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Soil Water Potential: Effects on Soybean Looper Feeding on Soybean Leaves

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ABSTRACT

Defoliation by soybean looper, *Pseudoplusia includens* (Walker), often is uniformly high over portions of soybean [*Glycine max* (L.) Merr.] fields but is uniformly low, or progresses more slowly, over other portions of the same fields. Through the use of insect bioassays the effect of soil water potential (SWP) and two soil types were investigated to determine if they are factors associated with observed soybean looper defoliation patterns. Tests were conducted using excised leaves from greenhouse-grown plants and laboratory-reared insects. In Test I, a significant ($P \leq 0.01$) reduction in 10-d larval weights and an increase in larval development periods was caused by plants grown at reduced SWP for 15 d before bioassay initiation. No differences in 10-d larval weights or development periods associated with Dubbs silt loam (fine-Silty, mixed, thermic Typic Hapludalf) or Sharkey clay (very-fine, montmorillonitic, nonacid, thermic Vertic Haplaquept) soils occurred in Test I. In Test II, a large, significant reduction occurred in 10-d larval weights and an increase occurred in development periods that was associated with plants grown at reduced SWP for 27 d before bioassay initiation. A small, significant decrease in 10-d larval weights and an increase in larval development periods under reduced SWP was associated with Sharkey clay in Test II. In Test III, a small, significant reduction in 10-d larval weights and an increase in development periods was associated with plants grown for 24 d at moderately reduced SWP. The effects observed in these tests are great enough to be taken into consideration when conducting host-plant resistance research and when making insect control decisions.

SOYBEAN LOOPER (SBL) is a major defoliator of soybean in the U.S. Gulf Coast and South Atlantic States. Populations of SBL are reported to be randomly distributed within soybean fields (Shepard and Carner, 1976). However, our general observations, made during many years of research in the Mississippi Delta, are that defoliation patterns by SBL populations often are uniformly high over portions of a field and uniformly low, or progress more slowly, over other portions of the same field. For a randomly distributed insect, this suggests a possible difference in larval development and/or mortality within field locations. Defoliation patterns have been observed to follow soil type and soil water distribution patterns within a field. Defoliation usually is highest on soybean plants growing in silt loam soils or under irrigated conditions and lowest on plants growing in clay soils or under nonirrigated conditions.

Much of the Mississippi Delta might be described as having either loam or clay soil textures (Brown et al., 1970). Plants growing in clay soils have less total available water and less water available per unit of time than plants growing in silt loam soils (Heatherly and Russell, 1979a). Defoliation patterns we observed could be the result of soil type and/or soil water conditions under which plants were growing. Therefore, as a first step toward identifying the cause(s) of the observed defoliation patterns, we bioassayed plants grown in clay and silt loam soils with varied SWP to determine their influence on SBL development.

MATERIALS AND METHODS

Soil was collected from areas described as Dubbs silt loam and Sharkey clay on the Delta Branch Experiment Station

Abbreviations: SBL, soybean looper; SWP, soil water potential.

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at Stoneville, MS. Each soil was processed through a soil grinder, thoroughly mixed to assure uniformity, and then analyzed to determine particle size distribution and fertility. Equal numbers of 8-L plastic pots, 26 cm deep and 23 cm in diam. with six 6.4-mm-diam. drain holes in the bottoms, were filled with soil of each type and placed in a randomized complete-block design on benches in a greenhouse.

Three separate tests (I, II, and III) were conducted and fresh soil from the same source was used for each. Silt loam and clay soils with two SWPs were used in Tests I and II. In Test III, only silt loam soil was used, with three SWPs.

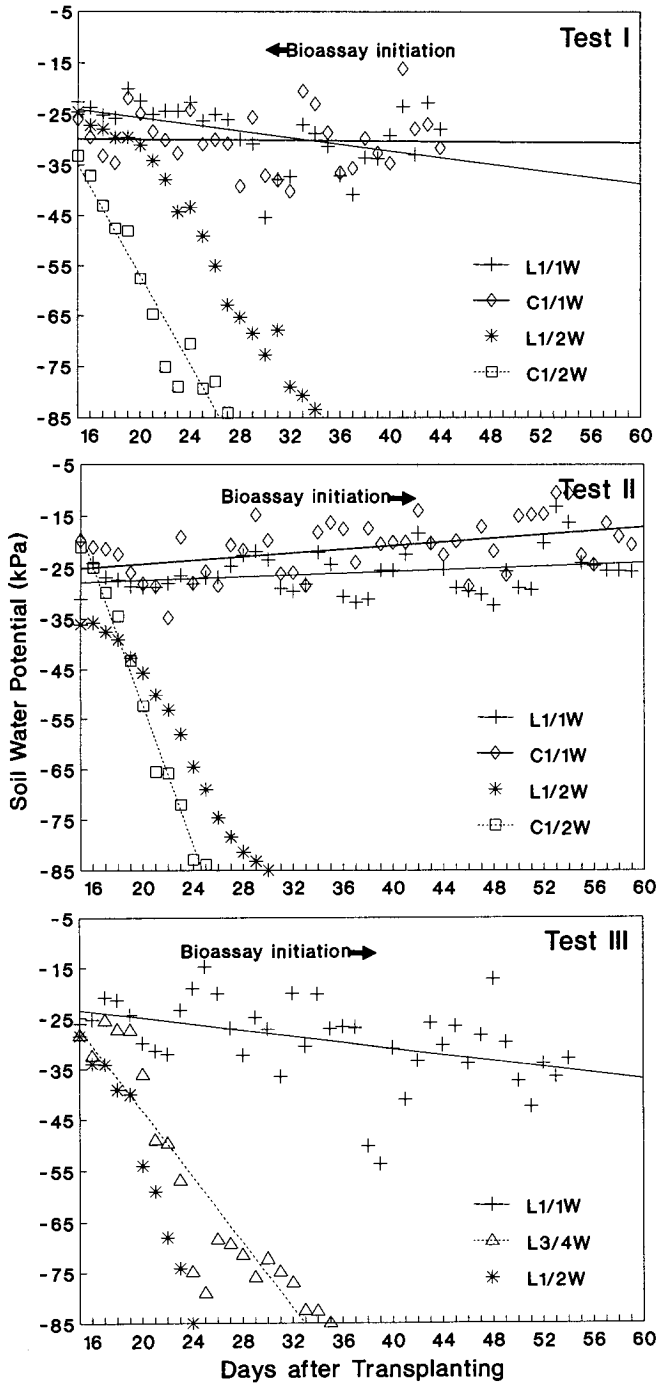

Fig. 1. Daily soil water potentials (SWP) and trend lines for Tests I, II, and III. Prefixes L and C designate treatments that received water estimated to maintain a SWP of −20 kPa, and suffixes 1/2W and 3/4W designate treatments which received, respectively, 1/2 and 3/4 the amount of water as 1/1W.

Seeds from a single source of 'Centennial' soybean, a cultivar known to be susceptible to insect feeding damage (Lambert and Hamer, 1988), were germinated in vermiculite for each test. When plants were in the seedling stage, soil in all pots was saturated with water and four uniformly vigorous seedlings were transplanted to each pot. Tensiometers were installed randomly in eight pots of each replicate at transplanting to monitor SWP and were read at 0800 CST each day. A recording thermometer was placed in the center of the greenhouse room to continuously monitor ambient temperature. To prevent plants from fruiting, the light period was extended with artificial lighting to 16 h.

A watering regime was initiated 15 d after transplanting, when the mean of all tensiometer readings was −20 kPa (Fig. 1). All watering was done at 0800 h and plants were observed for wilting at 0800 and 1500-h CDT each day. Treatments were designated L1/1W, C1/1W, L3/4W, L1/2W, and C1/2W. The L and C prefixes designate loam and clay soils, respectively. The 1/1W suffix designates treatments which, based on mean tensiometer readings, received each day an amount of water estimated to maintain a SWP of −20 kPa. The 3/4W and 1/2W suffixes designate treatments which received 3/4 and 1/2 the amount of water, respectively, as treatments with the 1/1W suffix. To prevent severe drought stress, treatments with 1/1W, 3/4W, and 1/2W suffixes received at least 100, 75, and 50 mL of water, respectively, each day regardless of tensiometer readings. Treatments C1/1W and C1/2W occurred only in Tests I and II; treatment L3/4W occurred only in Test III.

Insect bioassays were begun 15, 27, and 24 d after initiation of watering for Tests I, II, and III, respectively (Fig. 1). Just prior to watering each day, fully expanded leaves nearest the apex of plants in each treatment were excised, sealed in plastic bags, and labeled to identify source. Leaves were immediately transported to a laboratory and placed in 80-mL clear plastic cups with tight-fitting, labeled lids. At test initiation, two neonate (< 1-h old) SBL larvae from a laboratory culture, which had been reared for >10 generations, were added to each cup. Cups were placed in a randomized complete-bock design with 50, 50, and 125 replicates for Tests I, II, and III, respectively, and held in an environmental control chamber at 25 ± 0.5 °C, 75 ± 5% relative humidity, and a 10-h photoperiod. After 48 h, larvae were randomly thinned to one per cup, fresh leaves were placed in clean cups, and larvae were transferred to the leaves. Thereafter, larvae were transferred to clean cups with fresh leaves every 24 h until they pupated or died. Larval weights were determined 10 d after hatching. Cups were monitored every 12 h for larval pupation or adult emergence.

Leaf water concentration was determined at the end of each bioassay to measure the amount of diet water available to insects. To determine leaf water concentration prior to exposure to insects, excised leaves were weighed, dried for 70 h at 60 °C, and weighed again. The average water concentration of leaves on which insects fed was determined by exposing leaves to the same environment as leaves with larvae and determining water concentration before and after exposure. Average leaf water concentration was determined to be: mean leaf water content at the end of the exposure period plus one-half the mean water loss during exposure.

To determine if treatments influenced the nutritional value of leaves, N and caloric content of leaves from each treatment were measured at the end of Test II. Leaves were dried for 70 h at 60 °C, ground in a Wiley mill, and sealed in glass vials. Nitrogen concentration was determined by Kjeldahl digestion analysis, and caloric content was determined by use of a bomb calorimeter. Mississippi State University Chemical Laboratory conducted the analyses.

All data were analyzed by the analysis of variance procedure of SAS (SAS Institute, 1985) and mean separations were accomplished by Duncan's Multiple Range Test.

RESULTS AND DISCUSSION

Soil particle distribution analysis showed the soils to be nearly identical in texture to the Dubbs silt loam and Sharkey clay soils used by Heatherly and Russell (1979b) in a previous study at this location. For the period from transplanting to test completion, the mean 0900 to 1700-h ambient temperatures were 28.3, 26.6, and 27.9 °C, and the mean 1700 to 0900-h CDT ambient temperatures were 21.1., 20.7, and 23.4 °C for Tests I, II, and III, respectively.

Mean SWP reached −20kPa and watering regimes were begun 15 d after transplanting for all tests. In Test I, treatment C1/2W exceeded a SWP of −85 kPa 3 d before, and treatment L1/2W exceeded a SWP of −85 kPa 5 d after, bioassay initiation (Fig. 1). Treatments L1/2W and C1/2W, respectively, exceeded −85 kPa 10 and 18 d prior to bioassay initiation in Test II. Therefore, plants grew under stress conditions much longer in Test II than in Test I. In Test III, SWP in treatments L1/2W and L3/4W was lower than −85 kPa for 16 and 5 d, respectively, before bioassay initiation. No wilting occurred on any day in any of the three tests. There was a slight, observable reduction in plant height in the partly watered treatments compared with the fully watered treatments.

In Test I, leaf water concentration (Table 1) of plants in treatments L1/1W and C1/1W were nearly equal, as was the leaf water concentration of plants in treatments L1/2W and C1/2W. However, the difference in leaf water concentration between the 1/1W and 1/2W treatments was significant. In Test II, water concentration was significantly less in leaves from treatment L1/1W than in leaves from treatment C1/1W. Also, there was significantly less water in leaves from both treatments L1/2W and C1/2W than in leaves from treatments L1/1W and C1/1W. There was no difference in leaf water concentration between treatments L1/2W and C1/2W. In Test III, leaf water concentration was significantly different among the three treatments. Leaf water concentration, before exposure to insects, averaged 825 g kg^{-1} for treatments 1/1W.

There were no significant differences among soil water treatments for N or caloric content of leaves (data not shown); however, both parameters were numerically higher for leaves from plants grown in clay soil than for leaves from plants grown in silt loam soil regardless of SWP. This indicates a possible significant soil effect on these parameters that the tests were not sensitive enough to detect.

In Test I, there were no significant differences in 10-d larval weights or in developmental rates between treatments L1/1W and C1/1W, or between treatments L1/2W and C1/2W (Table 2). However, both parameters in treatments L1/1W and C1/1W were significantly different from those in treatments L1/2W and C1/2W. These results indicate a SWP effect and no soil effect in this test. In Test II, differences in 10-d larval weights were significantly different among all treatment combinations; however, the difference in larval weights between soils was much smaller than the difference among SWP. Larval development was much longer on leaves from plants grown in the L1/2W and C1/2W treatments than for those grown in L1/1W and C1/1W treatments. There was no soil effect on time for larval development between treatments L1/1W and C1/1W, but there was a slight soil effect between treatments L1/2W and C1/2W. In Test III, all treatments were significantly different for both larval weights and larval development days; however, differences in both parameters between treatments L1/1W and L3/4W were much smaller than the differences between L3/4W and L1/2W.

These data show that soybean plants grown under less than optimum SWP conditions have an adverse effect on SBL development. The longer plants were grown under these conditions, the greater the effect. Also, the lower the SWP, the greater the effect. This shows a plant response to water stress which influences insect development. There appeared to be a small soil effect that was exhibited only after plants were grown in the two soils for >30 days. This may also be a plant stress response, since plants grown in clay soil normally yield less than plants grown in loam soil under the same growing conditions, indicating greater stress (Heatherly, 1984). Test III results show that the effect is present at small water deprivation levels, and appears to increase rapidly as SWP decreases.

The factor(s) responsible for this phenomenon is unknown. It does not appear to be a nutritional effect, since no differences in nutritional levels were detected among SWP treatments. Leaves from plants in treatments 1/1W contained 825 g kg^{-1} water, suggesting that SBL larvae feeding on intact, adequately watered soybean plants are normally exposed to a food sub-

Table 1. Leaf water concentration of soybean plants grown on a loam or clay soil at three soil water potentials.

Treatment†	Water		
	Test I	Test II	Test III
	g kg^{-1}		
L1/1W	793a‡	758b	776a
C1/1W	789a	776a	–
L3/4W	–	–	755b
L1/2W	766b	706c	734c
C1/2W	765b	714c	–

† Prefixes L and C designate loam and clay soil, respectively; suffix 1/1W designates treatments that received water estimated to maintain a soil water potential −20 kPa; and suffixes 1/2W and 3/4W designate treatments which received, respectively, 1/2 and 3/4 the amount of water as 1/1W.
‡ Within columns (tests), means followed by the same letter are not significantly different at $P \leq 0.01$.

Table 2. Weights and development periods of soybean looper larvae reared on soybean plants grown on a loam or clay soil at three soil water potentials.

Treatment†	10-d larval weight			Development period		
	Test I	Test II	Test III	Test I	Test II	Test III
	mg			d		
L1/1W	213.8a‡	246.9a	235.9a	20.0a	19.8a	22.0a
C1/1W	227.2a	199.1b	–	19.8a	20.2a	–
L1/4W	–	–	210.3b	–	–	22.6b
L1/2W	158.9b	72.5c	120.1c	20.8b	23.6b	24.0c
C1/2W	155.0b	47.3d	–	20.5b	25.6c	–

† Prefixes L and C designate loam and clay soil, respectively. Suffix 1/1W designate treatments which received water estimated to maintain a soil water potential of −20 kPa, and suffixes 1/2W and 3/4W designates treatments which received, respectively, 1/2 and 3/4 the amount of water as 1/1W.
‡ Within columns (test), means followed by the same letter are not significantly different at $P \leq 0.01$.

strate that is greater than 800 g kg^{-1} water. The 706 to 793 g kg^{-1} water concentration of leaves on which insects fed in these tests does not appear, however, to be a causal factor. In Test II, larval weights were smaller for those reared on leaves from plants in treatment C1/1W than from plants in treatment L1/1W, even though the leaf water concentration was greater for treatment C1/1W. Also, in Test II, larval weights were smaller and development periods longer for those reared on leaves from plants in treatment C1/2W than from plants in treatment L1/2W, even though water concentration was the same. Studies conducted with Mexican bean beetle, *Epilachna varivestis* Mulsant, reared on soybean plants grown with water deficits showed a reduction in survival, growth rate, and pupal weight (McQuate and Conner, 1990). However, studies conducted with whitebacked planthopper, *Sogatella furcifera* Horvath, reared on rice, *Oryza sativa* L., plants grown with salinity stress showed an increase in assimilation of food, growth rate, adult longevity, fecundity, and population increase (Salim et al., 1990).

The differences in larval development that occurred in these tests appear to be the result of chemical or physical changes within plants. These changes were initiated by plant stress due to either water deprivation or increased leaf temperatures resulting from reduced plant water. The SWP effect in these tests was very pronounced, and is probably the major causal factor for the differential defoliation patterns we have observed. Since clay soils have less available water than silt-loam soils and the water is available at a slower rate, plants growing in clay soils experience water deprivation much sooner than plants growing in loam soils (Heatherly and Russell, 1979a). Thus, if plant water deprivation is the causal agent, defoliation patterns should follow soil type, with defoliation being greater on loam soils or under irrigated conditions just as we have observed.

The SWP effects observed in these tests are great enough to be taken into consideration when conducting insect resistance studies and when making insect control recommendations. When studies are being conducted to evaluate genetically controlled plant resistance, it is imperative that SWP be monitored along with the many other factors that affect insect development and plant damage. When drought conditions prevail and a potentially damaging insect population is present, it may be possible to (i) apply an insecticide to only a portion of a field, (ii) delay insecticide application until conditions improve, or (iii) avoid the use of an insecticide as a result of larval mortality due to the induced resistance and the action of entomophagous organisms. Research designed to answer these questions is planned.

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