Effect of Larvae of Western Corn Rootworm (Coleoptera: Chrysomelidae) and of Mechanical Root Pruning on Sap Flow and Growth of Corn

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ABSTRACT Little information is available on the growth response of corn, *Zea mays* L., to either mechanical root injury or infestation by western corn rootworm, *Diabrotica virgifera virgifera* LeConte. Studies were conducted in the greenhouse to determine growth and sap flow rates in corn when known proportions of the root system were damaged by mechanical root pruning and infestations of corn rootworm larvae. Corn was transplanted into boxes that divided the roots into four sections. Roots in various sections were mechanically pruned or infested with 100 neonate larvae of the western corn rootworm. Sap flow was measured using a heat balance technique, and root and shoot growth were measured. Mechanical pruning of roots decreased sap flow, fresh and dry weight of stalks and roots, and plant height. Infesting roots with rootworm larvae did not significantly affect sap flow, fresh or dry weight of stalks, or plant height. Fresh and dry weights of roots were reduced in boxes infested with rootworm larvae.

KEY WORDS Insecta, *Diabrotica virgifera virgifera*, root pruning, sap flow

MORE INSECTICIDE IS USED to control *Diabrotica* spp. than for any other insect pest in the province of Ontario (Moxley 1989). However, Sutter et al. (1989) have reported that root protection in corn, *Zea mays* L., by insecticides is highly variable and is dependent on year and population density. Until improved methods of monitoring are available or until we know more about the interactions of corn plants and corn rootworms, however, prophylactic insecticide use may be the optimal strategy for control (Foster et al. 1986).

The effect of root damage by the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, on corn plant physiology and growth has received little attention. Western corn rootworm larvae feed on the nodal (primary adventitious) roots and lateral (secondary adventitious) roots. Kahler et al. (1985) reported root damage by western corn rootworm caused significant and complex effects on nutrient accumulation in shoot tissues and grain. They also suggested that root pruning may interact with soil fertility to affect yields. Spike & Tollefson (1989) reported that rootworm feeding can lead to disruption of phenology in reproductive organs of corn and that root injury may interfere with nitrogen uptake. In a detailed study of water relations in corn and rootworm feeding, Riedell (1990) reported that rootworm larvae damage roots that contribute little to providing water to the shoots during the period of maximum larval damage. He observed significant effects of rootworm feeding on water relations only when corn plants developed to the tassel stage, and he speculated that observed changes in water potential at this stage were related to stomatal closure, photosynthesis inhibition, decreased solute accumulation, or hormonal imbalance in plants with rootworm damage.

Most reports relating western corn rootworm damage to yield loss in corn are based on comparing grain yield with root damage ratings or egg density of western corn rootworm (Branson et al. 1980, Chiang et al. 1980, Spike & Tollefson 1989). It has been suggested, however, that excessive precipitation during larval establishment may affect larval survival and root damage (Spike & Tollefson 1988, Sutter et al. 1989).

Mechanical root pruning has been used to establish known levels of root injury in simulating rootworm feeding damage. Landis (1988) reported on the effect of mechanical injury to corn seedlings in studies that simulated feeding by the southern corn rootworm, *D. undecimpunctata howardi* Barber. The effect of mechanical root pruning on above-ground growth in corn has been described by Spencer (1941) and Fitzgerald et al. (1968). Whitfield (1992) conducted field trials using mechanical root pruning to simulate rootworm damage and reported that during ideal growing conditions, plants are able to withstand a short period of limited root pruning with minimal effect on yield but that during periods of

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drought, plants are less able to recover from root damage. Riedell (1990) compared feeding injury by western corn rootworm to mechanical root pruning and reported that mechanical root pruning had a much greater effect on relative water content, leaf water potential, and stomatal conductance in corn.

A major obstacle in studies on the effect of rootworm damage to corn is the difficulty in inflicting root damage to known amounts of root mass. Assessment of root damage also requires that the root system be removed from the soil and evaluated for pruning damage (Branson 1986). Tan et al. (1981) described a method of growing tomato plants in sectional root boxes to provide for known proportions of the root system to be treated separately. This technique was also useful for growing corn plants with divided root systems for physiological studies (Gavloski et al. 1992). In this paper, we report on the use of this technique for providing information on the growth and sap flow rates in greenhouse-grown corn plants when known proportions of the root system are mechanically pruned or infested with western corn rootworm larvae.

Materials and Methods

Two experiments were conducted in a 1990 greenhouse study. One involved mechanical root pruning and the other infestation by western corn rootworm. The design for each experiment was a randomized complete block.

General Methodology. The greenhouse was maintained at 25–28°C during the day and not <17°C during night hours. No supplementary lighting was supplied. One corn seed ('Pioneer' corn hybrid 3707) was planted in each of 20 plastic pots (12.7 cm diameter [five-in standard]) containing a 1:1 mix of sandy loam soil and peat moss. Plants were fertilized 14 d after planting with Peters general purpose 20-20-20 (N-P-K) fertilizer (J. R. Johnson, St. Paul, Minn.). Root boxes were prepared to transplant corn according to Tan et al. (1981). Plastic bags (82.7 by 36 cm) used to line the root-boxes were cut to a length of 60 cm, and five holes (1.0 cm diameter) were made with a cork borer approximately 2 cm from the bottom and spaced 2–3 cm apart on each side of the bag. One bag was placed in each section of the box, and the holes were aligned along the bottom of the box for drainage. Plastic flaps extending above the top of each section were folded over the top edges of the wood, and the bags were stapled in place. Plastic bags prevented wood from warping and allowed soil and roots to be removed easily from each section at the completion of the experiment.

Coarse gravel was placed in each section to a depth of ≈2.5 cm, and boxes were then filled to within 5 cm of the top with a steam-sterilized Brookston clay soil (15.5% sand, 46.0% silt, 38.8% clay). Soil was watered daily for 3 d to maintain a slightly moist clay for transplanting. After 21 d, individual corn plants were transplanted into the root boxes following the method of Gavloski et al. (1992), which divided the root system into four sections. Root boxes containing the plants were watered at 1100 hours (EST) every 2–3 d to the drip point at the drainage holes.

To measure sap flow, sap-flow gauges (Dynagage, Dynamax Inc., Houston, Tex.) were attached to plants along the lower stalk. Lower leaves (fourth and fifth from the base) were removed from all plants so stems of plants with attached gauges would be in direct contact with the heater element of the gauge. An electrical insulating compound (Compound #4, Dow Corning, Midland, Mich.) was applied to the area of the stem that would be covered by the gauges and also to the inside of the gauges. As recommended by the manufacturer, the insulating compound was also used to seal any gaps between the plant and upper and lower edges of the gauges. Wire leads attached to the gauges were connected to an AM16 multiplexer (Campbell Scientific Corp., Logan, Utah) which was connected to a CR21X (Campbell) datalogger. The multiplexer allowed data from eight gauges to be processed sequentially by the datalogger. The gauges were powered by an external power source (Elanco Electronics Inc., Wheeling, Ill., model XP750) to maintain 3 V. The rate of sap flow measured by each gauge was recorded by the datalogger every 30 min. General methodology and use of the gauges to measure sap flow has been described by Steinberg et al. (1989).

At the completion of each experiment, plants were severed at ground level, leaves were removed, and the stalks were split lengthwise. The length of each internode from node 4 to 14 (numbered from the base) was measured, and fresh and dry weights of stalks were recorded.

The soil in each root box section was carefully examined to recover any roots. Roots were placed in containers filled with water and soaked overnight to ease the removal of soil. Roots were then washed, and dry weights were determined.

Experiment 1. Effect of Mechanical Root Pruning. Plant height was measured at 48 d of growth to the nearest 0.1 cm as the height from the ground to the top of the leaf with the greatest upward extension. The same day, plants were randomly assigned to one of five root pruning treatments. Plants had no, one, two, three, or four (all) sections of roots pruned using a flat steel blade (6 cm wide) (plane blade by Stanley Corp., Burlington, Ontario) attached to an implement handle. Within a root box section, all roots were pruned by forcing the blade to a depth of 15 cm at a distance of 5 cm from the base of the corn stalk. Two replications per treatment were performed during one time period.

Table 1. Effect of mechanical root pruning on sap flow (mean ± SE), fresh and dry weight of stalks, and percentage water in stalks of corn

Sections pruned[a]	Sap flow (g/h) on d after pruning			Fresh stalk wt, g	Dry stalk wt, g	% Water in stalk
	−1[b]	4	7			
0	58.6a ± 3.28	138.3a ± 8.97	134.2a ± 9.14	354.47a ± 26.579	38.22a ± 1.960	89
1	—	73.2ab ± 5.08	63.6b ± 9.92	277.29b ± 13.958	31.75b ± 2.403	89
2	—	—	—	213.48c ± 7.680	24.14c ± 1.159	89
3	50.7a ± 4.26	62.5b ± 3.93	37.9bc ± 6.13	205.36c ± 10.677	20.55c ± 1.425	90
4	41.4a ± 2.49	36.5b ± 4.18	16.5c ± 1.75	143.31d ± 9.199	9.72d ± 0.922	93

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Tukey's studentized range (HSD) test [SAS Institute 1987]).

[a] Corn seedlings were transplanted into boxes divided into four equal sections. Treatments consisted of mechanical pruning of roots in a certain number of sections.

[b] One day before root pruning.

Sap flow (grams per hour) was measured 1 d before roots were mechanically pruned and each day after pruning until completion of the experiment. A maximum of eight gauges could be used at one time; therefore, sap flow was measured on plants for treatments where 0, 1, 3, and 4 sections of roots were to be pruned.

Plant height was measured 6 and 11 d after root pruning. Gauges were removed 11 d after pruning, and internode lengths and fresh and dry stalk and root weights were measured. A total of four replications was obtained by repeating the study under the same growing conditions.

Experiment 2. Effect of Infestation by Western Corn Rootworm. Eggs of the western corn rootworm were obtained from beetles collected from corn and maintained for egg production using the rearing methods of Branson et al. (1975). Eggs were placed on moist filter paper in Petri dishes, incubated at 25°C, and examined for first hatch every 3–4 d. At peak hatch, larvae ≤1 d old were retained for infestation purposes.

Boxes had no, one, two, three, or four sections each infested with 100 neonate western corn rootworm larvae at 43 d of corn growth. The method of Riedell (1989) for infesting corn plants in the greenhouse with western corn rootworm larvae was followed.

Sap flow gauges were attached to plants 1 d before infestation with rootworm larvae. A maximum of eight gauges could be used at one time, therefore sap flow was measured on two plants in root boxes that had no, one, and four sections infested and on one plant in root boxes that had two and three sections infested.

Plant height was measured the day of rootworm infestation and 6, 13, and 18 d thereafter in the same manner described previously. Sap flow gages were removed 19 d after rootworm infestation, and internode lengths and fresh and dry stalk and root weights were recorded. Nodal root axes were examined before roots were dried for damage by rootworm larvae. Up to 10 nodal root axes in an infested section were examined for pruning, tunneling, or surface feeding caused by the larvae.

The study was repeated under the same growing conditions, but treatments of two or three infested sections had only one replication because of a limited number of larvae available for infestation.

Data Analysis. The two periods of time in which each experiment was performed were treated as blocks and data combined. To correct for any differences in plant height observed in pretreatment measurements, analysis of covariance (ANCOVA) (SAS Institute 1987) was used to analyze plant height. Fresh and dry weights of roots and stalks were analyzed by analysis of variance (ANOVA) procedures, and treatment means were compared using Tukey's studentized range (HSD) test (SAS Institute 1987).

Sap flow was analyzed as a randomized complete block design (SAS Institute 1987) for each of the days after treatment. Intervals of 30 min (from 1200 to 1500 hours) were used as the time component. Sap flow should be greatest and maximum differences between treatments could be expected during this time period. Treatment means for sap flow (grams per hour) were compared using Tukey's HSD test.

Results and Discussion

Experiment 1. Effect of Mechanical Root Pruning. Mechanical pruning of roots decreased the sap flow in corn (Table 1). Four days after pruning, sap flow was less in plants where roots in three or four sections were pruned than it was in the control plants ($F = 7.91$; df = 3, 11; $P < 0.01$). Sap flow was also less ($F = 22.66$; df = 3, 11; $P < 0.001$) 7 d after pruning in plants where one, three, or four sections of the roots were pruned. There was no evidence of any detrimental effects from the use of the sap flow gauges or insulating compound with the corn plants.

Downey & Mitchell (1971) reported that when 75% of the root system of corn was stressed by withholding water or by being pruned, the plants were unable to maintain turgidity (reduced relative water content) at a vapor pressure deficit of 40 mb or higher. Similarly, Riedell (1990) re-

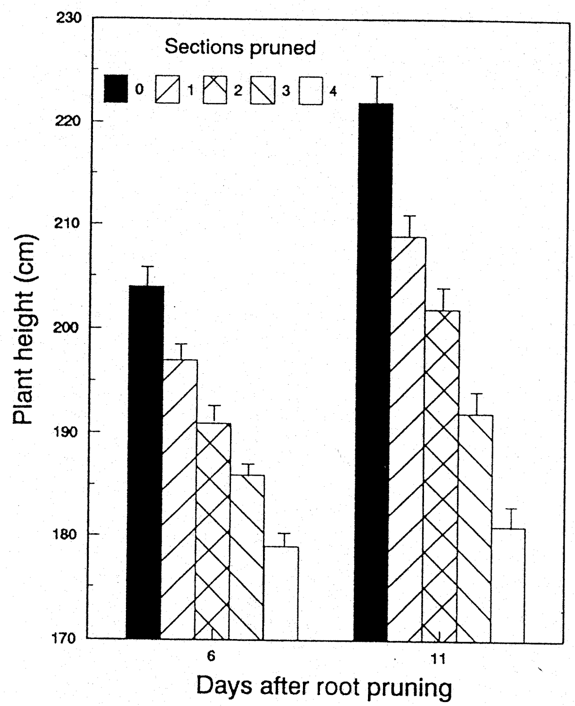

Fig. 1. Effect of mechanical root pruning on height ($\bar{x}$ + SE) of corn plants grown in sectional boxes (n = 4). Means were adjusted using ANCOVA procedures.

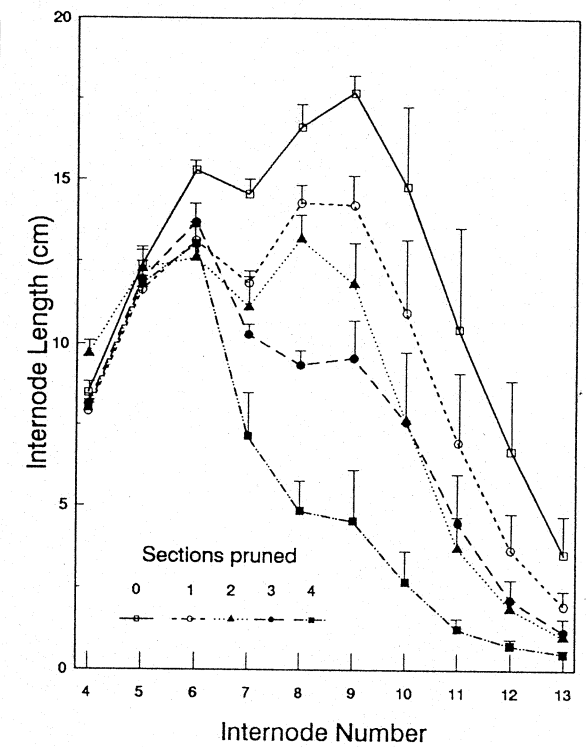

Fig. 2. Effect of mechanical root pruning on internode length in corn grown in sectional boxes (n = 4).

ported that relative water content of corn grown in a greenhouse soil bed was significantly lower than the control after 75% of the roots had been pruned, but not when only 25% of the roots had been pruned. Stomatal conductance, however, was significantly lower after only 25% of the roots had been pruned. Our results showing reduced sap flow after pruning of 25% of the root system suggested that sap flow, like stomatal conductance, is sensitive to changes in the ability of the root system to provide water to the shoot.

Root boxes with one or more sections of roots pruned had lower fresh (F = 43.83; df = 4, 14; P < 0.001) and dry (F = 65.20; df = 4, 14; P = 0.001) weights of stalks compared with the control plants (Table 1). Stalk weight decreased in proportion to the number of sections that were pruned, suggesting that stalk assimilates were used to provide energy for respiration. Dry weight of stalks from boxes with four root sections pruned were less than half the dry weight of stalks in any of the other treatments.

Six days after root pruning, plant height was progressively shorter as the number of sections that were pruned increased (F = 66.18; df = 4, 13; P < 0.001) (Fig. 1). Differences in plant height between treatments were even larger 11 d after pruning (F = 69.75; df = 4, 13; P < 0.001). Internode lengths for nodes 7–13 were highest in the unpruned plants and generally decreased in response to increased root pruning (Fig. 2).

Whitfield (1992) observed that plant height decreased as the amount of mechanical root pruning increased. In their study of the effects of root pruning on apple trees, Geisler & Ferree (1984) reported agreement with other authors that reduced growth of shoots after root pruning can be explained by a combination of limited water absorption (lower leaf water potential), reduced mineral uptake and assimilation, and reduced synthesis of hormones.

Root pruning decreased the dry weights of roots (F = 19.78; df = 4.13; P < 0.001) when four sections of roots were pruned compared with the controls (Table 2). Pruning all four root sections resulted in a 78% decrease in dry weights of roots compared with the undamaged plants. Pruning three sections resulted in a 30% reduction in dry weights of roots respectively, compared with the unpruned plants. These results can be explained if plants with up to three sections pruned are able to compensate for some of the damage by increasing the growth of roots in nonpruned sections. No compensatory lateral root growth was observed where all four sections were pruned; however, considerable lateral root growth was observed for those pruned sections in boxes where less than all four sections of the box were pruned.

Table 2. Effect of mechanical root pruning of corn on dry root weight

Sections pruned[a]	Dry root wt, g			
	Per section		Total ± SEM	% In nonpruned sections
	Pruned	Nonpruned		
0	—	2.06	8.22a ± 0.967	100
1[b]	1.84	2.07	7.68a ± 0.571	81
2	1.40	1.82	6.42a ± 0.248	57
3	1.36	1.67	5.76a ± 0.405	29
4	0.45	—	1.78b ± 0.292	—

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Tukey's studentized range (HSD) test [SAS Institute 1987]).

[a] Corn seedlings were transplanted into boxes divided into four equal sections.

[b] Dry root weight in mechanically pruned sections and total dry root weight calculated from three replications instead of four.

Whitfield (1992) reported that moderate and severe pruning of adventitious roots with mechanical devices resulted in a decrease in initiation of nodal root axes. He also observed significant increases in lateral root development on nodal root axes that had been pruned. Spencer (1941) observed that when one side of the root system of corn was pruned on three different dates, pruning reduced the average weight of main roots by 8% and increased the weight of lateral roots by 28%.

Increased growth of roots after root pruning may occur at the expense of above-ground growth. In an experiment where roots of holly, *Ilex crenata* Thunb., were pruned, Randolph & Wiest (1981) concluded that reduced growth of shoots may have led to an increased translocation of photosynthate to the remaining roots and caused the compensatory growth of roots. In an experiment in which roots of blue gamagrass, *Bouteloua gracilis*, were pruned, Detling et al. (1980) found that for several days following root pruning, the proportion of photosynthetically fixed ^{14}C allocated to roots of treated plants was lower than in control plants. This proportion increased until, by 3 wk after treatment, the proportion allocated to roots of treated plants significantly exceeded that of controls. In our experiment, root pruning decreased shoot growth more than root growth.

Experiment 2. Effect of Infestation by Western Corn Rootworm. Infestation of root boxes with larvae of the western corn rootworm did not reduce sap flow in corn 9 d ($F = 0.41$; df = 4, 8; $P > 0.70$), 12 d ($F = 0.50$; df = 4, 9; $P > 0.70$), or 17 d ($F = 0.78$; df = 4, 10; $P > 0.50$) after infestation (Fig. 3). Although root boxes with three or four sections infested had sap flow rates that were on average lower than root boxes with no to two sections infested, the differences were not significant.

In a greenhouse experiment where corn was infested with 50 and 150 second-instar western corn rootworm larvae per plant, Riedell (1990) showed that relative water content, stomatal conductance, and water potential of the leaves were not significantly different from the controls at the ninth leaf stage, at a time when the majority of larvae were in the prepupal stage of development (i.e., larval feeding concluded). However, after 19 d, when plants were in the tassel stage

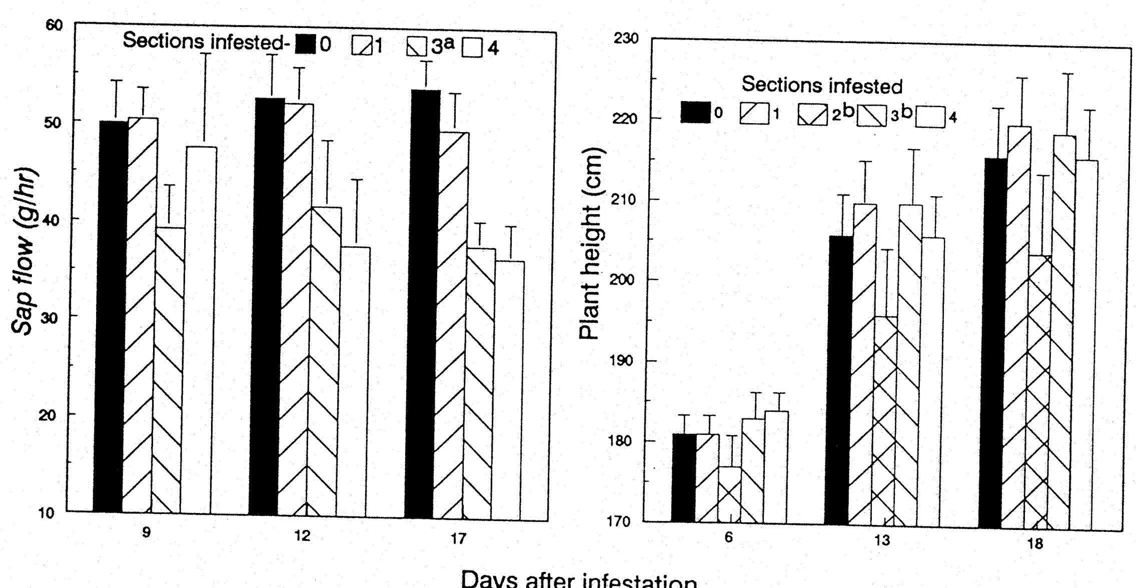

Fig. 3. Effect of larvae of the western corn rootworm on sap flow ($\bar{x}$ + SE) and plant height ($\bar{x}$ + SE) in corn grown in sectional boxes with 100 larvae per infested section (n = 4) except for a (n = 2) and b (n = 3). Means for plant height adjusted using ANCOVA procedures.

Table 3. Effect of larvae of the western corn rootworm on dry root weight, fresh and dry stalk weight, and percentage water in stalks of corn grown in sectional root boxes

Sections infested[a]	Dry root wt, g				Fresh stalk wt, g ± SEM	Dry stalk wt, g ± SEM	% Water in stalk
	Per section		Total ± SEM	% in uninfested sections			
	Infested	Uninfested					
0	—	1.86	7.45a ± 0.677	100	226.60a ± 12.798	29.71a ± 4.548	87
1	1.23	2.03	7.34a ± 0.884	83	209.17a ± 13.783	30.00a ± 5.669	86
2[b]	1.16	1.86	6.04ab ± 0.478	62	205.43a ± 22.382	29.18a ± 5.489	86
3[b]	1.46	2.04	6.43a ± 0.647	32	223.51a ± 7.462	32.35a ± 4.493	86
4	1.18	—	4.70b ± 0.561	—	206.83a ± 12.687	30.08a ± 5.071	85

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Tukey's studentized range (HSD) test [SAS Institute 1987]).

[a] Corn seedlings were transplanted into boxes divided into four equal sections; 100 larvae of the western corn rootworm were placed in each infested section.

[b] Treatments performed on three replications instead of four.

and western corn rootworm had completed development to the adult stage, leaf water potential was significantly higher (less negative) and stomatal conductance was significantly less in infested plants than in the controls ($P < 0.05$).

Results of the present experiments are in agreement with findings by Riedell (1990) that feeding by rootworms does not significantly affect water relations in corn from the time of infestation to the time when root damage is greatest. At the highest rates of infestation, sap flow began to fall below that of the controls at the time of maximum damage (Fig. 3). Because the experiments were terminated before tassel stage, however, differences in sap flow due to rootworm infestation were not determined.

There were no significant differences in fresh ($F = 0.72$; df = 4, 12; $P > 0.50$) or dry ($F = 1.23$; df = 4, 12; $P > 0.30$) weights of stalks between the different levels of infestation (Table 3). The percentage moisture of the stalk did not differ between the treatments. There was no difference in plant height 6 d ($F = 2.75$; df = 4, 11; $P > 0.08$), 13 d ($F = 1.25$; df = 4, 11; $P > 0.30$), or 18 d ($F = 0.80$; df = 4, 11; $P = 0.50$) after treatment (Fig. 3). Similarly, infesting root boxes with rootworm larvae did not affect internode length of the corn (data not shown).

Our results differ from those of Riedell (1989) in which he infested corn with 150 second-instar western corn rootworm per plant and reported shoot characteristics (height of plants, ear length and width, ear dry weight, husk dry weight) that were less than those of uninfested plants. Conversely, plants infested with 50 larvae had shoot characteristics that were greater than those of uninfested plants. Riedell reported that fourth and fifth nodes of roots were completely pruned in pots with 150 corn rootworms; however, the same nodes from pots with 50 rootworms had only minor pruning and extensive tunneling. Similarly, in the present study, because first instars were used for infestation, assessment of root damage in infested root box sections revealed a high percentage of roots had been fed on and damaged by larvae (75–89%), but a much lower percentage of roots had actually been pruned (26–38%) (Table 4). Root box sections were pruned at 47 d of corn growth or infested with western corn rootworm larvae at 43 d of growth after the method of Riedell (1989). He infested corn plants in the greenhouse at 49 d of growth and observed similar timing of infestation and response of the roots to western corn rootworm in infested plants in the field. In the present experiments, western corn rootworm larvae in infested sections were in the final instar and prepupal stage when the experiments were terminated. The low to moderate level of root damage may account for the lack of significant differences in above-ground plant growth among the infestation treatments.

Root boxes infested with rootworm larvae in all four sections had roots that had lower dry weights ($F = 13.11$; df = 4, 12; $P < 0.001$) than the controls (Table 3).

Spike & Tollefson (1989) proposed that, within the pest categories given by Boote (1981), the corn rootworm can be classified as a "turgor reducer" in that root feeding disrupts the water balance of the corn plant. They also suggested that a reduction in turgor caused by rootworm feeding led to observed physiological asynchrony in tassel and silk development. No direct

Table 4. Percentage of corn roots pruned or damaged (tunneling, surface feeding, and pruning) per infested section by larvae of the western corn rootworm

Sections infested[a]	n[b]	% Roots pruned			% Roots damaged		
		$\bar{x}$	Max	Min	$\bar{x}$	Max	Min
1	4	26	40	14	89	100	80
2	6	36	50	20	75	100	60
3	9	38	71	17	77	100	33
4	16	38	83	0	85	100	67

[a] Corn seedlings were transplanted into boxes divided into four equal sections; 100 larvae of the western corn rootworm were placed in each infested section. Feeding damage was evaluated per infested section.

[b] Number of sections in which roots were examined.

evidence of turgor reduction due to rootworm feeding, however, was provided. Infesting roots with rootworm larvae in our study did not significantly affect sap flow, suggesting that the effect of rootworm feeding on the physiology of corn growth may be more complex than disruption of the water balance. Riedell (1990) also concluded that the effects of rootworm infestation on corn plant physiology must be described more fully before exact mechanisms are known.

Mechanical pruning of corn roots in our study revealed that even a loss of 25% of the root system of corn can decrease sap flow and growth. These results are similar to those of Riedell (1990), who found that one period of severe mechanical damage to corn roots reduced the ability of the root system to provide adequate water to the shoot to a much greater extent than did prolonged and moderate damage by corn rootworms. This is not unexpected because feeding by rootworm larvae usually extends over a period of several weeks (Ortman & Fitzgerald 1964). Continuous root feeding for a long period of time may affect compensatory growth of lateral roots on pruned nodal root axes in a different way than when roots are pruned at one time. If mechanical pruning devices are to be used to damage corn roots, they should be used over a period of several weeks to better simulate continuous feeding by larvae of corn rootworms (Whitfield 1992).

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