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# Affects of Larval Injury by Western Corn Rootworm (Coleoptera: Chrysomelidae) on Gas Exchange Parameters of Field Corn

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J. Econ. Entomol. 86(5): 1546-1556 (1993)

**ABSTRACT** The effect of larval-induced root injury by western corn rootworm, *Diabrotica virgifera virgifera* LeConte, on plant physiological parameters of field corn (*Zea mays* L.) was examined in a 2-yr field study. Controlled infestations of 200, 500, and 1,000 eggs per 30.5 row-cm were established in an irrigated, silty clay loam soil in 1989 and in silty clay loam, loam, and sandy loam soil textures with irrigated and dryland treatments in 1990. Infestations were made 16 d after planting and at planting in 1989 and 1990, respectively. Gas exchange parameters were examined before egg hatch, during the injury period, and ≈2 wk following the cessation of the injury. During both years, corn photosynthetic rates at full sunlight were reduced by an average of 7.9% coinciding with the initial period of larval injury; i.e., feeding by primarily first and second instars. During the periods of maximum injury and postinjury, western corn rootworm injury to corn roots resulted in either no significant effect on photosynthetic rate (1990) or in an apparent stimulatory effect (by up to 11.2%) on photosynthetic rate (1989). The photosynthesis effects were not consistently related to changes in stomatal conductance or intercellular CO<sub>2</sub> concentration. Plant response to root injury was similar in all three soil textures and in differing soil moisture levels (occurring during postinjury period only) in 1990; however, soil texture and soil moisture did have significant direct effects on plant physiology. Plant developmental stage at the time of injury may be an important factor in determining the plant response to injury. Peak injury occurred in the V12-V15 and V9-V11 stages of development in 1989 and 1990, respectively. The increased amount of photosynthetically active biomass (i.e., leaf tissue) may have enhanced the plants' compensatory response in 1989.

**KEY WORDS** *Diabrotica virgifera virgifera*, corn, photosynthesis

THE WESTERN CORN ROOTWORM, *Diabrotica virgifera virgifera* LeConte, is a serious insect pest of field corn, *Zea mays* L., in much of the United States. This pest is part of the *Diabrotica* complex which accounts for crop losses and control costs estimated at \$1 billion annually (Metcalfe 1986). The most substantial plant damage is inflicted by the larvae, which feed almost exclusively on corn roots (Branson & Ortman 1970). This injury has been shown to reduce corn grain yield (Turpin et al. 1972, Sutter et al. 1990) and vegetative yield (Spike & Tollefson 1991), to increase plant lodging (plants leaning more than 30° from vertical) (Sutter et al. 1990), and to alter the nutrient content of the grain (Kahler et al. 1985).

Neonate western corn rootworm larvae feed on root hairs and on outer cortical tissue (Chiang 1973). In a laboratory study, Riedell & Kim (1990) showed that second and third instars fed

primarily on the cortex tissues of excised root sections. Third instars did not damage the vascular system; it was hypothesized that the endodermis acted as a barrier to entry into the stele. However, in the field, western corn rootworm larvae not only tunnel roots but also prune roots; i.e., completely destroy root sections (Branson 1986, Riedell 1990). Root pruning may result from larvae that enter the stele at the root tip of intact plants or from deterioration of injured roots by root rot pathogens (Palmer & Kommedahl 1969).

Although western corn rootworm injury has been shown to detrimentally affect corn plant productivity, effects of western corn rootworm larval injury on corn plant physiology, primarily photosynthesis, have not been characterized. Several researchers (e.g., Pedigo et al. 1986) have identified host plant physiological response to arthropod injury as an area needing expanded research efforts. Information in this area will be useful for refinement of economic thresholds, for devising predictive models of pest interactions, and possibly for designing alternative control strategies. The effects of leaf tissue destruction

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(defoliation and mesophyll injury) comprise the majority of all studies conducted on plant physiological response to arthropod-induced injury with 29 and 27 studies, respectively (Welter 1989). Results with mesophyll feeders have shown consistent reductions in photosynthetic rates, whereas studies with defoliators have shown a variable response. The effects of indirect plant injury from arthropods (i.e., injury to tissues other than the photosynthetically active tissues) on plant gas exchange are poorly understood because studies in this area are extremely limited. Welter (1989) cited only two studies on the effects of stem tunneling on plant physiology (injury to dogwood by *Thamnosphexia scitula* [Harris], [Heichel & Turner 1973] and injury by *Sirex noctilio* F. to Monterey pine [Madden 1977]). Godfrey et al. (1991) showed that stem tunneling by European corn borer, *Ostrinia nubilalis* Hübner, significantly reduced corn photosynthetic rates by an average of 16.9% for a manually established infestation of five larvae per plant. Other effects of the tunneling were decreased stomatal conductances, decreased intercellular CO<sub>2</sub> concentrations, and increased leaf temperatures. The insect-plant synchrony (plant growth stage at the time of injury) and length of time after the injury was shown to influence the interaction.

Studies on the influence of root injury, another form of indirect plant injury, on plant physiology are also limited. Detling et al. (1980) reported on the effects of root injury (simulated damage) to blue gramma. In addition, Kramer & Kozlowski (1979) reported, from simulated root damage to apple trees, an initial decline in photosynthesis followed by significantly higher assimilation rates compared with undamaged plants. Riedell (1990) found, in a greenhouse study, that feeding by 50 and 150 western corn rootworm larvae (second and third instars) did not significantly affect leaf water potential or stomatal conductance of V9 stage corn (Ritchie et al. 1986) at 12 d after infestation. However, on VT stage corn, western corn rootworm-injured plants had lower stomatal conductance and higher leaf water potential values than uninjured plants. Western corn rootworm injury had minimal effects on the plant compared with a treatment that removed 75% of the root tissue from the plant.

Corn roots serve many significant roles in corn plant growth and development. In addition to anchorage of the plant in the soil, roots function in absorbance of water and nutrients from the soil and subsequent conductance into the shoots. Roots also function in the synthesis of numerous plant hormones such as cytokinins and gibberellins which are critical for normal plant functioning (Skene 1975, Rendig & Taylor 1989). Altered plant hormone levels may upset plant photosynthesis and development as detailed by Chapin (1991). In addition, roots may "communicate"

with and exert control over shoots (through plant hormones) during periods of stress (Blackman & Davies 1985). Several researchers have theorized that root injury by western corn rootworm reduces water conductance from the soil and that this effect magnifies yield losses during soil water deficit conditions (Owens et al. 1974, Branson et al. 1980). The objectives of our study were to characterize the effect of western corn rootworm larval injury on corn gas exchange parameters and to examine the potential interactions of larval-induced root injury with soil texture and moisture on these plant physiological parameters.

### Materials and Methods

Research was conducted at the University of Nebraska Agricultural Research and Development Center near Mead, NE, in 1989 and 1990. Corn, 'Pioneer 3377', was planted on 24 May 1989 and on 6 May 1990. The seeding rate was 60,500 kernels per ha in 76.2-cm (center to center) rows.

In 1989, plots were located on a silty clay loam soil with overhead sprinkler irrigation. The fertilization and herbicide regimes used were anhydrous ammonia (applied on 13 April 1989) at 112 kg/ha nitrogen and atrazine (applied preemergence) at 3.36 kg (AI)/ha, respectively. Western corn rootworm eggs were infested at 200, 500, and 1,000 eggs per 30.5 row-cm. Western corn rootworm eggs, suspended in 0.125% agar water, were manually infested in the soil by excavating a trench (7.6 cm deep) in the soil (6 cm from the seed furrow), trickling the egg suspension into this trench, and then covering the trench with moist soil. The egg concentration was varied in the suspensions to obtain various infestation densities. This procedure was a modification of that developed by Sutter & Branson (1986). Plots were infested on 9 June 1989 when the corn was in the V2-V3 growth stage (Ritchie et al. 1986). The soil at this time was moist from 2.6 cm of rain during 2 d before to 2 d after the infestation. Field corn had been grown in this plot area the previous year and a slight background western corn rootworm egg infestation ( $2.5 \pm 1.6$  eggs per 0.5 liter soil) was present (egg infestation was determined with soil core samples to a depth of 7.6 cm taken in the fall of 1988 and processed following the methods of Shaw et al. [1976]). Therefore, a fonofos treatment (112 g [AI]/1,000 row-m) was also included to quantify any confounding effects from native western corn rootworm larvae. The soil insecticide was applied with a hand-operated applicator mounted on bicycle wheels equipped with a Noble metering unit (Mayo 1986) and incorporated into the soil with a rake. Godfrey & Holtzer (1992) showed that fonofos had minimal direct effects on corn photosynthesis. Including the uninfested treatment, five treatments were used in 1989.

Treatments were replicated four times in a randomized complete-block design. Within each of the four blocks, each treatment was placed in two adjacent rows (9.1 m long) with at least one untreated row between each treatment.

In 1990, soil texture (three levels) and soil moisture (two levels) were included as independent variables, in addition to the western corn rootworm egg density. Studies were conducted in a series of plots established in November 1989 within an area fallowed the previous year. The native soil (a silty clay loam) was removed to a depth of 0.46 m. A specified soil texture was then placed in each plot (6.1 by 12.2 m) to the previous soil surface level. Each plot was surrounded by a 6.1-m border of undisturbed soil. Soil textures used (and percentages of sand, silt, and clay as determined by gravimetric analysis) were a silty clay loam; i.e., the native soil (8.0% sand, 63.6% silt, and 28.4% clay), a loam (34.4% sand, 44.0% silt, and 21.7% clay), and a sandy loam (75.6% sand, 14.6% silt, and 9.7% clay). Each soil texture was represented once in each of four blocks. Two soil moisture treatments, dryland (i.e., only natural precipitation) and furrow irrigation, were established in 3.05-m-wide subplots (four corn rows) of each soil texture main plot. Western corn rootworm eggs were infested using a modification of the pressurized tractor-mounted mechanical technique of Sutter & Branson (1986). Infestation densities were 200, 500, and 1,000 eggs per 30.5 row-cm in addition to an uninfested treatment. The egg infestation densities were randomly assigned within each soil moisture subplot. Thus, the experimental design was a split split-plot with the soil textures forming the main plots, soil moisture comprising the subplots, and egg infestation level forming the sub-subplots. Atrazine (3.36 kg [AI]/ha) was applied to all plots before planting. The fertilization program was designed to provide adequate fertilization to all treatments and was based on interpretation of soil nutrient analysis of each soil texture (Wiese & Penas 1979). A yield goal of 11,300 kg/ha was used for quantification of nitrogen requirements. This resulted in nitrogen fertilization rates of 56.0, 224.1, and 246.5 kg/ha for the silty clay loam, loam, and sandy loam treatments, respectively. The nitrogen in the loam and sandy loam soil textures was split evenly into an application at planting and on 16 June.

During both 1989 and 1990, irrigation and precipitation amounts were recorded. In addition, western corn rootworm larval density and root damage were estimated at about weekly intervals following the initiation of egg hatch until pupation (Godfrey et al. 1993). Larval density was estimated from 15.2-cm soil cube samples using the methods of Bergman et al. (1981). In addition, larvae were forced from corn roots by suspending root systems over water in the presence of heat. Root damage was evaluated during

the early stages of larval feeding (7 July 1989 and 18 and 25 June 1990) by calculating the percentage of nodal roots with corn rootworm larval feeding scars (number of damaged roots per total number of roots). During and after periods of peak damage (14 and 26 July 1989 and 2 and 16 July 1990), root injury was rated on a 1–6 scale in 1989 (Hills & Peters 1971) and on a 1–9 scale in 1990 (Musick & Suttle 1972). Two samples (larval and root) were examined per block per treatment combination for each sampling period. Sample dates in 1989 are somewhat later than those expected with a natural western corn rootworm population because the infestation was not established until 16 d after planting, and the planting date was relatively late compared with common agronomic practices in the area. Sample dates in 1990 were typical for the corn–corn rootworm system in Nebraska.

In 1990, percentage soil moisture was evaluated in all plots with soil core samples at 7.6, 15.0, and 30.0 cm on 20 June, 28 June (before irrigation), and 9 July (after irrigation). Wet weights and dry weights (following drying for 48 h at 60°C) were recorded. In addition, soil water potential at a 15-cm depth was monitored in one block of the sandy loam and loam soils (irrigated and without irrigation treatments) from 13 June to 3 August. Potential was measured with gypsum soil moisture blocks (Model 221 Delmhorst; Campbell Scientific, Logan, UT) and recorded with a data logger (Model CR-21; Campbell Scientific).

Corn plant physiological parameters were monitored with a LI-6200 portable photosynthesis system (LI-COR, Lincoln, NE). Upon enclosure of a fully illuminated (by solar radiation) corn leaf in the 1.0-liter Lexan (General Electric, Chicago, IL) leaf chamber, the system monitored the changes in CO<sub>2</sub> and water vapor concentrations within the chamber over about a 30-s period. Using the recorded air temperature and leaf temperature, the instrument calculated and recorded plant photosynthetic rate, stomatal conductance, and intercellular CO<sub>2</sub> concentration. Gas exchange measurements were made on three plants per treatment combination (between 1100 and 1500 hours CDT) before the initiation of western corn rootworm feeding (1990 only), at about weekly intervals during the injury period, and at 2 wk following the injury. In 1989, measurements were made on 5 July (26 d after egg infestation), 12 July, 20 July, 1 August, and 11 August. Gas exchange measurements were evaluated on 7 June (6 d after egg infestation), 15 June, 21 June, 28 June, and 14 July in 1990.

**Statistical Analysis.** Response variables were analyzed with analysis of variance (ANOVA) (SAS Institute 1985) using the appropriate statistical model (randomized complete-block design in 1989 and split-plot design in 1990 [split split-plot design for 14 July 1990 sampling date with

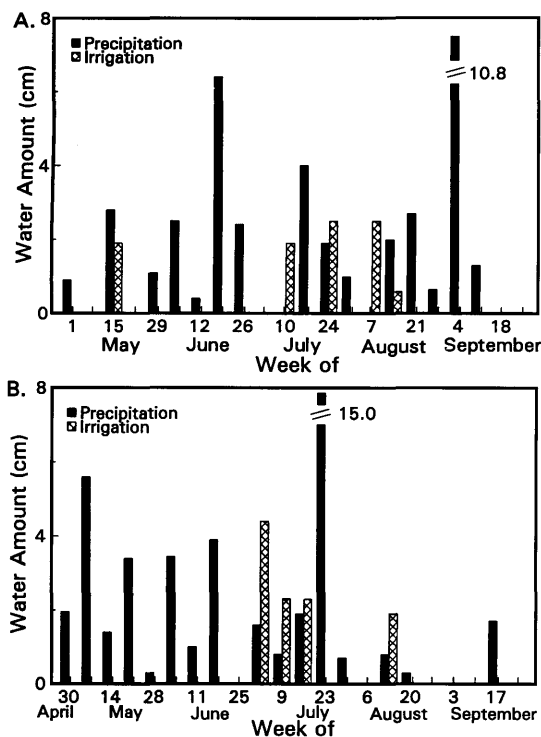


Fig. 1. Precipitation and irrigation totals. (A) 1989. (B) 1990.

the addition of soil moisture parameter]). Least significant differences test was used to separate means.

### Results

In 1989, moisture stress was limited because either precipitation or irrigation, usually exceeding 1.9 cm, occurred almost weekly (Fig. 1A). Some transient drought stress existed between 30 June and 15 July and between 25 July and 19 August. Irrigations on 10 July and on 28 July helped to alleviate the stress, but during periods of peak evapotranspiration some moisture deficit conditions existed.

In 1990, irrigation (averaging 2.3 cm) was provided on 2, 5, 11 and, 18 July and 16 August (Fig. 1B). Precipitation was limited during July, August, and September with the exception of a 15.0-cm rainfall on 25 July. Percentage soil moisture averaged 17.7, 15.0, and 9.3% in the silty clay loam, loam, and sandy loam soils on 20 June and 11.0, 7.8, and 6.7% in the silty clay loam, loam, and sandy loam soils on 28 June, respectively. On 9 July (4 d after the second irrigation), soil moisture was  $\approx 2\%$  higher in irrigated than in dryland treatments in the silty clay loam and loam soils and was similar between the two treatments in the sandy loam soil. Soil water potential was much lower in the nonirrigated treatment

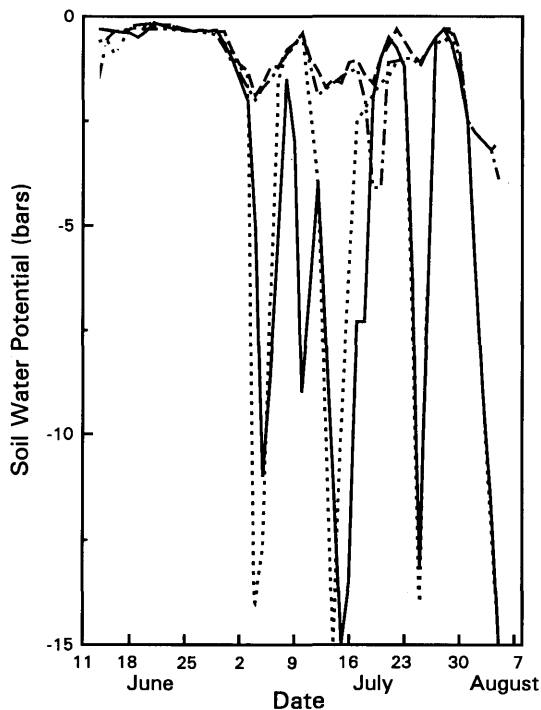


Fig. 2. Soil water potential (bars) in 1990; —, loam soil, dryland; ---, loam soil, irrigated; ····, sandy loam soil, dryland; — · —, sandy loam soil, irrigated.

compared with the irrigated treatment (Fig. 2). Water potential from 13 June to 2 July averaged  $-0.34$  bars in both treatments. From 2 July to 3 August, potential in the irrigated treatment was generally  $> -2$  bars. In the non-irrigated treatment, the water potential was  $< -5$  bars during much of this period and was at or near the permanent wilting point for 4 d; these deficit soil moisture conditions were clearly exhibited by the corn plants. The irrigated and nonirrigated treatments are referred to as irrigated and dryland, respectively.

Complete data on larval density and root damage at each sampling date are presented by Godfrey et al. (1993). In summary, in 1989, larval densities averaged 2.1, 2.5, 7.6, 13.2, and 16.6 per 15.2-cm soil cube for the insecticide-treated, uninfested, 200, 500, and 1,000 eggs per 30.5-row-cm treatments, respectively. Root damage ratings (1–6 scale) averaged 2.0 (insecticide-treated), 2.0 (uninfested), 2.2 (200 eggs per 30.5 row-cm), 2.6 (500 eggs per 30.5 row-cm), and 3.3 (1,000 eggs per 30.5 row-cm). Larval population densities in 1990 were similar to those seen in 1989. Averaged across the soil texture and moisture treatments, densities were 1.0, 5.2, 13.5, and 14.8 larvae per 15.2-cm soil cube for the uninfested, 200, 500, and 1,000 eggs per 30.5-row-cm treatments, respectively. No significant differ-

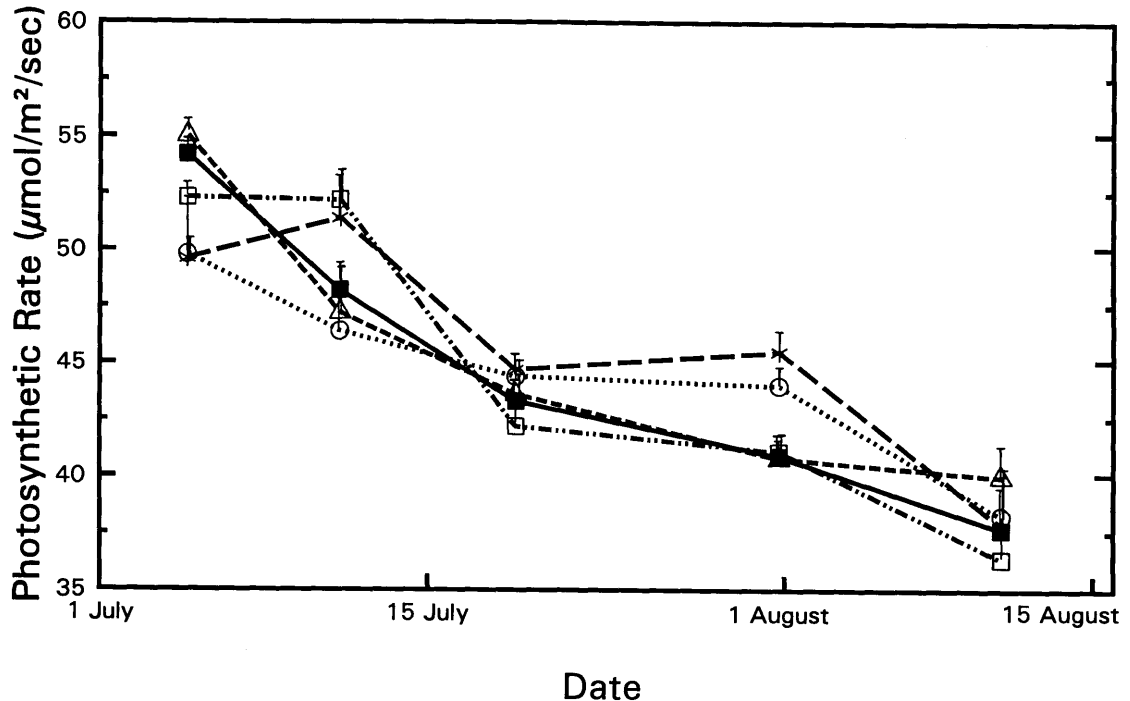


Fig. 3. Influence of western corn rootworm density on corn photosynthetic rates in 1989 (mean  $\pm$  SEM);  $\blacksquare$ , uninfested;  $\blacktriangle$ , 200 eggs per 30.5 row-cm;  $\ominus$ , 500 eggs per 30.5 row-cm;  $-\cdot-\cdot-$ , 1,000 eggs per 30.5 row-cm;  $\square$ , insecticide-treated.

ences were noted among the soil textures. Root damage ratings (1–9 scale) averaged 2.0 (uninfested), 2.6 (200 eggs per 30.5 row-cm), 5.6 (500 eggs per 30.5 row-cm), and 6.5 (1,000 eggs per 30.5 row-cm).

**Gas Exchange Parameters, 1989.** Plant development of uninfested plants (based on Ritchie et al. [1986]) on the date coinciding with quantification of gas exchange parameters was V10 (5 July), V12 (12 July), V15 (20 July), V18 (1 August), and VT (11 August) in 1989. The initial evaluation was done 26 d after the western corn rootworm egg infestation. Larval development at this time (as represented by samples taken on 7 July) was 21.4% first instar, 21.4% second instar, 46.0% third instar, and 11.3% pupae and, on 14 July, the development was 0.0% first instar, 9.6% second instar, 69.1% third instar, and 19.8% pupae. Maximum injury occurred near 20 July, thus the latter two samples represent a period of time following western corn rootworm injury; i.e., plant recovery phase.

Corn photosynthetic rates were significantly affected by western corn rootworm larval injury on 5 July ( $F = 3.91$ ;  $df = 4, 12$ ;  $P < 0.05$ ), 12 July ( $F = 4.25$ ;  $df = 4, 12$ ;  $P < 0.05$ ), and on 1 August ( $F = 4.94$ ;  $df = 4, 12$ ;  $P < 0.05$ ). The block effect was not significant for any date. Plants stressed by larval infestations resulting from the 500 and 1,000 eggs per 30.5-row-cm treatments had significantly reduced photosynthetic rates (on 5

July) compared with plants from the uninfested treatment (Fig. 3). However, during the period of peak injury on 12 July, plants with root injury from the highest infestation rate and plants from the fonofos treatment had significantly higher photosynthetic rates (by 6.2% and 8.3%, respectively) than uninjured plants. Photosynthetic rates did not differ significantly among the five treatments on 20 July; however, on 1 August, plants injured by the high infestation rate again had significantly higher photosynthetic rates than the uninfested, insecticide-treated, and 200 eggs per 30.5-row-cm treatments. Rates of plants from the 500 eggs per 30.5 row-cm were intermediate. No significant differences in photosynthetic rates were found among treatments on the last sampling date (11 August).

Stomatal conductance also responded to western corn rootworm-induced root injury (Table 1). Significant effects were seen on 12 July ( $F = 5.21$ ;  $df = 4, 12$ ;  $P < 0.05$ ) and on 11 August ( $F = 4.15$ ;  $df = 4, 12$ ;  $P < 0.05$ ). The block effect was not significant. On 5 July, no significant differences were seen in stomatal conductance values among the treatments; however, as with the photosynthetic rate, plants from the two highest western corn rootworm levels tended to have the lowest conductance values. On the second sampling date (12 July), stomatal conductance values associated with the insecticide and 200 eggs per 30.5-row-cm treatments differed significantly

**Table 1. Gas exchange parameter means ( $\pm$  SEM) for stomatal conductance, intercellular CO<sub>2</sub> concentration, and leaf temperature parameters in 1989**

Infestation level	Stomatal conductance, mol/m <sup>2</sup> /s	Leaf temp, °C	Intercellular CO <sub>2</sub> concn, ppm
5 July			
Uninfested	0.62 (0.05)a	35.8 (0.5)a	113.2 (6.6)a
Insecticide-Trt.	0.58 (0.11)a	36.2 (0.4)a	103.9 (10.9)a
200 eggs <sup>a</sup>	0.64 (0.03)a	35.0 (0.1)a	116.7 (4.4)a
500 eggs	0.53 (0.05)a	35.6 (0.3)a	101.5 (7.9)a
1,000 eggs	0.52 (0.03)a	35.6 (0.4)a	100.7 (5.6)a
12 July			
Uninfested	0.48 (0.03)ab	35.5 (0.2)a	117.1 (6.9)ab
Insecticide-Trt.	0.55 (0.03)a	35.5 (0.3)a	127.2 (6.9)ab
200 eggs	0.52 (0.04)a	35.4 (0.2)a	131.7 (11.6)a
500 eggs	0.43 (0.03)b	35.9 (0.2)a	104.1 (6.8)b
1,000 eggs	0.49 (0.04)ab	35.4 (0.3)a	113.2 (7.9)b
20 July			
Uninfested	0.43 (0.03)a	30.4 (0.4)a	107.1 (6.3)a
Insecticide-Trt.	0.42 (0.02)a	30.6 (0.3)a	105.1 (5.9)a
200 eggs	0.45 (0.02)a	30.4 (0.2)a	104.7 (5.2)a
500 eggs	0.46 (0.03)a	30.5 (0.4)a	105.3 (6.7)a
1,000 eggs	0.53 (0.01)a	30.7 (0.4)a	120.1 (3.0)a
1 Aug.			
Uninfested	0.43 (0.03)a	34.4 (0.3)b	96.9 (16.7)a
Insecticide-Trt.	0.39 (0.07)a	34.7 (0.7)ab	84.5 (1.4)a
200 eggs	0.48 (0.02)a	33.9 (0.6)b	105.5 (19.5)a
500 eggs	0.45 (0.05)a	35.6 (1.0)a	104.2 (34.2)a
1,000 eggs	0.47 (0.07)a	35.6 (0.3)a	109.3 (16.7)a
11 Aug.			
Uninfested	0.27 (0.01)b	31.5 (0.7)a	87.3 (6.3)a
Insecticide-Trt.	0.32 (0.02)ab	31.5 (0.5)a	93.1 (5.1)a
200 eggs	0.37 (0.03)a	31.8 (0.5)a	97.5 (6.5)a
500 eggs	0.28 (0.03)b	31.8 (0.8)a	94.6 (5.4)a
1,000 eggs	0.28 (0.03)b	32.0 (0.6)a	86.7 (11.6)a

For each sample date, means within columns followed by the same letter are not significantly different ( $P < 0.05$ ; LSD; SAS Institute [1985]).

<sup>a</sup> No. eggs per 30.5 row-cm.

from the 500 eggs per 30.5-row-cm treatment. A concomitant increase in stomatal conductance was not associated with the increase in photosynthetic rate, which was noted for the 1,000 eggs per 30.5-row-cm treatment. No significant differences were seen in stomatal conductance among the five treatments on the 20 July and 1 August sampling dates. Again, the apparent overcompensatory response seen in photosynthetic rate of plants injured by the highest western corn rootworm infestation rate was accompanied by only a slightly increasing trend in stomatal conductance. On the last sampling date, stomatal conductance values of plants injured by the lowest infestation rate were significantly higher than that of plants from the uninfested, 500, and 1,000 eggs per 30.5-row-cm treatments.

Leaf temperature was significantly affected by the western corn rootworm treatments only on 1 August ( $F = 3.56$ ;  $df = 4, 12$ ;  $P < 0.05$ ). The leaf temperature of plants stressed by larvae from the two highest infestation rates was significantly

higher than plants from the uninfested and 200 eggs per 30.5 row-cm treatments (Table 1). In addition, the block effect was significant on 5 July ( $F = 3.90$ ;  $df = 3, 12$ ;  $P < 0.05$ ), 20 July ( $F = 36.28$ ;  $df = 3, 12$ ;  $P < 0.05$ ), and 11 August ( $F = 13.05$ ;  $df = 3, 12$ ;  $P < 0.05$ ). A 3°C range of leaf temperatures was seen over the four blocks. This difference probably occurred because of the time required to sample the four blocks and the resulting diurnal temperature cycle.

Intercellular CO<sub>2</sub> concentration was significantly affected only on 12 July by the western corn rootworm infestations ( $F = 3.85$ ;  $df = 4, 12$ ;  $P < 0.05$ ); plants stressed by the 500 and 1,000 eggs per 30.5-row-cm treatments averaged 108.6 ppm, which differed significantly from those of the 200 eggs per 30.5-row-cm treatment (Table 1). No significant differences were found among the western corn rootworm treatments on the other sampling dates or from the block effect.

**Gas Exchange Parameters, 1990.** Corn plant development in the uninfested treatment, coinciding with gas exchange evaluations in 1990, was V5 (on 8 June), V7 (on 15 June), V9 (on 22 June), V11 (on 30 June), and V15 (on 14 July). Development in infested treatments was slightly delayed (Godfrey et al. 1993). The first evaluation was before western corn rootworm egg hatch, whereas western corn rootworms were primarily first and second instars (28.2% first, 52.9% second, and 18.8% third instar) at the 15 June evaluation (as indicated by larval sampling on 18 June), second and third instars (3.1% first, 36.7% second, 60.2% third instar, and 0.2% pupae) at the 22 June evaluation (as indicated by larval sampling on 25 June), and third instars and pupae (0.0% first, 7.4% second, 62.0% third instar, and 30.7% pupae) at the 30 June evaluation (as indicated by larval sampling on 2 July). The final evaluation corresponded with the period after injury; i.e., pupation.

At the first evaluation, corn photosynthetic rates did not differ significantly among the three soil textures and averaged 27.7  $\mu\text{mol}/\text{m}^2/\text{s}$  (Fig. 4). Trends in photosynthetic rates were found during the subsequent three sampling periods, and significant differences were found among the soil texture treatments on 15 June ( $F = 5.25$ ;  $df = 2, 6$ ;  $P < 0.05$ ) and on 30 June ( $F = 5.81$ ;  $df = 2, 6$ ;  $P < 0.05$ ). In all cases, rates were lower (by an average of 16.5%) from plants in the sandy loam soil compared with the other two soil textures. No significant differences were identified on the final sampling date, 14 July.

Stress from western corn rootworm larval injury significantly reduced corn photosynthetic rates on 22 June ( $F = 3.50$ ;  $df = 3, 16$ ;  $P < 0.05$ ) (Fig. 5). Photosynthetic rates from plants in all three infestations rates were reduced compared with the untreated. Similar trends were seen on 15 June; however, the differences were not significant. These dates corresponded with the ini-

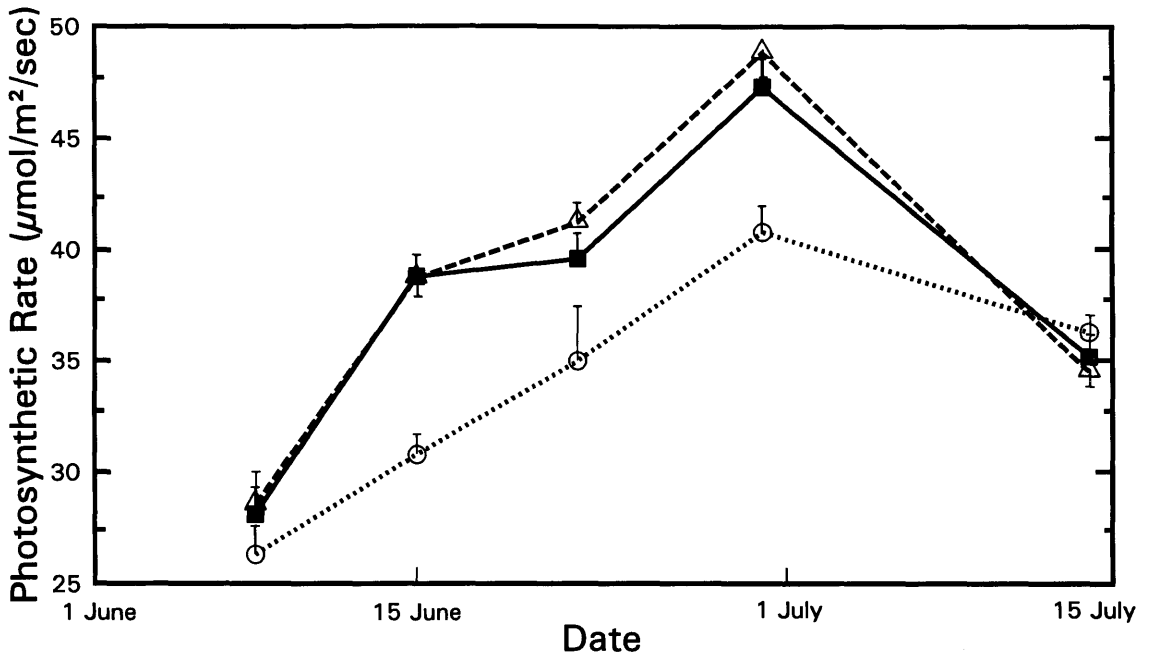


Fig. 4. Influence of soil texture on corn photosynthetic rates in 1990 (mean  $\pm$  SEM);  $\blacksquare$ , silty clay loam soil;  $\blacktriangle$ , loam soil;  $\ominus$ , sandy loam soil.

tial to peak stages of larval-induced injury. The 1,000 eggs per 30.5-row-cm infestation had the most severe effects on photosynthesis; however,

the differences were not as great as that seen from the soil texture main effect. Photosynthetic rate reductions of 6.9 and 7.0% were seen in

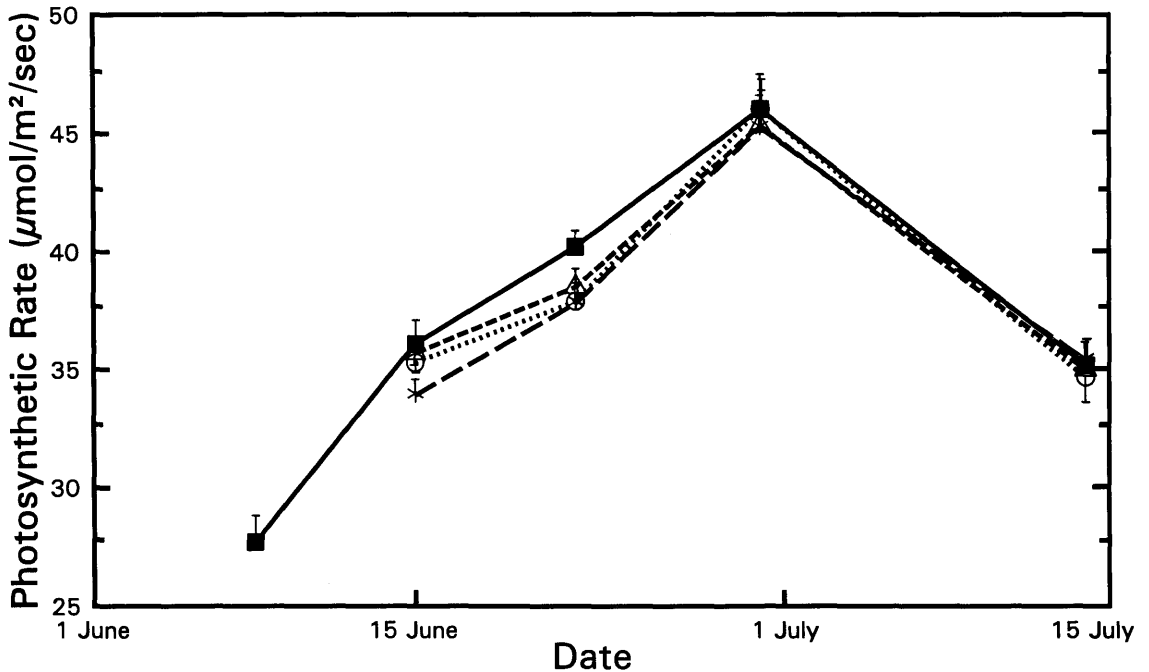


Fig. 5. Influence of western corn rootworm density on corn photosynthetic rates in 1990 (mean  $\pm$  SEM);  $\blacksquare$ , uninfested;  $\blacktriangle$ , 200 eggs per 30.5 row-cm;  $\ominus$ , 500 eggs per 30.5 row-cm;  $-\ast-, 1000 eggs per 30.5 row-cm.$



**Table 2. Gas exchange parameter means ( $\pm$  SEM) for stomatal conductance, intercellular CO<sub>2</sub> concentration, and leaf temperature parameters in 1990**

Soil texture	Stomatal conductance, mol/m <sup>2</sup> /s	Leaf temp, °C	Intercellular CO <sub>2</sub> concn, ppm
8 June			
Silty clay loam	0.24 (0.01)a	32.4 (0.8)a	126.2 (6.3)a
Loam	0.26 (0.01)a	31.8 (0.7)a	137.5 (9.1)a
Sandy loam	0.24 (0.01)a	32.8 (0.8)a	133.8 (6.4)a
15 June			
Silty clay loam	0.40 (0.01)a	33.1 (0.2)a	117.6 (4.4)b
Loam	0.39 (0.01)a	33.4 (0.2)a	110.7 (3.6)b
Sandy loam	0.34 (0.01)b	34.2 (0.3)a	132.7 (4.2)a
22 June			
Silty clay loam	0.37 (0.01)a	28.4 (0.2)a	96.4 (2.3)a
Loam	0.39 (0.01)a	28.2 (0.2)a	99.2 (2.7)a
Sandy loam	0.32 (0.01)a	28.3 (0.2)a	109.8 (5.2)a
30 June			
Silty clay loam	0.45 (0.02)a	38.2 (0.2)a	98.6 (8.2)a
Loam	0.47 (0.02)a	37.2 (0.1)b	114.9 (8.8)a
Sandy loam	0.41 (0.01)a	37.7 (0.2)ab	129.8 (6.5)a
14 July			
Silty clay loam	0.34 (0.02)a	31.6 (0.2)a	97.7 (2.6)a
Loam	0.32 (0.01)a	31.7 (0.2)a	100.7 (2.6)a
Sandy loam	0.36 (0.01)a	31.1 (0.2)a	106.7 (2.7)a

For each sample date, means within columns followed by the same letter are not significantly different ( $P < 0.5$ ; LSD; SAS Institute [1985]).

plants from the 1,000 eggs per 30.5-row-cm infestation compared with the uninfested plants on 15 June and 22 June, respectively. Slight reductions in assimilation were also detected associated with the 200 and 500 eggs per 30.5-row-cm infestations on 22 June. No significant differences in photosynthetic rates were noted among the infestation densities on the last two sampling dates; i.e., the periods of maximum injury and after injury. The corn plants apparently responded to (i.e., compensated for) the injury during and after the period of maximum injury. In addition, the interaction between soil texture and infestation level was not significant.

The influence of soil moisture level (irrigation) could be evaluated only on the last sampling date. Plants from irrigated soils averaged 37.6  $\mu\text{mol/m}^2/\text{s}$  compared with 33.2  $\mu\text{mol/m}^2/\text{s}$  for plants from nonirrigated soils ( $F = 16.88$ ;  $df = 1, 6$ ;  $P < 0.01$ ). The soil texture-by-soil moisture interaction was also significant ( $F = 5.28$ ;  $df = 2, 6$ ;  $P < 0.05$ ). In the silty clay loam and loam soil textures, corn photosynthetic rates responded positively to the irrigation (by an average of 6.0  $\mu\text{mol/m}^2/\text{s}$ ), but no response was seen in plants from the sandy loam soil (34.6 compared with 34.2  $\mu\text{mol/m}^2/\text{s}$  for the dryland and irrigated treatments, respectively). In plots without irrigation, plants from the sandy loam soil had a higher photosynthetic rate than plants from the other two soil textures, whereas the inverse occurred in the ir-

**Table 3. Gas exchange parameter means ( $\pm$  SEM) for stomatal conductance, intercellular CO<sub>2</sub> concentration, and leaf temperature parameters in 1990**

Infestation level	Stomatal conductance, mol/m <sup>2</sup> /s	Leaf temp, °C	Intercellular CO <sub>2</sub> concn, ppm
8 June			
Uninfested	0.25 (0.01)	32.4 (0.8)	132.5 (7.3)
15 June			
Uninfested	0.39 (0.02)a	33.6 (0.3)a	121.8 (5.1)a
200 eggs <sup>a</sup>	0.36 (0.02)a	33.6 (0.4)a	115.1 (5.2)a
500 eggs	0.39 (0.02)a	33.5 (0.3)a	123.3 (4.5)a
1,000 eggs	0.37 (0.01)a	33.7 (0.2)a	121.9 (4.9)a
22 June			
Uninfested	0.36 (0.02)a	28.4 (0.2)a	94.4 (2.3)a
200 eggs	0.35 (0.02)a	28.4 (0.2)a	103.3 (4.1)a
500 eggs	0.38 (0.01)a	28.3 (0.3)a	103.7 (4.0)a
1,000 eggs	0.35 (0.02)a	28.3 (0.2)a	105.8 (5.8)a
30 June			
Uninfested	0.45 (0.02)a	37.7 (0.2)a	115.8 (5.3)ab
200 eggs	0.42 (0.02)a	37.6 (0.2)a	106.8 (4.2)b
500 eggs	0.44 (0.02)a	37.8 (0.2)a	113.0 (4.6)ab
1,000 eggs	0.45 (0.02)a	37.7 (0.2)a	122.2 (5.6)a
14 July			
Uninfested	0.35 (0.02)a	31.2 (0.2)a	105.1 (3.3)a
200 eggs	0.35 (0.02)a	31.6 (0.2)a	102.2 (3.3)a
500 eggs	0.35 (0.02)a	31.4 (0.2)a	101.2 (3.1)a
1,000 eggs	0.33 (0.01)a	31.5 (0.2)a	99.1 (2.7)a

For each sample date, means within columns followed by the same letter are not significantly different ( $P < 0.05$ ; LSD; SAS Institute [1985]).

<sup>a</sup> No. eggs per 30.5 row-cm.

rigated soils. The soil moisture-by-infestation level and soil texture-by-soil moisture-by-infestation level interactions were not significant.

Stomatal conductance was affected significantly by soil texture in a manner similar to the photosynthetic rate response (Table 2). Stomatal conductance was similar among the soil texture treatments for 8, 22, and 30 June and 14 July sampling dates. However, significant differences in stomatal conductance were found for the 15 June ( $F = 6.01$ ;  $df = 2, 6$ ;  $P < 0.05$ ) sampling date. The trend for this sampling date (and for the 22 June and 30 June sampling dates, although the differences were not significant) was for a reduced conductance in the sandy loam soil compared with the silty clay loam and loam soils. No significant differences were found among the western corn rootworm infestation levels for the stomatal conductance parameter (Table 3). Values ranged from 0.25 (8 June) to 0.44 mol/m<sup>2</sup>/s (30 June). These data are in contrast with the results from the soil texture treatments, when the stomatal conductance data more closely mirrored the photosynthetic rate data. The interaction between infestation level and soil texture on stomatal conductance was not significant. The dryland treatment on 14 July significantly ( $F = 11.18$ ;  $df = 1, 14$ ;  $P < 0.05$ ) reduced corn stomatal conductance compared with irrigated conditions.

The plant response to the moisture deficit was manifested by a 0.06 mol/m<sup>2</sup>/s reduction (0.37 versus 0.31 mol/m<sup>2</sup>/s). The interactions of infestation level and soil texture with soil moisture were not significant.

The western corn rootworm infestation level had no significant effect on corn leaf temperature (Table 3); moreover, the soil texture effect was significant ( $F = 7.85$ ;  $df = 2, 6$ ;  $P < 0.05$ ) only on the 30 June sampling date (Table 2). In this case, leaf temperatures were greater (by 1.0°C) from plants grown in the silty clay loam soil than the loam soil. Within a sampling date, the greatest range of leaf temperature, over the levels of western corn rootworm, was 0.3°C. The interaction terms between infestation level and soil texture were not significant. Soil moisture level (14 July) significantly ( $F = 12.57$ ;  $df = 1, 6$ ;  $P < 0.01$ ) affected corn leaf temperature. The irrigated soil conditions resulted in plants with an average of 0.9°C cooler leaf surface temperatures than the plants from the dryland treatment. In addition, a significant interaction ( $F = 5.29$ ;  $df = 2, 6$ ;  $P < 0.05$ ) occurred between soil moisture and soil texture on leaf temperature. Similar to the photosynthetic rate response, plants in the silty clay loam and loam soils responded to the soil moisture (i.e., cooler leaf temperatures with irrigation); however, plants from the sandy loam soil had similar leaf temperatures in irrigated and dryland conditions.

Intercellular CO<sub>2</sub> concentration was affected significantly ( $F = 5.69$ ;  $df = 2, 6$ ;  $P < 0.05$ ) by the soil texture on 15 June (Table 2). Plants from the sandy loam soil had a higher concentration than plants from the other two soil textures. This corresponds with the lower photosynthetic rate recorded for plants from the sandy loam soil compared with the silty clay loam and loam soils. A similar photosynthetic rate response was noted on 22 and 30 June; however, there were no significant differences in intercellular CO<sub>2</sub> concentration (although there was a trend for a lower concentration in the sandy loam soil by 17.5 ppm). Western corn rootworm injury had a significant ( $F = 3.20$ ;  $df = 3, 18$ ;  $P < 0.05$ ) effect on intercellular CO<sub>2</sub> concentration only on 30 June (Table 3). Plants injured by larvae from the 1,000 eggs per 30.5-row-cm infestation had a significantly higher concentration than plants injured by larvae from the 200 eggs per 30.5-row-cm infestation. However no significant photosynthetic rate differences, among infestation levels, were found on this date. The dryland conditions significantly ( $F = 7.08$ ;  $df = 1, 6$ ;  $P < 0.05$ ) reduced the internal CO<sub>2</sub> concentration by an average of 10.8 ppm (107.3 compared with 96.5 ppm). The interactions of soil moisture with soil texture and infestation level were not significant.

## Discussion

Western corn rootworm larval injury to root systems resulted in significant modification of corn plant physiology and the magnitude of the effect was generally related to the larval density (i.e., severity of injury). During the early phases of injury (feeding by primarily first and second instars), a detrimental effect on photosynthetic rate was recorded. In 1989, larvae from the 500 and 1,000 eggs per 30.5-row-cm infestations resulted in an 8.7% reduction in photosynthetic rate and, in 1990, the highest infestation density reduced the rate by 7.0%. However, these detrimental effects were transient during both years. On two of the three subsequent sampling dates in 1989, the most severely injured plants had significantly higher photosynthetic rates than the uninjured plants and, in 1990, photosynthetic rates were equal among the infestation regimes following the initial differences. These responses in 1989 and 1990 are consistent with overcompensatory and compensatory responses, respectively, as described by Belsky (1986). The apparent overcompensatory response in the 1,000 eggs per 30.5-row-cm treatment, compared with the uninfested, was 13.0 and 17.8% on 12 July 1989 and 1 August 1989. Results on 20 July 1989 may have been altered by the excessively wet soil conditions (a total of 6.1 cm of precipitation fell during the preceding 5 d). In addition, the fonofos treatment resulted in high photosynthetic rate values during the first two sampling periods (significantly greater than the uninfested on 12 July 1989). This result is in contrast to that found by Godfrey & Holtzer (1992).

The photosynthetic rate data generally mirror the plant biomass accumulation (Godfrey et al. 1993). In 1989, plant biomass was initially reduced by larval injury; however, on 26 July, injured plants were larger than the uninjured plants. For instance, leaf wet weight was 8.8% greater from injured plants by larvae from the 1,000 eggs per 30.5-row-cm treatment than uninjured plants on this date. In 1990, plant biomass was again initially reduced by larval injury, but by 2 July there were no differences in plant biomass between the two treatment groups.

The mechanisms involved in these plant responses, detrimental and compensatory phases, are uncertain. A disruption of stomatal function or a change in plant chemistry (i.e., enzymes and hormones) are possible hypotheses. Stomatal conductance values among the western corn rootworm treatments were not consistently related with either increased or decreased photosynthetic rates. In 1989, stomatal conductance in plants stressed by the 500- and 1,000-egg infestation rates tended to be reduced in accordance with the reduced photosynthetic rate, but in 1990 there were no trends. The apparent compensatory photosynthetic rate response was not

related to increased stomatal conductance during either year. In addition, intercellular CO<sub>2</sub> concentration did not differ significantly among the western corn rootworm levels on the dates when the photosynthetic rate was affected (15 and 22 June). Therefore, a disruption of plant chemistry appears to be the most likely explanation. Effects on photosynthetic rate from the other variables (i.e., soil moisture and soil texture) were generally more closely related to stomatal conductance (e.g., on 14 July 1990, the 11.7% decrease in photosynthetic rate and the 16.2% reduction in stomatal conductance from the dryland treatment compared with the irrigated treatment).

The differing magnitude of compensatory response between 1989 and 1990 may be related to the insect-plant synchrony (the plant growth stage at the time of injury), although environmental conditions and nutrient levels may also be important factors. In 1989, because of the delay in infestation (16 d after planting), the plants were in the V12-V15 growth stages during the period of maximum injury. In comparison, in 1990, the plants were only in the V9-V11 growth stages as the maximum injury occurred. The greater biomass (i.e., photosynthetically active leaf tissue) in 1989 compared with 1990 may have augmented the response. During the period of peak third-instar population, the uninfested plants averaged  $\approx 7,600$  and  $4,800$  cm<sup>2</sup> leaf tissue in 1989 and 1990, respectively (Godfrey et al. 1993). Riedell (1990) also showed differing corn plant response, by phenological stages, to corn rootworm larval injury initiated at the V5 stage. At the V9 stage, the larval root injury had no effects on water relations; however, at the tassel stage, the stomatal conductance was significantly reduced in the injured plants compared with the uninjured plants.

The plant response to root injury was similar in all three soil textures. Plants were not under appreciable moisture stress during the period of western corn rootworm larval feeding. Plant response may be different under drought stress conditions, thus may be influenced by soil type as manifested by different water-holding capacities. In addition, soil texture may influence larval survival (Turpin & Peters 1971) and indirectly affect the damage potential.

Western corn rootworm larval feeding (at the level evaluated) did not appear to disrupt corn plant physiology as severely as tunneling by European corn borer larvae (Godfrey et al. 1991). Stem tunneling was shown to reduce photosynthetic rates and stomatal conductance values, which resulted in decreased intercellular CO<sub>2</sub> concentrations (presumably through a limitation of CO<sub>2</sub> entry into the leaf) and in increased leaf temperatures (from less evaporative cooling on the leaf surface). These results indicate that western corn rootworm and European corn borer have different modes of disruption of plant phys-

iology. Stem tunneling and root injury are types of indirect injury (not to the photosynthetically active tissues). Stem tunneling alters photosynthetic rates by disrupting stomatal function (Godfrey et al. 1991), but root injury appears to alter photosynthesis with no consistent relationship to stomatal conductance. However, root injury by western corn rootworm larvae in our study did result in significant reductions of grain yield (Godfrey et al. 1993). Gas exchange evaluations based on single leaf measurements at one point during the day are not necessarily indicative of canopy photosynthesis. More detailed evaluations such as photosynthetic light response, an estimate of dark respiration, and diurnal photosynthetic cycles need to be conducted. However, the detrimental effects of western corn rootworm injury on corn leaf biomass accumulation (Godfrey et al. 1993) coupled with transient effects on photosynthesis reported herein indicates significant damage potential of this pest.

#### Acknowledgments

We thank M. Barnhart, J. Brown, and S. Spomer (Department of Entomology, University of Nebraska) for their technical assistance, J. Tollefson (Department of Entomology, Iowa State University) for the use of the mechanical egg infester, and L. Higley (Department of Entomology, University of Nebraska) and T. Arkebauer (Department of Agronomy, University of Nebraska) for manuscript reviews. This research was supported by USDA-CSRS under grant 89-34103-4326 and the University of Nebraska Agricultural Experiment Station, Projects 17-043 and 17-046. This is paper no. 10178 of the Journal Series of the University of Nebraska Agricultural Research Division and Contribution No. 794 of the Department of Entomology, University of Nebraska-Lincoln.

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Received for publication 30 December 1992; accepted 22 April 1993.