
60% lower	1	87.05	58.04	104.08	125.45	17.86**	80.68	79.40	69.20	
	2	107.31	31.73*	71.31	96.52	72.18	70.62	32.44*	56.92	
	1+2	96.61	45.57*	88.55	111.72	43.55*	75.89	57.15	63.36	
60% upper	1	25.64*	108.74	62.50	108.23	46.05	29.66*	63.14	74.30	
	2	81.41	63.31	97.59	24.84*	77.36	28.39*	63.31	72.39	
	1+2	52.05*	87.21	79.08	68.74	60.85	29.05**	63.20	73.37	

Table 8. Continued

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		Time of defoliation (in days after planting)								
		30	40	50	60	70	80	90	100	
80% lower	1	41.77	69.96	113.33	71.24	31.57*	56.12	81.95	70.15	
	2	101.99	51.28	81.26	26.40*	32.29*	53.23	64.23	56.07	
	1+2	70.25	61.11	98.12	50.03*	31.90**	54.73	73.54	63.47	
80% upper	1	18.49**	52.42	46.68	68.24	26.28*	36.80*	29.15*	29.34*	
	2	26.05*	37.97	132.36	28.74*	56.07	37.40	39.89	43.08	
	1+2	22.06**	45.57*	87.21	49.53*	40.26**	37.11**	34.25**	35.83**	
100%	1	5.26**	14.67**	31.57*	33.29*	15.31**	19.90**	44.77	35.24*	
	2	12.78**	9.23**	84.95	57.84	39.74	18.45**	35.49*	31.41*	
	1+2	8.80**	12.09**	56.82	44.90*	26.86**	19.21**	40.36**	33.41**	

^aMean yield per plant for the control: USDA grade 1, 156.8 g; USDA grade 2, 140.9 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 9. Influence of defoliation of 'Walter' tomato plants on the mean yield of all large fruit in the second harvest of the spring crop of 1978.

Defoliation level ^c	Fruit grade	Mean yield per treatment as a percentage of the mean yield of the controls ^{a,b}									
		30	40	50	60	70	80	90	100		
20% lower	1	87.00	77.38	147.90	80.31	98.44	82.60	154.50	104.85		
	2	123.79	120.89	72.53	129.59	77.85	171.66	267.31*	97.20		
	1+2	94.98	87.81	118.88	92.41	88.23	106.93	183.39*	98.39		
20% upper	1	100.27	107.33	95.42	88.56	86.54	23.81	77.56	140.11		
	2	32.40	58.99	74.47	151.35	116.05	32.88	113.64	166.83		
	1+2	75.39	88.23	85.25	104.54	92.29	25.69	85.72	142.89		
40% lower	1	167.12	128.39	133.88	151.10	122.25	94.96	155.68	114.65		
	2	105.90	102.03	95.74	114.11	122.34	152.80	130.56	183.75		
	1+2	141.70	115.29	116.91	133.81	117.50	109.14	141.88	131.54		
40% upper	1	134.16	106.69	105.49	91.58	118.32	74.63	44.87	96.15		
	2	91.39	131.04	41.59	151.84	95.26	97.20	71.57	113.15		
	1+2	115.71	110.07	81.66	106.63	106.63	78.67	51.37	97.67		
60% lower	1	174.45	81.69	93.59	92.95	119.69	44.41	61.36	78.30		
	2	231.14	107.83	74.47	99.61	133.95	105.42	192.94	120.89		
	1+2	185.19*	86.62	84.05	91.40	119.47	61.53	99.58	88.41		
60% upper	1	35.26	120.88	46.43	112.18	114.47	129.58	157.97	103.02		
	2	26.11	116.54	33.85	127.66	106.38	105.90	112.19	130.56		
	1+2	31.06	114.81	40.74	112.60	107.53	117.20	137.69	107.53		

Table 9. Continued

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	50.82	66.58	147.44	90.84	100.46	119.69	15.76*	75.55	
	2	27.56	110.25	83.66	189.07	152.80	101.55	124.27	179.30	
	1+2	41.64	77.48	121.98	117.68	112.72	109.44	48.69	104.66	
80% upper	1	29.03	46.89	3.67*	112.82	38.92	68.22	71.61	38.19	
	2	0	104.93	0	207.93	112.67	121.86	144.10	115.47	
	1+2	18.94	63.02	2.39*	137.81	60.16	82.14	91.22	60.63	
100%	1	15.57*	49.64	32.69	36.63	46.89	27.66	50.09	54.67	
	2	33.85	63.35	55.13	98.16	66.25	118.96	25.63	74.95	
	1+2	20.61	51.97	38.35	54.18	51.08	54.78	40.62	58.84	

^aMean yield per plant for the control: USDA grade 1, 115.7 g; USDA grade 2, 51.7 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 10. Influence of defoliation of 'Walter' tomato plants on the mean yield of all large fruit in the first two harvests of the spring crop of 1978.

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the controls ^{a,b}									
		30	40	50	60	70	80	90	100		
20% lower	1	106.79	75.49	129.61	90.09	91.82	78.24	74.94	58.97		
	2	132.01	89.04	66.20	73.99	46.99	119.78	105.50	87.85		
	1+2	117.17	81.07	103.31	83.39	73.22	95.42	87.58	70.92		
20% upper	1	84.29	88.26	93.58	88.51	77.43	85.21	58.06	77.32		
	2	81.78	55.56	62.41	104.88	77.36	75.80	78.40	96.57		
	1+2	83.22	74.68	80.64	95.25	77.37	81.28	66.45	85.26		
40% lower	1	102.83	97.62	115.49	111.19	100.00	66.50	79.08	66.68		
	2	89.93	82.81	98.39	87.75	95.12	110.70	81.52	107.74		
	1+2	97.46	91.45	108.36	101.44	97.94	84.78	80.06	83.64		
40% upper	1	109.43	105.94	92.37	98.90	111.56	62.75	38.42*	66.06		
	2	66.30	65.26	40.24	67.34	43.35	56.85	48.81	63.34		
	1+2	91.55	89.08	70.75	85.79	83.28	60.28	42.70*	64.90		
60% lower	1	120.00	66.12	97.43	109.43	58.24	54.22	70.28	71.99		
	2	140.55	52.18	72.17	97.35	88.79	79.96	75.55	74.09		
	1+2	128.45	60.33	86.93	104.38	70.86	70.71	72.43	72.36		
60% upper	1	28.88**	111.01	54.57	107.23	72.37	68.99	99.63	84.04		
	2	66.56	77.62	80.48	52.44	85.15	49.17	76.43	88.00		
	1+2	44.49*	97.14	65.27	84.50	77.63	60.76	89.98	85.64		

Table 10. Continued

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		Time of defoliation (in days after planting)								
		30	40	50	60	70	80	90	100	
30% lower	1	44.40*	66.97	124.29	77.43	58.42	80.26	53.47	70.64	
	2	82.04	67.08	81.88	70.09	64.64	66.20	80.32	89.15	
	1+2	59.96	66.99	106.71	74.36	60.97	74.40	64.58	78.27	
80% upper	1	22.28**	48.99*	28.33**	84.48	30.72**	48.51*	45.50*	32.18**	
	2	19.06**	55.92	96.83	76.84	71.24	60.07	67.86	62.56	
	1+2	20.95**	51.84*	56.67	81.28	47.50*	53.30*	54.74	44.75*	
100%	1	9.25**	28.33**	31.27**	33.84**	27.60**	22.57**	45.87*	42.20*	
	2	18.43**	23.73**	76.85	68.64	46.83	45.43	32.81*	43.09	
	1+2	13.05**	26.43**	50.18*	48.25*	35.57**	32.02**	40.45**	42.55**	

^aMean yield per plant for the control: USDA grade 1, 272.5 g; USDA grade 2, 192.6 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 11. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large plus large fruit in the first harvest of the spring crop of 1978.

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}									
		30	40	50	60	70	80	90	100		
20% lower	1	96.38	101.42	99.10	114.94	125.91	110.45	20.56**	38.03*		
	2	144.86	100.43	81.67	90.54	63.38	108.44	74.44	87.53		
	1+2	118.85	100.98	91.40	104.18	98.31	109.56	44.36*	59.90		
20% upper	1	84.94	101.79	73.44	96.85	86.89	113.08	47.93	33.86*		
	2	89.18	88.90	46.50	114.77	74.13	107.35	74.52	80.58		
	1+2	86.83	96.10	61.54	104.78	81.25	110.56	59.68	54.50*		
40% lower	1	74.21	73.04	124.83	91.74	74.89	74.21	25.66**	57.11		
	2	111.06	73.86	107.54	98.55	100.90	120.83	82.85	97.69		
	1+2	90.49	76.85	117.21	94.77	86.40	94.80	50.92*	75.04		
40% upper	1	75.66	129.56	77.30	90.35	104.73	73.65	50.93	45.30*		
	2	73.08	62.13	75.42	56.55	46.78	52.05	61.43	76.08		
	1+2	74.52	99.78	76.47	75.44	79.15	64.13	55.58	58.90		
60% lower	1	86.58	75.14	97.87	106.68	17.78**	73.65	85.71	104.89		
	2	124.15	42.99	97.89	103.95	74.44	97.77	45.53	66.82		
	1+2	103.18	60.94	97.88	105.47	42.81**	84.32	67.96	88.07		
60% upper	1	28.20**	106.28	88.90	102.26	58.60	43.75*	65.55	74.89		
	2	67.80	74.44	89.09	27.16*	88.12	46.97	69.56	89.57		
	1+2	45.69*	92.21	88.99	69.08	71.64	45.18*	67.32	81.39		

Table 11. Continued

Defoliation level ^c	Fruit grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	44.12*	86.27	118.49	52.94	23.25**	42.12*	49.69	78.85	
	2	76.08	60.06	114.11	33.49*	35.56*	76.48	56.75	62.41	
	1+2	58.26	74.69	116.55	44.36*	28.69**	57.31	52.82*	71.59	
80% upper	1	14.22**	49.94	50.71	54.73	41.90*	34.32*	38.40*	40.20*	
	2	29.58**	48.85	117.62	28.02*	63.60	43.26	49.82	61.74	
	1+2	21.01**	49.46*	80.27	42.93**	51.48*	38.27**	43.45**	49.72*	
100%	1	4.24**	28.82**	34.38*	26.19**	12.83**	28.29**	50.93	39.18*	
	2	9.46*	11.61*	92.30	34.39*	39.16*	28.53*	31.85*	52.95	
	1+2	6.56**	21.23**	59.99	29.81**	24.46**	28.40**	42.50**	45.26*	

^aMean yield per plant for the control: USDA grade 1, 323.3 g; USDA grade 2, 255.9 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 12. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large plus large fruit in the second harvest of the spring crop of 1978.

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}									
		30	40	50	60	70	80	90	100		
20% lower	1	92.19	78.42	137.48	77.84	101.25	101.62	158.10	115.76		
	2	97.56	95.27	81.10	102.13	76.52	170.73	244.97	117.38		
	1+2	93.90	83.87	119.11	85.71	93.15	124.07	186.35	116.23		
20% upper	1	92.93	103.24	81.00	96.24	88.88	19.15	88.14	156.63		
	2	25.46	46.49	58.69	139.48	99.09	71.65	124.54	190.09		
	1+2	70.97	84.71	73.70	110.27	92.16	36.23	100.00	167.49		
40% lower	1	155.38	116.13	135.13	151.84	122.24	138.44	172.31	115.98		
	2	98.62	89.18	102.44	89.94	120.43	193.14	111.28	153.20		
	1+2	136.82	107.30	124.42	131.61	121.59	156.18	152.36	128.04		
40% upper	1	124.59	101.40	107.88	86.30	134.39	96.09	52.28	104.20		
	2	71.95	111.28	32.77	119.66	108.54	76.52	61.28	106.25		
	1+2	107.44	104.57	83.37	97.12	125.91	89.68	55.19	104.81		
60% lower	1	159.79	69.59	94.77	95.51	178.72	39.40	58.32	71.43		
	2	190.85	125.00	70.43	78.51	129.76	101.37	167.99	115.09		
	1+2	169.83	87.59	86.85	89.93	161.39	59.55	94.04	85.61		
60% upper	1	32.02	114.29	53.53	127.39	104.71	141.38	157.00	90.57		
	2	20.58	91.77	34.60	130.64	105.18	106.25	103.20	128.05		
	1+2	28.29	106.95	47.39	128.39	104.81	129.88	139.45	102.73		

Table 12. Continued

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	44.70	57.95	157.58	104.57	94.77	119.07	12.67	65.32	
	2	21.65	86.89	67.38	158.54	155.03	88.41	123.48	187.04	
	1+2	37.22	67.34	128.14	122.08	114.39	109.03	48.73	104.96	
80% upper	1	27.61	54.12	6.77	114.87	31.30	67.01	72.90	42.12	
	2	0	89.94	9.91	210.67	97.10	104.42	113.57	113.11	
	1+2	18.61	65.76	7.79*	146.00	52.70	79.16	86.10	65.26	
100%	1	16.72	53.02	30.71	29.46	41.38	39.03	49.85	62.22	
	2	34.30	49.85	52.59	77.29	84.60	119.97	28.96	75.76	
	1+2	22.43	51.96	37.82	45.01	55.43	65.36	43.03	66.60	

^aMean yield per plant for the control: USDA grade 1, 135.8 g; USDA grade 2, 65.6 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 13. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large plus large fruit in the first two harvests of the spring crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the controls ^{a,b}									
		30	40	50	60	70	80	90	100		
20% lower	1	96.47	94.62	110.45	103.99	118.62	107.84	61.24	61.02		
	2	135.17	99.35	81.53	92.88	66.08	121.11	109.20	93.59		
	1+2	112.40	96.56	98.54	99.40	96.97	113.29	81.00	74.43		
20% upper	1	87.33	102.24	75.68	96.69	87.48	85.30	59.82	70.17		
	2	76.18	80.22	48.97	119.78	79.20	100.03	84.73	102.92		
	1+2	82.73	93.16	64.67	106.19	84.07	91.37	70.07	83.65		
40% lower	1	98.21	90.16	127.87	109.54	88.89	93.21	69.03	74.52		
	2	108.52	76.96	106.50	96.77	104.85	135.57	88.62	108.99		
	1+2	102.45	84.71	119.05	104.26	95.47	110.64	77.09	88.71		
40% upper	1	90.16	121.23	86.35	89.18	113.50	80.29	51.33*	62.72		
	2	72.82	72.14	66.70	69.40	59.39	57.06	61.41	82.25		
	1+2	83.01	101.00	78.24	81.02	91.20	70.71	55.47	70.75		
60% lower	1	108.23	73.50	96.95	103.38	65.37	63.52	77.64	94.99		
	2	137.75	59.70	92.26	98.73	84.89	98.48	70.49	76.65		
	1+2	120.37	67.81	95.02	101.45	73.40	77.92	74.68	87.42		
60% upper	1	29.33**	108.67	78.51	109.69	72.23	72.63	92.60	79.53		
	2	58.15	77.95	77.95	48.26	91.57	59.08	76.40	97.39		
	1+2	41.20**	96.00	78.24	84.39	80.19	67.04	85.93	86.89		

Table 13. Continued

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	44.32*	77.90	130.05	68.21	44.43*	64.90	38.76**	74.85	
	2	64.99	65.52	104.54	58.99	59.92	78.89	70.34	87.84	
	1+2	52.82	72.80	119.54	64.41	50.80	70.65	51.76	80.19	
80% upper	1	18.18**	51.18*	37.72**	72.52	38.76**	43.99*	48.61*	40.77**	
	2	23.54**	57.21	95.62	65.30	70.43	55.72	62.81	72.20	
	1+2	20.39**	53.66	61.56	69.54	51.80	48.82*	54.45	53.72	
100%	1	7.95**	35.98**	33.32**	27.16**	21.28**	31.47**	50.63*	45.99*	
	2	14.52**	19.43**	84.17	43.13	48.41	47.17	31.25*	57.59	
	1+2	10.65**	29.16**	54.26	33.74**	32.46**	37.93**	42.64*	50.77	

^aMean yield per plant for the control: USDA grade 1, 459.1 g; USDA grade 2, 321.5 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 14. Influence of defoliation of 'Walter' tomato plants on the mean yield of all medium size fruit in the first harvest of the spring crop of 1978.

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}									
		30	40	50	60	70	80	90	100		
20% lower	1	130.86	110.51	77.54	80.47	110.25	46.88*	25.09**	28.44**		
	2	176.07**	108.23	73.76	91.23	40.58*	89.87	32.29*	41.47*		
	1+2	151.85*	109.42	75.76	85.45	77.82	66.86	28.43**	34.49**		
20% upper	1	105.87	112.16	78.83	70.07	100.82	102.78	30.91**	16.33**		
	2	175.65**	77.13	46.62	93.15	80.57	115.23	48.70	26.78**		
	1+2	138.29	95.87	63.83	80.77	91.38	108.54	39.17**	21.21**		
40% lower	1	90.16	59.61	102.27	59.87	86.04	55.13	23.44**	33.59**		
	2	68.42	70.62	79.98	56.10	89.45	65.46	43.25*	47.10		
	1+2	80.03	64.74	91.87	58.13	87.60	59.92	32.64**	39.86**		
40% upper	1	89.49	106.90	49.30	98.66	98.25	60.79	45.44*	19.17**		
	2	78.79	68.72	80.57	33.59*	40.40*	69.02	65.99	27.25**		
	1+2	84.49	89.12	63.83	68.37	71.35	64.60	54.96*	22.92**		
60% lower	1	48.17	60.79	68.52	55.49	34.36**	62.18	66.05	80.22		
	2	72.69	68.54	72.27	54.50	59.36	63.80	47.51	41.88*		
	1+2	59.56	64.38	70.25	55.01*	46.01*	62.95	57.44	62.40		
60% upper	1	63.73	92.22	72.39	76.76	53.43	35.29**	39.00*	40.03*		
	2	140.11	79.21	74.47	52.84	82.35	50.36	38.51*	49.88		
	1+2	99.23	86.14	73.33	65.52	66.86	42.29**	38.76**	44.63*		

Table 14. Continued

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	57.96	41.06*	74.03	43.12*	35.03**	37.72*	61.57	27.56**	
	2	131.81	23.82**	70.50	34.95*	55.69	47.10	59.66	35.84*	
	1+2	92.29	33.06**	72.37	39.31**	44.63*	42.07**	60.66	31.40**	
80% upper	1	61.67	37.71*	66.98	56.00	38.23*	29.11**	47.40*	42.76*	
	2	73.16	34.95*	124.53	13.74**	48.28	38.92*	36.73*	33.47*	
	1+2	67.00	36.42**	93.72	36.36**	42.89**	33.66**	42.42**	38.43**	
100%	1	17.36**	18.65**	33.85**	34.88**	18.29**	11.33**	34.00**	41.06*	
	2	31.10*	25.47**	62.62	40.11*	32.29*	11.97**	35.25*	54.32	
	1+2	23.75**	21.82**	47.25*	37.33**	24.79**	11.63**	34.57**	47.25*	

^aMean yield per plant for the control: USDA grade 1, 194.1 g; USDA grade 2, 168.8 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 15. Influence of defoliation of 'Walter' tomato plants on the mean yield of all medium size fruit in the second harvest of the spring crop of 1978.

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}									
		30	40	50	60	70	80	90	100		
20% lower	1	53.35*	67.54	106.84	99.04	100.94	96.48	99.04	107.04		
	2	70.88	88.60	98.44	105.79	76.17	81.60	114.31	96.09		
	1+2	61.96**	77.88	102.71	102.35	88.78	89.17	106.54	101.66		
20% upper	1	68.53	73.35	103.43	87.68	95.54	54.54*	73.27	90.01		
	2	48.10*	93.01	92.18	110.64	83.01	78.61	86.54	102.62		
	1+2	58.50**	83.01	97.91	98.96	89.39	66.36*	79.79	96.22		
40% lower	1	142.08*	77.19	85.75	104.99	94.98	84.00	104.14	104.14		
	2	74.79	74.93	102.85	78.17	70.88	74.64	65.24	85.66		
	1+2	109.02	76.08	94.15	91.81	83.15	79.40	85.03	95.06		
40% upper	1	90.30	100.37	104.00	79.60	85.13	118.81	92.79	90.15		
	2	87.19	83.51	89.19	108.93	71.76	71.32	68.38	82.63		
	1+2	88.78	92.10	96.72	94.01	78.56	95.50	80.80	86.47		
60% lower	1	107.46	63.14	91.43	115.55	82.63	109.96	63.34	71.85		
	2	96.30	73.08	74.26	83.46	67.06	48.25*	113.49	86.60		
	1+2	101.99	68.02*	83.01	99.78	75.00	79.64	87.99	79.11		
60% upper	1	79.31	89.67	67.40	80.36	49.66*	86.18	81.07	96.77		
	2	56.77	60.01	73.82	93.15	69.26	98.06	48.19*	75.73		
	1+2	68.24*	75.10	70.55	86.65	59.29**	92.03	64.92*	86.43		

Table 15. Continued

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	38.51**	36.38**	86.12	52.70*	66.26	84.34	31.84**	67.96	
	2	35.56**	64.21	122.60	87.78	66.91	85.87	69.35	85.28	
	1+2	37.06**	50.05**	104.04	69.94*	66.58*	85.10	50.27**	76.47	
80% upper	1	46.88**	61.63	32.92**	90.01	35.19**	84.28	37.60**	50.14*	
	2	42.32**	54.86*	24.68**	78.52	74.79	67.59	64.85	54.28*	
	1+2	44.64**	58.32**	28.87**	84.38	54.64**	76.08	50.99**	52.19**	
100%	1	27.44**	50.43*	34.82**	33.48**	26.39**	35.24**	27.10**	57.60*	
	2	25.33**	51.72*	59.80	80.28	57.95	39.23**	52.66*	54.28*	
	1+2	26.42**	51.06**	47.09**	56.47**	41.89**	37.20**	39.66**	55.97**	

^aMean yield per plant for the control: USDA grade 1, 352.4 g; USDA grade 2, 340.3 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 16. Influence of defoliation of 'Walter' tomato plants on the mean yield of all medium size fruit in the first two harvests of the spring crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}									
		Time of defoliation (in days after planting)									
		30	40	50	60	70	80	90	100		
20% lower	1	80.86	82.78	96.41	92.43	104.23	78.85	72.76	79.13		
	2	105.77	95.11	90.26	100.96	64.37*	84.36	87.12	77.98		
	1+2	92.87	88.73	93.44	96.54	85.01	81.51	79.68	78.57		
20% upper	1	81.78	87.12	94.68	81.41	97.42	71.66	58.21**	63.85*		
	2	90.40	87.74	77.10	104.83	82.20	90.75	73.99	77.49		
	1+2	85.93	87.43	86.19	92.71	90.08	80.87	65.83*	70.42*		
40% lower	1	123.62	70.93	91.60	88.95	91.79	73.73	75.47	79.07		
	2	72.68	73.50	95.27	70.85	77.04	71.60	57.94*	72.87		
	1+2	99.05	72.18	93.37	80.23	84.68	72.70	67.01*	76.08		
40% upper	1	90.01	102.67	84.56	86.35	89.77	98.19	75.96	64.95*		
	2	84.40	78.61	86.33	83.97	61.38*	70.56	67.57	64.27*		
	1+2	87.31	91.07	85.41	85.20	76.08	84.87	71.92*	64.62**		
60% lower	1	86.39	62.29	83.28	94.22	65.50*	92.97	64.31*	74.83		
	2	88.49	71.60	73.60	73.86	64.53*	53.43**	91.63	71.79		
	1+2	87.40	66.78*	78.62	84.39	65.02**	73.90	77.48	73.36		
60% upper	1	73.77	90.56	69.15	79.07	50.99**	68.09*	66.14*	76.60		
	2	84.40	66.39	74.05	79.79	73.60	82.24	44.98**	67.18		
	1+2	78.90	78.90	71.51*	79.42	61.90**	74.92	55.93**	72.06		

Table 16. Continued

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}								
		30	40	50	60	70	80	90	100	
80% lower	1	45.41**	38.05**	81.81	49.30**	55.16**	67.78*	42.39**	53.60**	
	2	67.47	50.82**	105.32	70.26	63.19*	73.01	66.14	68.89	
	1+2	56.06**	44.21**	93.16	59.41**	59.03**	70.31*	53.85**	60.98**	
80% upper	1	52.14**	53.15**	45.01**	77.94	36.26**	64.67*	41.07**	47.51**	
	2	52.54**	48.26**	57.79*	57.06*	66.00	58.08*	55.53**	47.38**	
	1+2	52.33**	50.79**	51.17**	67.87*	50.60**	61.50**	48.05**	47.45**	
100%	1	23.87**	39.15**	34.49**	33.97**	23.51**	26.75**	29.55**	51.72**	
	2	27.24**	43.02**	60.74*	66.98	49.44**	30.19**	46.89**	54.31**	
	1+2	25.50**	41.01**	47.15**	49.89**	36.02**	28.42**	37.91**	52.97**	

^aMean yield per plant for the control: USDA grade 1, 546.6 g; USDA grade 2, 509.1 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 17. Influence of defoliation of 'Walter' tomato plants on the mean fresh weight of all above ground plant parts, excluding fruit, at the time of completion of the third harvest of the spring crop of 1978.

Defoliation level ^c	Mean fresh weight per plant (in grams) ^{a,b}		
	Time of defoliation (in days after planting)		
	30	60	100
80% lower	11062*	8080	6928
80% upper	10960*	7100	8175
100%	14177**	7595	7785

^aMean fresh weight per control plant: 8545 g.

^bWeight is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

Table 18. Gross revenue in dollars per hectare of 'Walter' tomatoes based on all marketable fruit of sizes extra large through small. Influence of defoliation on the first harvest of the spring crop of 1978.

Defoliation level ^b	Price range ^c	Gross revenue in dollars per hectare ^a		
		Time of defoliation (in days after planting)		
		30	40	50
20% lower	low	8082.09	6550.75	5324.03
	medium	12637.24	10303.40	8493.80
	high	21392.33	17327.15	14268.75
20% upper	low	6545.31	6193.58	3872.43
	medium	10280.84	9754.46	6281.72
	high	17327.81	16428.61	10748.39
40% lower	low	5382.35	4579.86	6870.04
	medium	8378.81	7279.11	10919.89
	high	14092.30	12251.89	18362.76
40% upper	low	4756.31	6316.15	4511.49
	medium	7543.69	10130.75	7076.46
	high	12751.90	17052.51	11725.68
60% lower	low	5453.36	4049.70	5620.91
	medium	8520.16	6440.70	8852.95
	high	14178.30	10791.39	14785.40
60% upper	low	3991.70	5667.20	5267.03
	medium	6143.33	9069.60	8346.68
	high	10387.59	15295.96	14047.32
80% lower	low	4358.11	3854.30	6331.63
	medium	6787.66	6185.50	10011.80
	high	9246.99*	10316.42	16681.33
80% upper	low	2348.83**	2951.32**	5259.78
	medium	3619.87**	4644.44**	8123.45
	high	6215.82**	7791.31**	13707.45
100%	low	805.63**	1397.73**	3517.23*
	medium	1242.04**	2236.14**	5362.91*
	high	2126.91**	3722.67**	8967.95*

^aA significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^bFor an explanation of the defoliation level codes see page 26.

Table 18. Extended

Gross revenue in dollars per hectare ^a				
Time of defoliation (in days after planting)				
60	70	80	90	100
6173.47	6009.88	6039.37	2433.01**	3177.35*
9767.64	9644.90	9527.27	3643.43**	4884.31**
16265.67	16276.05	15813.27	6048.10**	8159.86**
6147.28	5318.10	6807.10	3296.79*	2662.18**
9617.88	8434.99	10794.19	5132.76*	4083.64**
16063.85	14265.29	18167.70	8572.06*	6791.28**
5095.03	5408.71	5311.34	2788.05**	3964.52
8046.67	8472.88	8200.71	4222.35**	6119.93
13434.95	14299.88	13663.95	7027.70**	10155.79
4591.06	4845.43	4057.60	3680.82	2952.63**
7398.22	7845.84	6443.66	5693.40*	4537.35**
12597.86	13281.38	10778.38	9493.99*	7474.33**
5419.59	2693.48**	4990.19	4065.18	5113.31
8656.90	4081.66**	7772.03	6541.85	8183.41
14481.44	6870.53**	13029.51	10983.16	13747.98
4337.84	4331.91	2842.58**	3612.12	4244.26
7106.12	6742.85	4417.75**	5712.84	6678.10
12011.36	11282.84	7327.38**	9548.36*	11109.36
2665.81**	2128.23**	3211.95*	3348.36*	3748.70
4296.49**	3315.41**	4963.23*	5350.39*	5976.93
7263.29**	5608.72**	8288.86**	9150.98*	9943.92
2542.74**	3098.60*	2298.74**	2725.11**	2931.05**
4154.81**	4803.75**	3598.78**	4259.09**	4535.05**
7114.36**	8036.95**	6025.53**	7187.50**	7599.87**
1923.61**	1491.64**	1466.60**	2522.31**	2880.97**
3087.23**	2285.07**	2297.76**	4051.18**	4466.68**
5310.85**	3845.90**	3790.05**	6796.89**	7453.91**

^cPrices used in the computations are given in Table 3.

Note: Gross revenue per hectare of the control plants was for the low price range, \$6194.11, for the medium range, \$9829.29, and for the high range, \$16607.44

Table 19. Gross revenue in dollars per hectare of 'Walter' tomatoes based on all marketable fruit of sizes extra large through small. Influence of defoliation on the second harvest of the spring crop of 1978.

Defoliation level ^b	Price range ^c	Gross revenue in dollars per hectare ^a		
		Time of defoliation (in days after planting)		
		30	40	50
20% lower	low	4563.55	5193.22	6543.17
	medium	7104.97	8039.75	10308.02
	high	12227.51	13900.53	17950.72
20% upper	low	4059.58	5135.56	5833.43
	medium	6412.53	8048.32	9111.45
	high	11250.22	13881.75	16003.55
40% lower	low	7001.67	5337.04	6090.78
	medium	11108.37	8376.83	9568.95
	high	19569.22	14530.70	16476.06
40% upper	low	5774.95	5781.54	5732.94
	medium	9103.87	9070.75	9001.06
	high	15836.17	15851.00	15687.90
60% lower	low	7004.47	4477.72	5343.14
	medium	11105.89	6946.81	8374.69
	high	19362.29	12010.86	14674.69
60% upper	low	3737.50*	5059.28	3982.64
	medium	5796.53*	8021.46	6185.83
	high	10259.42*	14072.86	10740.81
80% lower	low	2570.91**	3413.60*	6723.57
	medium	3989.40**	5286.63**	10580.51
	high	6938.90**	9039.12**	18171.65
80% upper	low	2426.76**	3676.05*	1704.49**
	medium	3763.36**	5729.15*	2602.21**
	high	6585.18**	9997.80*	4614.78**
100%	low	1595.76**	3260.88**	2719.68**
	medium	2469.10**	5088.44**	4171.45**
	high	4322.69**	8866.79**	7113.04**

^aA significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^bFor an explanation of the defoliation level codes see page 26.

Table 19. Extended

Gross revenue in dollars per hectare ^a				
Time of defoliation (in days after planting)				
60	70	80	90	100
5998.51	5101.78	5819.10	7340.06	6273.81
9313.43	8080.12	9117.71	11550.22	9846.72
16178.68	14145.02	15908.33	19939.24	17153.50
6105.44	5359.28	3796.15	4976.57	6812.87
9500.42	8417.19	5738.87*	7778.30	10674.09
16398.13	14726.59	9851.99*	13439.07	18326.84
6074.29	4353.30	5855.84	6083.85	6255.19
9670.44	8468.43	9186.73	9729.58	9832.39
16904.73	14808.63	15841.28	17019.07	17188.43
5612.67	5186.47	5752.87	4440.31	5391.91
8740.10	8248.49	9039.45	6935.28	8474.69
15059.05	14323.77	15933.21	12216.80	14736.47
5828.49	5634.25	4310.82	5208.09	5128.97
9158.40	9012.27	6779.92	8053.43	7931.51
16080.99	15584.60	12185.33	13803.00	13724.42
5720.42	4041.95	5883.35	4826.49	5462.75
9020.13	6392.43	9293.65	7786.70	8576.18
15500.08	10943.62	16007.51	13607.61	15051.30
4547.24	4602.10	5306.89	3023.64**	4784.15
7174.33	7225.73	8399.23	4585.30**	7433.97
12249.09	12505.11	14574.35	7838.43**	12846.14
5702.62	3233.86**	4486.12	3425.79*	3267.80**
8980.14	4956.31**	7044.50	5382.52**	5081.03**
15615.57	8444.54**	12366.56	9210.46**	8841.09**
3101.73**	2773.88**	2835.33**	2289.19**	3533.70*
4760.92**	4247.23**	4346.08**	3591.53**	5538.86*
8075.67**	7173.83**	7478.12**	6094.89**	9654.95*

^cPrices used in the computations are given in Table 3.

Note: Gross revenue per hectare of the control plants was for the low price range, \$6286.20, for the medium range, \$9798.74, and for the high range, \$17064.17.

Table 20. Influence of defoliation of 'Walter' tomato plants on the total yield of marketable fruit, the weight of the culled fruit, and the total yield of marketable fruit plus culled fruit in the first harvest of the spring crop of 1978.

Defoliation level ^c	Fruit type ^d	Mean yield per treatment (in grams) ^{a,b}									
		Time of defoliation (in days after planting)									
		30	40	50	60	70	80	90	100		
20% lower	total 1	13328	10343	8343	9448	9290	9238	3683**	4898**		
	culls	757	647	290	825	735	915	627	947		
	total 2	14085	11990	8633	10273	10025	10153	4310**	5845*		
20% upper	total 1	10955	9730	6368	9600	8470	10830	5113**	4010**		
	culls	527	815	765	897	980	510	1120	902		
	total 2	11482	10545	7133	10497	9450	11340	6233	4912**		
40% lower	total 1	8320	7300	10735	7703	8678	8145	4323**	5948		
	culls	265	777	920	635	1105	1005	1055	1230		
	total 2	8585	8077	11655	8338	9783	9150	5378*	7178		
40% upper	total 1	7598	9980	6943	7235	7560	6360	5895*	4345**		
	culls	952	612	382	1122	1240	545	2080	810		
	total 2	8550	10592	7325	8357	8800	6905	7975	5155**		
60% lower	total 1	8305	6460	8743	8250	4378**	7895	6293	7838		
	culls	992	1312	517	1065	1757	832	1027	840		
	total 2	9297	7772	9260	9315	6135	8727	7320	8678		
60% upper	total 1	6955	8963	8293	6915	6783	4415**	5543*	6378		
	culls	345	825	815	780	1362	1325	945	1300		
	total 2	7300	9788	9108	7695	8145	5740*	6488	7678		

Table 20. Continued

		Mean yield per treatment (in grams) ^{a,b}									
Defoliation level ^c	Fruit type	Time of defoliation (in days after planting)									
		30	40	50	60	70	80	90	100		
80% lower	total 1	7468	5748*	9550	4255**	3573**	4963**	5555*	5715*		
	culls	717	452	330	552	1190	1472	1247	972		
	total 2	8185	6200	9880	4807**	4763**	6435	6802	6687		
80% upper	total 1	4193**	4700**	8695	4063**	4868**	3645**	4295**	4525**		
	culls	135	705	645	502	770	800	1062	642		
	total 2	4328**	5405*	9340	4565**	5638*	4445**	5357*	5167**		
100%	total 1	1488**	2183**	5613*	3268**	2415**	2158**	3983**	4498**		
	culls	72	55	405	182	635	870	670	1340		
	total 2	1560**	2238**	6018*	3450**	3050**	3028**	4653**	5838*		

^aMean yield per 10 plants. Mean yield for the control per 10 plants: total marketable fruit, 10443 g; culled fruit, 552 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: total 1 = total yield of all marketable fruit; culls = total weight of culled fruit; total 2 = total yield of marketable fruit plus culled fruit.

Table 21. Influence of defoliation of 'Walter' tomato plants on the total yield of marketable fruit, the weight of the culled fruit, and the total yield of marketable fruit plus culled fruit in the second harvest of the spring crop of 1978.

Defoliation level ^c		Fruit type		Mean yield per treatment (in grams) ^{a,b}									
				Time of defoliation (in days after planting)									
				30	40	50	60	70	80	90	100		
20% lower	total 1	8855	10240	12502	11708	9535	10902	13603	11810				
	culls	712	720	510	667	1055	460	887	652				
	total 2	9567	10960	13012	12375	10590	11362	14490	12462				
20% upper	total 1	7935*	9908	11547	11647	10247	7510*	9305	12575				
	culls	382	577	900	640	555	477	522	1027				
	total 2	8317*	10485	12447	12287	10802	7987*	9827	13602				
40% lower	total 1	13315	10310	11458	11435	9870	10570	11257	11938				
	culls	452	625	537	557	452	722	945	982				
	total 2	13767	10935	11995	11992	10322	11292	12202	13920				
40% upper	total 1	11115	11115	11078	10792	9442	11060	8600	10170				
	culls	657	887	362	390	485	465	387	512				
	total 2	11772	12002	11440	11182	9927	11525	8987	10682				
60% lower	total 1	13170	8565	10380	11220	10047	8298	9992	10017				
	culls	700	662	422	540	855	812	325	385				
	total 2	13870	9228	10802	11760	10902	9110	10317	10402				
60% upper	total 1	7502*	9647	7745*	10618	7432*	10883	8763	10463				
	culls	590	810	347	547	585	837	632	592				
	total 2	8092*	10457	8092*	11165	8017*	11720	9395	11055				

Table 21. Continued

		Mean yield per treatment (in grams) ^{a,b}									
Defoliation level ^c	Fruit type ^c	Time of defoliation (in days after planting)									
		30	40	50	60	70	80	90	100		
80% lower	total 1	5153**	6648**	12772	8245	8557	9957	5882**	8957		
	culls	342	712	600	170	585	610	270	580		
	total 2	5495**	7360**	13372	8415*	9142	10567	6152**	9537		
80% upper	total 1	4837**	7067**	3500**	10480	6288**	8557	6385**	6182**		
	culls	420	705	120	445	372	735	640	365		
	total 2	5257**	7772*	3620**	10925	6660**	9292	7025**	6547**		
100%	total 1	3117**	6365**	5290**	6020**	5272**	5402**	4255**	6695**		
	culls	250	765	600	595	375	205	400	770		
	total 2	3367**	7130**	5890**	6615**	5647**	5607**	4655**	7465**		

^aMean yield per 10 plants. Mean yield for the control per 10 plants: total marketable fruit, 12218 g; culled fruit, 589 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: total 1 = total yield of all marketable fruit; culls = total weight of culled fruit; total 2 = total yield of marketable fruit plus culled fruit.

Table 22. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large fruit in the first harvest of the fall crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}						
		30	40	50	60	70	80	
60% upper	1	34.25*	67.60	35.92*	112.77	113.08	151.19	
	2	57.57	15.67*	39.98	73.03	99.36	75.16	
	1+2	39.55**	55.79	36.79	103.73	109.96	133.91	
80% lower	1	31.59*	83.97	67.50	93.01	78.64	130.80	
	2	55.12	63.11	60.77	91.15	104.16	93.28	
	1+2	36.96**	79.25	65.97	92.58	84.46	122.27	
80% upper	1	11.04**	74.34	61.07	70.17	111.98	104.05	
	2	25.27*	37.31	103.62	42.32	91.90	60.23	
	1+2	14.30**	65.92	70.77	63.86	107.42	94.09	
100%	1	5.02**	23.75*	19.67**	27.82*	96.61	82.03	
	2	29.32*	75.16	24.20	51.92	31.66	41.26	
	1+2	10.54**	35.43	20.72**	33.33**	81.85	72.76	

^aMean yield per plant for the control: USDA grade 1, 159.4 g; USDA grade 2, 46.9 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 23. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large fruit in the second harvest of the fall crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}						
		30	40	50	60	70	80	
60% upper	1	34.36	120.27	37.80	144.33	71.13	63.57	
	2	70.00	258.50	50.00	27.50	22.50	121.00	
	1+2	48.68	175.86	42.60	96.35	51.12	86.61	
80% lower	1	79.04	0	40.21	34.36	21.31	23.02	
	2	136.00	32.50	0	57.50	0	0	
	1+2	101.83	13.18	23.73	43.61	12.58	13.59	
80% upper	1	34.36	60.14	0	0	0	0	
	2	0	83.50	0	0	0	0	
	1+2	20.28	69.37	0	0	0	0	
100%	1	38.49	0	0	35.05	0	0	
	2	0	0	0	31.00	0	0	
	1+2	22.72	0	0	33.47	0	0	

^aMean yield per plant for the control: USDA grade 1, 14.6 g; USDA grade 2, 10.0 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 24. Influence of defoliation of 'Walter' tomato plants on the mean yield of all large fruit in the first harvest of the fall crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^a						
		30	40	50	60	70	80	
60% upper	1	85.81	92.09	52.47*	100.82	95.65	149.68*	
	2	61.99	53.64	131.76	76.84	65.42	85.30	
	1+2	79.11	81.27	74.78	94.07	87.15	131.56	
80% lower	1	66.71	80.30	97.65	95.20	90.99	127.45	
	2	33.40	75.82	125.61	87.60	143.03	79.92	
	1+2	57.34**	79.04	105.54	93.07	105.64	114.07	
80% upper	1	70.83	82.26	85.91	68.86	96.55	116.01	
	2	55.84	67.21	107.33	66.09	64.40	115.63	
	1+2	66.61*	78.03	91.94	68.08	87.51	115.92	
100%	1	48.86*	36.02**	46.79*	86.62	94.24	135.47	
	2	22.80*	53.02	70.18	58.15	66.09	90.16	
	1+2	41.52**	40.80**	53.37**	78.60	86.32	122.72	

^aMean yield per plant for the control: USDA grade 1, 249.2 g; USDA grade 2, 97.6 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 25. Influence of defoliation of 'Walter' tomato plants on the mean yield of all large fruit in the second harvest of the fall crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}						
		30	40	50	60	70	80	
60% upper	1	65.79*	75.89	28.32**	58.71**	43.65**	63.54*	
	2	87.89	108.07	67.11	143.42	129.39	100.88	
	1+2	69.62	81.46	35.03**	73.37	58.49*	70.00	
80% lower	1	67.77*	28.96**	34.75**	31.72**	47.79**	37.47**	
	2	163.60	58.33	160.96	150.44	46.67	63.33	
	1+2	84.35	34.04**	56.59*	52.26**	47.60**	41.94**	
80% upper	1	82.77	55.50**	27.03**	37.74**	52.34**	40.40**	
	2	32.63	73.25	87.89	130.00	59.65	74.74	
	1+2	73.64	58.56*	37.58**	53.70**	53.60**	46.34**	
100%	1	64.32*	16.38**	6.98**	22.77**	28.32**	39.39**	
	2	87.46	58.77	77.19	112.89	60.53	37.28	
	1+2	68.33	23.72**	19.13**	38.37**	33.89**	39.02**	

^aMean yield per plant for the control: USDA grade 1, 272.3 g; USDA grade 2, 57.0 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 26. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large plus large fruit in the first harvest of the fall crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}						
		30	40	50	60	70	80	
60% upper	1	65.71	82.54	46.01**	105.48	102.45	150.27*	
	2	60.55	41.35	101.97	75.61	76.47	82.01	
	1+2	64.36*	71.77	60.63**	97.67	95.65	132.42*	
80% lower	1	53.01*	81.74	85.90	94.35	86.17	128.76	
	2	40.48	71.70	104.57	88.75	130.45	84.26	
	1+2	49.73**	79.11	90.77	92.88	97.73	117.12	
80% upper	1	47.50**	79.17	76.24	69.38	102.57	111.36	
	2	45.92	57.51	106.12	58.37	73.36	97.65	
	1+2	47.09**	73.51	84.04	66.50*	94.93	107.76	
100%	1	31.75**	31.23**	36.22**	63.69	95.17	114.62	
	2	24.91*	60.21	55.26	56.12	54.91	74.29	
	1+2	29.96**	38.80**	41.19**	61.71**	84.65	104.09	

^aMean yield per plant for the control: USDA grade 1, 408.6 g; USDA grade 2, 144.5 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 27. Influence of defoliation of 'Walter' tomato plants on the mean yield of all extra large plus large fruit in the second harvest of the fall crop of 1978.

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}						
		Time of defoliation (in days after planting)						
		30	40	50	60	70	80	
60% upper	1	64.18*	78.12	28.80**	63.05*	45.06**	63.53*	
	2	85.16	130.50	64.50	126.03	113.35	103.80	
	1+2	68.15	88.02	35.55**	74.96	57.98*	71.14	
80% lower	1	68.33	27.49**	35.04**	31.85**	46.45**	36.73**	
	2	159.36	54.55	136.84	136.47	39.67	53.84	
	1+2	85.55	32.58**	54.31**	51.65**	45.16**	39.97**	
80% upper	1	79.78	55.73**	25.66**	35.82**	49.68**	38.35**	
	2	27.74	74.72	74.72	110.51	50.71	63.53	
	1+2	69.92	59.32*	34.96**	49.96**	49.86**	43.11**	
100%	1	63.01*	15.55**	6.62**	23.39**	26.88**	37.39**	
	2	74.35	49.96	65.62	100.67	51.45	31.69	
	1+2	65.14	22.06**	17.80**	38.02**	31.53**	36.30**	

^aMean yield per plant for the control: USDA grade 1, 286.9 g; USDA grade 2, 67.0 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 28. Influence of defoliation of 'Walter' tomato plants on the mean yield of all medium sized fruit in the first harvest of the fall crop of 1978.

Defoliation level ^c	Fruit grade ^d	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}						
		30	40	50	60	70	80	
60% upper	1	150.33	150.33	121.64	161.80	74.10	122.13	
	2	90.63	81.01	201.92	99.04	124.28	84.13	
	1+2	126.10	122.20	154.04	136.32	94.45	106.62	
80% lower	1	114.75	138.85	163.44	194.59	114.26	133.11	
	2	103.37	104.57	124.28	131.01	164.66	91.35	
	1+2	110.03	124.83	147.52	168.65	134.57	116.07	
80% upper	1	132.20	99.18	121.31	125.41	164.75	149.28	
	2	121.88	71.39	185.10	102.64	70.91	78.13	
	1+2	128.04	87.83	147.03	116.07	126.58	120.25	
100%	1	65.08	57.38	162.30	126.23	129.51	251.97**	
	2	67.31	38.46	199.52	50.48	124.28	165.87	
	1+2	65.92	49.66	177.22	95.42	127.26	216.85**	

^aMean yield per plant for the control: USDA grade 1, 30.5 g; USDA grade 2, 20.9 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 29. Influence of defoliation of 'Walter' tomato plants on the mean yield of all medium sized fruit in the second harvest of the fall crop of 1978.

Defoliation level ^c	Fruit ^d grade	Mean yield per treatment as a percentage of the mean yield of the control ^{a,b}						
		30	40	50	60	70	80	
60% upper	1	100.32	101.88	53.72*	35.65**	53.43*	77.63	
	2	92.25	121.71	114.50	117.98	150.39	129.22	
	1+2	98.81	105.60	65.14*	51.11**	71.62	87.32	
80% lower	1	93.91	57.40*	48.86**	34.85**	41.17**	26.49**	
	2	108.53	56.74	150.54	183.72*	47.67	56.98	
	1+2	96.66	57.29**	67.94*	62.77*	42.39**	32.21**	
80% upper	1	81.26	63.63	33.60**	39.59**	45.14**	48.33**	
	2	74.03	71.32	123.02	81.78	61.78	44.96	
	1+2	79.90	65.07*	50.39**	47.51**	48.28**	47.70**	
100%	1	76.16	49.97**	14.44**	18.53**	37.98**	46.39**	
	2	98.99	59.46	135.43	167.44	53.64	51.16	
	1+2	80.44	51.77**	37.15**	46.46**	40.93**	47.29**	

^aMean yield per plant for the control: USDA grade 1, 279.4 g; USDA grade 2, 64.5 g.

^bYield is significantly different from the control if indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^cFor an explanation of the defoliation level codes see page 26.

^dCodes: 1 = USDA grade 1; 2 = USDA grade 2; 1+2 = USDA grades 1 plus 2.

Table 30. Gross revenue in dollars per hectare of 'Walter' tomatoes based on all marketable fruit of sizes extra large through small. Influence of defoliation on the first harvest of the fall crop of 1978.

Defoliation level	Price ^c range	Gross revenue in dollars per hectare ^a					
		30	40	50	60	70	80
Time of defoliation (in days after planting)							
60% upper	low	2768.44*	3097.86	2668.36*	4167.82	4014.85	5427.49
	medium	4662.07	5277.57	4375.16*	6997.47	6703.88	9201.40
	high	7851.69	8845.21	7416.67*	11646.11	11067.43	15246.78
80% lower	low	2194.87**	3404.54	3828.69	4059.42	4064.77	4879.21
	medium	3687.08**	5692.16	6400.91	6762.62	6715.25	8213.97
	high	6172.65**	9502.07	10774.83	11303.02	11235.63	13620.30
80% upper	low	2077.16**	3064.42	3599.77	2881.63	4070.70	4445.34
	medium	3515.91**	5174.77	5945.30	4829.45	6813.11	7487.43
	high	5964.66**	8629.39	9943.84	8073.69	11324.19	12517.06
100%	low	1284.88**	1611.08**	2007.96**	2572.06*	3624.81	4535.05
	medium	2180.87**	2626.10**	3324.06**	4355.31*	6131.38	7695.75
	high	3671.51**	4394.85**	5661.76**	7336.69*	10210.73	12935.76

^aA significant difference from the control is indicated by * for P < 0.05 or by ** for P < 0.01.

^bFor an explanation of the defoliation level codes see page 26.

^cPrices used in the computations are given in Table 3.

Note: Gross revenue per hectare of the control plants was for the low price range, \$4128.54, for the medium range, \$6885.49, and for the high range, \$11444.88.

Table 31. Gross revenue in dollars per hectare of 'Walter' tomatoes based on all marketable fruit of sizes extra large through small. Influence of defoliation on the second harvest of the fall crop of 1978.

Defoliation level	Price range ^c	Gross revenue in dollars per hectare ^a						
		Time of defoliation (in days after planting)						
		30	40	50	60	70	80	
60% upper	low	3665.75	4220.29	2156.24**	2723.47*	2781.95*	3392.18	
	medium	6036.72	6928.85	3488.23**	4511.00*	4529.45*	5577.41	
	high	10748.23	12207.90	6153.71**	7762.73**	7909.11*	9786.34	
80% lower	low	3884.95	1901.86**	2546.20**	2395.78**	1892.06**	1580.03**	
	medium	6383.61	3116.89**	4124.82**	3841.87**	3177.76**	2633.93**	
	high	11280.03	5586.31**	7217.49**	6621.35**	5568.35**	4585.87**	
80% upper	low	3284.85	2690.02*	1842.64**	2080.37**	2102.86**	1899.64**	
	medium	5518.85	4660.08*	2969.93**	3413.36**	3526.45**	3163.92**	
	high	9720.85	7854.49*	5165.87**	5994.81**	6185.50**	5602.54**	
100%	low	3073.80	1595.76**	1127.38**	1744.78**	1563.14**	1811.75**	
	medium	5109.94	2576.34**	1762.32**	2792.25**	2572.06**	3012.93**	
	high	9006.25	4647.00**	3021.91**	4761.99**	4556.05**	5327.08**	

^aA significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^bFor an explanation of the defoliation level codes see page 26.

^cPrices used in the computations are given in Table 3.

Note: Gross revenue per hectare of the control plants was for the low price range, \$4339.46, for the medium range, \$7244.96, and for the high range, \$12724.42.

Figure 1. Influence of defoliation of 'Walter' tomato plants on the total yield of marketable fruit in the first harvest of the fall crop of 1978. A significant difference from the control (0) is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation level codes see page 26.

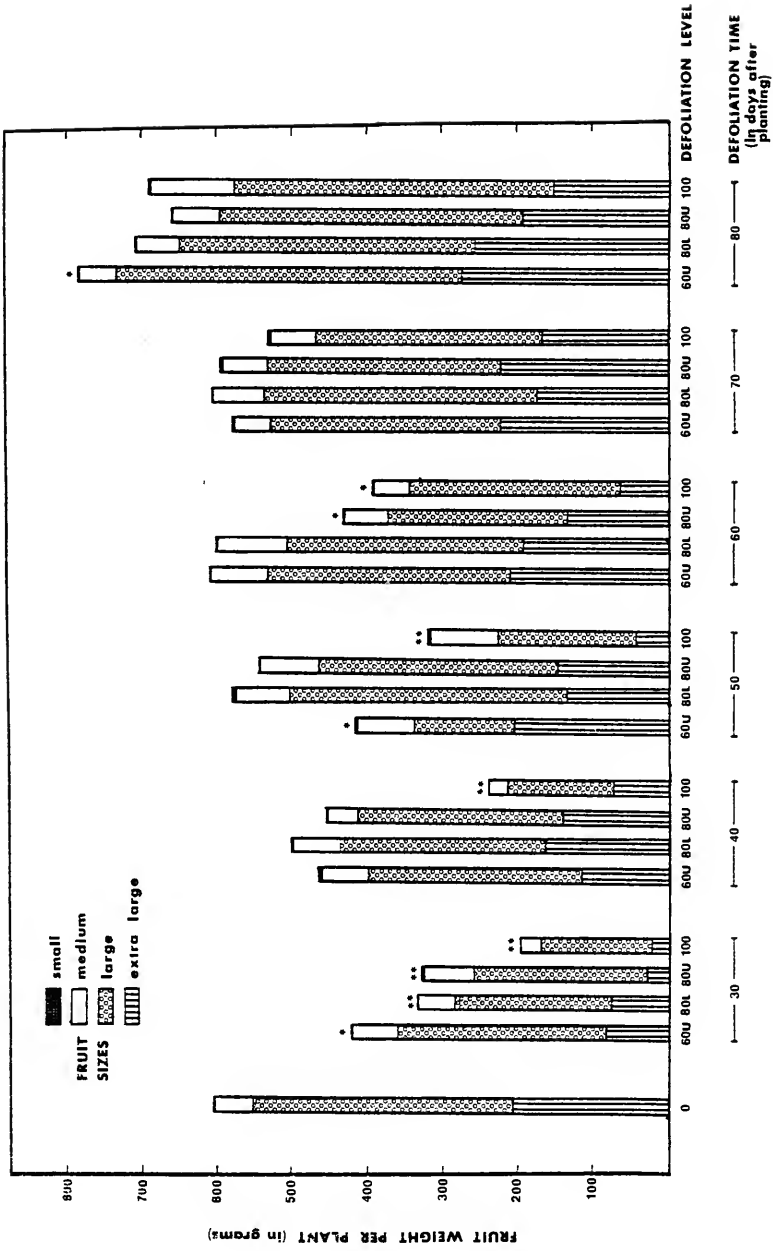
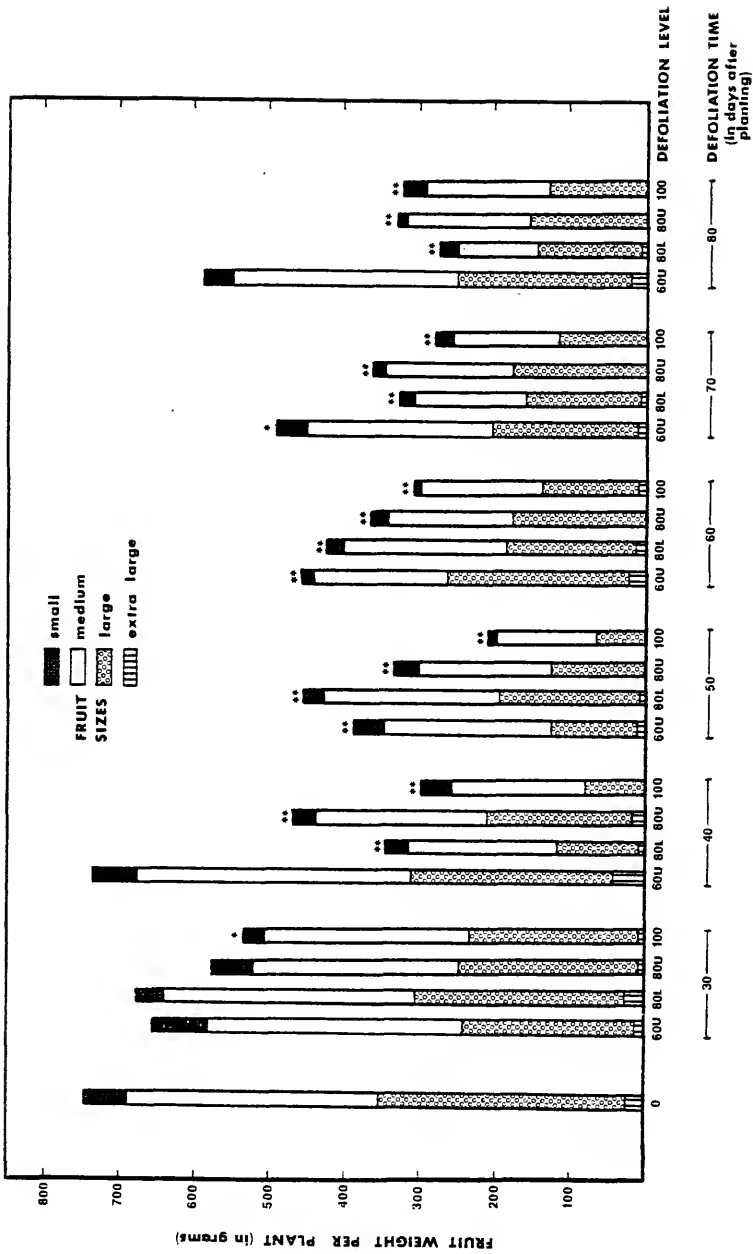


Figure 2. Influence of defoliation of 'Walter' tomato plants on the total yield of marketable fruit in the second harvest of the fall crop of 1978. A significant difference from the control (0) is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation level codes see page 26.



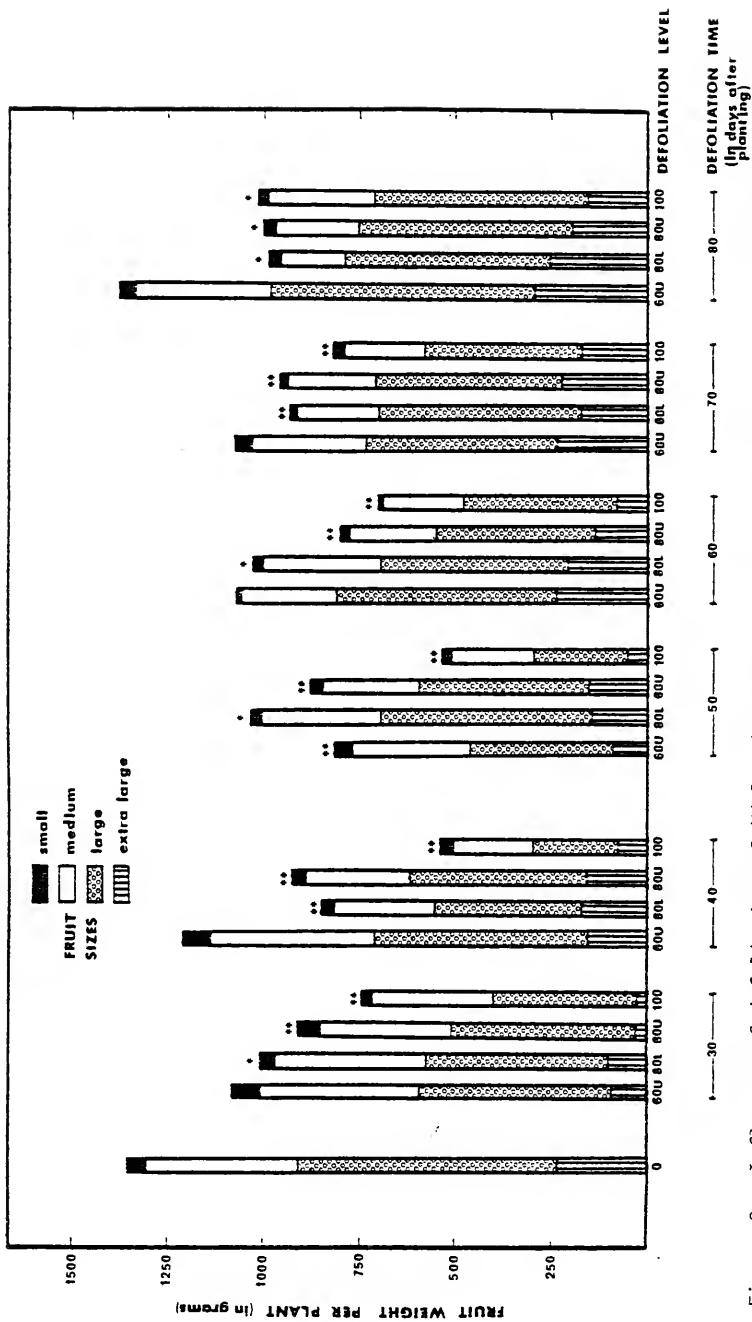


Figure 3. Influence of defoliation of 'Walter' tomato plants on the total yield of marketable fruit in the first two harvests of the fall crop of 1978. A significant difference from the control (0) is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation level codes see page 26.

Figure 4. Influence of defoliation of 'Walter' tomato plants on the mean weight of all extra large fruit in the first harvest of the spring crop of 1979. A significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation level codes see page 26.

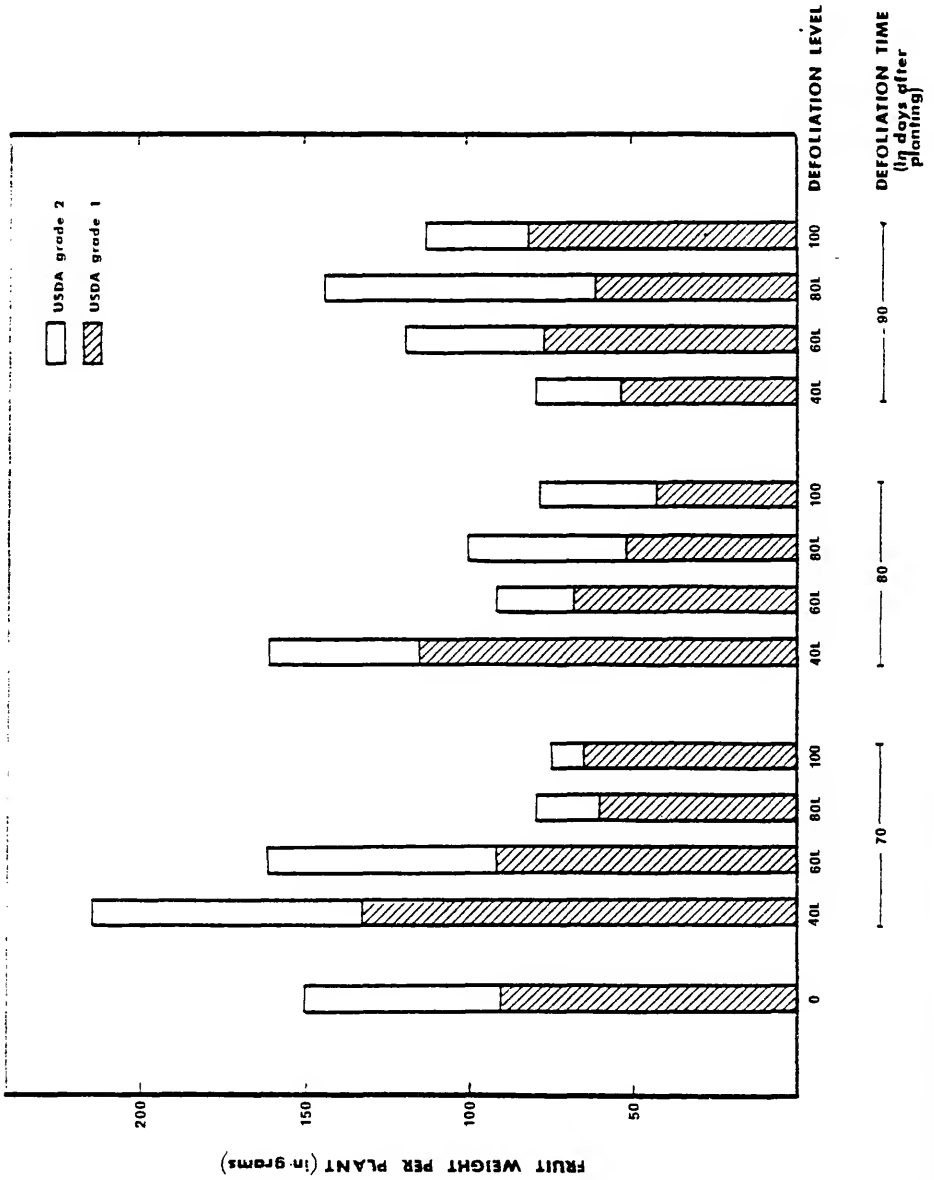
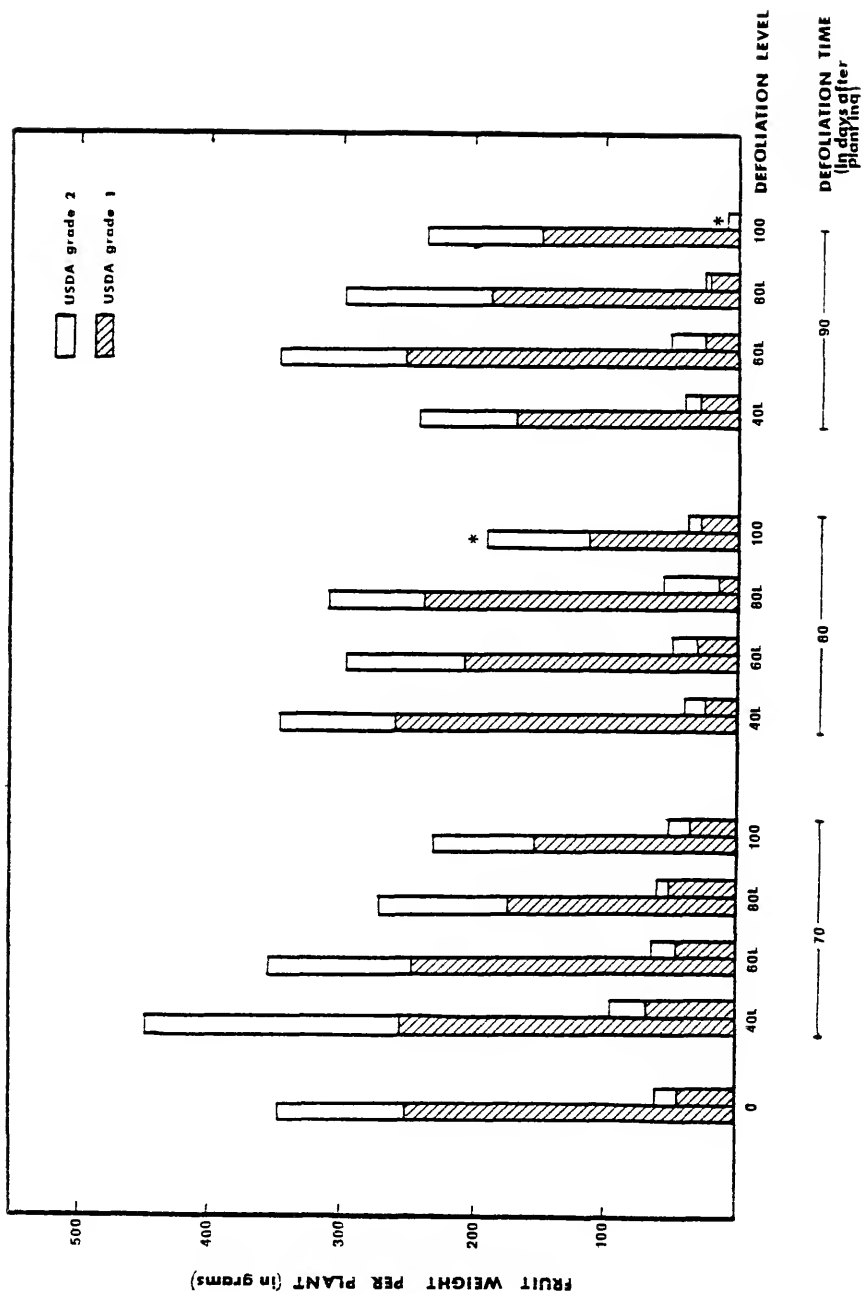


Figure 5. Influence of defoliation of 'Walter' tomato plants on the mean weight of all large fruit in the first (left column of each pair) and the second (right column) harvest of the spring crop of 1979. A significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation codes see page 26.



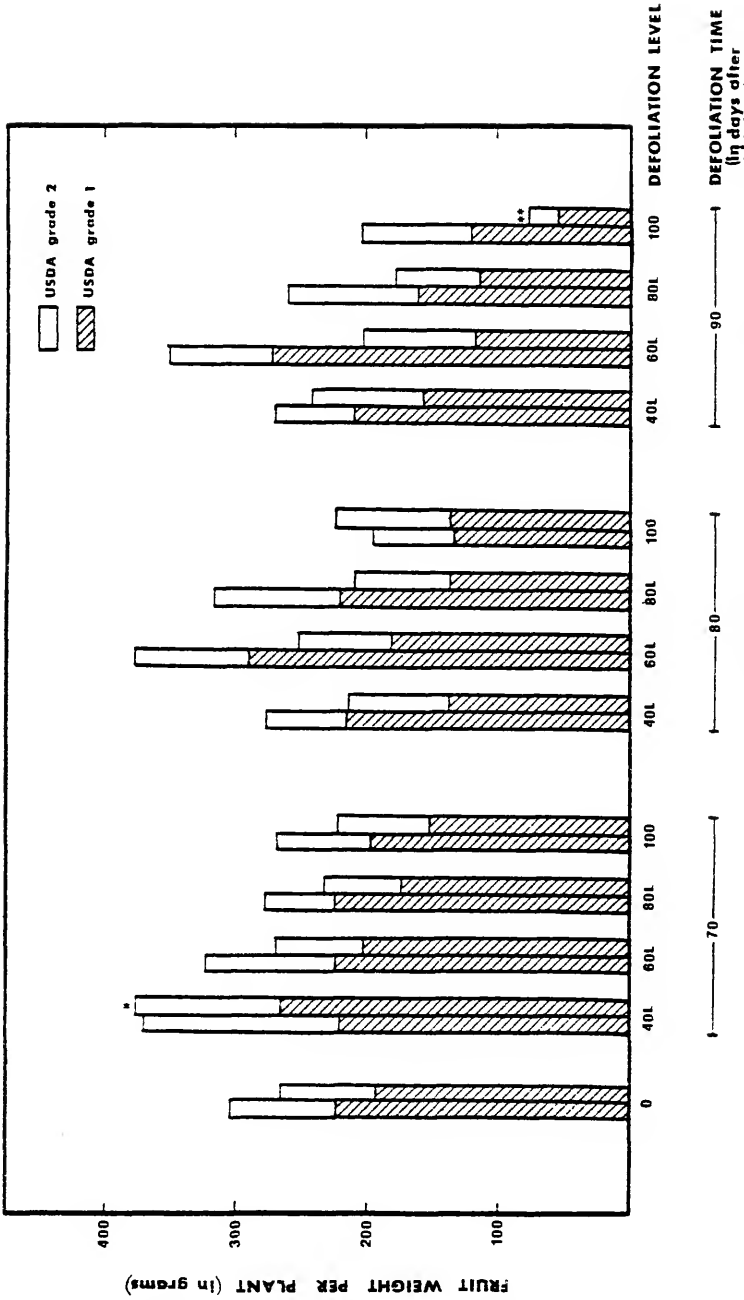


Figure 6. Influence of defoliation of 'Walter' tomato plants on the mean weight of all medium sized fruit in the first (left column of each pair) and the second (right column) harvest of the spring crop of 1979. A significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation level codes see page 26.

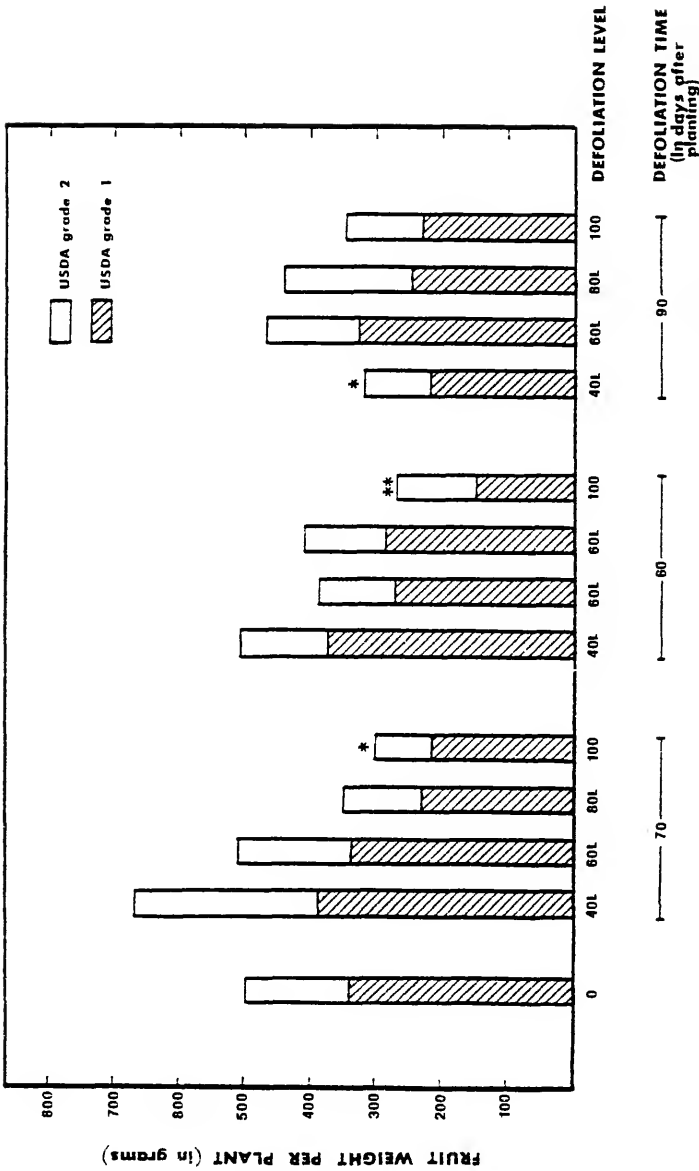
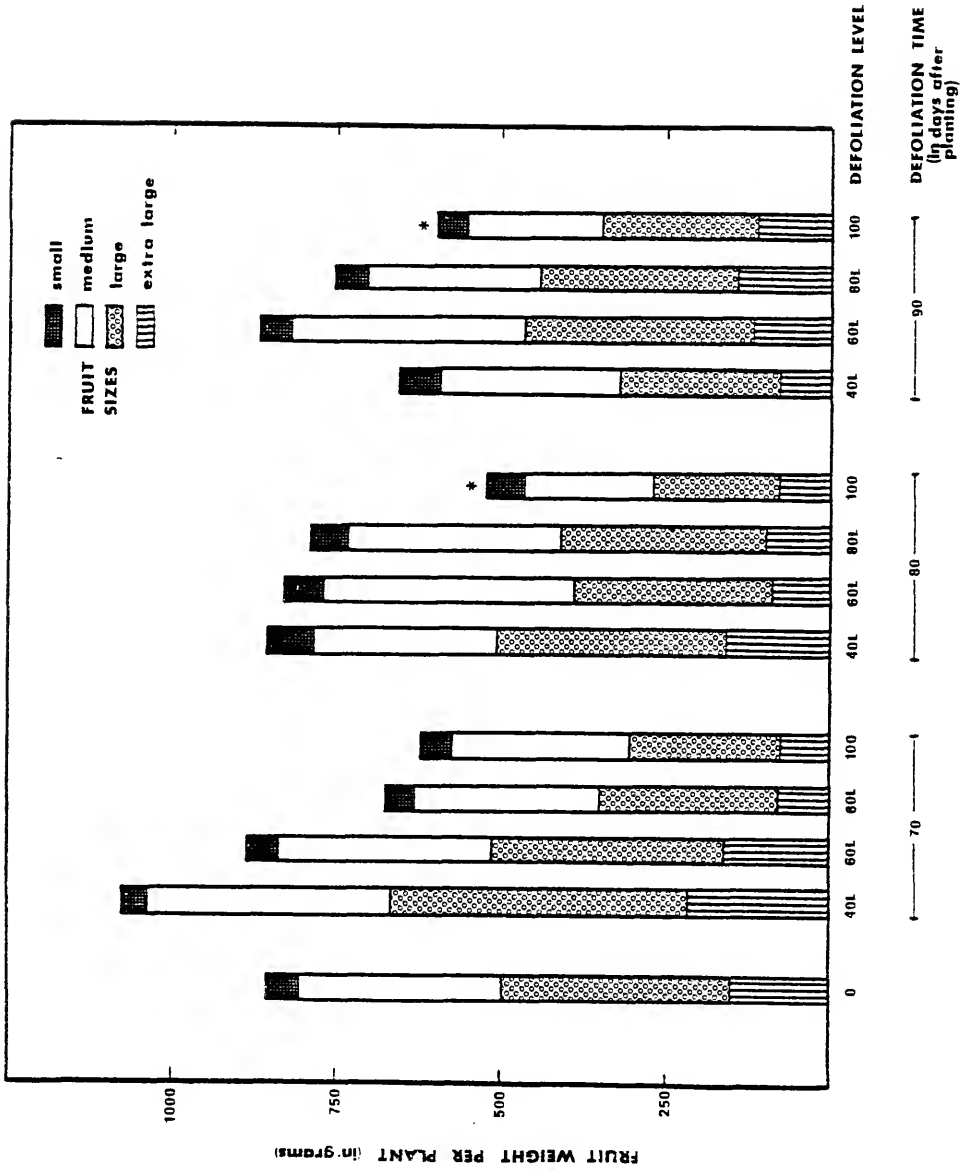


Figure 7. Influence of defoliation of 'Walter' tomato plants on the mean weight of all extra large plus large fruit in the first harvest of the spring crop of 1979. A significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation level codes see page 26.

Figure 8. Influence of defoliation of 'Walter' tomato plants on the total yield of marketable fruit in the first harvest of the spring crop of 1979. A significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation level codes see page 26.



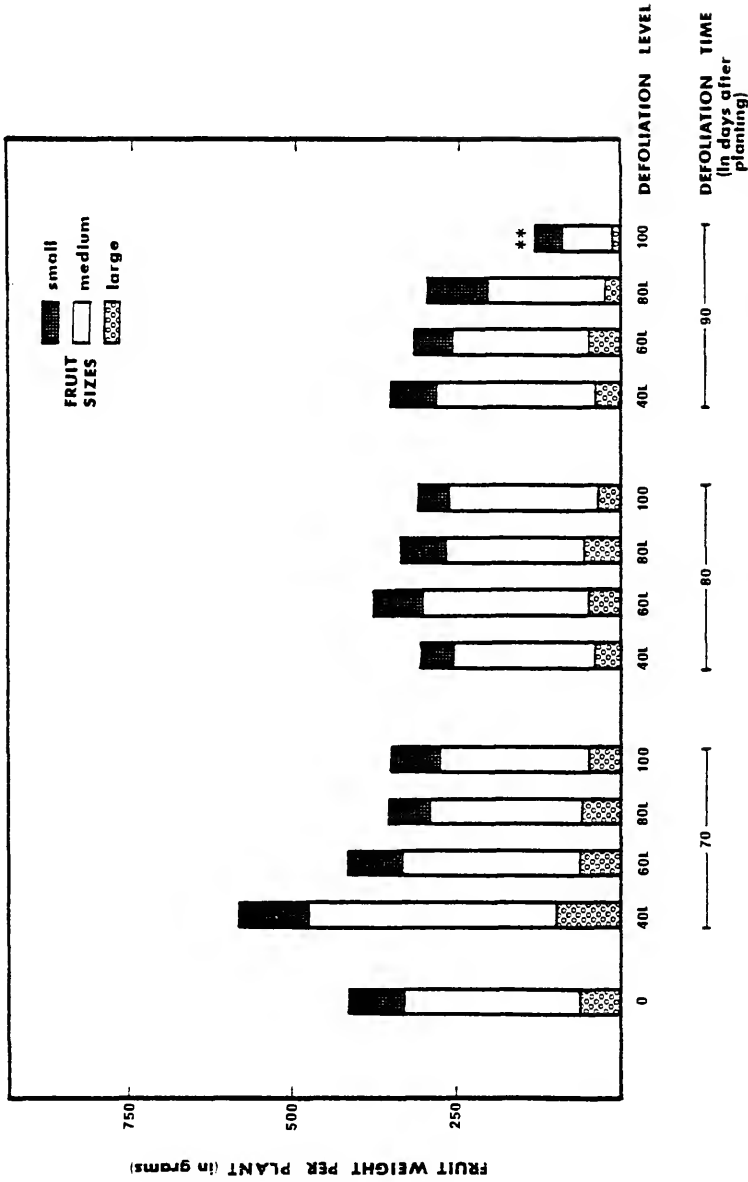


Figure 9. Influence of defoliation of 'Walter' tomato plants on the total yield of marketable fruit in the second harvest of the spring crop of 1979. A significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$. For an explanation of the defoliation level codes see page 26.

Table 32. Gross revenue in dollars per hectare of 'Walter' tomatoes based on all marketable fruit of sizes extra large through small. Influence of defoliation on the first harvest of the spring crop of 1979.

Defoliation level ^b	Price range ^c	Gross revenue in dollars per hectare ^a		
		Time of defoliation (in days after planting)		
		70	80	90
40% lower	low	6669.04	5261.75	3866.00
	medium	10782.49	8657.34	6316.70
	high	18404.99	14862.78	11009.63
60% lower	low	5446.27	4878.66	5231.33
	medium	8864.27	7990.99	8598.03
	high	15208.09	13941.17	14916.82
80% lower	low	4021.30	4737.85	4622.42
	medium	6603.69	7739.91	7412.39
	high	11543.96	13356.20	12663.16
100%	low	3684.56	3101.79*	3667.31
	medium	6050.79	4981.35*	5962.71
	high	10528.45	8599.68*	10165.67

^aA significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^bFor an explanation of the defoliation level codes see page 26.

^cPrices used in the computations are given in Table 3.

Note: Gross revenue per hectare for the control plants was for the low price range, \$5246.52, for the medium range, \$8575.55, and for the high range, \$14728.45.

Table 33. Gross revenue in dollars per hectare of 'Walter' tomatoes based on all marketable fruit of sizes extra large through small. Influence of defoliation on the second harvest of the spring crop of 1979.

Defoliation level ^b	Price range ^c	Gross revenue in dollars per hectare ^a		
		Time of defoliation (in days after planting)		
		70	80	90
40% lower	low	3049.83	1595.98	1818.72
	medium	4862.73	2522.09	2881.90
	high	8683.05	4505.01	5171.14
60% lower	low	1972.38	1950.85	1645.29
	medium	3108.48	3088.61	2590.07
	high	5658.80	5558.63	4602.54
80% lower	low	1876.49	1727.45	1474.94
	medium	3026.00	2701.55	2296.16
	high	5460.66	4834.29	4082.92
100%	low	1812.90	1613.11	653.07**
	medium	2876.96	2552.07	1023.86**
	high	5165.98	4533.45	1815.34**

^aA significant difference from the control is indicated by * for $P < 0.05$ or by ** for $P < 0.01$.

^bFor an explanation of the defoliation level codes see page 26.

^cPrices used in the computations are given in Table 3.

Note: Gross revenue per hectare for the control plants was for the low price range, \$2152.65, for the medium range, \$3430.95, and for the high range, \$6181.35.

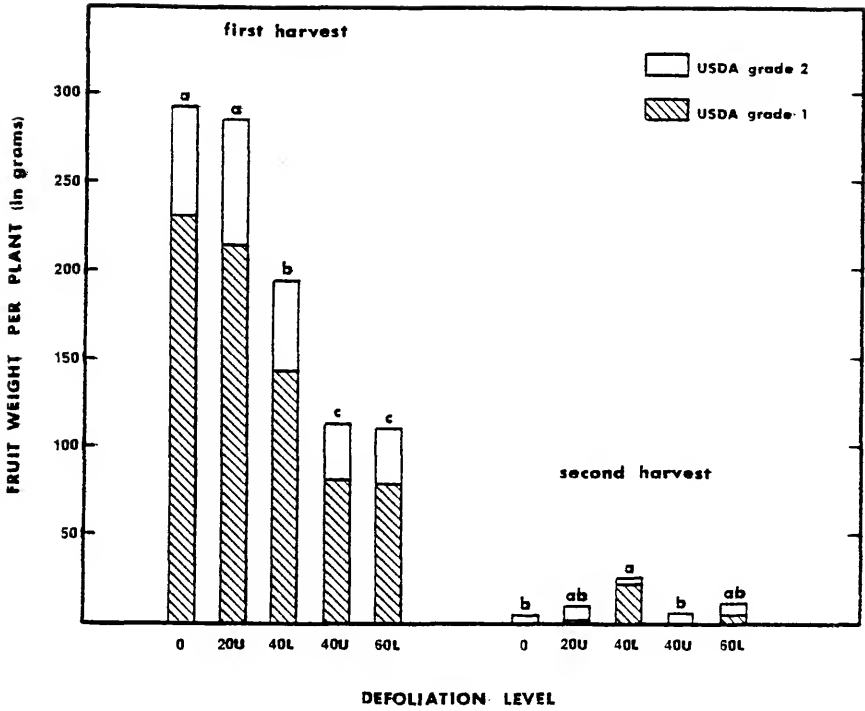


Figure 10. Influence of repeated defoliation of 'Walter' tomato plants on the mean yield of all extra large fruit (3 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

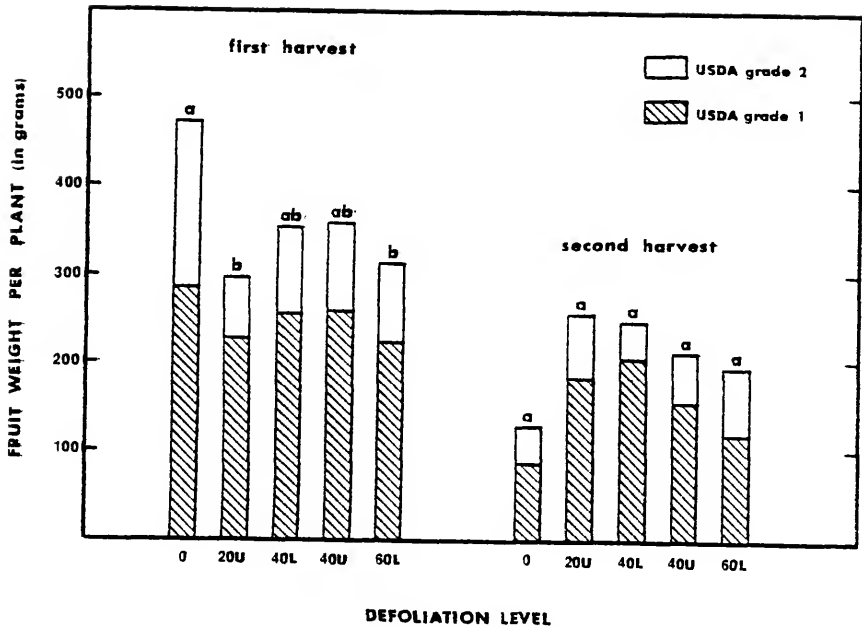


Figure 11. Influence of repeated defoliation of 'Walter' tomato plants on the mean yield of all large fruit (3 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

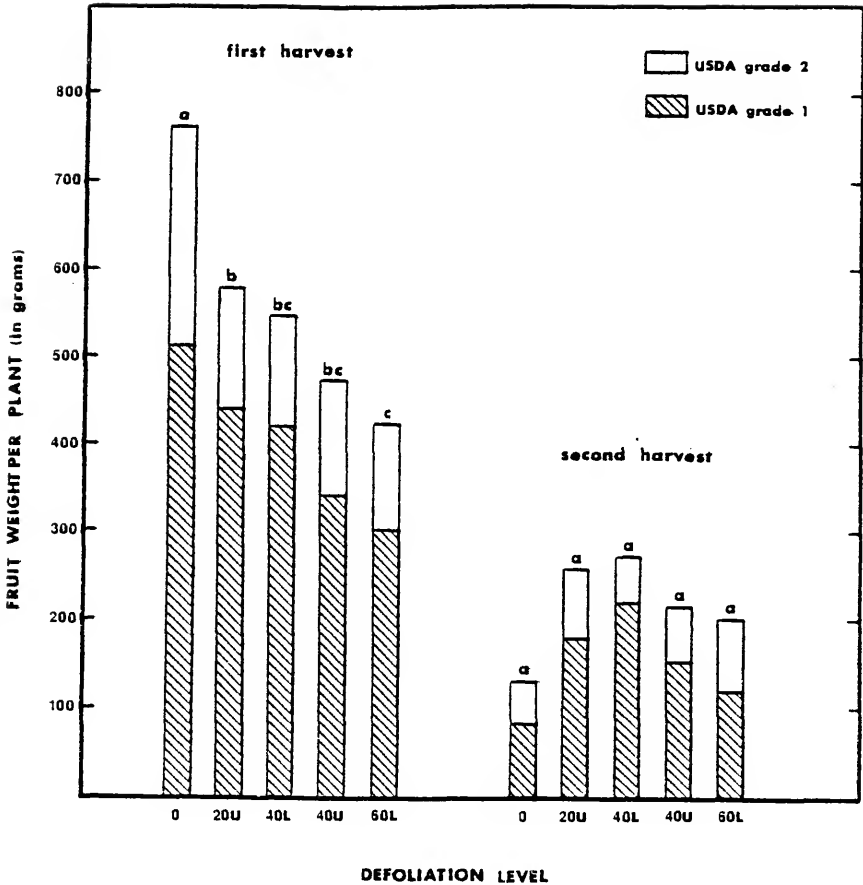


Figure 12. Influence of repeated defoliation of 'Walter' tomato plants on the mean yield of all extra large plus large fruit (3 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

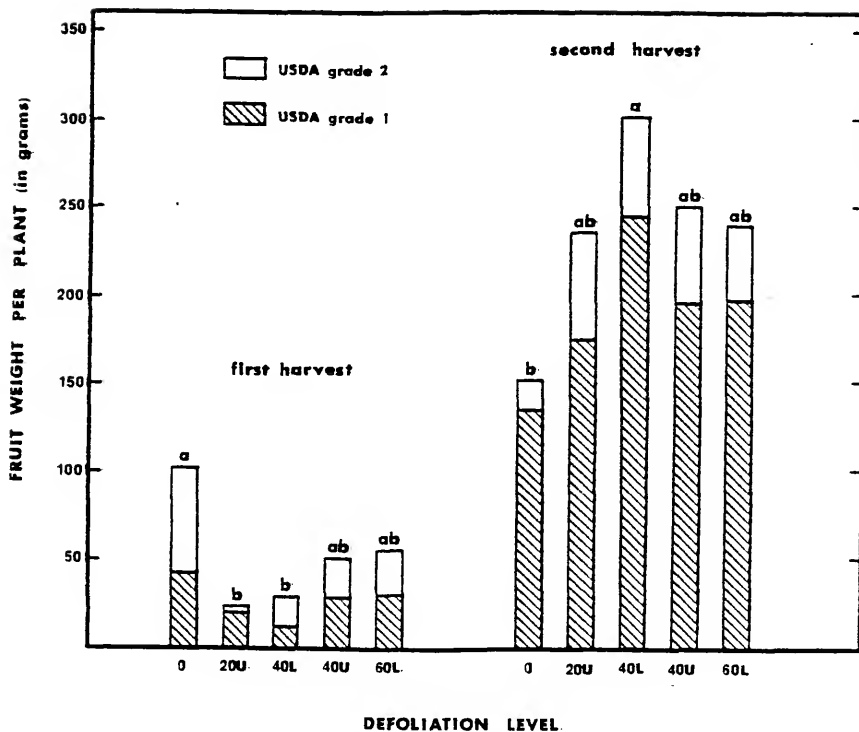


Figure 13. Influence of repeated defoliation of 'Walter' tomato plants on the mean yield of all medium sized fruit (3 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

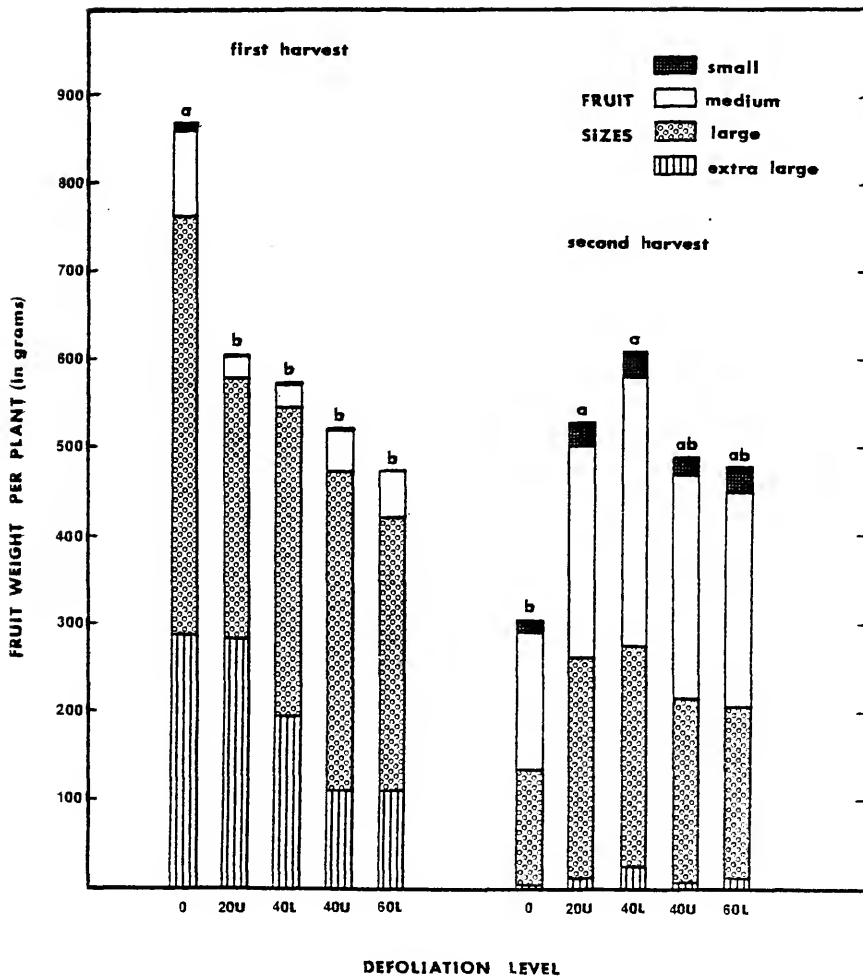


Figure 14. Influence of repeated defoliation of 'Walter' tomato plants on the mean total yield of all marketable fruit (3 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

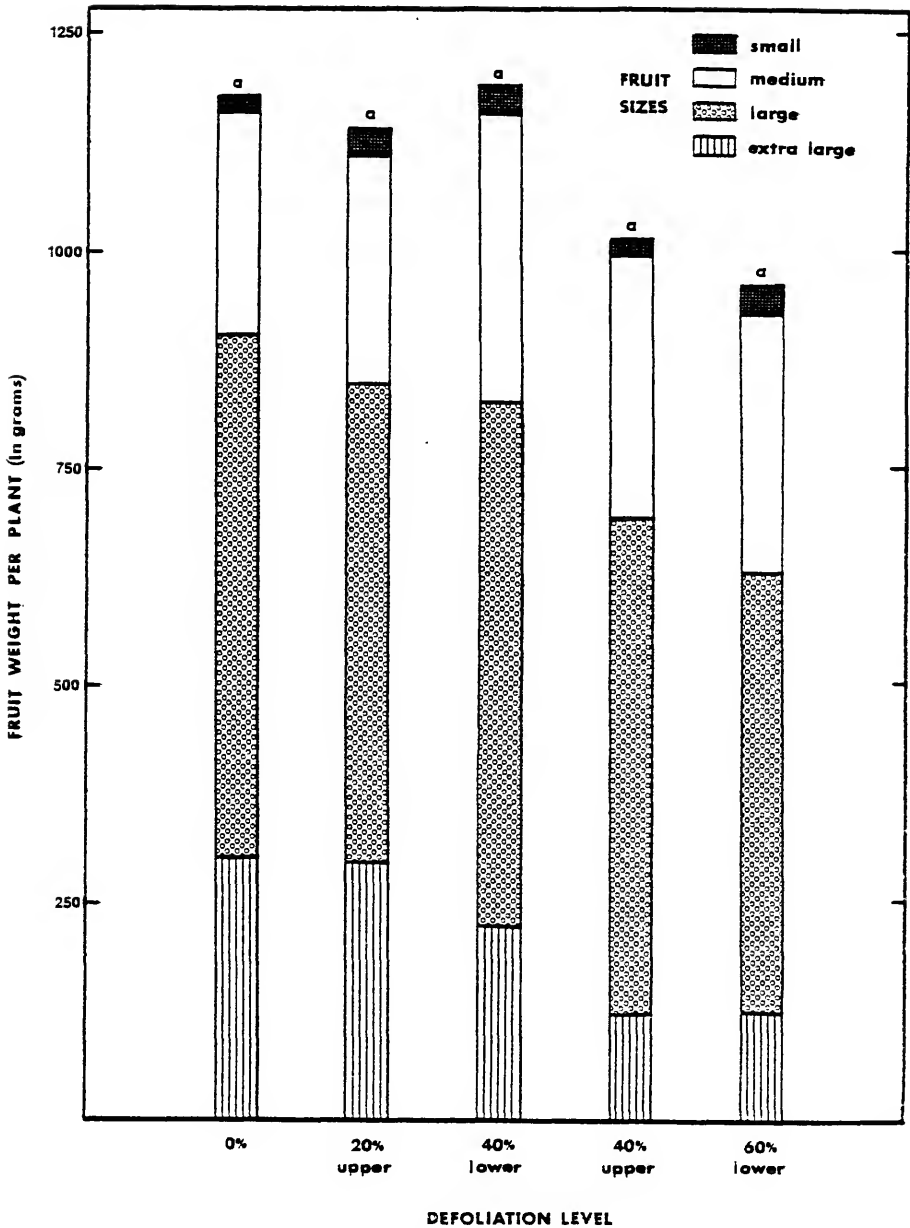


Figure 15. Influence of repeated defoliation of 'Walter' tomato plants on the mean total yield of all marketable fruit in the first two harvests (3 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

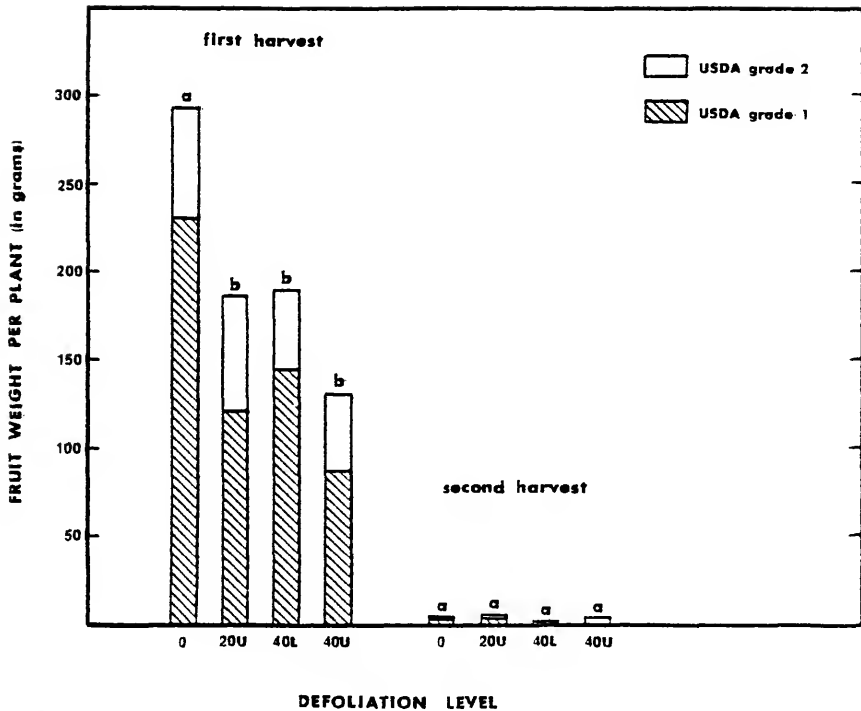


Figure 16. Influence of repeated defoliation of 'Walter' tomato plants on the mean yield of all extra large fruit (6 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

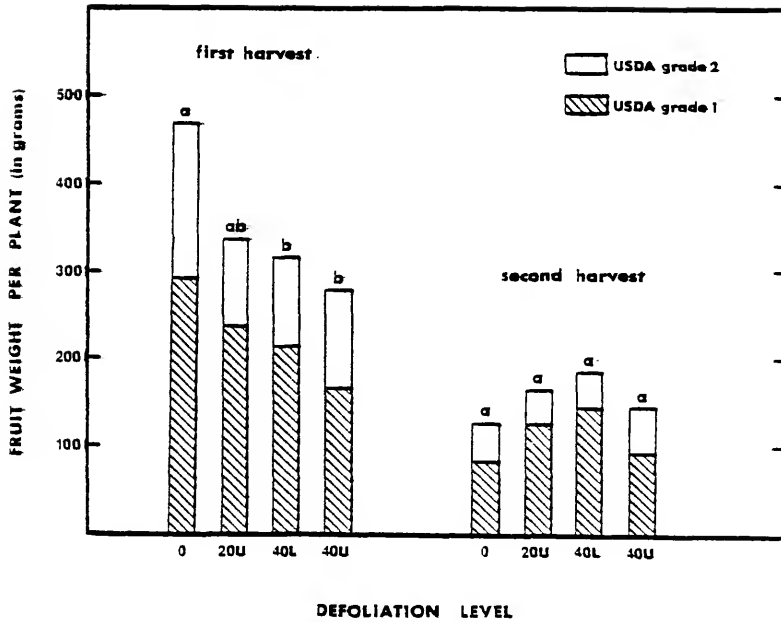


Figure 17. Influence of repeated defoliation of 'Walter' tomato plants on the mean yield of all large fruit (6 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

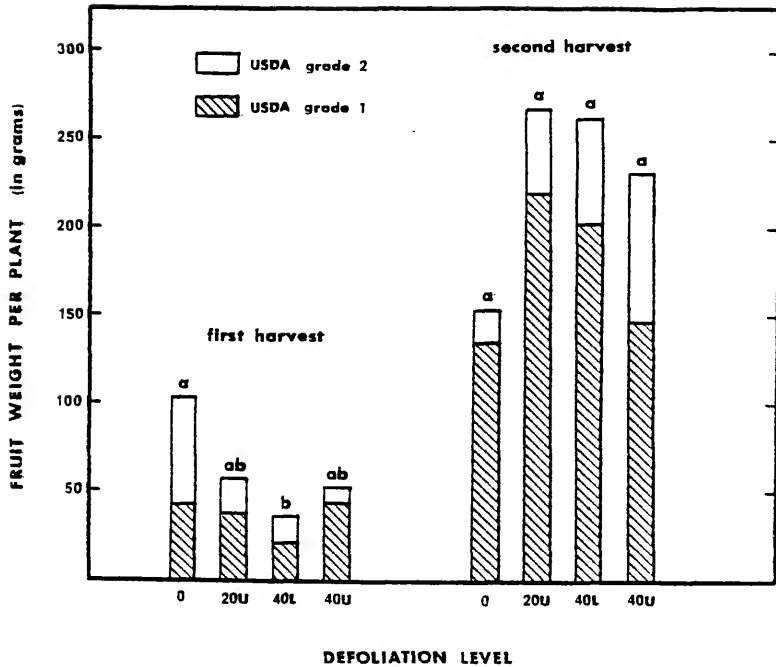


Figure 18. Influence of repeated defoliation of 'Walter' tomato plants on the mean yield of all medium sized fruit (6 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

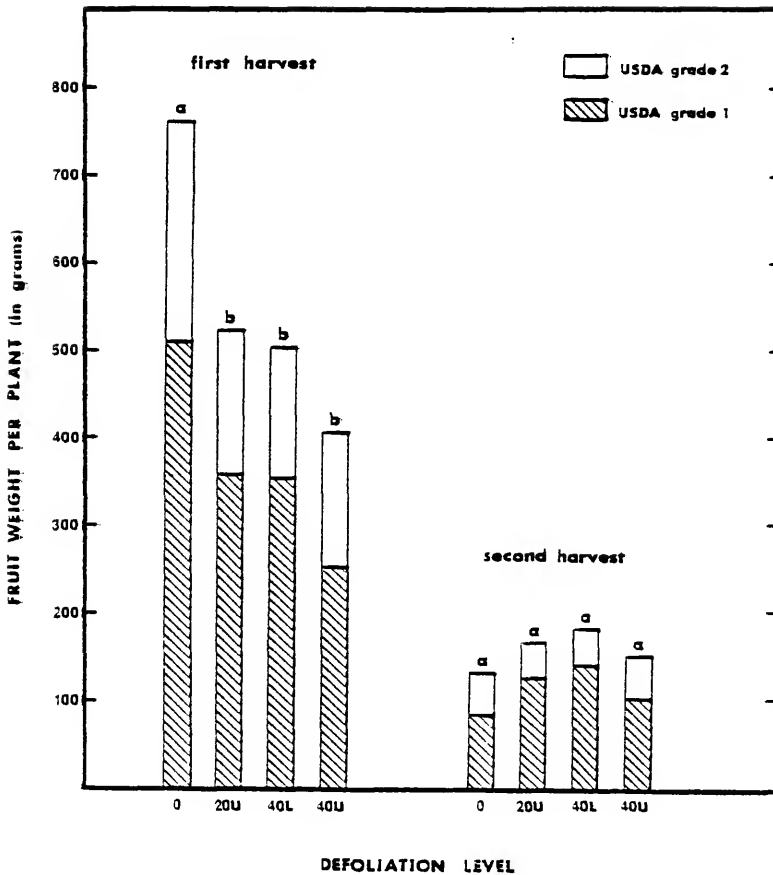


Figure 19. Influence of repeated defoliation of 'Walter' tomato plants on the mean yield of all extra large plus large fruit (6 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

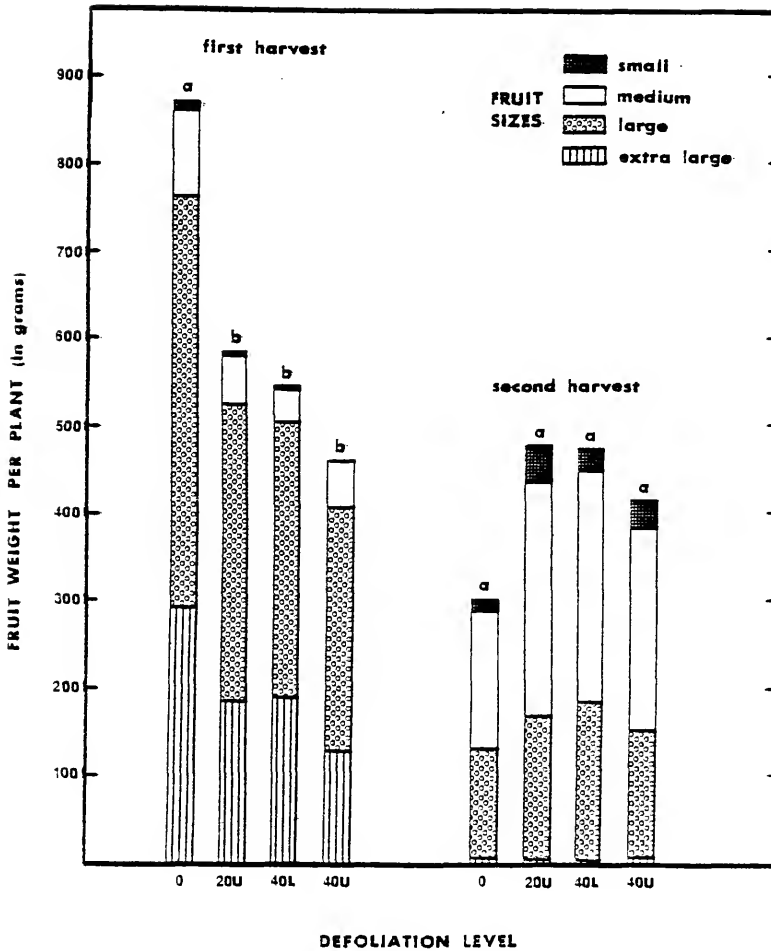


Figure 20. Influence of repeated defoliation of 'Walter' tomato plants on the mean total yield of all marketable fruit (6 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

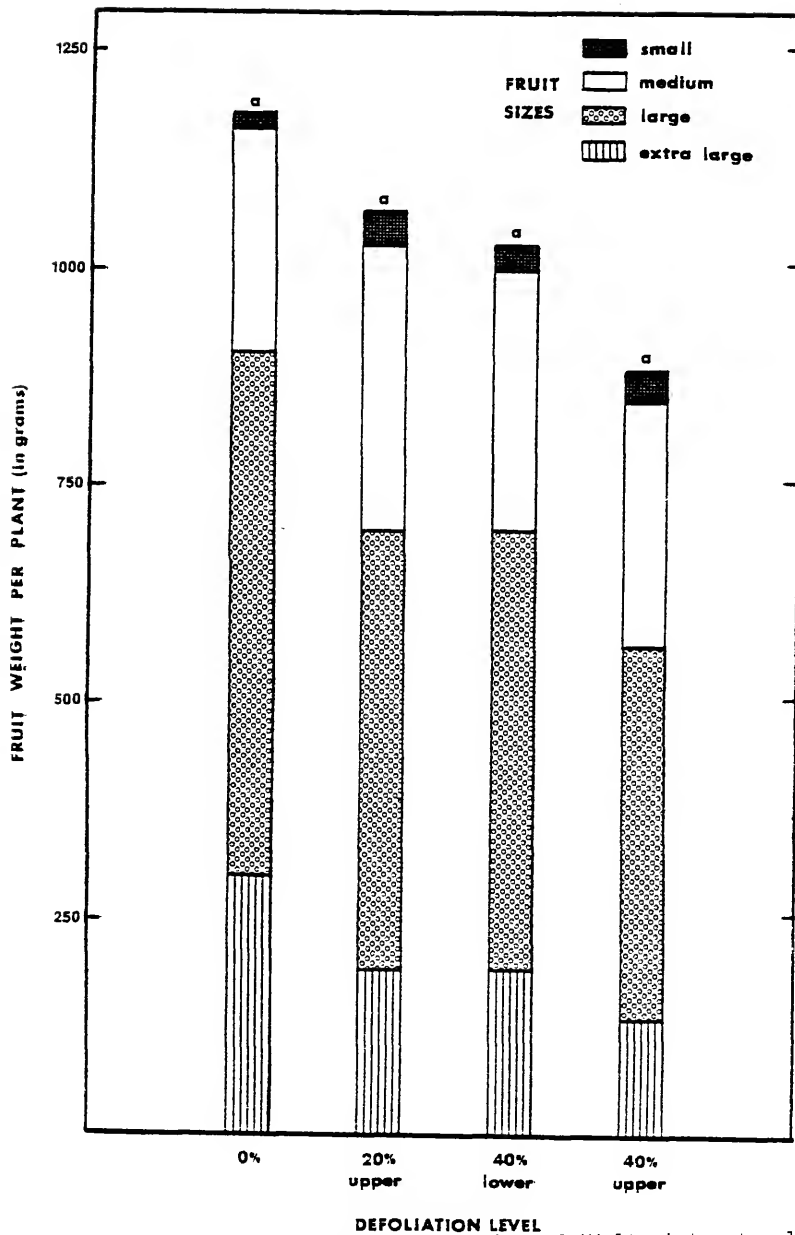


Figure 21. Influence of repeated defoliation of 'Walter' tomato plants on the mean total yield of all marketable fruit in the first two harvests (6 defoliations). Columns not marked by the same letter represent significantly different weights ($P < 0.05$), Duncan's multiple range test. For an explanation of the defoliation level codes see page 26.

development, seriously slowed its growth. Defoliation at that time may also affect the initial stages in ovary and embryo development resulting in reduced sizes of the fruit. Although Houghtaling (1935) postulated that the ultimate fruit size is determined early in its development, defoliation around mid-season, both in Experiments 1 and 2, resulted in a reduction of the fruit size. This observation suggests that mid-season is a critical time for photosynthate mobilization to growing fruit. Defoliation of the tomato plants at the lower levels (20% to 60% near the soil level) has little, if any, effect on fruit set, development or quality, especially when it occurs in the first two months of the season. It appears that the foliage remaining on the plant is capable of synthesizing sufficient amounts of nutrients necessary for the normal development of the fruit. Since the foliage of unstaked tomato plants is normally very dense, the lower leaves which are approaching senescence toward the middle of the season will not contribute significantly to the plant's net photosynthesis. They are probably even beyond the compensation point, using more photosynthate than they produce. The upper 20% to 40% of the foliage has in fact been shown to account for more than half of the net photosynthetic activity of entire tomato plants (Acock et al., 1978), since the upper leaf layers obviously intercept and utilize the largest amount of light. In addition, defoliation has been found to have a stimulatory effect on the remaining leaves, possibly even resulting in an increase of 30% to 50% of the exported photosynthates (Khan and Sagar, 1969). The amount of nutrients entering the fruit apparently also increased. The leaves remaining on the plant after many have died due to leafminer infestation and subsequent disease development are,

therefore, well able to compensate for the loss of photosynthetically active leaf area.

Removal of foliage from the tomato plant has an influence on both temperature and air flow within the canopy. Especially high levels of defoliation expose a large amount of the fruit to more direct sun radiation. Subsequent temperature increase may influence the metabolic equilibrium within the fruit, hastening the ripening process, whereas under normal conditions division and enlargement of the pericarp cells still would be the most important activities in the fruit. This temperature effect will have an especially profound effect when the ripening process is well under way, towards the end of the season and the plants' energy production is almost entirely directed toward reproductive development. Replacement of vegetation removed is then negligible and damage to the fruit by sunscald and decay becomes more likely. Sunscald may not occur if defoliation is a week or less before harvest but the ripening process will still be favored over cell enlargement. Yield loss due to sunscald may be prevented if the fruit can be harvested earlier than normal although this would only be applicable if the entire field were defoliated to the same extent and there were no border effects.

If the defoliation is serious enough to expose a large number of flower clusters to direct sun radiation, fertilization may be affected. Shading has been shown to affect the percentage of misshapen fruit, higher levels of shade increasing this percentage (Marr and Hillyer, 1968). On the other hand, exposure may mean temperature increases to levels where fruit set may be affected (Marlowe, 1977). Inadequate fertilization will cause poor locular jelly development and the

resulting fruit will be misshapen. This may explain not only why the total weight of culled fruit did not drop proportionally to the total yield (Tables 20 and 21) but also why yield reductions usually occurred in the USDA grade 1 fruit and not in the grade 2 fruit. The combination of these two effects could compensate each other and, although changes in fruit number and quality of an entire plant will be affected, the number of marketed fruit would remain the same.

Since the leafminers usually attack the lower and middle leaves first (Wilcox and Howland, 1952) their effect on net photosynthesis will be minimal. The younger leaves which are the most important to the plant and the removal of which would harm the plant more than the removal of the lower ones (Harper, 1977), are normally only slightly damaged. Only in case of very serious outbreaks of the vegetable leafminer will the mine intensity in the upper portion of the plant increase dramatically and pose a threat to fruit production.

Repeated defoliation at lower levels (20% to 60%) does as much harm to the tomato plant as a high level defoliation does over a short period of time when considering the first harvest. Vigor and transpiration are affected more often and the plant will have to divert a large portion of its energy supply to the healing process, delaying development of both vegetative growth and fruit development. In comparison to similar foliar damage in staked tomatoes one would expect less reduction of fruit yield in the unstaked plants. That at least 60% of the foliage has to be removed to significantly reduce yield of staked 'Walter' tomatoes (Jones, 1980) is probably due to the fact that in Jones' experiments no damage was inflicted to the plants in the especially sensitive pre-bloom period. The minimal reduction of total yield in the repeated

defoliation experiments in this study shows that the overall response of the tomato plants to defoliation is very similar in staked and unstaked tomatoes. However, continuous leaf abscission due to infection of even small numbers of leaf mines is a more gradual process than repeated mechanical defoliation and may, therefore, be less detrimental to the plant.

A reduction in the weight of extra large and large fruit is the most serious effect of high levels of defoliation at different times. Since these two largest fruit sizes account for the largest portion of the grower's revenue from the tomato crop, a reduction in their weight will affect his total income from the tomato harvest most. When comparing the influence of defoliation on yield of all extra large and large fruit with that on gross revenue (Tables 11 and 18; and Tables 26 and 30), the importance of these fruit sizes to growers is obvious.

Although the weight of the medium size fruit may also be reduced, the effect of this reduction is a relatively small component of the total yield. As a result, a significant reduction in total yield corresponds to a significant reduction in gross revenue so that, from a practical point of view, total yield data give a very good indication of the gross revenue a grower may expect from his tomato crop.

In the present study all marketable fruit, irrespective of its position within the canopy was harvested for further analysis. In a tomato grower's field this may not be the case. Pickers will easily overlook some mature fruit, especially the smaller sizes, if the plant's foliage is very dense. Defoliation resulting from leafminer infestations followed by disease development, especially in the last weeks before harvest may therefore be an advantage. Even if the actual fruit set is

reduced and the absolute number of extra large and large fruit is less than that of non-defoliated plants, the amount of fruit picked from the defoliated plants and shipped for further processing may well be equal or even greater than that originating from healthy plants. In fact the use of defoliants to increase the number of fruit picked has been suggested (Vittum, 1957).

Considering the differential sensitivity to defoliation in the course of the development of the tomato plants, the economic threshold of the leafminer varies during the season. Monitoring of the infestation levels is especially advisable early in the season and at mid-season.

Conclusion

Depending on the time and the frequency of leafminer outbreaks, the effect of defoliation, resulting from infestation of tomato plants, on both fruit yield and quality varies. Low levels of defoliation are tolerated very well by the tomato plants since the remaining foliage, which nearly always consists of actively photosynthesizing tissue, is responsible for nearly all the nutrient supply necessary for fruit development. Even occasional intermediate defoliations do not result in yield losses because of an increase in photosynthetic activity of the remaining foliage. Repeated defoliation at intermediate levels can be detrimental to yield and quality of the tomatoes because of more continuous interference with the plants' metabolism and diversion of the energy supply from the fruit to the vegetative parts of the plants in order to optimize its photosynthetically active leaf area. Before and

at anthesis, the removal of foliage interferes most with subsequent fruit development because of possible growth delay and impaired fertilization. At mid-season increased sensitivity to defoliation also occurs when interference with nutrient translocation from the leaves to the fruit is very important.

Near harvest the fruit is especially sensitive to radiation exposure which may result in sunscald or decay or both. At this time the reduction of the fruit weight will in practice be offset by the larger number of fruit harvested by pickers because of the greater ease with which the fruit can be located and, therefore, the greater speed with which the pickers can fulfill their set quota.

The following recommendations can be made to the grower. If the defoliation level of the lower canopy in the period before bloom exceeds 30%, specific insecticidal treatment for leafminer control should be applied. After bloom, no control measures need be undertaken until defoliation exceeds the 50% level. If, after specific insecticidal treatments for leafminer control have been applied, a further defoliation of 10% or more occurs, additional treatments are indicated. In general, if defoliation levels throughout the season do not exceed 30% in the lower canopy, no specific insecticidal treatments for leafminer control are warranted.

CHAPTER IV
MICRO-ORGANISMS ASSOCIATED WITH MINES OF
Liriomyza sativae BLANCHARD

Introduction

In several crops leaf mines have frequently been observed to be the center of an area characterized by yellowing, necrosis, or both.

Leaf mining insects occur in a very large number of plant species (Needham et al., 1928; Hering, 1951; Spencer, 1973a) and have been reported to cause various kinds of damage to the leaves. Relatively few reports have been made suggesting that these symptoms were associated with organisms other than the leaf mining insects themselves. The mines have been recognized as niches with an ideal environment for the development of fungi and other micro-organisms, mainly as parasites of the larvae (Hering, 1951). Discoloration of the mines and the leaf tissues in their vicinity has been explained by decay of portions of the tissue, by substances produced by either host plant or leafminer larvae, or by the undernourishment of some cells adjacent to the mine (Hering, 1951).

Wounds created by the piercing of the leaf epidermis by leafminer adults have been suggested as ports of entry for saprophytic micro-organisms (Portier, 1930; Hering, 1951) and plant pathogens (Eichman, 1943; Spencer, 1973a; Andaloro and Peters, 1977; Kamm, 1977). A relation between leaf damage by mining insects and subsequent disease

development has been shown for needle blight and Cecidomyid gall midges which mine red pine needles (Haddow and Adamson, 1939; Haddow, 1941), citrus canker and the citrus leafminer, Phyllocnistis citrella Stainton, which mines leaves of rough lemon (Sohi and Sandhu, 1968), and celery heart rot and the miners Scaptomyza graminum and Elachiptera costata which mine the petioles of celery plants (Leach, 1927).

A very large number of micro-organisms may be present in the phylloplane of plants (Dickinson, 1976) the majority of which reaches the leaf by wind or rain (Gregory, 1971). Leafminer adults have been shown capable of transmitting pathogenic viruses (Costa et al., 1958; Zitter and Tsai, 1977) and bacteria (Leach, 1927; Singh et al., 1977).

The objectives of this study were to

- (1) identify the organism or organisms responsible for the yellowing and necrosis associated with leaf mines in tomato,
- (2) identify any micro-organisms, especially fungi, associated with both healthy leaves and leaves mined but not showing any disease symptoms, and
- (3) find possible associations of the pathogen(s) with the leaf-miner adults.

Materials and Methods

Isolation from Leaves

Leaves were collected in a number of commercial tomato fields in the Homestead area of Dade County, Florida. Tomato plants of the

cultivar Walter growing either on open ground or on plastic mulch were sampled. Care was taken that the leaflets collected for isolations did not show any signs of senescence so that the yellowing associated with the mines was not the result of natural deterioration of the leaf tissues. Leaflets which were mined but did not show any yellowing as well as healthy leaves were collected from comparable areas within the plant canopy.

Surface sterilization was carried out in two ways. One was by cutting discs with a diameter of approximately 3 mm out of the leaf with a cork borer, immersing these in a 1% sodium hypochlorite solution, containing 1 drop of Tween-20 per 100 ml, for 1 to 2 minutes followed by three rinses in sterile distilled water. The other method used consisted of gently rubbing both leaf surfaces with a cotton swab soaked in 70% ethyl alcohol for 2 to 3 seconds, followed by cutting leaf discs as described above. The latter method proved more consistent and resulted in fewer contaminated cultures than the first, and, therefore, was employed more frequently.

The discs were cut from diseased leaves in such a way that they contained both yellowed and healthy tissue, or yellowed and necrotic tissue plus a very small portion of the mine. Discs from non-yellow mines were cut to contain apparently healthy leaf tissue plus a very small portion of the mine. Healthy leaves were cut in areas comparable to those where leaf mines occurred in the infested leaflets.

The discs were transferred onto potato dextrose agar (PDA) containing 100 ppm streptomycin sulphate and 150 ppm benomyl in petri dishes (PSBA plates). Benomyl was added because it has been shown ineffective in controlling the disease associated with the leaf mines.

The dishes were examined for fungal growth originating at the discs after 3 to 4 days of incubation in the dark at 25⁰C. Individual colonies were then transferred to PDA plates, a process which was repeated, when necessary, to obtain pure cultures. Any bacterial colonies arising from leaf discs were also transferred to PDA dishes. All cultures were incubated for 1 to 2 weeks in the dark at 25⁰C. When the fungal mycelium covered approximately 60% of the agar's surface, the cultures were exposed for alternating periods of 12 hours to U.V. radiation and to darkness for three days in order to induce sporulation.

Pathogenicity Tests

Tomato plants of the cultivar Walter were grown at a temperature of 21 ± 1⁰C in a growth chamber in pots containing a peat:vermiculite (1:1, v/v) mixture.

Fungal tests.

Of the fungal cultures obtained by isolation from yellowed mines, 8 were chosen for pathogenicity tests; of those from non-yellowed mines, 4 were tested. These isolates were inoculated on the third or fourth oldest leaf of 30-50 cm tall plants. Some of the tomato leaflets were wounded with a mounted needle before inoculation. Inoculum was obtained by scraping the surface of 1 month-old cultures with a sterile nichrome wire loop and then flooding the dishes with 10 ml sterile distilled water. The largest mycelial fragments were removed by filtering the suspension through two layers of cheesecloth. Half of the filtrate was diluted by adding an equal volume of distilled water, while to the other half an equal amount of a 1% (w/v) sucrose solution was

added. Thirty two tomato plants were divided into 8 treatment groups with 4 plants in each group. The leaflets were sprayed with a hand atomizer (Table 34). The leaflets were then allowed to dry and enclosed in a plastic bag for 24 hours to maintain high humidity. The plants were examined 4 to 6 days after inoculation for the development of disease symptoms.

Bacterial tests.

Inoculation was carried out on plants similar to those used in the fungal tests. Again 8 cultures originating from diseased mines were tested. Bacterial suspensions were obtained by flooding petri-dish cultures with distilled water. The suspensions were then cotton-swabbed on the upper surface of both the wounded and unwounded leaflets of four different plants for each treatment. The inoculated leaflets were subsequently wetted with distilled water by a hand atomizer and then enclosed in plastic bags for 24 hours. The plants were examined for necrotic lesions with yellow halos 6 to 8 days after inoculation.

Isolation from Flies

Adult female leafminers ovipositing on tomato leaves in the field were aspirated into sterile plastic vials. Of these flies some were released into a petri dish containing PSBA in the laboratory, one fly per dish, and allowed to move around for 15 minutes. Other flies were surface sterilized in groups of 5 as described by Noble et al. (1978) and crushed in 3 ml sterile water. Of the resulting suspension 1 ml was then plated on PSBA in petri dishes which subsequently were incubated in the dark at 25⁰C. Pure culture of any fungi developing on the plates

Table 34. Treatments of tomato leaflets to test the pathogenicity of fungal isolates.

Leaflet	Atomized with
Unwounded	distilled water only
	0.5% sucrose only
	conidial suspension in distilled water
	conidial suspension in 0.5% sucrose solution
Wounded	distilled water only
	0.5% sucrose only
	conidial suspension in distilled water
	conidial suspension in 0.5% sucrose solution

were obtained and their sporulation achieved as with the leaf disc isolates described above.

Results

Symptoms

The symptoms developing around the infected portion of the mine varied considerably. In some cases the diseased area was rather small, approximately 2 to 3 mm in diameter, and consisted of necrotic tissue surrounded by a narrow, often faint, yellow halo. Occasionally yellowing of up to 75% of the entire leaflet area was symptomatic. No necrosis was then evident except in the leaf mine itself. Most infected mines showed symptoms somewhere between these two extremes. On a few occasions two separate zones of necrosis and yellowing were associated with the same mine.

Very rarely was the entire mine surrounded by a chlorotic or necrotic zone. If the leaflet was severely mined and more than one mine was infected, a shriveling of the infected area or death of the entire leaflet often resulted.

The percentage of mines with yellow tissue varied from 5.0% to 88.9% per plant in 1978 in one field of the Homestead Agricultural Research and Education Center.

Isolations from Leaves and Flies

Very few fungi were isolated from surface sterilized, apparently healthy leaflets (Table 35). Surface sterilization with ethyl alcohol resulted in fewer isolates obtained than with sodium hypochlorite.

Table 35. Micro-organisms isolated from surface-sterilized, apparently healthy leaflets on field-grown tomato plants in the Homestead area of Dade county, Florida.

Field ^a	Sampling date	Method of surface sterilization ^b	Micro-organism				Total # of discs tested
			<u>Alternaria</u> spp.	<u>Cladosporium</u> spp.	Other fungi ^c	Nil	
1	1/17/79	A	3	1	1	40	45
		B	1	0	0	44	45
2	2/3/79	A	2	1	2	27	32
		B	0	1	0	31	32
3	3/30/80	A	3	2	2	28	35
		B	1	0	1	33	35
4	1/25/79	A	5	2	2	43	52
		B	2	0	1	49	52

^aIn fields 1, 2, and 3 tomatoes were grown with plastic mulching, in field 4 they were grown on open ground.

^bA = surface sterilization using sodium hypochlorite; B = surface sterilization using ethyl alcohol.

^cIncluding Aspergillus spp. and unidentified fungi.

Alternaria spp. and Cladosporium spp. were the most frequently encountered organisms.

Non-yellowed leaf mines apparently harbor a variety of saprophytic micro-organisms, Alternaria spp. and Cladosporium spp. being the most common (Figure 36). Only one of the four cultures, all Alternaria, isolated from non-yellow mines and tested for pathogenicity, incited faint yellowing of a small area of the inoculated leaflets. The other three isolates incited no disease symptoms at all.

The organism most frequently isolated from diseased mines was Alternaria (Table 37). Of the isolates tested for pathogenicity, seven were Alternaria alternata (Fries) Keissler (= A. tenuis Nees, Neergaard, 1945). All of these incited symptoms which were similar to those observed in the field and occurred only on wounded leaflets if the inoculum contained sucrose. Subsequent reisolation invariably resulted in the same fungus originally used for the inoculation. The other fungal isolate tested, Stemphylium sp., did not incite any symptoms in any of the tests. All bacterial isolates, which had yellow colonies on both PDA and PSBA, tested for pathogenicity resulted in development of small lesions. The largest number of bacterial isolations, from fields 2 and 5 (Table 37) coincided with the prevalence of bacterial spot on many tomato plants in those fields.

Exposure of PSBA to live flies resulted in only a few fungal cultures (Table 38). Surface sterilization produced even fewer, ethyl alcohol apparently killing all conidia and mycelial fragments present.

Table 36. The microflora isolated from non-yellowed leaf mines on field-grown tomato plants in the Homestead area of Dade County, Florida.

Field ^a	Sampling date	Micro-organism						Total # of discs tested
		<u>Alternaria</u> spp.	<u>Stemphylium</u> spp.	<u>Cladosporium</u> spp.	Other ^b fungi	Bacteria	Nil	
1	1/17/79	11	1	10	5	0	43	70
2	2/3/79	11	2	7	8	5	54	87
3	3/30/80	8	5	9	2	1	43	68
4	1/25/79	6	3	8	3	2	72	94

^aIn fields 1, 2, and 3 tomatoes were grown with plastic mulching, in field 4 they were grown on open ground.

^bIncluding Aspergillus spp., Mucor spp., and unidentified fungi.

Table 37. The microflora isolated from yellowed leaf mines on field-grown tomato plants in the Homestead area of Dade County, Florida.

Field ^d	Sampling date	Micro-organism						Total # of discs tested
		Alternaria spp.	Stemphylium spp.	Curvularia spp.	Other ^b fungi	Bacteria ^c	Nil	
1	1/16/79	15	1	0	0	8	51	75
2	1/17/79	48	3	2	1	19	43	116
3	1/21/79	17	2	0	1	13	29	62
4	1/25/79	18	0	1	0	6	55	80
5	2/3/79	41	0	1	3	24	56	125
6	3/30/80	17	2	0	0	13	38	70
7	1/22/79	17	1	1	0	6	59	84
8	1/25/79	28	0	0	0	9	71	108

^dIn fields 1 through 6 tomatoes were grown with plastic mulching, in fields 7 and 8 they were grown on open ground.

^bIncluding Pestalotia spp., Cladosporium spp., Drechslera spp., and yeasts.

^cAll bacterial cultures were yellow on both PDA and PSBA.

Table 38. Fungi isolated from female leafminer flies

Fungus	Live flies ^b		Flies surface sterilized by ^a	
	Mean	Range	Sodium hypochlorite	Ethyl alcohol
	Mean	Range	Mean	Range
<u>Cladosporium</u> spp.	1.2	1-4	2.3	2-6
<u>Alternaria</u> spp.	0.9	0-4	1.0	0-3
<u>Stemphylium</u> spp.	0.7	0-3	0	-
<u>Drechslera</u> spp.	0.4	0-2	0	-
Other ^c	1.5	0-5	1.2	0-3

^aPer group of 5 flies, out of a total of 10 groups.

^bPer adult fly of the 25 flies tested.

^cIncluding Aspergillus spp., Mucor spp., and unidentified fungi.

Discussion

Fungi have been found as internal leaf colonizers of healthy leaves on several occasions (Norse, 1972; Spurr and Welty, 1972, 1975). The sporadic isolations of fungi from non-mined apparently healthy tomato leaflets obtained in this study indicate the absence of endophytic fungi from most tomato leaves in the Homestead area. The presence of trichomes on the leaf epidermis could conceivably prevent the complete destruction of propagules of fungi associated with them during surface sterilization by sodium hypochlorite as has been shown to be the case for pathogenic bacteria (Schneider and Grogan, 1977). Surface sterilization by ethyl alcohol may well have a drastic effect in many cases on any microflora present inside healthy or diseased leaf tissue. The results presented in Tables 35, 36, and 37, therefore, do not necessarily present accurate quantitative data on the endophytes or invaders of tomato leaves.

The more frequent isolation of fungi and bacteria from surface sterilized, mined leaves (Tables 36 and 37) indicates that these organisms are associated with the mines and their surrounding tissues. The pathogenic Alternaria isolates proved to be weak parasites, as was suggested earlier (Baranowski, 1958), because of their failure to incite symptoms in uninjured leaves and in injured leaves without an exogenous nutrient source. The absence of an adequate amount of carbohydrates may well be the reason why no infections have been observed around leaf punctures produced for feeding by adult flies or for oviposition if this did not result in larval development. A similar increased virulence of a number of pathogen on some hosts has been demonstrated by the addition

of glucose or leaf washings to the inoculum (Bashi and Rotem, 1977; Blakeman, 1968; Deverall and Wood, 1961; Milholland, 1970) and by the presence of pollen on the leaf surface (Chou and Preece, 1968). In particular the penetration and subsequent lesion expansion by Alternaria solani is affected by the tomato leaves' sugar conditions (Horsfall et al., 1974).

Although Alternaria species are ubiquitous and are present in large numbers on many plant surfaces (Dickinson, 1976; Sinha, 1971), a potential pathogenicity should not be precluded. In fact another fungus, Aureobasidium pullulans, also present everywhere, and also generally occurring as a saprophyte, is believed to be a weak parasite by some authorities (Browne, 1968) and is capable of inciting disease in some injured tissue (Haddow, 1941). Alternaria alternata has been shown to require either weakened or injured tissue in which to germinate and develop (McColloch and Worthington, 1952).

Since Alternaria species are usually present on leaf surfaces, and leaves in fact have been actually considered spore traps (Gregory, 1971), it is unlikely that the leafminer adult would be solely or even for the most part responsible for the transmission of the pathogen invading the leaf mines. Although some Alternaria conidia may be shaken off the adult leafminer (Table 38), the number is negligible when compared to that probably already present on the leaf surface and that in the atmosphere around it. Necrosis and yellowing also do not always occur around the fly's oviposition puncture. Other ports of entry may be created by piercing of the upper epidermis by exiting leafminer larvae or by ovipositing leafminer parasites. As concluded by Martin (1918) from his studies of the dissemination of Alternaria solani, the pathogen's conidia

are primarily transported by wind. The leafminers in this study provide excellent means for the penetration of the potentially parasitic Alternaria because of the wounding of the tomato leaves as do flea beetles for Alternaria solani (Martin, 1918).

The adult leafminer probably does not carry any fungal conidia internally. Surface sterilization by sodium hypochlorite resulted in very few isolations, the original propagules of which possibly escaped destruction by their association with the fly's setae as those on the leaf surface do by their association with trichomes.

Mines without associated yellowing frequently contained Alternaria colonies (Table 36). At no time has a vacated non-diseased mine been observed to develop yellowing or extensive necrosis in its vicinity for as long as the mined leaflets were monitored for disease symptoms (minimum of one month after tagging). The primary colonizer of the mine seemed to have prevented the establishing of pathogenic micro-organisms. Once the mining activity has ceased, the free nutrient content of the leaf interior will probably be depleted by the saprophyte present, thereby often effectively checking the development and harmful effect of a weakly parasitic Alternaria possibly entering the mine at a later time either through the oviposition puncture or through the larva's exit hole. This is probably one of the most important reasons for the apparent inhibition of the development of weakly pathogenic Alternaria in those mined leaves and the subsequent failure of those mines to turn yellow. Biological control of phylloplane pathogens by other micro-organisms has been reported elsewhere (Fokkema and Lorbeer, 1974; Heuvel, 1971; Spurr, 1977).

The leaf tissue around the mine can acquire an immunity to the pathogen by the action of the saprophyte present, as was found experimentally by the inoculation of sweet potato roots with pathogenic isolates of Ceratocystis fimbriata following inoculation with non-pathogenic isolates of this fungus (Weber and Stahman, 1964).

In addition to depletion of the nutrient content of the mine by saprophytes and the possibly acquired immunity, the resulting death of the cell layers surrounding the mine can provide a physical barrier to weak parasites.

The occurrence of chlorosis as one of the symptoms associated with diseased mines is indicative of Alternaria parasitism of some tomato leaves. Several Alternaria species are known to synthesize phytopathogenic toxins; twelve different compounds can be produced by Alternaria alternata alone (Harvan and Pero, 1976). The type of carbon source has been demonstrated to have an effect on the toxin production by Alternaria tenuis (Fulton and Bollenbacher, 1968). Chlorosis is a common symptom associated with infection of many plants by this fungus (Luke and Biggs, 1976). From the failure to isolate any organism from the chlorotic areas of tomato leaflets, it seems reasonable to assume that the pathogenic Alternaria thallus remains restricted to the leaf mine and its immediate necrotic surroundings. With the increasing age of the infected leaves, the fungus advances further probably due to a decrease in the resistance of the leaf tissues. A stimulation of the synthesis of maceration enzymes by the fungus when the carbohydrate source becomes exhausted may also play a role in the further necrosis of the leaf as was suggested for Alternaria solani (Horsfall et al., 1974). Differences in virulence of the Alternaria colonies may account

for the variation in the extent of the diseased tissue. The affected area increased beyond the presence of the fungus itself by the production of one or more toxins which have been repeatedly shown capable of inciting symptoms typical of the disease that the fungus itself causes (Gilchrist and Grogan, 1976); Luke and Biggs, 1976; Pound and Stahman, 1951; Templeton et al., 1967).

The pathogenic bacterium, probably Xanthomonas vesicatoria (Doidge) Dows., found to incite necrosis and yellowing around some leaf mines occurs only sporadically depending on the prevalence of bacterial spot in tomato fields. Its occurrence in and around leaf mines is not surprising since wounds provide ideal ports of entry into leaf tissue for bacterial pathogens.

Conclusions

Micro-organisms normally incapable of penetrating tomato leaves are provided the opportunity to colonize the leaf interior as soon as the leaf epidermis is pierced by a leafminer adult. The chance of a pathogen entering through the puncture into the developing mines depends on its presence on or near the injured leaf and on competition with other potential leaf colonizers.

Because Alternaria is one of the most common phylloplane inhabitants, it has a good chance of exploiting the ideal niche provided by the leafminer larvae. Weakly parasitic Alternaria species, to which the tomato is normally immune, can do damage to their host plant because of the carbohydrate supply originating from the mesophyll cells macerated by the leafminer.

Varying degrees of virulence of this pathogen will, therefore, result in varying degrees of leaf damage, most of which is done as a result of the production of one or more toxins by this fungus.

Competition on the leaf surface or inside the leaf mine can prevent pathogenic Alternaria from penetrating the leaf or establishing itself inside the mine.

Development of disease symptoms is favored by aging of the leaves. Therefore, the lower leaves of the tomato plants are especially susceptible to the pathogen and likely to show the most extensive damage symptoms including leaf abscission.

Adult leafminers are very likely to carry conidia of various fungi since they are in continuous contact with air containing a large number of propagules of micro-organisms. However, in relation to the number of conidia already present in the phylloplane of tomatoes the flies contribute only a small amount to the potential leaf invaders.

For all practical purposes the only function the leafminer performs in the development of the disease associated with leafminer in tomato, is providing a means of entry into the leaf for the pathogens and an easy access to the nutrient-rich contents of the mesophyll cells.

CHAPTER V

EFFECT OF THE VEGETABLE LEAFMINER, *Liriomyza sativae* BLANCHARD, ON THE PHOTOSYNTHETIC ACTIVITY OF INDIVIDUAL TOMATO LEAFLETS

Introduction

Leafminers reduce the photosynthesis potential of a green leaf by removing cells containing chlorophyll. If a plant's metabolism would be affected seriously by the presence of a large number of mines, a significant reduction in the synthesis of carbohydrates and other compounds essential for normal vegetative growth and reproductive capacity would result. This would mean a possible reduction in both fruit set and fruit size.

The study presented here was undertaken to determine the quantitative effect, if any, of the presence of a leaf mine on the photosynthetic activity of an entire tomato leaflet.

Materials and Methods

Tomatoes of the variety 'Walter' were grown in the field as described earlier (Chapter III, Experiment 2). Leaflets were removed in pairs from adjacent positions on the same, fully expanded leaf. The cut petiole was immediately placed in distilled water. Of each pair, one leaflet had at least one mine while the other was undamaged. Photosynthetic measurements of five pairs of leaflets were carried out

in a leaf chamber with a volume of approximately 245 ml. Air containing 234 ppm carbon dioxide was admitted to the chamber via a water trap to saturate the air with water vapor. The entering air flow was regulated with a needle valve at 43 ml min^{-1} . Air leaving the leaf chamber was forced to pass through another water trap in order to keep the pressure inside the leaf chamber as constant as possible. Light was provided by fluorescent tubes at a photosynthetic photon flux density of $230 \mu\text{Einsteins m}^{-2} \text{ sec}^{-1}$. The entire apparatus was kept at a temperature of $22.5 \pm 0.5^\circ\text{C}$.

The carbon dioxide content of the air samples taken from air entering and leaving the chamber was analyzed by means of a gas chromatograph. A Varian 3700 Gas Chromatograph with a thermal conductivity detector was utilized. The detector temperature was kept at 150°C and that of the filament at 230°C , resulting in a current of 258 mA. The oven temperature was maintained at 35°C and the carrier gas, helium, was used at a rate of 30 ml min^{-1} .

From preliminary observations it was concluded that accurate measurements could be taken between 20 and 30 minutes after placing the leaflet in the leaf chamber and closing it. At that time the carbon dioxide concentration of the air leaving the chamber had reached its minimum level and remained constant for the entire period of the experiment.

Results

The amount of carbon dioxide consumed by the leaflet was taken as a measurement of the total photosynthetic activity of that leaflet.

The rate of consumption was calculated on the basis of the area of the entire leaflet and on the basis of the area of the leaflet excluding the mined area.

The rate of carbon dioxide consumption of a non-mined leaflet based on the entire leaflet area was significantly different from that of a mined leaflet ($P < 0.05$) (Table 39). If the leaf area occupied by the mine was excluded from the area assumed photosynthetically active no significant difference ($P < 0.05$) was found (Table 39).

Discussion

The effect of a leafminer larva tunnelling in a tomato leaf, on the photosynthesis capacity, appears to be the result of removal of metabolically active tissue only, as was shown for injured apple leaves by Hall and Ferree (1976), even though in the tomato leaves only the palisade tissue is consumed and, therefore, some tissue containing chlorophyll still occupies the mined area. The immediate result of the mining activity can be twofold. The leafminer larva and any microorganisms associated with the mine increase the carbon dioxide content of the air inside the leaf resulting in an increase in the photosynthesis rate of the cells exposed to the mine's air. This rate increase may thereby partially compensate the loss of green cells due to consumption by the leafminer larva. On the other hand, the photosynthesis rate of the remaining tissue may be reduced for some time due to the injury inflicted by the leafminer as was shown for leaf tissue remaining after partial defoliation by clipping of grass (Detling et al., 1979).

Table 39. Consumption of carbon dioxide by undamaged and by mined 'Walter' tomato leaflets.

Leaflet	Total area in dm ² b	Percentage of the total area mined ^a	Amount of carbon dioxide consumed in mg dm ⁻² hr ⁻¹ a	
			Total area	Area excluding mine
non-mined	.240	-	5.27a	5.27a
mined	.279	4.5	4.56b	4.76a

^aMeans in a column not followed by the same letter are significantly different ($P < 0.05$).
Duncan's multiple range test.

^bMean value based on 5 replicates.

At low mine densities the effect on net photosynthesis will be minimal since most leaf mines occur near the leaf margins and do not sever any veins and, therefore, interfere only slightly, if at all, with nutrient transport within the leaf.

From measurements of the leaf area affected by the different instars of the vegetable leafminer, Liriomyza sativae Blanchard, and a number of other Agromyzid leafminers (Table 40) it is obvious that in case death of the larvae occurs in the first or second instar, the damage to the leaf tissues, which amounts to less than 0.5% of the area of a tomato leaflet for the vegetable leafminer, remains so small that the impact on overall photosynthesis activity of the leaflet becomes negligible.

However, as a result of serious leafminer outbreaks, the density of the mines may increase to such an extent that translocation of nutrients and thereby the metabolism of the mesophyll cells distal to the mines will be affected (Hering, 1951). In this case the photosynthesis rate of the tomato leaf will be reduced disproportionately to the actual injury. The impairment of the metabolism can become so severe that death of the entire affected leaf area results.

Conclusions

The effect of a single mine of the vegetable leafminer in a tomato leaflet reduces the net photosynthesis of the leaflet proportionally to the area that the mine occupies. A higher mine density in tomato leaflets will reduce the net photosynthesis rate more than the additive effect of individual mines due to interference with translocation of nutrients in the leaf's mesophyll.

Table 40. The area of the mines excavated by the different instars of some leafminer larvae.

Leafminer species	Total area of the mine in mm ²	Ratio of the total area per instar			Reference
		instar I	instar II	instar III	
<u>Liriomyza sativae</u>	103.6	1	2.3	26	This study
<u>Phytomyza</u> <u>syngenesiae</u>	328.2	1	4	44	Ibrahim and Madge, 1977
<u>Phytomyza lanati</u>	- ^a	1	4	40	Tauber and Tauber, 1968

^aNot given.

Control of the leafminer by means of efficient insecticides or Hymenopterous parasites which will kill the larvae in their first or second instar will result in a negligible effect on the photosynthesis potential of the tomato leaves.

CHAPTER VI
CONCLUSIONS

Although leafminers can do serious damage to the leaf tissues of tomato plants, the density of the leaf mines is rarely high enough to cause serious defoliation by itself. Only in the seedling stage when the total leaf area of the tomato plants is small will consumption of the entire photosynthetically active tissue occur easily. The most important factor in the occurrence of leaf deterioration and subsequent abscission is the weak pathogen, Alternaria alternata, which is capable of destroying an entire leaflet. This can happen even if only a single mine is present in a leaflet and becomes colonized by the fungus. Low leafminer densities are, therefore, not necessarily a measure of potential damage to the tomato plants. Additional damage associated with leaf mines can be caused by Xanthomonas vesicatoria which may enter the mines.

The lower leaves of the tomato plants which act more as metabolic sinks than as photosynthetically active organs are dispensable as can be concluded from the absence of effects of defoliation of lower plant canopies on fruit development. The upper leaves are more important to the plant than the middle and lower ones and, because of their younger age, are more resistant to infection. Since leafminers usually attack only the lower and middle leaves, infestations except at very high levels usually have relatively little effect on the yield and, therefore, on

the gross revenue of the tomato crop.

The tomato plants exhibit a differential sensitivity to defoliation during the growing season. The most sensitive times are early in the season and at mid-season. Still, at least 60% of the foliage has to be removed before significant reduction in the yield of the fruit in the two largest size categories as well as the total yield of marketable fruit can be observed.

Repeated defoliation is tolerated by the tomato plants at lower levels with removal of 40% of the foliage resulting in significant yield reduction.

The weight of all marketable fruit at any level of defoliation is significantly correlated with the gross revenue that the grower would obtain from that yield, based on different prices for the different size categories.

If large leafminer populations occur, then parasites, if they are present, can ensure that the leafminer larvae will be killed before the damage to the tomato leaflet becomes severe enough for the pathogen to establish itself sufficiently to affect the tissue around the mine.

An effective way to avoid concern about possible damage to tomato plants by the leafminer-Alternaria complex is, therefore, to ensure the presence of sufficient parasites in the field which can effectively control the leafminer population as was the case before the first serious outbreaks which resulted from the intensive use of pesticides. The application of sound pest management practices appears to offer the best chance of achieving maximum net revenue in crops where the leafminer can be a serious problem.

If, however, the parasite population is ineffective in controlling the vegetable leafminer, insecticide applications specifically to control the leafminer are required. Insecticides for leafminer control should be applied when the defoliation level reaches 30% in plants before anthesis and 50% in plants after anthesis. If further defoliation of 10% occurs after the insecticides have been applied, further treatment is advised.

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BIOGRAPHICAL SKETCH

Jozef Leo Willem Keularts was born on August 10, 1945, in Heerlen, The Netherlands. After completing secondary school at the St. Bernardinus College in Heerlen in 1963, he received a scholarship to the Catholic University of Nijmegen, The Netherlands. In 1969 Jozef graduated from the Catholic University of Nijmegen with the title of Doctorandus in Biology.

In the same year, Jozef fulfilled the compulsory Armed Services requirements of the Dutch Army, serving as a radio communications operator in the Cavalry Division. Following his military service in 1971, Jozef taught biology and agricultural science to senior forms in preparation for their Cambridge examinations at Mumbwa Secondary School, The Republic of Zambia, Africa. He left Zambia in 1976, returning to the Catholic University of Nijmegen to study the ultrastructure of mites.

From 1977 to 1980, Jozef has been a graduate student in the Department of Entomology and Nematology at the University of Florida. Upon completing the requirements for the degree of Doctor of Philosophy, he plans to take up a position as Lecturer of Entomology at the University of Malawi, The Republic of Malawi, Africa.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Van H. Waddill, Chairman
Associate Professor of Entomology
and Nematology

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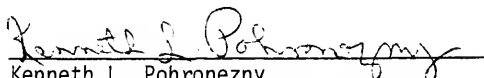
John R. Strayer
Professor of Entomology and
Nematology

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Robert T. McMillan, Jr.
Associate Professor of Plant
Pathology

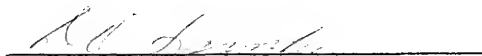
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Kenneth L. Pohronezny
Assistant Professor of Plant
Pathology

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Dean, College of Agriculture

Dean, Graduate School

