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Antibiosis in *Lycopersicon* to the Tomato Fruitworm (*Heliothis zea*)[1]

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Abstract. Leaves of *Lycopersicon hirsutum* Humb. & Bonpl. and *L. hirsutum* f. *glabratum* C. H. Mull. contained a factor highly antibiotic to tomato fruitworm, *Heliothis zea* (Boddie), larvae. The factor was extractable with ethanol and lethal to larvae fed on an artifical diet containing the extract. The antibiotic factor appeared to be inherited recessively. Because the early instars of *H. zea* larvae on tomato, *L. esculentum* Mill., plants depend on leaf tissue rather than fruit as a primary food source, this antibiotic factor may be a valuable source of resistance for commercial cultivars.

The tomato, *Lycopersicon esculentum* Mill., is subject to infestation by the fruitworm, *Heliothis zea* (Boddie), in several major North American production areas. At present, insecticides are the only effective control measures available. As tomato culture shifts toward an agronomic-type system, losses (including control costs) caused by the fruitworm become increasingly important. This economic consideration and the recent concern over the potential dangers of insecticide residues have heightened interest in development of resistant cultivars. Fery and Cuthbert (3, 5) reported on such aspects of resistance as the relationships between damage and earliness, fruit number, fruit size, vine size, and plant density. Canerday et al. (2) observed that small-fruited processing cultivars were less susceptible than fresh-market cultivars. Fery and Cuthbert (4) screened a world-wide collection of cultivars and found a wide range in susceptibility to fruitworm damage.

Observation of fruitworm infestations of tomatoes indicate that moths deposit their eggs on foliage, and the early instar larvae feed almost exclusively on leaf tissue. This early larval dependence on leaf tissue might be utilized in development of fruitworm resistant cultivars. The objectives of the present study were to determine the variability present within the genus *Lycopersicon* with respect to larval survival on leaf tissue and to assess antibiosis as a resistance mechanism.

Materials and Methods

Test I. Five-week-old plants of 4 *L. esculentum* accessions that had previously been selected as having moderate levels of fruitworm resistance, 2 susceptible *L. esculentum* cultivars, and single accessions of *L. pimpinellifolum* (L.) Mill., *L. peruvianum* (L.) Mill., and *L. hirsutum* f. *glabratum* C. H. Mull. were bioassayed for antibiosis against the tomato fruitworm[3]. The experiment was conducted on greenhouse ground beds, in a randomized complete-block design with 8 replications. Each plot consisted of 2 plants, surrounded by a greased aluminum lawn-edging barrier to prevent interplot larval movement. Plots in the first 2 replications were infested with 40 newly hatched larvae each, whereas plots in the remaining 6 replications were infested with 20 larvae each. The *H. zea* larvae used in this test, as well as in the other tests reported here, were obtained from a laboratory culture maintained on a pinto-bean diet introduced by Shorey and Hale (7) and modified by Burton (1). The test was terminated after 16 days, and the surviving larvae were collected.

Test II. Excised foliage of *L. hirsutum* Humb. & Bonpl. accessions, *L. hirsutum* f. *glabratum* accessions, *L. esculentum* cv. Floradel, the interspecific hybrid between 'Floradel' and *L. hirsutum* f. *glabratum* (P.I. 126449), and *L. pimpinellifolium* (P.I. 205009) was bioassayed for an antibiotic factor. Two or 3 young leaves from flowering greenhouse-grown plants were placed in 1-oz (30 cm^3) clear plastic cups with paper lids and infested with a single 1-day-old larva. Every other day, the leaves were exchanged for fresh ones, and the number of dead larvae were recorded. The experimental design was a randomized complete block with 4 replications in time of 20 cups per treatment. The average test lasted 13.2 days.

Test III. Excised foliage of *L. hirsutum* f. *glabratum* (P.I. 126449) and *L. esculentum* cv. Homestead-24 was bioassayed for an antibiotic factor by use of third- and fourth-instar larvae. The larvae were reared on the standard laboratory diet, grouped according to size, and starved for 4 hr before the test began. Leaves were exchanged for fresh ones, and larval survival was recorded daily. The experimental design was a randomized complete block, with 10 replications of 5 cups per treatment. This test was repeated. The means of the pooled data are reported here. On the average, each of these 2 tests lasted 6 days.

Test IV. The relative preference of *H. zea* larvae for fresh leaf tissue of *L. hirsutum* f. *glabratum* (P.I. 126449) and *L. esculentum* cv. Homestead-24 plants was determined by use of third- and fourth-instar larvae. Three or 4 young leaves were weighed and placed on moist filter paper in petri dishes. Each dish was infested with a single larva that had been reared on the standard diet, starved for 4 hr, and assigned to replication according to size. The experimental design was a randomized complete block, with 8 replications of 5 dishes per treatment. To adjust for differential rates of moisture loss, one uninfested dish per treatment was included in each replication. After the larvae had fed for 18 hr, the test was terminated and the remaining leaf tissue was weighed.

Test V. Extracts of leaf tissue from greenhouse-grown, flowering *L. hirsutum* f. *glabratum* (P.I. 126449) and *L. esculentum* cv. Homestead-24 plants were bioassayed for antibiosis factors. Young leaves were dried, pulverized, divided into 2 samples each, and extracted in a soxhlet extraction apparatus. The first sample was extracted with

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[3] The resistant and susceptible *L. esculentum* accessions were selected on the basis of fruit damage by F. P. Cuthbert, Jr., and O. L. Chambliss (unpublished data).

water, and the second was serially extracted with hexane and ethanol. The tissue residue from each extraction was saved. Cellulose powder was impregnated with appropriate amounts of the extracts, dried, and reground to a fine powder. The impregnated powder and tissue residues mixed with fresh cellulose powder were blended into a freshly mixed pinto-bean diet (1). The final mixture contained 1.96% cellulose and 654-mg equivalents of extract or tissue residue (based on fresh leaf wt) per g of diet. To prepare the control, only fresh cellulose powder was blended into the diet. The diet was poured into 1-oz (30 cm^3) clear plastic cups with paper lids. After the diet had cooled, each cup was infested with a single, newly hatched larva. The experimental design was a randomized complete-block, with 5 replications of 10 cups per treatment. The test was terminated after 14 days, and the number of survivors was recorded.

Results and Discussion

Test I. Survival rates of larvae fed on the intact plants ranged from 0.62 to 19.75% (Table 1). The survival rate of larvae on *L. hirsutum* f. *glabratum* plants (P.I. 126449) was only 3.3% of that of larvae on *L. esulentum* cv. Homestead-24 plants, and it was significantly lower than the survival rates of larvae on plants of any other accession. This high larval mortality on P.I. 126449 plants indicates the presence of an antibiotic factor that is either not present or present at a lower level in the *L. esculentum*, *L. pimpinellifolium*, and *L. peruvianum* accessions. Our failure to demonstrate significant differences in larval survival between plants of the *L. esculentum* accessions selected for moderate field resistance and the susceptible 'Chico Grande' indicated that antibiosis was not responsible for the observed resistances. Subsequent work showed that much of the resistance of these accessions may have been caused by some unknown factor associated with their large vine size (5).

Test II. Low survival rates on excised foliage with first-instar larvae confirmed the presence of an antibiotic factor in all the *L. hirsutum* and *L. hirsutum* f. *glabratum* accessions tested (Table 1). Survival rates on the *L. hirsutum* f. *glabratum* accessions, for example, ranged from 0 to 5.00%; the mean survival rate on these accessions was 2.08%, compared to the 28.75% on 'Floradel'. Analysis of the data failed to separate the *L. hirsutum* from the *L. hirsutum* f. *glabratum* means. Nevertheless, the average survival rates (2.08 vs 10.83%) differed in magnitude and all the *L. hirsutum* means were greater than the highest *L. hirsutum* f. *glabratum* mean. This suggests that the concentration of the antibiotic factor was greater in *L. hirsutum* f. *glabratum* than in *L. hirsutum* accessions.

Thirty-five percent of the larvae survived on foliage from plants of the interspecific hybrid, compared to 28.75 and 2.50% survival on the parents 'Floradel' and P.I. 126449, respectively. The antibiotic factor appeared to be lacking in the F_1 and is probably inherited in a recessive manner.

The high survival rate (46.25%) on P.I. 205009 shows that the field resistance previously observed in this *L. pimpinellifolium* accession was not caused by an antibiotic mechanism. Therefore, the moderate resistance of this entry to the fruitworm may be caused by other factors associated with its large vine size. Fery and Cuthbert (5) reported a high negative correlation between vine size and fruitworm damage.

Test III. Results of the excised-foliage test with third- and fourth-instar larvae showed that the antibiotic factor in P.I. 126449 was effective also against larger, more mature larvae (Table 1). Although the survival rates of the older larvae were considerably greater than those of the first-instar larvae in the earlier tests, larval survival on the *L. hirsutum* f. *glabratum* foliage was less than 1/7 of the survival rate on 'Homestead-24' foliage (12 vs 85%).

Test IV. Third- and fourth-instar larvae of *H. zea* differed significantly in preference for excised leaf tissue of 'Homestead-24' and *L. hirsutum* f. *glabratum* (P.I. 126449) (Table 2). Larvae feeding on leaf tissue of P.I. 126449 consumed 2.6 times as much tissue as larvae feeding on 'Homestead-24' leaf tissue. These data agree with our observations that first-instar larvae fed more when placed on *L. hirsutum* f. *glabratum* plants than when placed on *L. esculentum* plants. Preference for the *L. hirsutum* f. *glabratum* tissue rules out the presence of a feeding deterrent or the lack of a feeding stimulant to explain the antibiotic effect of the *L. hirsutum* and *L. hirsutum* f. *glabratum* accessions.

Test V. Larval survival on diets with the water and hexane extracts did not differ from the control (Table 3). However, the ethanol extract of both entries reduced larval survival. Survival on media containing the ethanol extracts of 'Homestead-24' and P.I. 126449 was 26 and 0% respectively, the difference being significant. Comparison of larval survival on diets with the tissue residues showed that the antibiotic factor in the residue from the water extract of P.I. 126449 was completely extracted by ethanol.

Assuming that the active material was not an extraction artifact, the success in extracting a factor from P.I. 126449 that resulted in 100% larval mortality when the factor was added to an artificial diet

Table 1. Average percent survival of *Heliothis zea* larvae fed on intact plants and excised foliage of various *Lycopersicon* species.

Treatment	% Survival[z]		
	Intact plants	Excised foliage	
	1st instar (Test I)	1st instar (Test II)	3rd–4th instar (Test III)
L. esculentum			
'Floradel'	—	28.75b	—
'Homestead-24'	18.75c	—	85.00b
'Chico Grande'	14.06bc	—	—
TF-1[y]	6.88b	—	—
TF-2[y]	14.06bc	—	—
TF-4[x]	7.50b	—	—
TF-5[w]	6.88b	—	—
Average	11.36	—	—
Interspecific Cross			
F_1 ('Floradel' × P.I. 126449)	—	35.00b	—
L. pimpinellifolium			
P.I. 126938	13.12bc	—	—
P.I. 205009	—	46.25b	—
L. peruvianum			
P.I. 126431	14.38bc	—	—
L. hirsutum			
P.I. 126445	—	15.00a	—
P.I. 127826	—	7.50a	—
P.I. 127827	—	10.00a	—
Average	—	10.83	—
L. hirsutum f. *glabratum*			
P.I. 126449	0.62a	2.50a	12.00a
P.I. 129157	—	0.00a	—
P.I. 134417	—	1.25a	—
P.I. 134418	—	1.25a	—
P.I. 251304	—	2.50a	—
P.I. 251305	—	5.00a	—
Average	—	2.08	—

[z] Arcsin $\sqrt{\%}$ transformation used in all analyses. Means in same column followed by same letter do not differ significantly, as determined by Duncan's multiple-range test, at the 5% level.
[y] Fruitworm-resistant selection from STEP 494.
[x] Fruitworm-resistant selection from P.I. 128214.
[w] Fruitworm-resistant selection from P.I. 128258.

Table 2. Relative preference of third- and fourth-instar larvae of *Heliothis zea* for *Lycopersicon esculentum* and *L. hirsutum* f. *glabratum* as determined by their feeding response to fresh excised leaf tissue (Test IV).

Treatment	Tissue consumed (g)[z]
L. esculentum cv. Homestead-24	0.05
L. hirsutum f. *glabratum* (P.I. 126449)	0.13

[z] Means significantly different, as determined by the F-test, at the 5% level.

Table 3. Average percent survival of *Heliothis zea* larvae fed for 14 days on diets with leaf extracts and tissue residue (Test V).

Treatment	% Survival[z]				
	Water		Hexane-ethanol		
	Water	Residue	Hexane	Ethanol	Residue
L. esculentum cv. Homestead-24	54	48a	48	26b	54
L. hirsutum f. *glabratum* (P.I. 126449)	44	22b	50	0c	54
Control[y]	56	56a	56	56a	56

[z] Arcsin $\sqrt{\%}$ transformation used in all analyses. Means within columns followed by the same letter do not differ significantly, as determined by Duncan's multiple-range test, at the 5% level.
[y] Standard diet plus cellulose.

confirms that the resistance in *L. hirsutum* f. *glabratum* was caused by an antibiotic mechanism and that it is chemical in nature. An ethanol-soluble antibiotic factor was present in both *L. esculentum* and *L. hirsutum* f. *glabratum* plants. Thus, the antibiotic effect of the *L. hirsutum* and *L. hirsutum* f. *glabratum* accessions noted in the intact plant and excised foliage tests may be caused, not by a compound unique to this species, but instead by a higher concentration of a compound also present in *L. esculentum*. This is not surprising, in light of our observations that the tomato is a relatively poor host of *H. zea*, as compared to some of its other host crops.

Conclusions

Because the early instars of *H. zea* larvae on the tomato plant depend on leaf tissue as a primary food source, any increase in the antibiotic effect of this tissue should increase resistance measurably. Thus, the *L. hirsutum-L. hirsutum* f. *glabratum* antibiotic factor reported here is potentially a valuable source of fruitworm resistance for *L. esculentum* cultivars, especially since these 2 species are cross-compatible. Because *L. hirsutum* f. *glabratum* accessions have been reported to be resistant also to the carmine spider mite and the tobacco flea beetle (6, 8), this antibiotic factor might confer resistance to more than one insect species.

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Effect of Soil Moisture and Irrigation Method on Tipburn and Edgeburn Severity in Greenhouse Lettuce[1]

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Abstract. Lettuce (*Lactuca sativa* L.) cvs. Domineer and Grand Rapids were grown in the greenhouse at 4 soil moisture levels using 2 irrigation methods. Tipburn developed on immature 'Domineer' plants but not on 'Grand Rapids' in the high soil moisture beds 63 days after transplanting. Tipburn was observed on both cultivars when harvested at maturity 93 days after transplanting. Mature plants of 'Domineer' were more severely tipburned than those of 'Grand Rapids.'

Edgeburn was first observed 53 days after transplanting on both cultivars at all soil moisture levels as pinpoint necrosis on outer leaves where the veins terminate at the leaf edge. The affected area enlarged with time and appeared to be associated with high levels of Mn.

Yields were higher at the 0.0-0.2 and 0.4 bar tension levels than at 2.0 bars. 'Domineer' gave higher yields than 'Grand Rapids.'

Tipburn and edgeburn are physiological disorders of lettuce confronting greenhouse growers. Leaf lettuce is seldom affected in the field, but will at times have quite severe tipburn when grown in the greenhouse (15). Numerous researchers have used crisphead and butterhead type lettuce cultivars for tipburn studies since these types are more susceptible to tipburn than leaf cultivars.

Environmental factors related to tipburn such as temperature (1, 7, 8, 18), light intensity (13, 18, 19), light duration (19), and humidity (11, 20) have been investigated. Nutrient deficiency or imbalance of B (3, 9, 10, 16), Ca (2, 16, 17), and an excess of N (2, 7) have been cited as causes of tipburn.

Soil moisture also affects severity of tipburn. Lettuce requires a constant and fairly high soil moisture content for rapid growth. Some investigators (1, 4, 7, 14) report tipburn is due to low soil moisture content while others have attributed the disorder to high soil moisture content (8, 12, 19). The conventional practice for watering greenhouse lettuce in the winter is for growers to maintain a high soil moisture content during the early part of the growing season. After the leaves enlarge and cover the soil surface, water is sprinkled sparingly and then only on bright sunny days. This is done to reduce the incidence of fungal diseases observed when the plants remain wet for long periods.

Edgeburn, the dark necrotic area on the edge of older lettuce leaves has been reported to be due to Mn toxicity (5). Susceptibility of

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