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Influence of Western Corn Rootworm (Coleoptera: Chrysomelidae) Larval Injury on Photosynthetic Rate and Vegetative Growth of Different Types of Maize

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ABSTRACT Two field experiments were conducted in 1995-1996 to determine if there are common photosynthetic and vegetative growth responses among genotypes of maize, *Zea mays* L., to larval western corn rootworm, *Diabrotica virgifera virgifera* LeConte injury. Specific variables measured from rootworm infested and noninfested plants were midday leaf photosynthetic rate, plant growth stage, and plant height during 9-18 leaf growth stages. Three yellow-dent hybrids, five white food-grade dent hybrids, and a popcorn hybrid were included in the study. Results suggest that there may be a common negative photosynthetic response within maize to larval injury during vegetative growth stages. Transient reductions in photosynthetic rate occurred in rootworm infested maize at both low to moderate levels of root injury, which after a lag period, led to significant reductions in plant height. This trend was consistent across hybrids in both experiments during each year. Plant growth stage was not significantly affected by rootworm injury during vegetative periods.

KEY WORDS *Diabrotica virgifera virgifera*, corn, photosynthesis, root injury, vegetative growth

THE WESTERN CORN ROOTWORM, *Diabrotica virgifera virgifera* LeConte is one of the most economically important insect pests of maize in the United States. Larvae feed on root hairs and cortical tissue (Chiang 1973, Riedell and Kim 1990), which can lead to root pruning and destruction of root sections of the plant (Branson 1986, Riedell 1990). Root damage may produce plant lodging (Sutter et al. 1990, Spike and Tollefson 1991), disrupt plant water relationships (Riedell 1990, Hou et al. 1997), and alter maize nutrient content (Kahler et al. 1985). Larval injury can also reduce leaf area and weight (Spike and Tollefson 1991, Godfrey et al. 1993a, Dunn and Frommelt 1998a), plant height (Roth et al. 1995, Allee and Davis 1996), and grain yield (Turpin et al. 1972, Apple et al. 1977, Spike and Tollefson 1991, Godfrey et al. 1993a, Gray and Steffey 1998).

Although the western corn rootworm can affect the productivity of maize plants, little is known about the physiological response mechanisms of maize to rootworm larval injury. Owens et al. (1974) suggested that feeding by even a small number of rootworm larvae inhibits the capacity of infested plants to assimilate water. Larval feeding by *Diabrotica* spp. may reduce the ability of roots to provide water to the plant, resulting in water deficits and subsequent yield loss (Riedell 1990, Riedell et al. 1992). However, results from several greenhouse studies are not conclusive. Mechanical pruning of maize roots decreased relative

water content and leaf water potential (Riedell 1990), sap flow, fresh and dry weight of stalks and roots, and plant height (Gavloski et al. 1992). In contrast, sap flow was not significantly affected when plants were infested with rootworm larvae (Gavloski et al. 1992). Rootworm injury did not affect relative water content or leaf water potential at the nine-leaf growth stage, but leaf water potential was significantly higher in injured versus noninjured plants at tassel (Riedell 1990). Dunn and Frommelt (1998b) also reported that relative water content was not affected by rootworm injury at 13 and 55 d after infesting six-leaf stage plants. Gavloski et al. (1992) concluded that the effect of rootworm feeding on the physiology of maize growth may be more complex than simple disruption of water balance.

Differences in canopy temperatures have been detected between severely infested and noninfested maize during the period of larval feeding (Schaafsma et al. 1993). These differences occurred at >200 eggs per plant, and differences increased with higher levels of egg infestation. Schaafsma et al. (1993) suggested that if rootworm injury affects water relations in the plant, there could be a link between rootworm injury-moisture interactions and canopy temperatures.

Several studies have characterized gas exchange responses in maize to larval western corn rootworm injury. In a greenhouse study, feeding by 50 or 150 western corn rootworm larvae did not affect stomatal conductance of nine-leaf stage maize; however, infested plants had significantly lower stomatal conductance than noninfested plants at tassel stage (Riedell 1990). In a field study, photosynthetic rates in full

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sunlight were reduced by an average of 7.9% in severely damaged maize (Godfrey et al. 1993b). This reduction occurred during the initial period of larval injury when larvae were first and second instars, but photosynthesis was not affected during the periods of maximum injury or postinjury (Godfrey et al. 1993b). There was no consistent relationship between photosynthesis and stomatal conductance or intercellular CO₂ concentration. In a study with the same hybrid, larval feeding resulted in a transient reduction of both maize leaf photosynthesis and stomatal conductance (Hou et al. 1997). A significant interaction between larval injury and soil moisture also occurred. Rootworm larval injury inhibited plants grown in a low-to-moderate soil moisture environment from using supplemental moisture to increase stomatal conductance and photosynthesis for a short period (Hou et al. 1997). Dunn and Frommelt (1998b) also reported a significant interaction between rootworm injury and soil moisture that affected plant gas exchange parameters. Maize grown under dry soil moisture conditions had significantly lower leaf photosynthetic rates and stomatal conductance than well-watered maize 24 d after larval infestation.

Previous experiments conducted to study gas exchange and growth responses of maize to rootworm injury during vegetative growth stages have only focused on a few yellow-dent hybrids. Little information on these response variables is available within or among different types of maize. Therefore, the objective of this study was to determine if there are common photosynthetic and plant growth responses within maize to larval western corn rootworm injury. One experiment was conducted to characterize photosynthetic and vegetative growth responses of yellow-dent, white-dent, and popcorn hybrids to larval injury. A second experiment focused on food-grade white-dent hybrids.

Materials and Methods

Studies were conducted at the University of Nebraska Agricultural Research and Development Center near Mead, NE. Three yellow-dent hybrids (Pioneer 3346, 3394 and 3377), a white-dent hybrid (Noble Bear 749W), and a popcorn hybrid (Purdue 612) were included in experiment 1. Four white-dent hybrids (Pioneer 3281W, 3287W; Noble Bear 739W, 742W), and a yellow-dent hybrid (Pioneer 3377) were included in experiment 2. All yellow and white hybrids were commercially available and widely grown at the time of the study except Pioneer hybrid 3377. Pioneer 3377 was included as a historical standard (1980s era hybrid) to allow comparison with past gas exchange work (Godfrey et al. 1993b, Hou et al. 1997). Hybrids were chosen that exhibited some trait differences (e.g., early growth, root strength, relative maturity) in an attempt to include genetic diversity within the study. A split-plot design with four replications was used. Hybrids were the whole plots and rootworm infestation levels were the subplots (experiment 1: 0, 1,000 eggs per 30.5-cm row; experiment 2: 0, 200, 500,

1,000 eggs per 30.5-cm row). Whole plots (each 6.1 m long) consisted of four rows in experiment 1 and eight rows in experiment 2 separated by two border rows. Each subplot was two rows.

Maize plots were established where soybeans had been grown the previous year in a Sharpsburg silty clay loam soil. Experiment 1 was planted on 18 May 1995 and 20 May 1996; experiment 2 was planted on 18 May 1995 and 17 May 1996. The seeding rate was 60,500 kernels per hectare in rows spaced 0.76 m apart. Total nitrogen applied was 92.1 kg/ha in 1995, and 138.3 kg/ha in 1996. Daily air temperature, rainfall, and water applied by irrigation were recorded during each experiment.

Eggs were suspended in a concentration of 0.125% agar-water, and infested at the two- to three-leaf growth stage, using a modification of the techniques described by Sutter and Branson (1986). To estimate western corn rootworm age structure, three 15.2-cm³ soil cubes each surrounding a maize plant were periodically taken and were processed using the method of Bergman et al. (1981). Larvae within roots were recovered by suspending each root system over a container of water and forcing larvae to move from roots with heat. In experiment 1, samples were taken on five dates during 1995 (26 June–11 July period), and on six dates during 1996 (25 June–15 July period). In experiment 2, samples were taken on four dates in 1995 (29 June–17 July period) and on six dates in 1996 (15 June–12 July period). To estimate larval population density and evaluate root damage, samples were taken during the peak damage period (experiment 1: 11 July 1995 and 15 July 1996; experiment 2: 17 July 1995 and 12 July 1996). Root damage was evaluated using a 1–6 damage rating scale (Hills and Peters 1971). In experiment 1, two plants in 1995 and one plant in 1996 were sampled per treatment per replication. In experiment 2, one plant was sampled per treatment per replication in both years. Adult emergence also was used as an indicator of the magnitude of larval infestation. Single plant emergence cages (Hein et al. 1985) were placed in plots before adult emergence. One cage was placed in each treatment subplot per replication. Voucher specimens have been deposited in the University of Nebraska State Museum, Lincoln.

Photosynthetic Rates. Maize leaf photosynthesis was measured in full sunlight (1,700–2,100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) near midday (1100–1400 hours CDT), with a portable photosynthesis system (LI-6200, LI-COR, Lincoln, NE). To measure gas exchange, a maize leaf was enclosed in a 1.0-liter chamber, and data were registered at 10-s intervals. Leaf photosynthesis was measured on the middle of the third fully expanded leaf from the leaf apex. Measurements were taken periodically during the larval period from three plants per treatment per replication (experiment 2: only in plots infested with 0 and 1,000 eggs per 30.5-cm row). In experiment 1, leaf photosynthesis was measured on four dates in 1995 (30 June–13 July period), and on seven dates in 1996 (28 June–18 July period). In experiment 2, measurements were made on three dates

in 1995 (7–18 July period) and on four dates in 1996 (27 June–13 July period).

Growth. Plant growth stage (Ritchie et al.1997) and extended leaf height (base of the stem to the tip of the tallest vertically extended, fully developed leaf) were measured from three plants per treatment per replication. In experiment 1, measurements were made on six dates in 1995 (29 June–31 July period) and five dates in 1996 (26 June–26 July period). In experiment 2, measurements were made on five dates each year (1995: 29–31 July period; 1996: 20 June–22 July period).

Statistical Analysis. All response variables were analyzed on each date with the MIXED procedure (SAS Institute 1985) so that both random and fixed effects could be appropriately modeled. The analysis reflected the split plot design with hybrids as main plots and infestation as subplots. Fisher protected least significant difference (LSD) test was used to determine significant differences among treatment means. A significance level of $P < 0.05$ was used for all experiments.

Results

Environmental Conditions. Rainfall plus irrigation applied to each experiment during 24 June–18 July 1995 and 22 June–18 July 1996 was 52.9 and 122.6 mm, respectively. In experiment 1, on dates that photosynthesis measurements were made, maximum temperatures ranged from 21.7 to 39.8°C in 1995 and 24.2 to 36.7°C in 1996. In experiment 2, maximum temperatures ranged from 30.5 to 37.6°C in 1995, and 26.3 to 32.1°C in 1996.

Rootworm Population Dynamics and Larval Injury. Larvae were predominantly first and second instars during 26–30 June each year (percentage of total individuals first or second instar, range across sampling dates: 69.2–100). Larval age structure became skewed toward third instar from 5 to 15 July in 1995 and 1996 (percentage of total individuals third instar, range across sampling dates: 47.2–93.3). Initial pupae were recovered on 6 July 1995 and 10 July 1996. Peak injury (maximum root biomass loss) occurred during mid-July each year.

Egg infestation rates resulted in significantly different rootworm populations per treatment, as measured by larvae per plant and adults per trap in each year (Table 1). Rootworm injury was greater in infested than noninfested plants each year, but the level of injury resulting from the highest infestation level was only above the commonly used economic injury index (>3.0 root damage rating, Mayo 1986) during 1 yr of each experiment (Table 1).

Photosynthesis, Experiment 1. Across hybrids, rootworm-infested plants had significantly lower midday leaf photosynthetic rates than noninfested plants on 10 July ($F = 10.82$; $df = 1, 15$; $P = 0.005$) and 13 July ($F = 13.97$; $df = 1, 15$; $P = 0.004$) 1995 (Fig. 1A), and on 1 July ($F = 7.27$; $df = 1, 15$; $P = 0.017$), 10 July ($F = 14.53$; $df = 1, 11$; $P = 0.003$), 12 July ($F = 14.98$; $df = 1, 15$; $F = 0.002$), and 18 July ($F = 13.88$; $df = 1, 15$; $P = 0.002$) 1996 (Fig. 1B). During each year, there were no

Table 1. Rootworm population and root injury parameters ±SE of plants across hybrids

Year	Infestation level ^a	Larvae per plant	Root injury rating ^b	Adults per trap ^c
Experiment 1				
1995	0	0.4 ± 1.7a	1.0 ± 0.1a	11.4 ± 6.5a
	1000	13.9 ± 1.7b	2.9 ± 0.1b	41.2 ± 6.5b
1996	0	0.00 ± 1.3a	1.0 ± 0.1a	4.25 ± 2.4a
	1000	9.55 ± 1.3b	3.9 ± 0.1b	25.6 ± 2.4b
Experiment 2				
1995	0	0.6 ± 1.2a	1.3 ± 0.15a	7.6 ± 6.0a
	200	3.8 ± 1.2b	2.2 ± 0.15b	22.7 ± 6.0b
	500	9.6 ± 1.2c	2.7 ± 0.15c	36.7 ± 6.0c
	1000	11.8 ± 1.2c	3.4 ± 0.15d	48.8 ± 6.0c
1996	0	0.0 ± 1.4a	1.2 ± 0.11a	4.5 ± 2.4a
	200	3.4 ± 1.4b	2.2 ± 0.11b	8.5 ± 2.4b
	500	5.7 ± 1.4b	2.6 ± 0.11c	14.5 ± 2.4bc
	1000	10.9 ± 1.4c	2.9 ± 0.11d	29.5 ± 2.4c

Means within year, experiment, and column followed by the same letter are not statistically different. ($P > 0.05$; Fisher protected LSD test). Each number is an average of 20 sample values except 1995 Experiment 1 larvae per plant and root injury ratings where sample size = 40.

^a Infestation level values are western corn rootworm eggs per 30.5 cm row.

^b Iowa 1–6 root rating scale (Hills and Peters 1971).

^c Total emergence from single plant emergence cages (Hein et al. 1985).

significant interactions between hybrid and larval injury on any date. Across infestation levels, leaf photosynthetic rates were not different among hybrids on any date in 1995, but statistical differences occurred among hybrids on 10 July ($F = 3.92$; $df = 4, 9$; $P =$

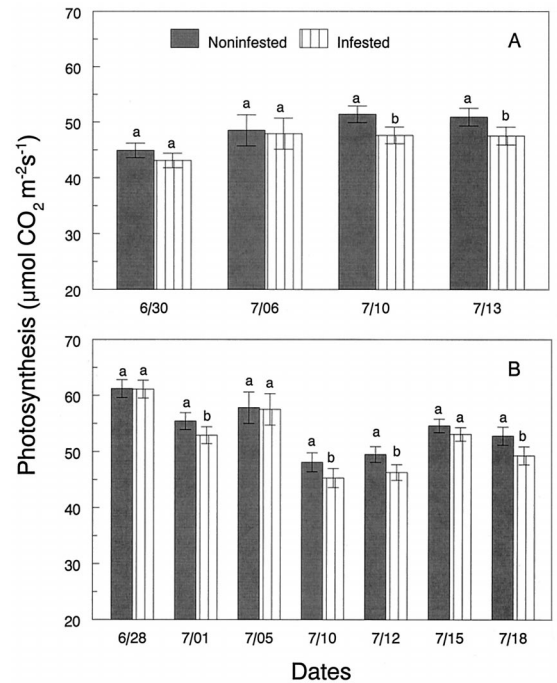


Fig. 1. Photosynthetic rates across hybrids in infested and noninfested plants. Experiment 1 (A) 1995 and (B) 1996.

Table 2. Midday photosynthetic rates \pm SE under full sunlight across infestation levels of different hybrids, experiment 1, 1996

Date	Hybrid	Photosynthetic rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$)
10 July	P3377	48.6 \pm 1.9a
	P3346	48.0 \pm 1.9ab
	Purdue 612	47.5 \pm 1.9ab
	P3394	45.2 \pm 1.9bc
	NB742	44.4 \pm 1.8c
12 July	Purdue 612	51.5 \pm 1.8a
	P3377	49.5 \pm 1.8ab
	P3346	48.3 \pm 1.8ab
	NB742	46.4 \pm 1.8bc
	P3394	43.9 \pm 1.8c

Means within date and column followed by the same letter are not statistically different ($P > 0.05$; Fisher protected LSD test; 10 July: $F = 3.92$; $df = 4, 9$; $P = 0.041$; 12 July: $F = 5.65$; $df = 1, 12$; $P = 0.009$); numbers are averages of 24 sample values.

0.041), and 12 July ($F = 5.65$; $df = 1, 12$; $P = 0.009$) 1996 (Table 2).

Photosynthesis, Experiment 2. Across hybrids, rootworm-infested plants had significantly lower leaf photosynthetic rates than noninfested plants on 11 July ($F = 5.62$; $df = 1, 13$; $P < 0.05$) and 18 July ($F = 6.58$; $df = 1, 15$; $P < 0.05$) 1995 (Fig. 2A), and on 2 July ($F = 5.40$; $df = 1, 15$; $P < 0.05$), and 8 July ($F = 9.5$; $df = 1, 15$; $P < 0.01$) 1996 (Fig. 2B). During each year, there were no significant interactions between hybrid and larval injury on any date. Across infestation levels, leaf photosynthetic rates were not significantly different among hybrids on any date in either year (Urías-López 1998).

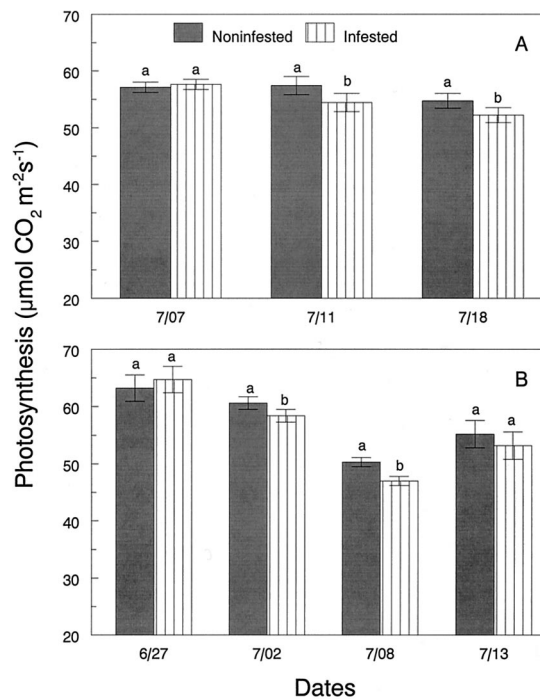


Fig. 2. Photosynthetic rates across hybrids in infested and noninfested plants. Experiment 2 (A) 1995 and (B) 1996

Plant Growth, Experiment 1. In each year, on all sampling dates, plant growth stage was not significantly affected by rootworm treatment, or hybrid by larval injury interaction. However, some hybrids did grow at different rates during each year (Urías-López 1998).

Plant height was affected in a similar way across hybrids in both years (Table 3). During the early rootworm injury period (first and second instar) there were no differences in plant height between infested and noninfested plants. During peak injury (third instar) to postinjury periods, noninfested plants were significantly taller than infested plants across hybrids (Table 3). Height differences occurred among hybrids on most dates; the yellow-dent hybrids were often taller than the white or popcorn hybrid (Urías-López 1998). During each year, the interaction between hybrid and rootworm injury did not significantly affect plant height on any date.

Plant Growth, Experiment 2. In each year, on all sampling dates, plant growth stage was not significantly affected by rootworm treatment, or hybrid by larval injury interaction. All hybrids grew at a similar rate during each year (Urías-López 1998).

Plant height was similar across hybrids in both years (Table 3) and followed the same pattern that was observed in experiment 1. Plant height was not significantly affected by rootworm infestation levels until peak injury occurred (Table 3). On the last two sampling dates each year, an inverse relationship between plant height and root injury level became apparent (Table 3). Differences in plant height occurred among hybrids on most dates each year (Urías-López 1998). However, the interaction between hybrid and rootworm injury did not significantly affect plant height on any date.

Discussion

Western corn rootworm injury reduced single leaf photosynthetic rates across hybrids on selected dates each year (Figs. 1 and 2). Leaf photosynthetic rates were consistent among hybrids in both experiments except for two dates during 1996 in experiment 1 (Table 2). The impact of rootworm injury on photosynthesis also was similar among hybrids as the hybrid by rootworm injury interaction was never significant. These data confirm and expand upon the field studies of Godfrey et al. (1993b) and Hou et al. (1997) who reported a transient reduction in photosynthetic rate in rootworm infested plants of a single hybrid (Pioneer 3377). In the previous work, the reduction in photosynthetic rate occurred primarily during the early larval injury period (predominantly first and second instars present). In our study, which included Pioneer 3377, significant reductions in photosynthetic rate were detected during the early injury period in 1996 (Fig. 1B: 1 July, Fig. 2B: 2 July), but in both years significant reductions also were detected during periods of maximum injury (third-instar to pupal stages) (Figs. 1 and 2A). The reason for this difference is unclear. In our study, fewer measurements were taken

Table 3. Extended leaf height (m) ±SE of plants across hybrids

Year	Infestation level ^a	Date						
		29 June	3 July	7 July	10 July	19 July	31 July	
1995	0	Experiment 1						
		0.94 ± 0.02a	1.12 ± 0.02a	1.33 ± 0.02a	1.53 ± 0.03a	2.02 ± 0.03a	2.42 ± 0.03a	
	1000	0.93 ± 0.02a	1.13 ± 0.02a	1.29 ± 0.02b	1.48 ± 0.03b	1.95 ± 0.03b	2.43 ± 0.03a	
		Experiment 2						
	0	0.91 ± 0.01	1.09 ± 0.02	1.31 ± 0.03	—	2.18 ± 0.03	2.70 ± 0.04	
	200	0.92 ± 0.01	1.09 ± 0.02	1.30 ± 0.03	—	2.11 ± 0.03	2.64 ± 0.04	
	500	0.90 ± 0.01	1.06 ± 0.02	1.29 ± 0.03	—	2.11 ± 0.03	2.62 ± 0.04	
	1000	0.91 ± 0.01	1.07 ± 0.02	1.26 ± 0.03	—	2.09 ± 0.03	2.58 ± 0.04	
	1996	0	Experiment 1					
			29 June	3 July	10 July	17 July	26 July	
0.77 ± 0.01a		1.19 ± 0.01a	1.59 ± 0.01a	2.00 ± 0.02a	2.39 (0.02)a			
1000		0.76 ± 0.01a	1.17 ± 0.01a	1.54 ± 0.01b	1.93 ± 0.02b	2.32 (0.02)b		
Experiment 2								
0		20 June	27 June	5 July	12 July	22 July		
0.54 ± 0.01		0.92 ± 0.02	1.43 ± 0.02	1.89 ± 0.02	2.48 ± 0.03			
200		0.54 ± 0.01	0.92 ± 0.02	1.42 ± 0.02	1.87 ± 0.02	2.45 ± 0.03		
500		0.55 ± 0.01	0.91 ± 0.02	1.42 ± 0.02	1.85 ± 0.02	2.40 ± 0.03		
1000		0.54 ± 0.01	0.91 ± 0.02	1.40 ± 0.02	1.81 ± 0.02	2.39 ± 0.03		

In experiment 1, means within year, experiment, and column followed by the same letter are not statistically different ($P > 0.05$; Fisher protected LSD test; 1995: 7 July $F = 5.07$; $df = 1, 15$; $P < 0.05$; 10 July $F = 9.51$; $df = 1, 15$; $P < 0.01$; and 19 July $F = 6.59$; $df = 1, 15$; $P < 0.05$; 1996: 10 July $F = 9.19$; $df = 1, 15$; $P < 0.01$; 17 July $F = 11.31$; $df = 1, 15$; $P = 0.01$; 26 July $F = 18.42$; $df = 1, 15$; $P < 0.01$). In experiment 2, rootworm injury significantly affected plant height on the last two dates each year (SAS MIXED procedure main effect; 1995: 19 July $F = 3.16$; $df = 3, 45$; $P < 0.05$; 31 July $F = 6.59$; $df = 3, 45$; $P < 0.01$; 1996: 12 July $F = 4.01$; $df = 3, 45$; $P < 0.05$; 22 July $F = 4.34$; $df = 3, 45$; $P < 0.01$). Each number is the average of 60 sample values.

^a Infestation level values are western corn rootworm eggs per 30.5 cm row.

during the first- and second-instar periods than in previous work because of cloudy weather, which may have precluded the measurement of differences that may have existed.

Environmental interactions with rootworm injury may have contributed to significant reductions in photosynthetic rate on selected dates during the period of maximum injury. Hou et al. (1997) and Dunn and Frommelt (1998) in greenhouse studies, documented that interactions between soil moisture level and rootworm injury could affect the photosynthetic rate of maize during maximum larval injury and postinjury periods, respectively. In another greenhouse study, Urías-López (1998) found that leaf-to-air vapor pressure deficit of infested plants was greater than that of noninfested plants when photosynthetic rates were reduced in infested plants.

In our study, heat stress interactions with larval injury may have reduced photosynthetic rates in infested plants on 10, 11, 13, and 18 July 1995, and 18 July 1996 (Figs. 1 and 2A) (maximum temperatures ranged from 32.2 to 39.8°C). On 8, 10, and 12 July 1996, when photosynthetic rates were significantly reduced in infested plants (Figs. 1B and 2B), heat stress was minimal (maximum temperatures ranged from 24.2 to 29.4°C). However, at this time moisture stress may have become an important interactive factor with rootworm injury, because only 5.5 mm rainfall was recorded from 28 June to 12 July. On 15 July 1996, differences in photosynthetic rates between rootworm treatments were not significant (Fig. 1B) even though the maximum temperature reached 32°C. Irrigation after gas exchange measurements completed

on 12 July may have had moderated existing moisture stress, resulting in greater photosynthetic rates across rootworm treatments than recorded on 10 or 12 July (Fig. 1B). This may have also reduced the negative impact of the rootworm-moisture stress interaction. Although the mechanisms driving rootworm-plant interactions are not clearly understood, results from this study and previous work collectively suggest that there may be a common photosynthetic response among maize hybrids to rootworm injury during vegetative growth stages.

Moderate rootworm injury did not significantly affect vegetative growth stage during our study. Godfrey et al. (1993a) also reported that rootworm injury did not affect plant growth stage during the larval period but did record a significant reduction in plant growth of rootworm injured plants after larvae had pupated. Allee and Davis (1996) reported that plant growth stage was not significantly affected by rootworm injury during the early larval period, but growth stage was reduced in rootworm infested versus noninfested plots during and just after the peak damage period. Spike and Tollefson (1989) reported that rootworm injury slowed plant development leading to asynchrony in tassel and silk development that resulted in a greater percentage of barren ears.

In both experiments, rootworm injury consistently resulted in plant height reduction. Although differences in plant height occurred among hybrids (both experiments, Urías-López 1998) all responded in the same general way to rootworm injury. Height of plants was not affected early in the larval injury period but a significant reduction in height of plants occurred during the late

larval and postlarval periods. Data suggest that under low to moderate rootworm injury a lag period occurs from initial reduction in photosynthetic rate before significant differences in plant height may be seen. Godfrey et al. (1993a) also reported a lag period after the initiation of injury at a low infestation level before plant height was significantly reduced. However, when injury was more severe (i.e., >1 node of roots pruned), reduction in height occurred fairly rapidly after initial injury. Allee and Davis (1996) reported a similar trend in that plant height was not affected by rootworm injury when larvae were predominantly second instar, but significant reductions in plant height occurred among rootworm infestation levels during peak and postinjury periods.

In conclusion, results from this study point to a common negative photosynthetic response within diverse maize genotypes to larval injury during vegetative growth stages. Transient reductions in photosynthetic rate occurred in rootworm-infested maize at both low and moderate levels of rootworm injury, which after a lag period led to plant height reduction. The transient nature of the photosynthetic response of maize to rootworm injury during vegetative growth stages and the growing body of evidence that links environmental stress with rootworm injury and leaf gas exchange in maize (i.e., Riedell 1990, Godfrey et al. 1993b, Hou et al. 1997, Dunn and Frommelt 1998b, Urías-López 1998) suggests that the environmental conditions under which gas exchange measurements are recorded may greatly contribute to the variability in plant responses that are measured over time. To more completely understand early season maize physiological responses to larval injury and potential impacts on maize reproductive physiology and yield, additional emphasis needs to be placed on season-long experiments to bridge maize physiological responses during the larval injury period with postinjury biomass partitioning, and to more formally address how environmental conditions influence the maize-rootworm interaction.

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References Cited

- Allee, L. L., and P. M. Davis. 1996. Effect of manure on maize tolerance to western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 89: 1608-1620.
- Apple, J. W., H. C. Chiang, L. M. English, L. J. French, A. J. Keaster, G. F. Krause, Z. B. Mayo, J. D. Munson, G. J. Musick, J. C. Owens, and others. 1977. Impact of northern and western corn rootworm larvae on field corn. North Central Research Publication 239. University of Wisconsin, Madison.
- Bergman, M. K., J. J. Tollefson, and P. N. Hinz. 1981. Sampling scheme for estimating populations of corn rootworm larvae. *Environ. Entomol.* 10: 986-990.
- Branson, T. F. 1986. Larval feeding behavior and host-plant resistance in maize, pp. 159-182. *In* J. L. Krysan and T. A. Miller [eds.], *Methods for study of pest Diabrotica*. Springer, New York.
- Chiang, H. C. 1973. Bionomics of the northern and western corn rootworm. *Annu. Rev. Entomol.* 18: 47-72.
- Dunn, J. P., and K. Frommelt. 1998a. Effects of below-ground herbivory by *Diabrotica virgifera virgifera* (Coleoptera) on biomass allocation and carbohydrate storage of maize. *Appl. Soil Ecol.* 7: 213-218.
- Dunn, J. P., and K. Frommelt. 1998b. Effects of below-ground herbivory by *Diabrotica virgifera virgifera* (Col., Chrysomelidae) and soil moisture on leaf gas exchange of maize. *J. Appl. Entomol.* 122: 179-183.
- Gavloski, J. E., G. H. Whitfield, and C. R. Ellis. 1992. Effect of larvae of western corn rootworm (Coleoptera: Chrysomelidae) and of mechanical root pruning on sap flow and growth of corn. *J. Econ. Entomol.* 85: 1434-1441.
- Godfrey, L. D., L. J. Meinke, and R. J. Wright. 1993a. Vegetative and reproductive biomass accumulation in field corn: response to root injury by western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 86: 1557-1573.
- Godfrey, L. D., L. J. Meinke, and R. J. Wright. 1993b. Affects of larval injury by western corn rootworm (Coleoptera: Chrysomelidae) on gas exchange parameters of field corn. *J. Econ. Entomol.* 86: 1546-1556.
- Gray, M. E., and K. L. Steffey. 1998. Corn rootworm (Coleoptera: Chrysomelidae) larval injury and root compensation of 12 maize hybrids: an assessment of the economic injury index. *J. Econ. Entomol.* 91: 723-740.
- Hein, G. L., M. K. Bergman, R. G. Bruss, and J. J. Tollefson. 1985. Absolute sampling technique for corn rootworm (Coleoptera: Chrysomelidae) adult emergence that adjusts to fit common row spacing. *J. Econ. Entomol.* 78: 1503-1506.
- Hills, T. M., and D. C. Peters. 1971. A method of evaluating postplanting insecticide treatments for control of western corn rootworm larvae. *J. Econ. Entomol.* 64: 764-765.
- Hou, X., L. J. Meinke, and T. J. Arkebauer. 1997. Soil moisture and larval western corn rootworm injury: influence on gas exchange parameters. *Agron. J.* 89: 709-717.
- Kahler, A. L., A. E. Olnes, G. R. Sutter, C. D. Dybing, and O. J. Devine. 1985. Root damage by western corn rootworm and nutrient content in maize. *Agronomy J.* 77: 769-774.
- Mayo, Z. B. 1986. Field evaluation of insecticides, pp. 183-203. *In* J. L. Krysan and T. A. Miller [eds.], *Methods for the study of pest Diabrotica*. Springer, New York.
- Owens, J. C., D. C. Peters, and A. R. Hallauer. 1974. Corn rootworm tolerance in maize. *Environ. Entomol.* 3: 767-772.
- Riedell, W. E. 1990. Rootworm and mechanical damage effects on root morphology and water relations in maize. *Crop Sci.* 30: 628-631.
- Riedell, W. E., and A. Y. Kim. 1990. Anatomical characterization of western corn rootworm damage in adventitious roots of maize. *J. Iowa Acad. Sci.* 97: 15-17.

- Riedell, W. E., R. D. Gustin, and D. L. Beck. 1992. Effect of irrigation on root growth and yield of plants damaged by western corn rootworm. *Maydica* 37: 143–148.
- Ritchie, S. W., J. J. Hanway, and G. O. Benson. 1997. How a corn plant develops. Iowa Coop. Ext. Serv. Spec. Rep. 48.
- Roth, G. W., D. D. Calvin, and S. M. Lueloff. 1995. Tillage, nitrogen timing, and planting date effects on western corn rootworm injury to corn. *Agron. J.* 87: 189–193.
- SAS Institute. 1985. SAS user's guide: statistics. SAS Institute, Cary, NC.
- Schaafsma, A. W., G. H. Whitfield, T. A. Gillespie, and C. R. Ellis. 1993. Evaluation of infrared thermometry as a non-destructive method to detect feeding on corn roots by the western corn rootworm (Coleoptera: Chrysomelidae). *Can. Entomol.* 125: 643–655.
- Spike, B. P., and J. J. Tollefson. 1989. Relationship of plant phenology to corn yield loss resulting from western corn rootworm (Coleoptera: Chrysomelidae) larval injury, nitrogen deficiency, and high plant density. *J. Econ. Entomol.* 82: 229–231.
- Spike, B. P., and J. J. Tollefson. 1991. Yield response of corn subjected to western corn rootworm (Coleoptera: Chrysomelidae) infestation and lodging. *J. Econ. Entomol.* 84: 1585–1590.
- Sutter, G. R., and T. F. Branson. 1986. Artificial infestation of field plots, pp. 147–157. In J. L. Krysan and T. A. Miller [eds.], *Methods for the study of pest Diabrotica*. Springer, New York.
- Sutter, G. R., J. R. Fisher, N. C. Elliott, and T. F. Branson. 1990. Effect of insecticide treatments on root lodging and yields of maize in controlled infestations of western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol.* 83: 2414–2420.
- Turpin, F. T., L. C. Dumenil, and D. C. Peters. 1972. Edaphic and agronomic characteristics that affect potential for rootworm damage to corn in Iowa. *J. Econ. Entomol.* 65: 1615–1619.
- Urías-López, M. A. 1998. Physiological and yield responses of different types of maize to western corn rootworm larval injury. Ph.D. dissertation, University of Nebraska, Lincoln.

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