Analysis of physiological, growth, and yield responses of celery to *Liriomyza trifolii*

John T. Trumble, Irwin P. Ting[1] & Loretta Bates[1]
Department of Entomology and[1] *Department of Botany-Plant Sciences, University of California, Riverside, California, USA*

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Abstract

Stomatal conductance, mesophyll conductance, transpiration and photosynthesis varied considerably by within-plant locations on celery (*Apium graveolens* L.), but specific opposite leaves proved equivalent. Using such comparable leaves, feeding damage by *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) larvae or adults was found to reduce significantly the capacity of celery for photosynthetic activity. In field trials where populations of *L. trifolii* were manipulated with pesticides, numbers of leaves, plant height, and numbers of petioles per plant were significantly greater in treatments with low leafminer densities. In treatments where *L. trifolii* was encouraged, harvest was delayed by up to 3 weeks. Related laboratory studies indicated that the pesticides used in the field trial neither promoted nor slowed celery growth. None of the physiological parameters measured at either 1.5 h or 7 days post-treatment was significantly affected.

Introduction

The destructive capacity of the polyphagous agromyzid, *Liriomyza trifolii*, has been documented by many researchers (Poe, 1982; Spencer, 1973). Although the crop losses attributed to this leafminer have recently stimulated considerable research designed to provide information on leafminer biology (Leibee, 1981, 1984; Parrella, 1984), chemical control strategies (Schuster & Everett, 1983; Webb *et al.*, 1983), resistance management (Keil & Parrella, 1982), and biological/integrated control programs (Trumble & Toscano, 1983), little effort has been made to determine physiological responses of the host plant to leafminer infestations. A notable exception is the study (M. W. Johnson *et al.*, 1983) on the effects of feeding by *L. sativae* Blanchard on a commercial variety of tomatoes, *Lycopersicon esculentum* (Mill.).

Until the development of the dual isotope porometer, statistical analysis of factors affecting photosynthesis and related processes was extremely difficult and tedious. This difficulty was primarily due to the variability in location and photosynthetic activity of chlorophyll in plants (Boulanger, 1958; Bruinsma, 1963). This problem was solved by the development of the porometer, which allows many samples to be taken in a short period of time (H. B. Johnson *et al.*, 1979). The research reported here studies the impact of adult leafminer feeding and larval mining on photosynthesis, transpiration, stomatal conductance and mesophyll conductance. Effects of various levels of leafminer damage on plant growth patterns and yield were investigated in experimental plantings in Orange County, California.

Materials and methods

Measurement of photosynthesis and related processes. Photosynthesis, transpiration, mesophyll conductance, and stomatal conductance by celery plants subjected to pesticide application or leaf-

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miner damage was measured with a dual isotope porometer. Specific design and operation of the porometer are described by H. B. Johnson *et al.* (1979). Gas exchange equations used to calculate the physiological parameters are based on the uptake of tritium (^3H_2O) and labeled CO_2 ($^{14}CO_2$), and calculated as follows:

Photosynthesis in mg CO_2/area/time =

$$\frac{\Delta CO}{R_s + R_m} \text{ and}$$

Transpiration in g H_2O/area/time =

$$\frac{\Delta H_2O}{R_s}$$

where ΔCO_2 = the difference in concentration of CO_2 between the atmosphere and the internal tissues of the leaf,

ΔH_2O = the difference in water vapor concentration between the leaf and the atmosphere,

R_s = the stomatal resistance to H_2O or CO_2 exchange in sec/cm,

R_m = the resistance of the mesophyll to assimilation of CO_2 in sec/cm.

R_s and R_m were calculated from ^3HOH and $^{14}CO_2$ uptake and then photosynthesis and transpiration were generated from the equations. Resistance data were converted to conductance (cm/s) by taking reciprocals.

Initially, twenty undamaged celery plants were 'mapped' with the porometer to compare photosynthesis and related parameters between specific leaves, petioles, and plants. All celery plants evaluated were of the same variety (5270-R) and seedlot, and grown under identical conditions in the greenhouse (i.e. soil type, moisture, light, etc.). Not all leaves, petioles or plants were equivalent physiologically, and direct, quantitative comparisons of rates of each physiological variable between separate plants, or even leaves on separate petioles within the same plant, would not be statistically valid. However, there were no statistical differences found for any of the physiological variables measured between the two opposite pairs of leaves nearest to the tips of those celery petioles which were vertically oriented. Therefore, these leaves were used exclusively for our experiments. Leaves on petioles with an increasing horizontal aspect are typically in advanced stages of senescence (Musgrave *et al.*, 1977; Van Steenwyk & Toscano, 1981) and proved too variable and unreliable for our purposes.

Due to variations between petioles and plants, analyses of porometer data were generated using a paired t-test which determined whether differences between opposite treated and control leaves were significant. Thus, the comparisons have been presented as levels of significance at which the null hypothesis, physiology of treatment leaves = physiology of control leaves, can be rejected.

Impact of L. trifolii *on celery physiology.* Larval mining on selected celery leaves was initiated by confining one female and two males on the upper surface of one of each pair of leaves for approximately 1 to 4 h using small styrofoam cages. Following oviposition, the cages were removed and plants were returned to the greenhouse where larvae completed development and exited the leaves within one week. Only leaves on which a single leafminer developed were tested. Porometer samples were taken distally on the test leaf, with the mined area between the petiole and the sample area. The same location was sampled from the opposite control leaf. Porometer samples were collected from 60 pairs of damaged versus undamaged leaves.

The physiological impact of damage caused by the adult female during feeding was evalated by confining newly emerged non-ovipositing females to the upper surface of one of each pair of opposite leaves in an area the size of the porometer sample (diam. = 9 mm). Following approximately 12 h of exposure, cages were removed and plants were transferred to the greenhouse and allowed to acclimate for 24 h prior to sampling with the porometer. The number of feeding punctures within each sample area was counted, allowing values to be readily converted to feeding punctures per cm^2. Again, opposite control leaves were sampled at the same location. Numbers of samples varied with each density of feeding punctures evaluated, and have been presented with the tabular information.

Impact of leafminers on celery growth and yield. A variety of plant growth parameters was monitored weekly for celery plugs and bare root transplants which were exposed to high and low levels of leafminer infestations in an experimental planting of 52–70 HK celery in Orange County, California, during 1982. All plants were germinated from the same seedlot and grown to transplant size with the same greenhouse operation. Plugs and bare root transplants were chosen for this test because these are the smallest and largest forms of celery, respectively, transplanted in California. We anticipated that equivalent leafminer populations would be more damaging on the smaller plants, and provide a maximum and minimum range of leafminer damage.

Populations of *L. trifolii* were manipulated in the field with weekly pesticide applications: methamidophos at 1.1 kg a.i./ha minimized leafminer density and methomyl at 1.0 kg a.i./ha maximized populations. Previous research had shown that methomyl application would increase leafminer density and, thus, the mean number of mined leaves/plant by greater than 75% as compared with celery treated with methamidophos (Trumble & Toscano, 1983).

Treatments of plugs and transplants were randomized in a complete block design with each treatment replicated four times. Each replicate consisted of four beds (2 rows/bed) × 20 m. Data on plant height, number of total leaves/plant and numbers of petioles/plant were collected randomly from the center two beds for 8 weeks following the first pesticide application. Plant growth was also evaluated at harvest. Leafminer densities were quantified using a modification of the pupal tray technique developed by M. W. Johnson *et al.* (1980), which collects larvae as they exit the leaves to pupate in the soil. Smaller trays (10 × 20 cm) were used in our experiments to permit insertion between rows of celery. Four trays were assessed per replicate per week once the plants reached a suitable size (ca. 25 cm). Comparisons of $\bar{x}$ plant growth parameters were generated with Duncan's new multiple range test (DNMRT).

An additional experiment was initiated to determine if the chemicals used to manipulate the leafminer populations were affecting photosynthesis, transpiration and stomatal and mesophyll conductance. Like the earlier porometer tests, opposite leaf pairs were utilized with one leaf serving as a control. Test leaves were treated to run-off with either methomyl or methamidophos at the rates used in the field trials. Porometer samples were then collected at ca. 1.5 h posttreatment (n = 21 comparisons/pesticide) and at 7 days posttreatment (n = 20 for methamidophos; n = 17 for methomyl).

Results and discussion

Impact of L. trifolii celery physiology. The impact of leafmining on celery physiology is presented in Table 1. A single leafmine significantly reduced stomatal conductance, mesophyll conductance, transpiration, and photosynthesis. These results are in agreement with those of Johnson *et al.* (1983), where *L. sativae* was shown to cause similar reductions in photosynthesis and transpiration on tomatoes. Mining causes a disruption of the vascular system in celery affecting the movement of water which, in turn, causes changes in turgor pressure. As guard cells collapse a reduction in stomatal conductance occurs which inhibits transpiration and photosynthesis. Although a reduction in photosynthesis by greater than 40% (Table 1) may be overestimating the loss to the leaf, since not all the leaf area was distal to the mine, the total loss of photosynthesis in the mined area (ca. one-tenth of the leaf area) and the frequent occurrence of more than a single mine per leaf under field conditions may result in much greater physiological effects in commercial operations.

The effects of feeding damage by adult *L. trifolii* on celery physiology have been presented in Table 2. Feeding punctures occurring at a density of less than ca. 13/cm^2 did not affect the physiological parameters evaluated. However, between 13 to 19 punctures/cm^2, a low level effect was seen on pho-

Table 1. Impact of leafmining by *L. trifolii* on selected physiological parameters of celery.

Physiological parameter	Units	Paired comparison analysis[a]	$\bar{x}$% reduction
Stomatal conductance	cm/s	< 0.001	36.25
Mesophyll conductance	cm/s	< 0.001	21.13
Transpiration	g H_2O/area/time	< 0.002	36.16
Photosynthesis	mg CO_2/area/time	< 0.001	42.64

[a] n = 60 comparisons, values indicate level at which the hypothesis 'physiology of damaged leaves = physiology of undamaged leaves' can be rejected.

Table 2. Relationship between density of feeding punctures of *L. trifolii* and celery physiology. Paired comparison analysis[a].

Feeding punctures/sq. cm	No. comparisons	Stomatal conductance	Mesophyll conductance	Transpiration	Photosynthesis
0 - 6.3	30	NS	NS	NS	NS
6.4–12.7	27	NS	NS	NS	NS
12.8–19.1	21	NS	NS	NS	0.1
19.1 +	20	0.01	0.001	0.02	0.001

[a] NS not significant at $P \leq 0.05$; indication of values, see Table 1.

tosynthesis. At densities above 19 punctures/cm^2, all processes measured were significantly reduced. Because the density of feeding/oviposition punctures frequently exceeds this level in the field, the previous view that such damage was negligible may not be valid.

Leafminer damage on celery growth and yield. The chemicals used to manipulate leafminer densities in the field did not significantly ($P \leq 0.1$, t-test) affect stomatal conductance, mesophyll conductance, transpiration or photosynthesis at either ca. 1.5 h or 7 days posttreatment. Similar results were found by Toscano *et al.* (1982) for methomyl applications on lettuce. Since no other insects or diseases attacked more than ca. 1% of the plants in our trial and no other pesticides were required or used, variations in plant growth and yield were assumed to be due to leafminer and cultural effects. Significantly higher populations of leafminers in methomyl treatments (Table 3) adversely affected the growth and development of celery as compared to plots where leafminer populations were suppressed with methamidophos. Plants treated with methomyl were smaller than those treated with methamidophos (Fig. 1). Differences in height were significant between chemical treatments on five of the eight sampling dates. Since smaller plants have fewer leaves and less leaf area per leaf, small plants would be more seriously affected by leafminer damage at a given infestation than plants with greater size.

The mean numbers of leaves per plant were also significantly different between treatments (Fig. 2). Transplants had more leaves than plugs on every sampling data, and transplants sprayed with methamidophos had significantly more leaves than those treated with methomyl on six of the eight sampling dates. In four of the last six samples, plugs treated with methomyl had significantly fewer leaves than plugs exposed to methamidophos.

As a result of slower growth due to leafminer damage, plugs sprayed with methomyl developed significantly fewer petioles after 4 weeks than all other treatments (Table 4). By the 7th week of sampling, plugs treated with methamidophos had as many petioles as transplants in the methomyl treatment. Only those transplants where leafminer damage was suppressed with methamidophos produced more petioles.

The cumulative effect of reduction in number of leaves, plant height, and number of petioles was evident when the plants were harvested. Transplants in plots where methamidophos was applied were the first to reach harvestable size. Weekly

Table 3. Population density of *L. trifolii* in selected chemicals and cultural treatments during 1982.

Treatment and rate	Cultural technique	$\bar{x}$ no. *L. trifolii*/tray/week[a]				
		OCT 11	OCT 18	OCT 26	NOV 1	NOV 8
Methomyl 1.0 kg/ha	Plugs	47.6 a	33.3 a	15.9 a	5.2 a	4.7 a
	Transplants	18.2 b	10.0 b	7.3 a	4.2 a	2.0 a
Methamidophos 1.1 kg/ha	Plugs	10.9 c	2.8 c	0.7 b	0.2 b	0.1 b
	Transplants	3.6 d	2.4 c	0.7 b	0.1 b	0.1 b

[a] Means of 4 trays/replicate and 4 replicates/treatment on each date; means within columns followed by same letter not significantly different at $P \leq 0.05$ level, DNMRT.

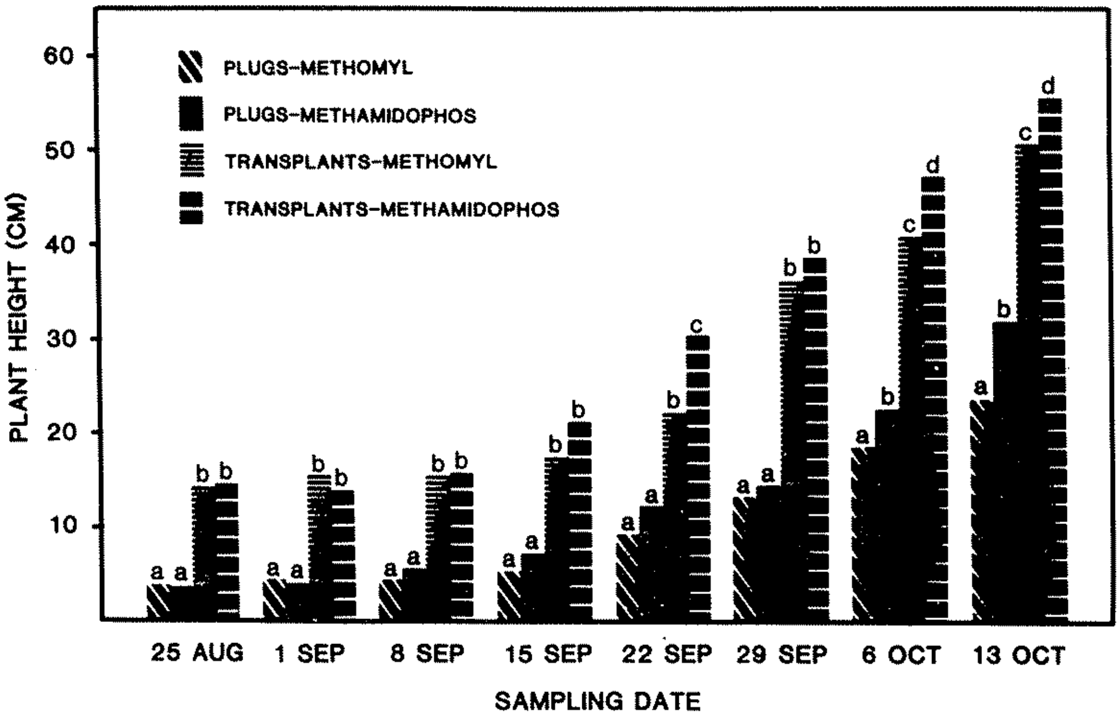

Fig. 1. Impact of leafminer damage on plant height for 5270-HK plugs and transplants in an experimental planting in Orange County, California during 1982. Data were collected from 20 plants/treatment/week. Significancies, see Table 3.

samples of 20 plants/replicate (80 plants/treatment) indicated that equivalent heights and weights were achieved by the metamidophos treated plugs and methomyl treated transplants after two additional weeks, and by the methomyl treated plugs following 3 weeks.

Such increases in time to harvest have substantial effects on the economic return to the grower, including reduced revenue due to additional labor, irrigation, rent and depreciation costs. Extending the time to harvest may also cause growers to miss the marketing period intended at the time of planting. Therefore, even the light-moderate infestation levels of *L. trifolii* which reduced plant vigour during this study may result in considerable economic loss.

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Table 4. Mean number of petioles/plant in celery plugs and transplants treated with methamidophos and methomyl.

Culture and treatment	Mean no. petioles/plant[a]						
	25 AUG	8 SEP	15 SEP	22 SEP	29 SEP	6 OCT	13 OCT
Plugs methomyl	3.2 b	3.9 c	4.5 c	6.1 c	7.4 c	14.2 c	16.6 c
Plugs methamidophos	3.2 b	3.5 b	5.7 c	8.6 b	9.7 c	18.0 b	22.0 b
Transplants methomyl	4.1 a	6.6 b	9.3 b	9.2 b	15.5 b	22.1 b	22.6 b
Transplants methamidophos	4.1 a	8.2 a	12.8 a	17.0 a	23.7 a	29.4 a	28.2 a

[a] 5 plants/replicate/date; significancies, see Table 3.

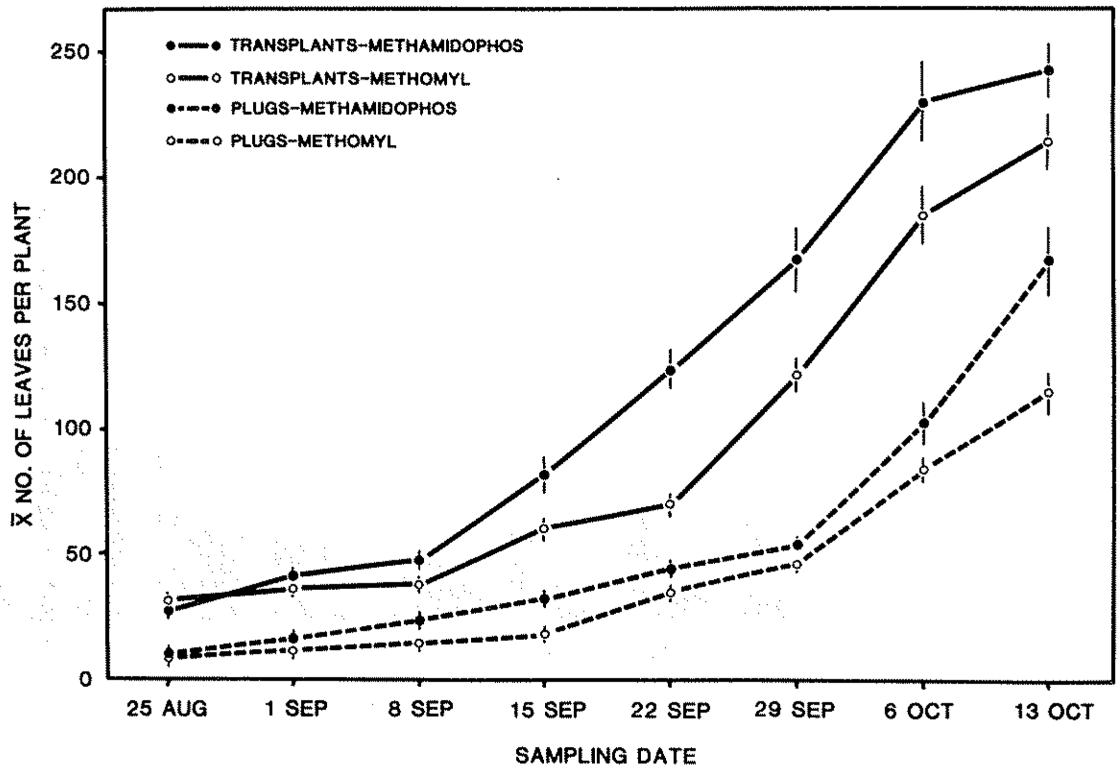

Fig. 2. Mean number of leaves per celery plant for 5270-HK plugs and transplants treated with methamidophos to suppress leafminer damage and methomyl to increase damage. Brackets on data points delineate s.e.'s. Data collected from 20 plants/treatment/week in an experimental planting in Orange County, California during 1982.

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Résumé

Etude des réactions physiologiques de la croissance et de la production de céleris attaqués par Liriomyza trifolii

Les conductances des stomates et du mésophylle, la transpiration et la photosynthèse varient considérablement suivant la position des feuilles dans un pied de céleri (*Apium graveolens* L.) mais ces paramètres sont identiques pour des folioles opposées.

En utilisant de telles folioles comparables, une réduction singificative de l'activité photosynthétique du céleri a été observée lors des dégâts alimentaires par les larves et les adultes de *Liriomyza trifolii* Burg. (Dipt. Agromyzidae). Dans des essais en champ où des populations de *L. trifolii* ont été contrôlées avec des insecticides, les nombres de pétioles et de folioles et la hauteur des plantes étaient significativement plus élevés là où les traitements avaient entraîné de faibles densités de mineuses. Dans les parcelles où *L. trifolii* avait été avantagé, la récolte avait été retardée jusqu'à 3 semaines. Des essais parallèles au laboratoire ont montré que les insecticides utilisés dans ces essais au champ, n'avaient ni accéléré, ni retardé la croissance du céleri. Aucun des paramètres physiologiques mesurés après 1,5 heure ou 7 jours après le traitement n'avait été modifié.

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