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Vegetative and Reproductive Biomass Accumulation in Field Corn: Response to Root Injury by Western Corn Rootworm (Coleoptera: Chrysomelidae)

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ABSTRACT A 2-yr field study was conducted to evaluate the effects of larval injury by western corn rootworm, *Diabrotica virgifera virgifera* LeConte, on vegetative and reproductive biomass accumulation of field corn, *Zea mays* L. Studies in 1989 were conducted in irrigated, silty clay loam soil, whereas in 1990, the possible interacting effects of soil texture (silty clay loam, loam, and sandy loam) and soil moisture (furrow-irrigated and dryland) were examined. In both years, during the early phases of injury (feeding by first and second instars), the vegetative biomass was detrimentally affected. Larval infestations reduced leaf area and leaf wet weight by up to 17.4%. However, during the period of peak injury by third instars and during the postinjury period, the plant biomass accumulation response differed slightly between the 2 yr. Overcompensatory and exact compensatory responses were noted in 1989 and 1990, respectively. In 1989, dry weights of injured plants were greater than the uninjured plants at ≈2 wk following pupation and in 1990, plants from the two treatments had similar biomass. The reason for the differing response was probably related to the plant development stage at the time of peak injury. In 1989, plants were in the V15 stage, averaging 8,350 cm^2 leaf area, whereas in 1990, plants were in the V8–V10 stage with 4,761.3 cm^2 leaf area. The greater amount of photosynthetically active tissue in 1989 compared with 1990 may have allowed the plants to respond better to the injury. In addition, rootworm-injured plants were unable to utilize, for the production of vegetative biomass, the supplemental soil moisture through irrigation compared with uninjured plants. The root injury apparently inhibited the plants from utilizing the soil moisture. Plant response to stress was generally similar in all three soil textures. The compensation and maintenance of unaltered levels of vegetative tissue biomass appeared to be at the sacrifice of reproductive tissue biomass. Western corn rootworm larval injury consistently reduced corn grain yield by up to 15.0% in 1989 and by 40.7% in 1990.

KEY WORDS *Diabrotica virgifera virgifera*, plant response, root injury

LARVAE OF WESTERN corn rootworm, *Diabrotica virgifera virgifera* LeConte, feed nearly exclusively on roots of corn, (*Zea mays* L.), and cause extensive injury to these structures. The larval tunneling activity interrupts the integrity of the root systems and root pruning; i.e., complete destruction of roots also results from larval feeding (Branson 1986). The western corn rootworm is a serious pest of continuous corn from the western Great Plains to the East Coast states.

Larval feeding by western corn rootworm has been shown to reduce corn grain yield (Turpin et al. 1972, Sutter et al. 1990) and vegetative biomass (Spike & Tollefson 1991), to increase corn stalk lodging (Sutter et al. 1990), and to alter corn nutrient content (Kahler et al. 1985). Several researchers have examined corn yield response to western corn rootworm larval injury. Turpin et al. (1972) identified several factors (percentage clay in soil, soil potassium and phosphorus levels, field slope and drainage, planting date, and plant population) that were correlated with corn rootworm damage to corn. Apple et al. (1977) examined corn yield with natural corn rootworm, *Diabrotica* spp., infestations for 4 yr in seven states and identified yield reductions in three of the states. Branson et al. (1980) found, from a controlled infestation of western corn rootworm, that larvae resulting from 300 and 1,200 eggs per 30.5 row-cm reduced corn yield by 5 and 16%, respectively. However, the correlation between yield and root damage was only 0.54. Turpin et al. (1972) established a root damage economic injury level of 2.5 (on a 1–6 rating scale); however, this level was increased to 2.75 (Stamm et al. 1985) and finally to 3.0 (Mayo 1986).

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Several interacting factors are important in determining corn response to corn rootworm injury. Spike & Tollefson (1989b) reported that "under conditions of normal to favorable agronomic conditions and favorable environmental conditions, yields of plants having rootworm injury were highly variable." Grain yield losses from corn rootworm injury have been speculated to be more severe under drought conditions (Branson et al. 1980, Chiang et al. 1980) and were more severe during a dry year (1985) compared with the normal year (1984) (Spike & Tollefson 1989a); however, this aspect of the rootworm–corn interaction has not been studied experimentally. Adequate nitrogen fertilization and low to normal plant densities have been shown to mitigate the effects of corn rootworm injury on corn (Spike & Tollefson 1989a). Gibb & Higgins (1991) showed that leaf dry weights of irrigated corn tended to compensate for rootworm larval injury during the season, but a similar compensation did not occur with stem weights.

Soil insecticides and crop rotation are the two primary control measures used to reduce damage from corn rootworm larvae. Soil insecticides in Nebraska are used either prophylactically or treatment needs are based on beetle density the previous summer and subsequent yield loss potential from larval feeding (Stamm et al. 1985). In Nebraska, 2.1 million kg of insecticide (AI) were used on corn in 1987, and the majority of these treatments were targeted for corn rootworm control (Baker et al. 1990). In addition to the well-documented environmental and social issues associated with soil insecticide usage, Sutter et al. (1990) found that soil insecticides did not consistently increase corn yields within plots with controlled western corn rootworm infestations. In addition, the correlation between rootworm-induced root injury and corn yield was not significant for the insecticide-treated plants, which was in contrast with the untreated plants.

Corn production in Nebraska occurs over a wide range of agronomic, edaphic, and environmental conditions. In the eastern section of the state, the soils range from clay loams to silty clay loams and precipitation ranges from 63.5 to 83.8 cm/yr (Elder 1969), thus much of the corn is grown without irrigation. In the central portion of Nebraska (especially south central); the soils are primarily loams and silt loams and the lower precipitation (48.3 to 63.5 cm/yr) necessitates supplemental irrigation for corn production (Elder 1969). Finally, in the western and northcentral part of the state, the soils are predominantly of sandy textures, and coupled with low precipitation (<48.3 cm/yr), irrigation is required for corn production (Elder 1969). This depicts the wide range of conditions for corn production in Nebraska and stresses the need to understand corn plant response to root injury under a wide range of environmental conditions. The objectives of our study were (1) to quantify the effect of corn rootworm larval injury on corn vegetative and reproductive biomass accumulation, and (2) to evaluate the potential interacting effects of soil texture and soil moisture on corn response to injury by corn rootworm larvae.

Materials and Methods

Studies were conducted at the University of Nebraska Agricultural Research and Development Center near Mead, NE. Controlled levels of western corn rootworm larvae were established in field plots of silty clay loam soil in 1989 and of three soil textures (silty clay loam, loam, and sandy loam) in 1990. Particle analyses of these soils was silty clay loam (8.0% sand, 63.6% silt, and 28.4% clay), loam (34.4% sand, 44.0% loam, and 21.7% clay), and sandy loam (75.7% sand, 14.6% loam, and 9.7% clay). In 1989, the plots were uniformly irrigated. In 1990, soil moisture level was an additional independent variable with two levels, irrigated and dryland (natural precipitation only).

Western corn rootworm infestations were initiated during both years at levels of 200, 500, and 1,000 eggs per 30.5 row-cm (and a treatment of 0 eggs per 30.5 row-cm). Western corn rootworm eggs, obtained from adults collected from northeastern Nebraska, were suspended in various concentrations in 0.125% agar water. In 1989, a manual infestation technique was used. A small trench (7.6 cm deep) was made adjacent to the corn seed furrow (16 d after corn planting; corn at the V2–V3 growth stage [Ritchie et al. 1986]), the egg suspension was trickled into the trench, and moist soil was applied over the trench to cover the eggs. In 1990, a modification of the pressurized tractor-mounted mechanical infestation technique (Sutter & Branson 1986) was used to infest the plots. The infestations were conducted on 6 May, which was immediately after corn planting. In addition, a planting-time insecticide treatment (fonofos at 112 g [AI]/1,000 row-m) was included in 1989 because a slight background infestation of western corn rootworm eggs was present in the plot area (corn had been grown in this area the previous year). This treatment was not necessary in the 1990 experiment because the plot area had been fallowed the previous year.

Plots were planted on 24 May 1989 and 6 May 1990 with 'Pioneer 3377' corn. Additional details of the herbicide and fertilization regimes are included in Godfrey et al. (1993). Treatments (western corn rootworm levels) were arranged in a randomized complete-block design with four blocks in 1989. Each treatment was applied to two adjacent corn rows (9.1 m long) per block. A split split-plot design was used in 1990 with four blocks. The soil textures formed the main plots (6.1 by 12.2 m, 0.46 m deep), with soil moisture

the subplots and the western corn rootworm levels randomly assigned to a single row within each subplot. Each soil texture plot was split into two 3.05-m-wide subplots; one subplot was furrow-irrigated beginning on 2 July, and in the other subplot dryland corn was grown. Irrigation was applied on 2 July (1.9 cm), 5 July (2.5 cm), 11 July (2.5 cm), 18 July (2.5 cm), and 16 August (1.9 cm). Complete data on precipitation and irrigation amounts, summarized by week from planting to harvest, are shown in Godfrey et al. (1993).

Soil moisture was monitored at a 15.0-cm depth from 13 June through 3 August with gypsum soil moisture blocks (Model 221 Delmhorst; Campbell Scientific, Logan, UT). Soil water potential was recorded in one block of the sandy loam and loam soil textures (irrigated and nonirrigated treatments); data are presented by Godfrey et al. (1993). Water potential in the irrigated treatments was generally >-2 bars compared with a water potential of <-5 bars in the nonirrigated treatments from 2 to 25 July. In the nonirrigated treatments, water potential was -15 bars (permanent wilting point) on several days. The deficit soil moisture conditions were most severe during July, which corresponded with the period of corn silking and pollination. The soil water potential was generally slightly lower in the sandy loam soil compared with the loam soil texture. These treatments (irrigated and nonirrigated) are referred to herein as irrigated and dryland, respectively.

Western corn rootworm larval population densities were quantified during both 1989 and 1990 at about weekly intervals from egg hatch to pupation. Samples (15.2-cm soil cubes surrounding a corn plant) were taken on 7, 14, and 26 July 1989 and on 18 and 25 June, and 2 July 1990. Samples were processed using the methods of Bergman et al. (1981). Larvae within roots were recovered by suspending root systems over water and forcing the larvae from the roots with heat. Root damage was estimated during the early stages of larval feeding by calculating the percentage of roots with western corn rootworm larval injury on 7 July 1989 and on 18 and 25 June 1990; the total number of roots and damaged roots per each sampled root system were counted. Root injury was rated on a 1–6 scale in 1989 (Hills & Peters 1971) and on a 1–9 scale in 1990 (Musick & Settle 1972). Damage was rated on 14 and 26 July 1989 and on 2 and 16 July 1990. Two larval and root damage samples were taken per each treatment combination per block on each sampling date.

Adult emergence was quantified as another indicator of the magnitude of the larval infestation. In 1989, unreplicated 1.83-m^2 screen cages (Hill & Mayo 1974) covering two corn rows (averaging 17.25 plants) were placed in plots in one block before adult emergence. Western corn rootworm beetles, retained by the cage, were collected and counted weekly from 2 July to 1 September. In 1990, single plant emergence cages (Hein et al. 1985) were placed in one block of the experiment (two cages per treatment combination). Western corn rootworm beetle density in these cages was quantified twice per week from 9 July to 23 August.

Plant biomass was sampled concurrently with the larval and root damage samples. Plants (two per treatment combination) were severed at the soil surface and separated into leaf, stem, and root tissues. Wet weights of leaf and stem tissues and the dry weights of leaf, stem, and root tissues (following drying for 48 h at 60°C) were recorded. In 1990, dry weights of brace root tissue were also recorded. Percentage moisture was calculated for leaf and stem tissues. The length and width of each photosynthesizing leaf was recorded, and total plant leaf area was calculated as the sum of the areas of the individual leaves (length by width by 0.75) (Grant et al. 1989). Photosynthesizing leaves were denoted as those with >50% of the leaf surface area not in a senescent state. Finally, plant growth stage (i.e., number of fully expanded leaves [Ritchie et al. 1986]), number of senesced leaves, and extended leaf height were recorded in 1990.

Corn grain yield was quantified at corn maturity in 1989 and 1990. Corn ears were harvested from five randomly selected plants and from one 4-m row section per treatment combination per block. Ears were dried for 72 h at 70°C, and the grain was shelled from the cob. Grain weights and moisture were recorded and the grain weight adjusted to 15.5% moisture (no. 2 yellow corn). In 1990, kernel number per plant and average kernel weight were determined for each yield sample. Kernels were counted with a seed counter (Davis Tool and Engineering, Montgomery, IL). Kernel number was quantified on each single plant sample and from a subsample of kernels from the 4-m row section samples. Average kernel weight was determined from the number of kernels and the total sample weight.

Statistical Analysis. Plant vegetative and reproductive biomass response variables were analyzed with analysis of variance (ANOVA) (SAS Institute 1985) using a randomized complete-block design in 1989 and split split-plot design in 1990. A split-plot design was used on samples taken before the establishment of soil moisture treatments. Percentage data were transformed as y = arcsine ($p^{0.5}$) before analyses; however, the untransformed values are reported herein. Least significant differences test was used to separate means. A significance level of $P < 0.05$ was used for all analyses.

Results

Western Corn Rootworm Density and Root Damage, 1989. Western corn rootworm larval population densities generally varied with the

Table 1. Western corn rootworm larval density and root ratings, 1989

Treatment[a]	7 July		14 July		26 July	
	Larvae/plant	% Damaged roots	Larvae/plant	Root rating[b]	Larvae/plant	Root rating[b]
0	2.1c	1.2a	2.8b	2.0a	0.0a	2.0a
200	7.3b	1.7a	7.9ab	2.1a	0.0a	2.3a
500	14.3a	10.7a	10.9ab	2.5ab	0.0a	2.6ab
1,000	16.0a	16.5a	17.1a	3.1b	0.0a	3.5b
Fonofos	2.5c	2.8a	1.6b	2.0a	0.0a	2.0a

Means within columns followed by the same letter are not significantly different with least significant differences test ($P < 0.05$) (SAS Institute 1985).
[a] Number of western corn rootworm eggs per 30.5 row-cm.
[b] 1–6 scale (Hills & Peters [1971]).

infestation treatments. Treatment effects were significant on 7 July ($F = 17.87$; df = 4, 12; $P < 0.01$) and on 14 July ($F = 3.91$; df = 4, 12; $P < 0.01$). On 7 July, larval densities were 7.3, 14.3, and 16.0 larvae per plant for 200, 500, and 1,000 eggs per 30.5 row-cm, respectively (Table 1). These densities differed significantly from those of the insecticide-treated and uninfested treatments. Larval densities in the uninfested and insecticide-treated plots averaged 2.3 larvae per plant and these two treatments did not differ significantly. On the second sampling date, larval densities were very similar to those on 7 July. However, only larval densities in the 1,000 eggs per 30.5-row-cm treatment differed significantly from those in the uninfested and insecticide-treated. Pupation had occurred by the sampling on 26 July.

Root damage (percentage damaged roots) was not significantly affected by larval density on 7 July; however, the damage tended to follow trends similar to the larval density data (Table 1). Western corn rootworm infestation level significantly affected root ratings on 14 July ($F = 3.96$; df = 4, 12; $P < 0.05$) and on 26 July ($F = 4.40$; df = 4, 12; $P < 0.05$). On 14 July, the root rating in the highest egg infestation level was significantly higher than that in the 200 eggs per 30.5 row-cm, uninfested, and fonofos treatments. Root rating results from the 26 July sampling date were similar to results obtained on 14 July. On 14 July and 26 July, the mean root rating from 1,000 eggs per 30.5 row-cm exceeded 3.0, which has been identified as the root rating threshold at which economic yield losses may occur (Mayo 1986).

Western corn rootworm beetle density averaged 2.4, 10.0, 29.6, and 46.6 beetles per plant in the uninfested, 200, 500, and 1,000 eggs per 30.5-row-cm treatments, respectively. These values for the 200 and 500 eggs per 30.5-row-cm infestations are comparable with results reported from similar egg infestation densities (Branson et al. 1980, Branson & Sutter 1985). However, adult emergence at the 1,000 eggs per 30.5-row-cm treatment (46.6 adults per plant) was substantially greater than that reported in these previous studies (an average of 33.0 adults per plant from an infestation of 1,200 eggs per 30.5 row-cm). The delayed infestation timing, relative to corn planting, probably resulted in larger root systems; this may have favored larval survival and subsequent adult emergence. However, this was not shown in a study by Fisher et al. (1990), which examined *D. virgifera virgifera* population dynamics with three corn planting dates and three infestation timings.

Western Corn Rootworm Density and Root Damage, 1990. Egg infestation treatments had significant effects on western corn rootworm larval densities on 18 June ($F = 7.93$; df = 3, 16; $P < 0.05$), 25 June ($F = 6.53$; df = 3, 16; $P < 0.05$), and 2 July ($F = 7.20$; df = 3, 16; $P < 0.05$). Soil texture had no significant effects on western corn rootworm larval density on the three sampling dates, which is in contrast to that found by Turpin & Peters (1971) and by L.D.G., L.J.M., R.J.W., and G. L. Hein (University of Nebraska, Scottsbluff) (unpublished data). On 18 June, larval densities were significantly higher in the 500 and 1,000 eggs per 30.5-row-cm treatments (averaging 16.7 larvae per plant) than in the 200 eggs per 30.5-row-cm and uninfested treatments (averaging 3.1 larvae per plant) (Table 2). Larval population density on 25 June was similar in the two highest egg infestation densities and averaged 15.8 larvae per plant. However, the larval density in the 500 eggs per 30.5-row-cm treatment was significantly higher than the 200 eggs per 30.5-row-cm and uninfested treatments and the density in the 1,000 and 200 eggs per 30.5-row-cm treatments did not differ significantly. Populations of larval western corn rootworms decreased on 2 July (coincident with pupation), but the trends among treatments were similar to those of the two earlier sampling dates.

Root damage, quantified with percentage of damaged roots, was significantly affected by egg infestation regimes on 18 June ($F = 13.79$; df = 3, 16; $P < 0.05$) and on 25 June ($F = 8.96$; df = 3, 16; $P < 0.05$). On 18 June, the percentage of damaged roots was significantly highest in the 1,000 eggs per 30.5-row-cm treatment, intermediate in the 500 eggs per 30.5-row-cm treatment, and

Table 2. Western corn rootworm larval density and root ratings, 1990

Treatment[a]	18 June		25 June		2 July		16 July
	Larvae/ plant	% Damaged roots	Larvae/ plant	% Damaged roots	Larvae/ plant	Root rating[b]	Root rating[b]
0	0.3b	0.3c	0.8c	2.2c	1.2c	1.8c	2.1c
200	5.9b	0.2c	6.0bc	29.8b	2.9bc	2.3c	3.4b
500	15.8a	8.0b	17.7a	57.2a	7.0ab	5.6b	5.7a
1,000	17.5a	17.6a	13.9ab	49.1ab	12.0a	7.4a	5.5a

Means within columns followed by the same letter are not significantly different with least significant differences test ($P < 0.05$) (SAS Institute 1985).

[a] Number of western corn rootworm eggs per 30.5 row-cm.

[b] 1–9 scale (Musick & Settle [1972]).

lowest in the 200 eggs per 30.5-row-cm and uninfested treatments (Table 2). Differences among the treatments on 25 June were similar to those on 18 June; however, the overall magnitude of damage was much higher (6.5% compared with 34.8% on 18 June and 25 June, respectively). Root ratings varied significantly among the egg infestation treatments on 2 July ($F = 26.81$; df = 3, 16; $P < 0.05$) and on 16 July ($F = 18.37$; df = 3, 16; $P < 0.05$). The block, soil texture, and soil moisture (16 July only) and all interactions were not significant. Root ratings were significantly highest in the infestation arising from the 1,000 eggs per 30.5-row-cm treatment on 2 July, followed by the 500 eggs per 30.5-row-cm treatment, then by the 200 eggs per 30.5-row-cm and uninfested treatments. On 16 July, the magnitude of damage was similar to that of 2 July, except the damage in the 500 and 1,000 eggs per 30.5-row-cm treatments did not differ significantly and the damage in the 200 eggs per 30.5-row-cm treatment was significantly greater than that in the uninfested treatment. Averaged over the other treatments, root ratings were 4.1 and 4.2 for the irrigated and dryland treatments, respectively. Overall, root ratings from the 500 and 1,000 eggs per 30.5-row-cm treatments exceeded the root rating threshold (for yield losses) of 5.0 on the 1–9 scale.

Adult emergence from single plant emergence cages averaged 2.3 beetles (uninfested treatment), 6.6 beetles (200 eggs per 30.5 row-cm), 19.5 beetles (500 eggs per 30.5 row-cm), and 11.2 beetles (1,000 eggs per 30.5 row-cm). Soil texture and soil moisture did not affect adult emergence. The higher emergence in the 500 than in the 1,000 eggs per 30.5-row-cm treatments may represent mortality from larval competition for roots in the higher egg infestation treatment. Similar results have been reported (Branson et al. 1980, Branson & Sutter 1985) for adult emergence arising from high western corn rootworm egg infestations. This result was probably magnified in 1990 over 1989 because of the smaller root systems during the feeding period in 1990.

Plant Biomass, 1989. *Root Biomass.* Western corn rootworm larval injury had no significant effects on corn root dry weights on 7 and 14 July (Fig. 1A). However, on 26 July, plants injured by larvae from the 1,000 eggs per 30.5-row-cm treatment had significantly ($F = 5.43$; df = 4, 12; $P < 0.05$) larger (by 26.3%) root weights than the other four treatments. In the most severely damaged plants, larval feeding on corn roots apparently stimulated regrowth, and produced a higher root weight than in the less severely injured root systems.

Leaf Area. Corn leaf area was significantly affected by western corn rootworm larval density on 7 July ($F = 4.00$; df = 4, 12; $P < 0.05$) and on 14 July ($F = 3.56$; df = 4, 12; $P < 0.05$) (Fig. 1B). Leaf area of plants stressed by larvae from the 1,000 eggs per 30.5-row-cm treatment was significantly lower than that of plants from both the fonofos-treated and uninfested treatments. The difference between the leaf areas of plants from the 1,000 eggs per 30.5-row-cm and fonofos treatments was 15.5%. On 26 July, no significant differences were found among the five treatments. However, there was a trend for a greater increase in leaf area (from the second to third sampling date) in the 1,000 eggs per 30.5-row-cm treatment than in the other four treatments.

Vegetative Biomass. Above-ground vegetative biomass accumulation was also affected by western corn rootworm larval injury. Leaf wet weight was significantly affected by larval root injury on 7 July ($F = 3.98$; df = 4, 12; $P < 0.05$) and on 26 July ($F = 4.34$; df = 4, 12; $P < 0.05$). On 7 July, plants injured by the highest larval density had significantly reduced leaf wet weight compared with the other treatments (Fig. 1C). Leaf biomass of plants from the 1,000 eggs per 30.5-row-cm treatment weighed 191.3 g, whereas the other four treatments averaged 230.8 g. The plant stress from larval-induced root injury apparently resulted in a reduction in leaf biomass accumulation. Godfrey et al. (1993) showed that during this part of the injury period, western corn rootworm larval injury significantly reduced corn photosynthetic rates. This reduction in assimilation appears to be manifested in the plant as a corresponding reduction in leaf biomass. On 14 July, leaf weights were similar among the five corn rootworm treatments; however, on 26 July, plants injured by larvae from the 1,000 eggs

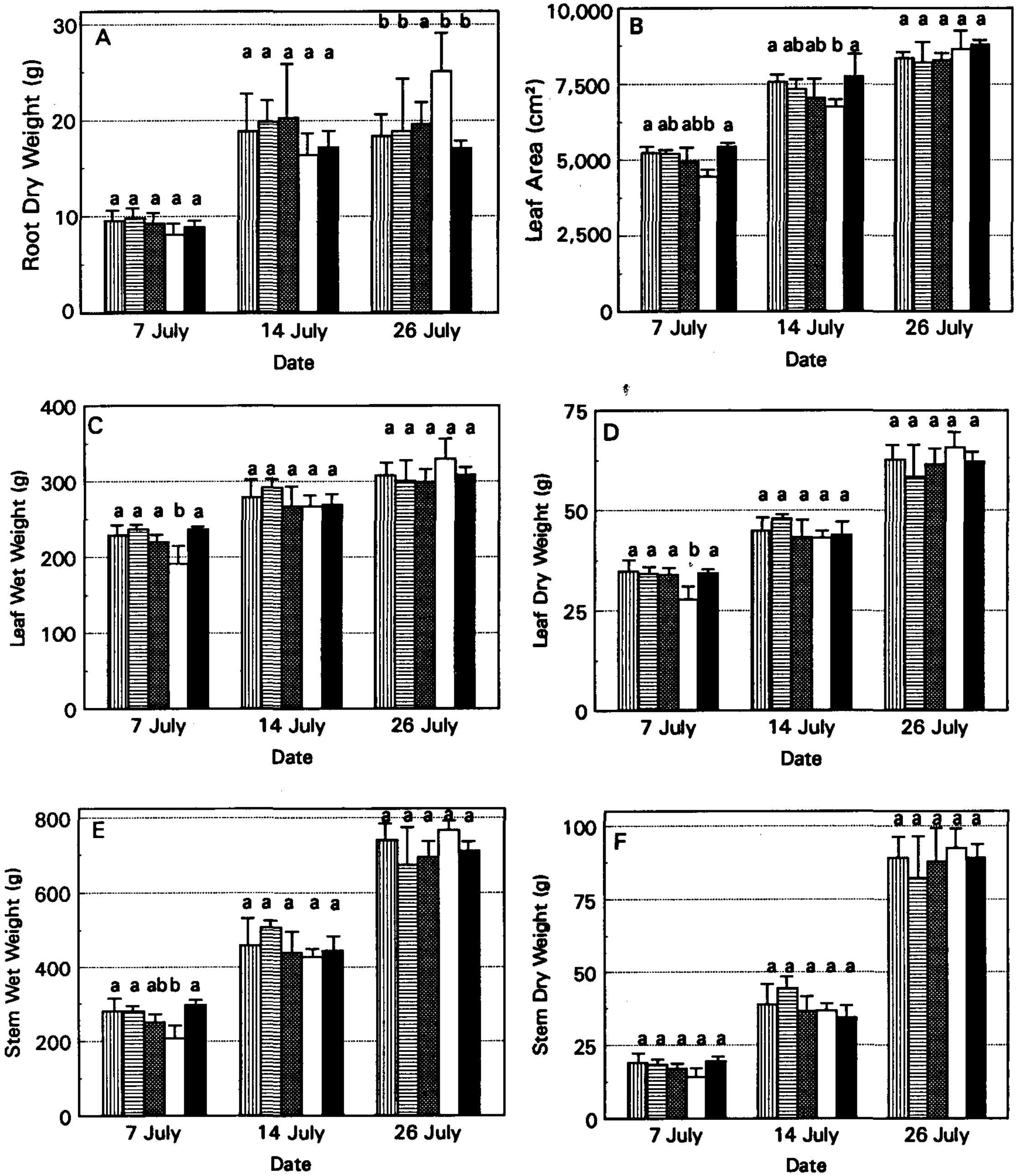

Fig. 1. Vegetative biomass (mean ± SEM) in 1989 for western corn rootworm infestation treatments: ▥, uninfested; ▤, 200 eggs per 30.5 row-cm; ▩, 500 eggs per 30.5 row-cm; □, 1,000 eggs per 30.5 row-cm; ■, fonofos-treated. (A) Root dry weight (g). (B) Leaf area (cm^2). (C) Leaf wet weight (g). (D) Leaf dry weight (g). (E) Stem wet weight (g). (F) Stem dry weight (g). Means within sample dates followed by the same letter are not significantly different with least significant differences test ($P < 0.05$) (SAS Institute 1985).

per 30.5-row-cm infestation had a significantly higher leaf biomass wet weight (by 25.4 g) than the other treatments. This again corresponds with the photosynthetic rate data (Godfrey et al. 1993). During the period from 12 July to 11 August, plants injured by the highest larval density generally had higher photosynthetic rates (by up to 10.1%) than the uninfested plants. This apparently resulted in a greater accumulation of leaf tissue in the severely injured plants compared with the uninjured plants.

Leaf dry weights were significantly reduced in plants injured by larvae from the 1,000 eggs per 30.5-row-cm treatment on 7 July (F = 4.46;

df = 4, 12; $P < 0.05$). (Fig. 1D). On 26 July, as with leaf wet weight response, the trend was for a higher leaf dry weight in plants from the highest western corn rootworm infestation compared with the other treatments.

The results for stem weights were similar to that of the leaf weight data (Fig. 1 E and F). In general, stem weights (wet and dry) of plants from the 1,000 eggs per 30.5-row-cm treatment were lowest on 7 July, intermediate on 14 July, and highest on 26 July among the five treatments. The only significant ($F = 3.76$; df = 4, 12; $P < 0.05$) difference was on 7 July for the wet stem weight data. In this case, plants from the 1,000 eggs per 30.5-row-cm treatment had a significantly lower stem weight than plants from the fonofos-treated, uninfested, and 200 eggs per 30.5-row-cm treatments.

Percentage Moisture. Water content of stem and leaf tissue was not significantly affected by the western corn rootworm treatments. Stem water content averaged 93.4, 91.6, and 87.8% on 7 July, 14 July, and 26 July, respectively. Leaf water content was 85.2% (7 July), 83.8% (14 July), and 80.0% (26 July).

Reproductive Biomass. Corn yield, based on single plant harvests, was significantly ($F = 2.82$; df = 4, 12; $P < 0.05$) affected by western corn rootworm infestation level (Fig. 2A). Grain yield was significantly higher in the insecticide-treated, uninfested, and 200 eggs per 30.5-row-cm treatments than in the 500 and 1,000 eggs per 30.5-row-cm treatments. The two highest infestation levels reduced the yield by an average of 14.8%. Corn yield, based on a 4-m-row section, did not differ significantly among the five treatments (Fig. 2A). However, the trends were similar to those from the single-ear harvest (a 10.0% yield reduction from the 1,000 eggs per 30.5-row-cm treatment compared with the uninfested). The block effects, with both evaluation methods, were not significant.

Plant Biomass, 1990. *Root Biomass.* Corn root biomass was not significantly affected by the western corn rootworm treatments on 18 and 25 June and 2 July (Fig. 3A). Weights averaged 1.9 and 4.7 g on 18 June and 25 June, respectively. On the third sampling date, roots from plants in infested plots tended to be smaller than those from uninfested plots (by up to 24.0%); however, the differences were not significant. On 16 July, a significant interaction was noted between the infestation level and soil moisture ($F = 3.71$; df = 3, 18; $P < 0.05$) on root weight. Root biomass was similar between the irrigated and dryland treatments with the uninfested, 200, and 500 eggs per 30.5-row-cm treatments (Fig. 3A). However, in the 1,000 eggs per 30.5-row-cm treatment, root biomass was 24.4% greater in the dryland than the irrigated treatment. As in 1989, root biomass generally increased with increasing amounts of damage for the uninfested, 200, and 500 eggs per 30.5-row-cm treatments. Under severe rootworm larval damage, apparently root regrowth is stimulated more by dry soil conditions than by moist soil conditions. The limited soil moisture in the dryland condition may place a greater importance on the moisture-absorbing roots than in the irrigated condition.

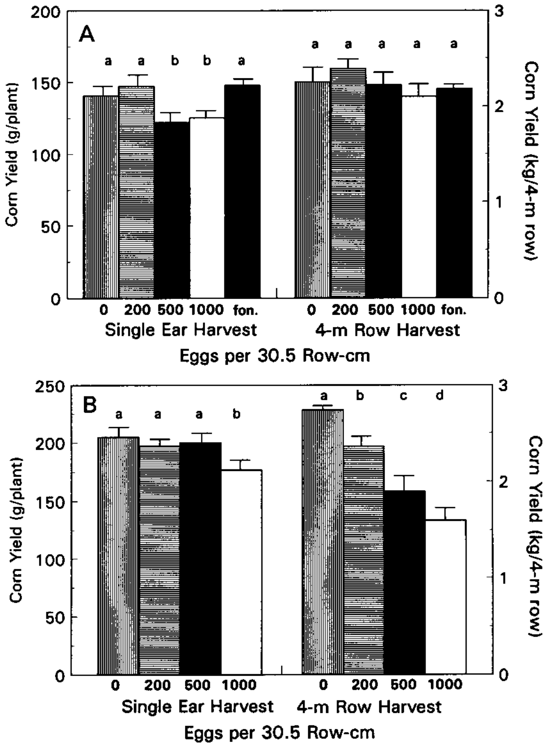

Fig. 2. Corn grain yield (mean ± SEM) for single-plant corn yield samples (g per plant) and for corn yield per 4-m-row section (A) 1989. (B) 1990. Means within harvest methods followed by the same letter are not significantly different with least significant differences test ($P < 0.05$) (SAS Institute 1985).

Corn root systems, averaged across infestation levels, were smaller from plants grown in the silty clay loam soil compared with the other two soil textures on the first three sampling dates and were significant on 18 June ($F = 15.31$; df = 2, 6; $P < 0.05$) and on 2 July ($F = 5.20$; df = 2, 6; $P < 0.05$) (Fig. 4A). On 2 July, roots from the silty clay loam averaged 8.4 g dry weight compared with 12.4 g for roots from the loam soil. Root biomass did not differ significantly among the soil texture treatments on 16 July (Fig. 4A). However, the infestation × soil texture interaction ($F = 2.83$; df = 6, 18; $P < 0.05$) occurred because of a low root weight for the sandy loam soil with 500 eggs per 30.5 row-cm (Fig. 5A). Root biomass among the soil textures was similar in the uninfested, 200, and 1,000 eggs per 30.5-row-cm treatments, therefore no biological basis could be identified for this interaction. The soil moisture × soil tex-

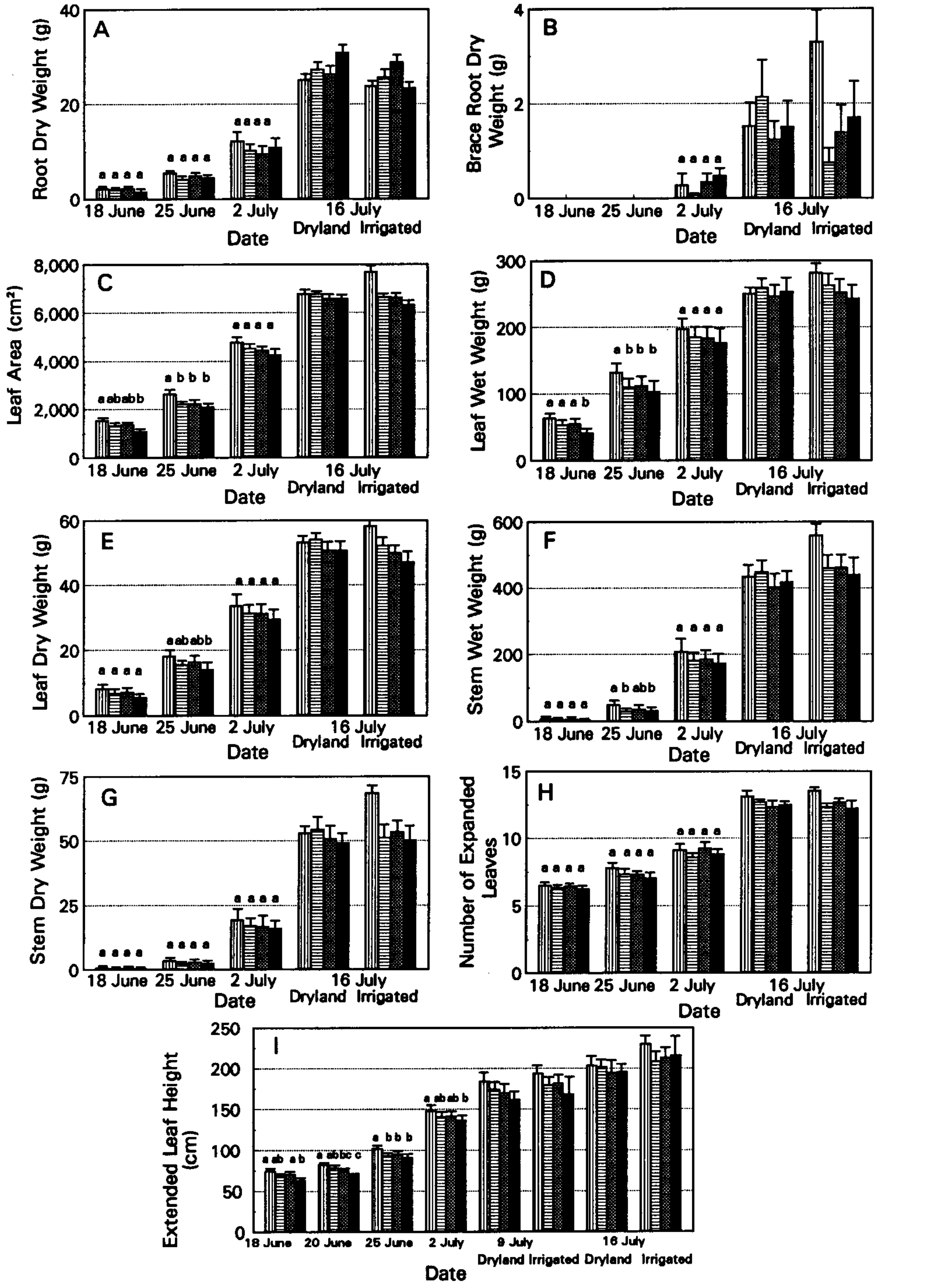

Fig. 3. Vegetative biomass (mean ± SEM) in 1990 for western corn rootworm infestation treatments and irrigation treatments (16 July only) (9 July and 16 July for corn growth data): ▥, uninfested; ▤, 200 eggs per 30.5 row-cm; ▩, 500 eggs per 30.5 row-cm; ■, 1,000 eggs per 30.5 row-cm. (A) Root dry weight. (g) (B) Brace root dry weight (g). (C) Leaf area (cm²). (D) Leaf wet weight (g). (E) Leaf dry weight (g). (F) Stem wet weight (g). (G) Stem dry weight (g). (H) Corn growth (number of fully expanded leaves). (I) Corn extended leaf height (cm). Means within sample dates followed by the same letter are not significantly different with least significant differences test ($P < 0.05$) (SAS Institute 1985).

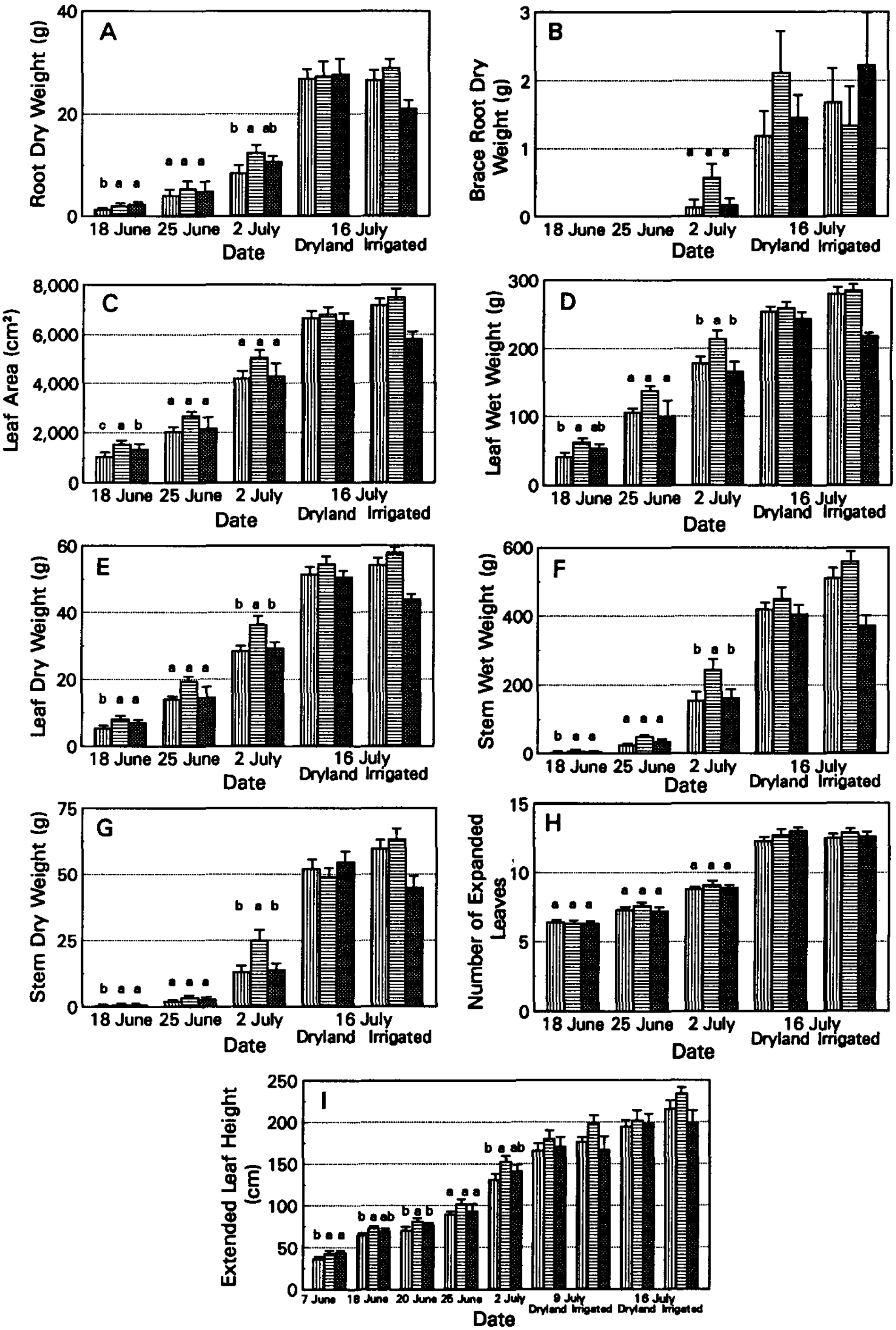

Fig. 4. Vegetative biomass (mean ± SEM) in 1990 for soil texture treatments and irrigation treatments (16 July only) (9 July and 16 July for corn growth data): ▥, silty clay loam; ▤, loam; ▩, sandy loam. (A) Root dry weight (g). (B) Brace root dry weight (g). (C) Leaf area (cm^2). (D) Leaf wet weight (g). (E) Leaf dry weight (g). (F) Stem wet weight (g). (G) Stem dry weight (g). (H) Corn growth (number of fully expanded leaves). (I) Corn extended leaf height (cm). Means within sample dates followed by the same letter are not significantly different with least significant differences test ($P < 0.05$) (SAS Institute 1985).

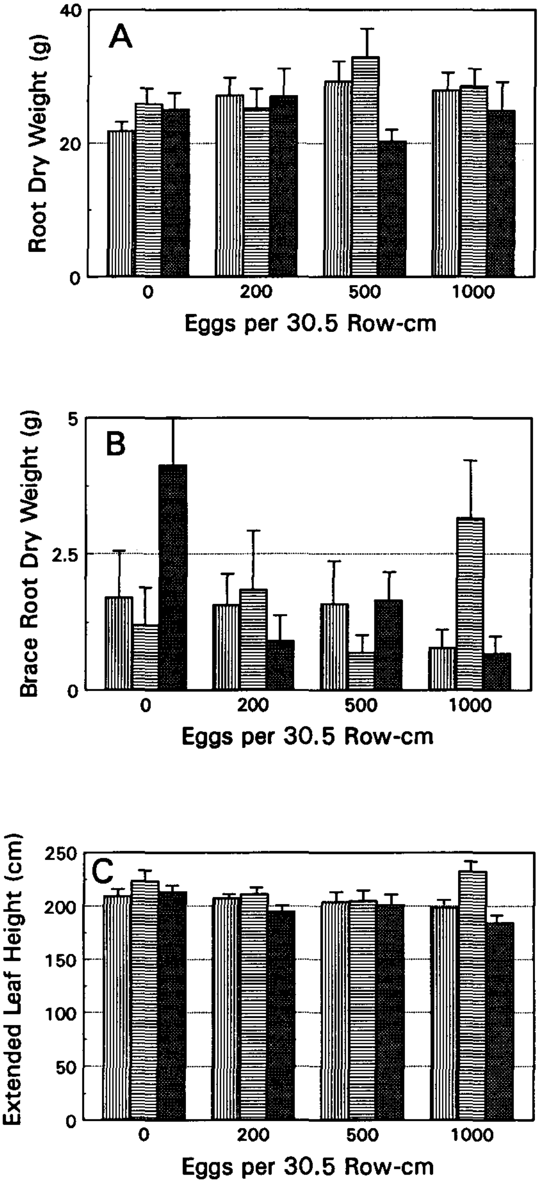

Fig. 5. Vegetative biomass (mean ± SEM) in 1990; interaction of western corn rootworm infestation level with soil texture on 16 July: ▥, silty clay loam; ▤, loam; ▩, sandy loam. (A) Root dry weight (g). (B) Brace root dry weight (g). (C) Corn extended leaf height (cm).

ture and infestation × soil moisture × soil texture interactions were not significant, as well as the soil moisture main effect (27.3 g in dryland and 25.5 g in irrigated).

Brace root development had not occurred on 18 and 25 June. However, on 2 July, brace root dry weight was not significantly affected by infestation level and ranged from 0.07 to 0.48 g per plant (Fig. 3B). On the last sampling date, brace root biomass was significantly affected by the interaction between infestation level and soil moisture ($F = 3.54$; df = 3, 18; $P < 0.05$). Irrigation, compared with dryland conditions, stimulated brace root development in uninfested plants (3.3 g compared with 1.5 g) (Fig. 3B). With slight root injury (200 eggs per 30.5 row-cm), brace root biomass was significantly greater in the dryland than in the irrigated treatment. The plants apparently responded to the soil moisture deficit coupled with slight root injury by producing brace root tissue. With more severe root injury, brace root weight did not differ between the irrigation treatments; the plants were either unable to respond with brace root development to the lack of soil moisture, or more likely, brace root development was delayed until after this last sampling date (2 wk after the cessation of feeding).

Brace root weights ranged from 0.14 to 0.57 g per plant over the soil texture treatments on 2 July (Fig. 4B). On 16 July, there was a significant interaction ($F = 4.19$; df = 6, 18; $P < 0.05$) between infestation level and soil texture on brace root development. In uninfested plants, brace root dry weight in the sandy loam soil was more than twice that in the silty clay loam or loam soil; however, in the infested treatments, brace root biomass was generally low in the sandy loam soil (Fig. 5B). Moreover, brace root development in the loam soil (1,000 eggs per 30.5 row-cm treatment) was >3 times the biomass in the other textures. The soil moisture main effect, soil moisture × soil texture, and three-way interaction were not significant.

Leaf Area. Total leaf area per plant was significantly affected by western corn rootworm density on 18 June ($F = 3.88$; df = 3, 18; $P < 0.05$) and on 25 June ($F = 3.86$; df = 3, 18; $P < 0.05$). On 18 June, leaf area of uninfested plants was significantly greater than plants stressed by the high infestation (Fig. 3C). On 25 June, primarily second and third instars were present, leaf areas of uninfested plants were significantly greater than plants from all three infestation regimes. The larval infestations resulted in a 17.4% reduction in leaf area. On the final sampling date, western corn rootworm infestation level interacted significantly ($F = 3.30$; df = 3, 18; $P < 0.05$) with soil moisture on corn leaf area. Plants in the uninfested treatment averaged 7,681.9 ± 468.1 and 6,780.4 ± 217.8 cm^2 in the irrigated and dryland treatments, respectively (i.e., a 901.5-cm^2 increase with irrigation) (Fig. 3C). Plants from plots infested with western corn rootworms did not respond with leaf area to the added soil moisture and, in fact, in two of the three infestation densities, plants from the irrigated treatments had slightly less leaf area than those from the dryland treatment. These results indicate that corn rootworm-induced root injury inhibited the plant from utilizing the supplemental soil moisture.

Significant effects from soil texture on leaf area were seen on 18 June ($F = 18.54$; df = 2, 6; $P < 0.05$), because the three textures differed significantly from each other (Fig. 4C). Leaf area was greatest in the loam soil, intermediate in the sandy loam soil, and lowest in the silty clay loam soil. No significant effects from soil texture were identified on 25 June, but the trends were similar to those on the previous date. On 2 July, significant interaction effects on leaf area ($F = 2.92$; df = 6, 18; $P < 0.05$) were found between western corn rootworm infestation level and soil texture (Fig. 6A). Leaf area in the silty clay loam and loam soil textures was generally low and high, respectively, across the infestation levels; whereas, leaf area declined with increasing larval density in the sandy loam soil. The biological basis for this interaction is unclear. Leaf area was also significantly ($F = 7.90$; df = 2, 6; $P < 0.05$) affected by soil texture on 16 July. Plants from the sandy loam soil had significantly less leaf area than plants from the silty clay loam or loam soils (Fig. 4C). No significant differences were seen between the irrigated (6,809.2 ± 187.9 cm^2 leaf area) and dryland (6,681.5 ± 126.9 cm^2 leaf area) treatment main effects.

Vegetative Biomass. Corn leaf wet weight was significantly affected by western corn rootworm infestation level on 18 June ($F = 3.23$; df = 3, 18; $P < 0.05$) and 25 June ($F = 4.22$; df = 3, 18; $P < 0.05$). On 18 June, leaf biomass in plants from the high infestation was significantly less than the biomass in the uninfested and two lower infestation rates (Fig. 3D). Leaf wet weight on 25 June in all three western corn rootworm infestation treatments were significantly less than that in the uninfested and averaged 108.2 g in the infested treatments compared with 131.2 g for the uninfested treatment (Fig. 3D). On 2 July, leaf wet weights did not differ significantly among the infestation regimes. Following the inclusion of the soil moisture effect (16 July), a significant interaction ($F = 3.77$; df = 3, 18; $P < 0.05$) was found between infestation level and soil moisture (Fig. 3D). The analysis and interpretation of this interaction is the same as with the leaf area parameter. Apparently, the root injury inhibited the plants from utilizing the supplemental soil moisture and from manifesting this irrigation as increased leaf biomass.

Soil texture had a significant effect on corn leaf wet weight on 18 June ($F = 9.88$; df = 2, 6; $P < 0.05$). On this date, leaf biomass was significantly higher from plants in the loam soil compared with plants from the silty clay loam texture (Fig. 4D). Soil texture had no significant effects on leaf biomass on 25 June; however, significant effects were again seen among the soil textures on 2 July ($F = 6.18$; df = 2, 6; $P < 0.05$) and on 16 July ($F = 7.32$; df = 2, 6; $P < 0.05$). In addition, the interaction between soil moisture and soil texture was significant ($F = 4.68$; df = 2, 6; $P < 0.05$). The plant benefited from irrigation (with more leaf biomass) in the silty clay loam and loam soil textures; however, in the sandy loam soil, plants grown without irrigation produced more leaf tissue than those grown with irrigation (Fig. 4D). Leaf wet weight values for the soil moisture treatments were 259.9 ± 6.8 and 252.4 ± 5.3 g for the irrigated and dryland, respectively.

Trends for leaf dry weight were similar to those of the leaf wet weight data. On 18 June, no significant differences were found among the

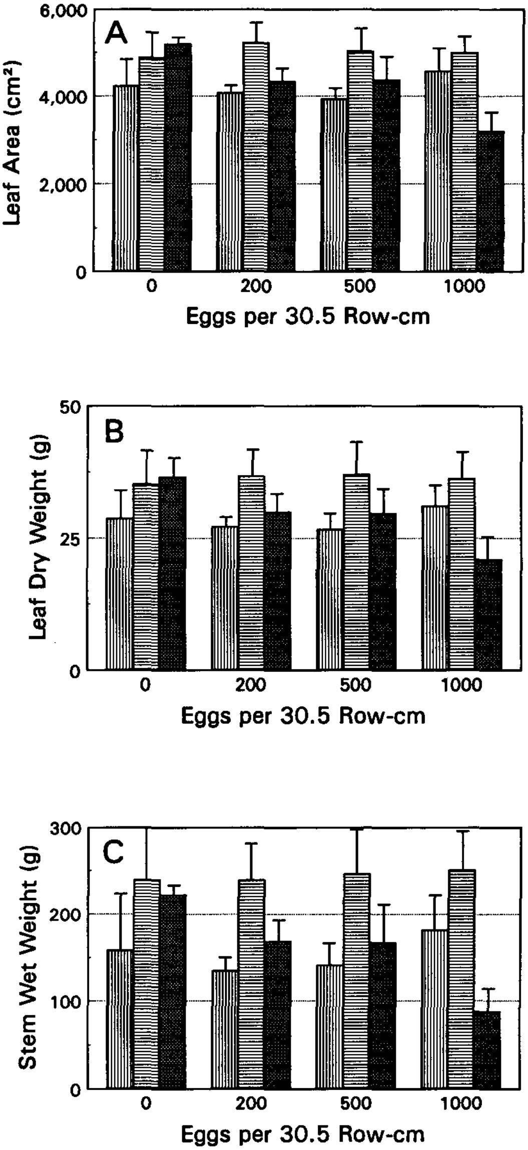

Fig. 6. Vegetative biomass (mean ± SEM) in 1990; interaction of western corn rootworm infestation level with soil texture on 2 July: ▥, silty clay loam; ▤, loam; ▩, sandy loam. (A) Leaf area (cm^2). (B) Leaf dry weight (g). (C) Stem wet weight (g).

four western corn rootworm treatments (Fig. 3E); however, the trends were similar to those for the leaf wet weight data. Leaf dry weight averaged 8.2 g from plants in the uninfested treatment compared with only 5.6 g in the 1,000 eggs per 30.5-row-cm treatment. On the second sampling date, leaf dry weight was significantly ($F = 3.33$; df = 3, 18; $P < 0.05$) greater in the uninfested plants (18.1 g) than in plants from the 1,000 eggs per 30.5-row-cm treatment (the other two treatments were intermediate). On 16 July, leaf dry weight was significantly affected by western corn rootworm infestation level ($F = 4.46$; df = 3, 18; $P < 0.05$). Leaf weights of uninfested plants were significantly greater than those of plants from the two highest infestation levels and similarly, the 200 and 1,000 eggs per 30.5-row-cm treatments differed (Fig. 3E). The range of the differences was 9.0 g (56.2 compared with 47.2 g).

The soil texture main effect significantly ($F = 10.81$; df = 2, 6; $P < 0.05$) affected corn leaf dry weight on 18 June in a manner similar to the leaf wet weight (Fig. 3D). Dry weight values were significantly lower in the silty clay loam than in the sandy loam or loam textures. No significant differences in leaf dry weights were noted among the soil textures on 25 June. However, on the 2 July sampling date, the leaf weight in the loam soil was significantly ($F = 5.29$; df = 2, 6; $P < 0.05$) greater than in the other two textures, and on 16 July, the dry weight biomass from plants in the loam and silty clay loam soil were significantly ($F = 7.98$; df = 2, 6; $P < 0.05$) greater than in the sandy loam soil. A significant interaction ($F = 2.84$; df = 6, 18; $P < 0.05$) for the leaf dry weight parameter was detected between infestation level and soil texture on 2 July (Fig. 6B). In the loam soil texture, leaf weights were universally high across the infestation levels and conversely, the values were generally low in the silty clay loam soil. However, in the sandy loam soil, the leaf dry weight values decreased with increasing larval density from 36.5 g in the uninfested to 21.0 g in the 1,000 eggs per 30.5-row-cm treatment. The soil moisture main effect and interaction terms with soil moisture were not significant.

Corn stem biomass (wet weight) was significantly reduced by western corn rootworm larval injury on 25 June ($F = 3.21$; df = 3, 18; $P < 0.05$). Stem wet weight was reduced by an average of 27.9% in infested plants (all three levels) compared with uninfested plants (Fig. 3F). On 16 July, a significant interaction occurred between western corn rootworm level and soil moisture ($F = 3.58$; df = 3, 18; $P < 0.05$). In the uninfested treatment, the soil moisture from irrigation resulted in a 124.8-g increase in stem wet weight compared with the dryland treatment (Fig. 3F). Increases of similar magnitude were not recorded in the western corn rootworm-infested plots; stem wet weight values were very similar among the infestation levels.

Soil texture significantly ($F = 10.80$; df = 2, 6; $P < 0.05$) affected stem dry weight on 18 June but not on 25 June (Fig. 4F). Stem weight was reduced in plants from the sandy loam soil compared with plants from the other two soil textures. On 2 July, a significant ($F = 3.32$; df = 6, 18; $P < 0.05$) interaction was found between infestation level and soil texture on the stem wet weight parameter. Graphically, this interaction was similar to the interactions seen with leaf area and leaf dry weight (Fig. 6C). Stem wet weight, in the sandy loam soil, decreased significantly with increasing infestation density (from 221.8 g per plant for the uninfested to 87.7 g per plant for the 1,000 eggs per 30.5-row-cm treatment), whereas stem weight did not respond to increasing density in the loam soil. Results were erratic in the silty clay loam soil. On 16 July, significant interactions occurred between soil moisture and soil texture ($F = 5.31$; df = 2, 6; $P < 0.05$). The soil moisture from irrigation resulted in a substantial increase in stem weight (averaging 99.5 g) in the silty clay loam and loam soils (Fig. 4F). Similar results were not noted in the sandy loam soil. The soil moisture main effect was also significant ($F = 6.83$; df = 1, 6; $P < 0.05$) on 16 July and the stem wet weight was greater in the irrigated treatment (478.7 ± 19.7 g) than in the dryland treatment (425.1 ± 15.6 g).

Stem dry weight was not significantly affected by western corn rootworm infestation level on 18 and 25 June and 2 July; however, trends in stem dry weight were similar to the stem wet weight data (Fig. 3G). Plants from the 1,000 eggs per 30.5-row-cm treatment consistently had the lowest stem dry weight among the four treatments. On 16 July, a significant interaction was found between soil moisture and infestation density ($F = 3.59$; df = 3, 18; $P < 0.05$). Analysis of this interaction was very similar to that shown with the same interaction terms on stem wet weight (Fig. 3F).

Stem dry weight was significantly affected by soil texture on 18 June ($F = 5.38$; df = 2, 6; $P < 0.05$) and on 2 July ($F = 6.32$; df = 2, 6; $P < 0.05$). On the first date, dry weights were significantly higher in the loam and silty clay loam soils than in the sandy loam soil (Fig. 4G). Weights differed by >2 times over the soil textures. On 2 July, stem weights were significantly higher from plants in the loam soil compared with the other two soil textures. On 16 July, a significant interaction was found between soil moisture and soil texture ($F = 10.27$; df = 2, 6; $P < 0.05$). As with stem wet weight, irrigation enhanced stem dry weights in the loam and silty clay loam soils, whereas the opposite result was found in the sandy loam soil.

Percentage Moisture. Corn leaf tissue percentage moisture was significantly ($F = 4.36$; df = 3,

18; $P < 0.05$) affected by larval injury on 18 June. Differences were slight; however, the percentage moisture was significantly lower in plants stressed by larvae from the 1,000 eggs per 30.5-row-cm treatment (86.4 ± 0.2%) than in the other three treatments (an average of 87.1 ± 0.2%). Percentage moisture in the stem tissue was not affected by infestation regime and averaged 88.2 ± 2.1%. Percentage moisture in the leaf tissue was not affected by infestation level on 25 June; however, western corn rootworm density significantly ($F = 5.50$; df = 3, 18; $P < 0.05$) affected the percentage moisture in the stem tissue. Values were significantly lower in the 500 eggs per 30.5-row-cm treatment (91.6% ± 0.3) compared with the uninfested, 200, and 1,000 eggs per 30.5-row-cm treatments (92.4 ± 0.2%). On 2 July, infestation level had no significant effects on percentage moisture (leaf or stem). Western corn rootworm infestation level had significant ($F = 5.50$; df = 3, 18; $P < 0.05$) effects on percentage leaf moisture on 16 July but no significant effects on stem percentage moisture. Plants injured by the highest larval density had significantly greater leaf moisture than plants from the lowest infestation density and from the uninfested treatment, whereas leaf moisture from plants from the 500 eggs per 30.5-row-cm treatment was significantly greater than that from uninfested plants.

The soil texture treatments had no significant effects on percentage moisture in leaf or stem tissues on 18 and 25 June and 2 July. Soil moisture significantly affected leaf percentage moisture ($F = 10.74$; df = 1, 6; $P < 0.05$) and stem percentage moisture ($F = 29.38$; df = 1, 6; $P < 0.05$) on 16 July. Percentage moisture in each tissue was altered by ≈0.7%. In addition, a significant interaction ($F = 18.27$; df = 2, 6; $P < 0.05$) occurred between soil moisture and soil texture on percentage stem tissue moisture. In the irrigated treatments, the percentage moisture averaged 88.6 ± 0.2% across the soil textures. In contrast, in the dryland treatment, the percentage stem moisture varied with the soil texture from a high of 89.1 ± 0.3% for plants from the loam soil to 86.8 ± 0.3% for plants from the sandy loam soil.

Plant Development. Corn plant development, recorded as the number of fully emerged leaves, was not significantly affected by infestation level on 18 and 25 June and 2 July (Fig. 3H). Plants averaged 6.4 ± 0.2, 7.4 ± 0.2, and 8.9 ± 0.2 leaves on 18 June, 25 June, and 2 July, respectively. However, on 16 July, western corn rootworm level significantly ($F = 3.96$; df = 3, 18; $P < 0.05$) affected corn development. Uninfested plants were significantly more developed (by about one leaf) than those from the rootworm infestation treatments. Moreover, the infestation level had no significant effects on the number of senesced leaves on any of the four sampling dates.

Corn plant development was not significantly affected by soil texture on 18 and 25 June and 2 and 16 July (Fig. 4H). In addition, soil moisture had no significant effects on corn development on 16 July. Soil texture significantly ($F = 5.35$; df = 2, 6; $P < 0.05$) affected the number of senesced leaves only on 25 June; the number of dried leaves was significantly greater in the sandy loam soil texture than in the other two textures.

Plant Height. Corn height was recorded seven times at about weekly intervals from 7 June to 16 July. The initial date was before western corn rootworm egg hatch. On each of the subsequent dates, the infestation level significantly affected corn extended leaf height (18 June: $F = 3.78$; df = 3, 18; $P < 0.05$, 20 June: $F = 4.46$; df = 3, 18; $P < 0.05$, 25 June: $F = 4.98$; df = 3, 18; $P < 0.05$, 2 July: $F = 3.28$; df = 3, 18; $P < 0.05$, 9 July: $F = 11.00$; df = 3, 18; $P < 0.05$, and 16 July: $F = 3.45$; df = 3, 18; $P < 0.05$). On 18 June, plant heights from the 1,000 eggs per 30.5-row-cm treatment differed significantly (a 15.6% decrease) from both the 500 eggs per 30.5-row-cm and the uninfested treatments (Fig. 3I). Plant heights averaged 82.4 cm (uninfested), 78.8 cm (200 eggs per 30.5 row-cm), 75.1 cm (500 eggs per 30.5 row-cm), and 69.0 cm (1,000 eggs per 30.5 row-cm) on 20 June. These trends (i.e., plants from infested treatments being shorter than plants from the uninfested treatment) continued through the 16 July sampling date. At this time, the height of plants from infested plots averaged 5.3% less than plants from uninfested plots.

Soil texture significantly influenced extended plant height on six of the seven sampling dates (7 June: $F = 13.48$; df = 2, 6; $P < 0.05$, 18 June: $F = 7.11$; df = 2, 6; $P < 0.05$, 20 June: $F = 5.99$; df = 2, 6; $P < 0.05$, 2 July: $F = 6.77$; df = 2, 6; $P < 0.05$, 9 July: $F = 5.44$; df = 2, 6; $P < 0.05$, and 16 July: $F = 24.86$; df = 2, 6; $P < 0.05$). On 7 June, plants from the sandy loam and loam soils were significantly taller than those from the silty clay loam soil (Fig 4I). Thereafter, plant growth in the sandy loam soil was slower than in the other soils, such that on 2 July, plants from the sandy loam and silty clay loam soils did not differ significantly. Significant interactions were found between soil texture and soil moisture on 9 July ($F = 5.50$; df = 2, 6; $P < 0.05$) and on 16 July ($F = 6.18$; df = 2, 6; $P < 0.05$). Plants responded, in terms of plant height, to irrigation in the silty clay loam soil (9 July) and in the silty clay loam and loam soils (16 July); however, no plant response was seen in the sandy loam soil. In addition on 16 July, a significant interaction ($F = 4.92$; df = 6, 18; $P < 0.05$) occurred between soil texture and infestation level; as the infestation level increased, the plant height generally remained constant, decreased, and increased (especially at 1,000 eggs per 30.5 row-cm) for the silty clay loam, sandy loam, and loam soil textures, respectively (Fig. 5C). The soil moisture

Table 3. Yield components, average number of kernels per plant, and average kernel weight (± SEM) from single-plant and 4-m-row section samples, 1990

Treatment[a]	Single-plant samples		4-m-row samples	
	No. kernels	Kernel wt, g	No. kernels	Kernel wt, g
		Western corn rootworm treatment		
0	805.1 (11.7)a	0.251 (0.004)a	11,526.0 (435.5)a	0.245 (0.005)a
200	792.4 (13.0)a	0.247 (0.004)a	10,343.3 (425.1)b	0.233 (0.006)b
500	798.6 (11.4)a	0.253 (0.004)a	9,104.3 (385.3)c	0.229 (0.006)b
1,000	753.8 (14.5)a	0.225 (0.005)b	7,083.0 (418.9)d	0.216 (0.007)c
		Soil texture		
Silty clay loam	792.5 (11.1)a	0.245 (0.004)a	9,006.8 (580.1)a	0.243 (0.005)a
Loam	800.8 (9.6)a	0.240 (0.003)a	9,897.0 (434.1)a	0.219 (0.005)a
Sandy loam	768.1 (12.3)a	0.245 (0.004)a	9,638.6 (397.5)a	0.231 (0.006)a
		Soil moisture		
Irrigated	768.5 (8.5)a	0.241 (0.003)a	9,654.4 (418.2)a	0.234 (0.005)a
Dryland	806.9 (9.4)a	0.247 (0.003)a	9,373.9 (361.3)a	0.227 (0.006)a

Means within columns followed by the same letter are not significantly different with least significant differences test ($P < 0.05$) (SAS Institute 1985).

[a] Number of western corn rootworm eggs per 30.5 row-cm.

main effect was significant on 16 July ($F = 12.82$; df = 1, 6; $P < 0.05$); the corn extended leaf height was increased 8.1% by the irrigation.

Reproductive Biomass. Western corn rootworm infestation level had significant ($F = 4.89$; df = 3, 18; $P < 0.05$) effects on corn yield based on single-plant harvests in 1990 (Fig. 2B). Grain yield was significantly reduced in the 1,000 eggs per 30.5-row-cm treatment (172.4 g per plant) compared with the other three treatments (average of 200.5 g per plant). Soil moisture (199.9 and 187.1 g per plant for the dryland and irrigated treatments, respectively) and soil texture (195.8, 193.8, and 190.4 g per plant for the silty clay loam, loam, and sandy loam treatments, respectively), as well as all interactions, were not significant.

Yield losses, in the single plant samples, from corn rootworm injury appeared to result from a reduction in individual kernel size rather than from a reduction in kernel number (Table 3). Kernel number per plant was not significantly affected by any of the main effects or interactions. Kernel weight was significantly ($F = 8.70$; df = 3, 18; $P < 0.05$) influenced by western corn rootworm level. Kernels from plants stressed by larvae from the 1,000 eggs per 30.5-row-cm treatment averaged 0.225 g compared with 0.251 g for the other three treatments. The number of kernels per plant tended to be lower associated with the 1,000 eggs per 30.5-row-cm treatment (753.8 per plant) but did not differ significantly from the other three treatments (798.7 per plant). Soil moisture and soil texture and all interactions had no significant effects on kernel weight or kernel number.

Grain yield, based on harvested 4-m-row sections, was significantly ($F = 57.09$; df = 3, 18; $P < 0.05$) affected by western corn rootworm density; the yield per 4-m-row section gradually decreased (from 2.7 to 1.6 kg) as the infestation density increased (Fig. 2B). However, there was also a significant ($F = 3.15$; df = 6, 18; $P < 0.05$) interaction between infestation density and soil texture. The yield response to infestation density was more apparent in the silty clay loam texture than in the other two soil textures (Fig. 7A). In the silty clay loam soil, grain yield decreased significantly from 2.85 to 1.30 kg per 4-m row as

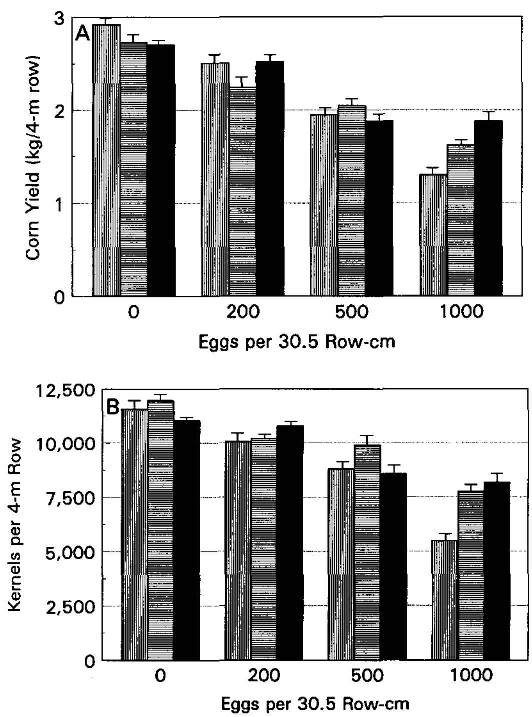

Fig. 7. Interaction of western corn rootworm infestation level and soil texture (mean ± SEM): ▥, silty clay loam; ▤, loam; ▩, sandy loam. (A) Corn grain yield. (B) Number of kernels from 4-m-row section samples in 1990.

the larval density increased from the uninfested to the 1,000 eggs per 30.5-row-cm treatment. In the loam and sandy loam soil textures, the yield response to injury was much less than in the silty clay loam soil and averaged 27.1% yield loss across the infestation densities. Corn yield was not significantly influenced by the other main effects or interactions. Treatment means were 2.2 kg for all three soil texture treatments and 2.3 and 2.1 kg for the irrigated and dryland treatments, respectively.

Western corn rootworm infestation density significantly affected kernel number (F = 46.49; df = 3, 18; P < 0.05) and kernel weight (F = 10.45; df = 3, 18; P < 0.05) in the 4-m-row section samples (Table 3). Kernel number was significantly highest in the uninfested treatment at 11,526 kernels per 4-m row; each successively higher infestation level produced a significantly lower kernel number. Plots infested with the 1,000 eggs per 30.5-row-cm treatment averaged only 7,083 kernels per 4-m-row section (the average number of plants per 4-m row did not differ significantly among the treatments). Kernel weight was significantly higher in the uninfested treatment (0.245 g), intermediate in the 200 and 500 eggs per 30.5-row-cm treatments (0.231 g), and lowest in the 1,000 eggs per 30.5-row-cm treatment (0.226 g). Soil texture, soil moisture, and all interactions were not significant for the average kernel weight variable, whereas the soil texture × infestation level was significant (F = 3.01; df = 6, 18; P < 0.05) for the number of kernels per 4-m-row section. Analysis of this interaction was similar to that on the yield parameter (Fig. 7B). Kernel number declined gradually as infestation level increased in the silty clay loam soil. In the loam and sandy loam soils, kernel number was similar for the 200 and 500 eggs per 30.5-row-cm and for the 500 and 1,000 eggs per 30.5-row-cm treatments, respectively.

Discussion

Injury from controlled populations of western corn rootworm larvae had significant effects on vegetative and reproductive biomass accumulation in 1989 and 1990. During both years, vegetative biomass (leaf and stem) was reduced, coinciding with injury from the first and second instars. However, the plants appeared to compensate for the injury during the period of peak feeding and during the period following injury. In 1989, the biomass of severely injured plants exceeded that of the uninjured plants and in 1990, the biomass of the injured and uninjured plants equilibrated. Belsky (1986), referring to defoliation injury, defined the type of responses observed in 1989 and 1990 as overcompensation and compensation, respectively. The difference in the response may be related to the plant size during the injury period (although there are other plausible explanations such as environmental effects). Because of late infestation timing in 1989 (16 d after planting), the uninjured plants averaged 8,350 cm^2 leaf tissue and 62.7 g dry weight leaf tissue during peak larval injury. In contrast, in 1990 during the peak injury period, the uninjured plants averaged only 4,761.3 cm^2 leaf tissue and 33.5 g dry weight leaf tissue. Therefore, the plants in 1989, with nearly twice the photosynthetically active tissue compared with plants in 1990, may have been able to respond better to the larval-induced stress. These results contrast with those of Spike & Tollefson (1991). They found reductions in corn leaf area index (indicative of plant leaf area) from rootworm injury but no compensatory response through 88 d after infestation. In our study, compensatory responses from rootworm injury were also seen with leaf as well as stem and root tissues. Tissue (leaf and stem) moisture content was generally not affected by larval injury. These data are in agreement with the results from a greenhouse study of Riedell (1990).

These data parallel the photosynthetic rate data from western corn rootworm injured plants (Godfrey et al. 1993). Photosynthetic rates of injured plants in 1989 were generally higher than those of uninjured plants during the peak injury period (rates were initially reduced by the injury). In 1990, photosynthetic rates were reduced by injury from early corn rootworm instars, and during the peak injury period, the rates of injured and uninjured plants were equal.

The compensatory response of vegetative tissue appears to be at the expense of the reproductive tissue. During both years, rootworm injury reduced corn grain yield. In 1989, yield reductions averaged 10.6 and 7.5% for the 500 and 1,000 eggs per 30.5-row-cm treatments, respectively. Yield reductions were more severe in 1990 with 19.0% (500 eggs per 30.5 row-cm) and 29.8% (1,000 eggs per 30.5 row-cm) losses. This magnitude of yield loss was similar to that reported by Sutter et al. (1990) and Spike & Tollefson (1989a, b); however, our root damage ratings were considerably lower (indicating less damage) than those reported in these previous studies for similar infestation densities. Yield reductions in 1990 were the result of a combination of reduction in kernel weight and number of kernels per plant. The reduction in kernel number per plant is frequently associated with environmental stress to the plant near the time of silking and pollination (R1 stage; Ritchie et al. 1986). Stress from larval injury may also reduce kernel number. The reduction in kernel weight likely occurred because of a limitation of photosynthate movement into the developing kernels. Western corn rootworm larval injury apparently disrupted the translocation/availability of photosynthates into the kernels. The production of photosynthates, based on single leaf instantaneous values,

was not affected by larval injury near the time of corn pollination in 1990 (Godfrey et al. 1993).

Corn rootworm larval injury inhibited the plant from utilizing supplemental soil moisture from irrigation for the production of aboveground vegetative biomass. Leaf and stem tissue biomass of the injured plants was similar in irrigated and dryland conditions. This was in contrast to the uninjured plants which consistently had more biomass for the irrigated than the dryland treatments. Root biomass production (injured plants) was generally greater in the dryland soil than the irrigated state, and results with brace root production were erratic. Grain production was not significantly affected by soil moisture and the interaction effects of soil moisture and infestation level were not significant. Following the end of the experiment on vegetative biomass accumulation in 1990 (16 July), adequate precipitation occurred which negated the moisture deficit conditions.

Corn rootworm interaction effects with soil texture were noted on several vegetative biomass parameters and also on grain yield (4-m-row samples). Plant vegetative response to larval densities was most pronounced in the sandy loam texture, whereas the grain yield responded to infestation level most noticeably in the silty clay loam soil.

These results on vegetative and reproductive tissue biomass accumulation along with the plant physiological response (Godfrey et al. 1993) provide insights into corn plant response to western corn rootworm larval injury. This interaction may be more fully explained through coupling rootworm injury into plant computer simulation models. In addition, generalized plant response to root injury, an area not previously examined in detailed studies, may be better explained because of these results.

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