Reprinted from JOURNAL OF AGRICULTURAL AND FOOD CHEMISTRY, 1994, 42.

Topical Toxicity of Tomato Sesquiterpenes to the Beet Armyworm and the Role of These Compounds in Resistance Derived from an Accession of *Lycopersicon hirsutum* f. *typicum*

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The topical toxicity of five sesquiterpenes to neonate beet armyworm (*Spodoptera exigua* [Hübner]) was determined to be sufficiently high (LD_{50} from 3 to 10 μg/larva) to implicate these compounds as resistance factors in sesquiterpene-producing accessions of *Lycopersicon hirsutum* f. *typicum* Humb. and Bonpl. (*hir*). Three sesquiterpenes (zingiberene and two isomers of elemene) were present at 33 μg/cm^2 on intact leaf surfaces of a genotype of *hir* accession PI 126445. Ten-day survival of *S. exigua* larvae on foliage of this genotype was 0%, but removal of 90% of the sesquiterpenes by wiping the foliage with methanol increased *S. exigua* survival to 65%. Although these data suggest that sesquiterpenes are resistance traits, other factors are also apparently involved. Ten-day larval weights on *hir* foliage wiped with methanol were still 8-fold lower than on susceptible commercial tomato plants, suggesting that lamellar resistance factors slowed larval growth. Also, *S. exigua* survival on plants from an F_2 and backcross population from an *hir* × *L. esculentum* cross was independent of the concentration of sesquiterpenes on the leaf surface. Sesquiterpene concentrations on foliage of the interspecific populations were only 10% as great as on the resistant parent and were perhaps too low to cause detectable effects on *S. exigua* larvae.

INTRODUCTION

Many accessions of *Lycopersicon hirsutum* are highly resistant to key insect and mite pests. Nevertheless, none of the resistance sources identified has been used successfully to develop insect-resistant varieties of cultivated tomato *Lycopersicon esculentum* (Farrar and Kennedy, 1992). PI 134417, an accession of *L. hirsutum* f. *glabratum* Mull., has been studied the most. Resistance to several tomato pests in this accession has been linked to the insecticidal methyl ketones, the dominant components of the secretions of the type VI glandular trichomes (Lin and Trumble, 1986; Kennedy and Dimock, 1983; Williams et al., 1980). Failure to develop resistant varieties from PI 134417 is a result of unfavorable linkages between trichome density, methyl ketone concentrations, and required horticultural traits. Study of other accessions of *L. hirsutum* may uncover sources and mechanisms of arthropod resistance better suited for developing resistant tomato varieties.

Insect-resistant accessions of *L. hirsutum* f. *typicum* Humb. and Bonpl. (*hir*) secrete sesquiterpenes from their type VI trichomes, instead of methyl ketones. These sesquiterpenes include zingiberene, γ- and δ-elemene, α-curcumene, and α-humulene (Eigenbrode and Trumble, 1993; Weston et al., 1989; Eigenbrode, unpublished results). Topical toxicity of zingiberene to Colorado potato beetle larvae (Carter et al., 1989a) and topical toxicity of sesquiterpene-containing trichome secretions from *hir* LA 361 to larvae of the beet armyworm, *Spodoptera exigua* (Hübner), and the tomato pinworm, *Kieferia lycopersicella* (Lin et al., 1987), suggest that these compounds are insect resistance factors in *hir* accessions.

We report here several experiments assessing the potential of a *hir* accession as a source of resistance to *S. exigua* and investigating the role of sesquiterpenes in conditioning this resistance. *S. exigua* was chosen as the study insect in these experiments because it is becoming the most important lepidopteran pest of tomatoes in California and Mexico (Brewer and Trumble, 1991), and alternatives to pesticides for managing this insect are needed. Specifically, we determined the topical toxicity of five tomato sesquiterpenes to *S. exigua* neonates. We also measured resistance to *S. exigua* in a genotype of *hir*, and the effect on this resistance of removing the sesquiterpenes from the leaf surface. Finally, we measured resistance to *S. exigua* in the F_2 and backcross populations derived from a *hir* × *L. esculentum* cross and examined the association between sesquiterpenes and resistance to *S. exigua* in these populations.

METHODS AND MATERIALS

Plant Culture. Twenty plants of a genotype of PI 126445 were propagated from cuttings obtained from C. D. Carter, South Dakota State University. These and 20 plants of the susceptible tomato cultivar VFN 7718 (Petoseed Co., Woodland, CA) were transferred to outdoor plots at the Agricultural Operations Facility of the University of California, Riverside, on April 8, 1991. Plants were spaced 40 cm within the row and 2 m between rows and furrow irrigated twice weekly. The soil was an Arlington loam, pretreated with 16–20–0 NPK at 450 kg/ha. Zingiberene for topical toxicity bioassays was isolated from the PI 126445 plants, as described below. Leaf tissue from PI 126445 and VFN 7718 was used in bioassays conducted in June and July 1991.

Plants for other experiments in the study were grown in the greenhouse at 28 °C, under ambient lighting conditions, in 12-L pots with University of California soil mix and fertilized weekly with an NPK and micronutrient supplement. These included additional plants of PI 126445 and VFN 7718 used in bioassays conducted during the winter of 1991–1992. Also, seed of the F_2 generation of a cross between tomato cv. Nova (Stokes Seed Co., Buffalo, NY) and PI 126445 and the backcross of the F_1 of this cross onto Nova (*NNH*) were obtained from C. D. Carter. Parentals, F_2, and *NNH* were planted in the greenhouse on August 1, 1991, and maintained through April 1992. Assays with these plants were conducted in January and March 1992. In April,

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0021-8561/94/1442-0807$04.50/0

clonal propagates of each plant were made and maintained in pots in the greenhouse until they were used in bioassays in August 1992.

Topical Toxicity of Individual Sesquiterpenes to *S. exigua*. Toxicities of zingiberene, β-elemene, α-curcumene, α-humulene, and β-caryophyllene were determined. Zingiberene was extracted from the field-grown plants of PI 126445 during the fall of 1991 and purified for use in topical bioassays. Batches of leaves (approximately 500 g each) were steeped in pentane (1500 mL) for 2–3 h at room temperature. The resulting mixture was filtered and concentrated on a rotary evaporator at 20 °C. The concentrate was loaded onto a silica gel column (83–200 mesh, 2.5 cm i.d. × 40 cm) which was then eluted with pentane (600 mL). The eluate was concentrated by rotary evaporation, leaving an oily residue containing hydrocarbons and waxes. The combined residue of six separate extractions was separated into volatile and nonvolatile fractions by Kugelrohr distillation (oven temperature, 95 °C; pressure, 0.1 mmHg; receiver flask cooled with dry ice). The distillate contained 92% zingiberene by GC analysis; minor components consisted primarily of other sesquiterpenes. A portion of the distillate (approximately 1 g) was purified further by flash chromatography on silica–silver nitrate [15% (w/w) $AgNO_3$ adsorbed on 230–400-mesh silica gel, 2.5 cm i.d. × 30 cm], eluted sequentially with 1 column volume each of 2%, 3%, and 5% ether in pentane, collecting 25-mL fractions. The resulting purified zingiberene (0.83 g) was >98% pure by GC.

β-Elemene and α-curcurmene were prepared as previously described (Millar et al., 1986). α-Humulene and β-caryophyllene were obtained from Sigma Chemical Co. (St. Louis, MO).

Topical toxicity of sesquiterpenes to neonate *S. exigua* was determined using methods similar to those of Lin et al. (1987). Doses of 0.0, 0.75, 1.50, 3.00, 6.00, 12.00, and 24.00 μg/ larva were applied in a 0.2-μL droplet of hexane, using a microapplicator. A single replicate consisted of 30 larvae, and for each sesquiterpene, each dose was replicated four times. Treated larvae were placed on a lima bean–agar artificial diet and evaluated for survival after 24 h. The diet was the same used to rear the *S. exigua* colony. Larvae in the bioassay were classified as dead if they did not react within a few seconds after prodding. Mortality in hexane-only controls was <3%.

Bioassays with Leaf Tissue. Beet armyworm larvae were reared from egg hatch on leaf tissue of field-grown PI 126445 and VFN 7718. Larvae were reared individually in 30-mL plastic cups partially filled with agar gel to maintain moisture (Diawara et al., 1992). The test was conducted in a growth chamber maintained at 29 °C and 16:8 light/dark, under ambient humidity (30–50% relative humidity). Leaf tissue, obtained from the fourth–fifth node below a branch terminal, was replaced every other day. Six groups of 10 larvae were reared on each genotype. Larval survival was determined after 10 days.

Larvae were also reared on leaflets from greenhouse-grown VFN 7718 and PI 126445 plants, which had been either wiped several times with a cotton swab soaked in methanol to remove trichome exudates or left untreated. Methanol was used rather than hexane or pentane to minimize damage to the leaves caused by removal of epicuticular leaf waxes along with the sesquiterpenes. In this experiment a replicate consisted of 10 larvae reared together in a single waxed-paper cup (200 mL) lined with agar gel. Leaflets were replaced every other day. Survival and larval weight were assessed at 10 days.

Larvae were reared from neonates on leaf tissue from 6 PI 126445, 6 Nova, and 20 *NNH* plants from January 24 to February 3. A second test was conducted from March 16–26 with 6 PI 126445, 6 Nova, 12 F_2, and 26 *NNH* plants. A third test was conducted from August 1–10 with 6 PI 126445, 6 Nova, 11 F_2, and 34 *NNH* plants. In these tests 10 larvae were reared in 200-mL paper cups. The January test included three replicate cups for each plant, the April test included two replicates for each plant, and the August test included four replicates for each plant. The mean percentage of larvae surviving on replicates for each plant was determined on the 10th day of each test.

The presence of sesquiterpenes on the leaf surface of all bioassayed plants was confirmed by GC and GC–MS analysis of hexane extracts of leaves. In the January and March tests, approximately 150 cm^2 of leaf tissue from the third node of each plant was extracted by agitating the tissue in hexane (30 mL) for 90 min. The solvent was decanted and evaporated just to dryness under a stream of nitrogen. The residue was redissolved in 1 mL of hexane containing either 87 μg of β-caryophyllene (January) or 73 μg of tetradecane (March) as an internal standards. Internal standards were chosen because their volatilities and retention times are similar to those of zingiberene. In the January and March tests only the presence or absence of the zingiberene peak was recorded. In the August test and the tests with PI 126445 and VFN 7718 the concentrations (μg/cm^2 of leaf surface) of zingiberene and two other sesquiterpenes, identified as elemene isomers, were determined. Approximately 30 cm^2 of leaf tissue from each plant was extracted with 10 mL of hexane containing 5.1 μg/mL of tetradecane as an internal standard.

Table 1. LD_{50} Values (Micrograms per Larva) for Sesquiterpenes Applied Topically to Neonate *S. exigua*

compound	LD_{50}	95% CI
α-zingiberene	3.8	3.4–4.3
α-humulene	4.5	3.0–6.6
β-elemene	5.0	3.3–7.9
α-curcumene	6.2	4.5–8.8
β-caryophyllene	9.7	6.7–15.9

All extracts were analyzed with a Hewlett-Packard (Avondale, PA) 5890 Series II gas chromatograph with a HP 7673 autosampler and a flame ionization detector. Injections were made in splitless mode onto a DB-5 column (J&W Scientific, Folsom, CA; 60 m × 0.25 mm i.d.). The temperature program was 100–200 °C at 15 °C/min, then 5 °C/min to 250 °C, and then 20 °C/min to 300 °C. The carrier gas was helium.

Identification of components was confirmed by GC–MS using a HP 5890 gas chromatograph interfaced to a HP 5870 mass selective detector. The retention time and mass spectrum of zingiberene isolated from leaf samples exactly matched those of an authentic sample of zingiberene isolated from ginger root. Two other major sesquiterpenes were tentatively identified as δ- and γ-elemene by comparing their mass spectra with those of literature spectra (EPA–NIH mass spectral database). Further corroboration of the identification of the structure of the compound identified as δ-elemene was obtained serendipitously; the mass spectrum and retention time of this compound exactly matched those of a minor impurity in a sample of synthetic β-elemene which had been isolated from a mixture of elemene isomers (Millar et al., 1986).

Immediately following the March and August bioassays, the densities of type IV and type VI trichomes were determined on each of the plants used in the respective tests. All trichomes were counted on a 2.2 mm^2 area of the upper and lower surface of each of four leaves (fourth–fifth node below the terminal) from each plant using a stereoscopic dissecting microscope at 60×. The mean number of each trichome type per mm^2 of each plant was calculated from these data.

LD_{50} values for individual sesquiterpenes were determined using the PROBIT procedure of SAS (1990). Statistical comparisons for leaf tissue bioassays were made using TTEST and GLM (for ANOVA) procedures of SAS (1990). Survival data were transformed to the arcsin $x^{1/2}$ to stabilize variances. Larval weights were not transformed before analysis. SAS procedure CORR was used to calculate correlation coefficients between mean survival and mean estimates of trichome densities and sesquiterpene concentrations.

RESULTS AND DISCUSSION

All five sesquiterpenes tested were highly toxic to *S. exigua* neonate larvae (Table 1). Zingiberene was more toxic than α-curcumene and β-caryopyllene, and β-caryophyllene was less toxic than all but α-curcumene (on the basis of nonnoverlapping 95% confidence intervals). Since the LD_{50}'s of all five sesquiterpenes were comparable to the 7 μg/larva reported for zingiberene to CPB neonates (Carter et al., 1989a), these compounds may have broad spectrum topical activity against potential insect pests. The sesquiterpene LD_{50}'s are also similar to the 3.4–3.5

Table 2. Sesquiterpene Concentrations (μg/cm²), 10-Day Survival (%), and 10-Day Weights (mg) of *S. exigua* Larvae Reared from Neonates on Leaf Tissue of a Susceptible Tomato Variety and a Resistant Genotype PI 126445 either Untreated or with Trichome Exudates Removed with Methanol

genotype	treatment	sesquiterpenes	survival[a]	larval wt[b]
VFN 7718	untreated	0	90 ± 7	24 ± 4b
	methanol-wiped	0	88 ± 3	60 ± 5a
PI 126445	untreated	51.0	0.0	
	methanol-wiped	4.2	65 ± 12	3 ± 0.2c

[a] No significant differences (survival on PI 126445 has no variance), $P = 0.0970$. [b] Means separated by protected LSD (0.05). Errors are SEM.

Table 3. Ten-Day Survival (Percent) of *S. exigua* Larvae on a Genotype of PI 126445 (*L. hirsutum* f. *typicum*), Tomato Cultivar Nova, and the F_2 and Backcross (*NNH*) of a Nova × PI 126445 Cross

	January test			March test			August test		
	n	mean[a]	range	*n*	mean[a]	range	*n*	mean[a]	range
PI 126445	6	0a	0–0	6	12a	0–30	6	5c	0–28
Nova	6	71b	56–82	6	66b	40–95	6	75a	53–88
F_2				10	9a	0–40	10	31b	0–78
NNH	21	37c	3–80	28	33ab	0–70	34	64a	0–88

[a] All means separated with LSD at 0.01.

μg/larva reported for the methyl ketones 2-tridecanone and 2-undecanone to *S. exigua* neonates (Lin et al., 1987).

The PI 126445 genotype tested was consistently highly resistant to *S. exigua* larvae, as determined by larval survival on foliage. Ten-day larval survival on foliage from field plots was 1.7 ± 1.7% on PI 126445 and 66.7 ± 6.7% on VFN 7718 ($P = 0.0001$). Similar differences were obtained on greenhouse-grown plants (Table 2).

Removal of methanol-soluble exudates greatly reduced the overall toxicity of PI 126445 plants to the insects (Table 2). Wiping with methanol removed 90% of the sesquiterpenes, from GC analysis of extracts of wiped leaves. This result implicates the sesquiterpenes as resistance factors in PI 126445. Methanol wiping also removed many other unidentified minor volatile components from the leaf surface, however, and these minor components could also be resistance factors. The larvae on methanol-wiped PI 126445 plants were still much smaller than those on VFN 7718. Exudate components that were not completely removed by wiping, or lamellar resistance factors, must account for the residual antibiosis on wiped leaflets of PI 126445.

Ten-day survival on VFN 7718 was not significantly affected by wiping with methanol, but the weight of larvae on VFN 7718 was significantly increased by this treatment. Therefore, even the susceptible plant possesses some antibiosis to *S. exigua* caused by extractable compounds on the leaf surface. These likely are phenolics present in type VI trichomes of cultivated tomatoes known to reduce the growth rates of *S. exigua* when incorporated into artificial diets (Duffey and Isman, 1981).

Ten-day survival of *S. exigua* on the F_2 and *NNH* populations was intermediate between those of the resistant and susceptible parents (Table 3). In all three tests, the range of *S. exigua* survival on *NNH* included that of the resistant parent and most of that of the susceptible parent.

Zingiberene and the elemenes were detected (>0.2 μg/cm² of leaf) on PI 126445, F_2, and *NNH* populations. Zingiberene was detected in 47% of all test plants in the *NNH* population and in 76% of all test plants in the F_2 population. γ-Elemene was detected in 53% of *NNH* and 66% of F_2 plants. δ-Elemene was only detected in one *NNH* plant but was present in 66% of the F_2 plants. Zingiberene was the dominant sesquiterpene in all plants tested, comprising 62–87% of the total of these three sesquiterpenes in the August test (Table 4). Sesquiterpene concentrations were much lower on F_2 and *NNH* plants than on the resistant parent.

Table 4. Sesquiterpenene Concentrations (μg/cm²) on Leaflets of Plants of PI 126445 (*L. hirsutum* f. *hirsutum*) and the F_2 and Backcross (*NNH*) Populations of an *esc* × PI 126445 Cross

compound	*n*	mean[a]	range
		PI 126445	
zingiberene	6	30.0 ± 11.5	5.6–72.3
α-elemene	6	3.0 ± 1.4	0.7–9.3
δ-elemene	6	1.3 ± 0.4	0.3–2.6
		F_2	
zingiberene	11	2.7 ± 1.1	0–94
γ-elemene	11	0.5 ± 0.2	0–1.7
δ-elemene	11	1.1 ± 0.3	0–2.7
		NNH	
zingiberene	35	0.9 ± 0.4	0–10.2
γ-elemene	35	0.2 ± 0.0	0–0.9
δ-elemene	35	0.01 ± 0.01	0–0.2

[a] No sesquiterpenes were detected on *esc* parent Nova. Errors are SEM.

S. exigua survival was not dependent on the presence of sesquiterpenes in the *NNH* or F_2 populations (Student's *t*-test at 0.05). There was no significant correlation between 10-day survival and the concentration of zingiberene, γ-elemene, δ-elemene, or the total of all three sesquiterpenes in any population (P for Pearson's coefficients all $\gg 0.05$). The presence of other resistance factors, as suggested by the leaf-wiping experiment, and the relatively low concentrations of sesquiterpenes on resistant *NNH* and F_2 plants probably account for the lack of relationship between sesquiterpenes and *S. exigua* survival. In the previous experiment showing a correlation between insect survival (Colorado potato beetle) and sesquiterpene concentrations on tomato, the sesquiterpene concentrations were more than an order of magnitude greater than in the present study (180–600 μg of zingiberene/cm²) (Carter et al., 1989b). The plants in the Carter et al. study were an F_2 population from a cross within *L. hirsutum*, rather than between *hir* and *L. esculentum*.

The unidentified traits contributing to resistance in *NNH* and F_2 plants may be minor components of the type VI trichome exudates, traits associated with type IV trichomes, or lamellar traits. Previous work in our laboratory suggests that sesquiterpenes alone do not account for resistance in another *hir* accession, LA 361 (Lin et al., 1987). The toxicity of crude type VI glandular exudates of *hir* accession LA 361 (LD_{50} of 0.048–0.306 μg/*S. exigua* neonate) is 10–100 times greater than the toxicity of the purified sesquiterpenes we report here, and LA 361 has lower concentrations of sesquiterpenes than PI 126445 (Lin et al., 1987).

Weak negative correlations between *S. exigua* survival and type IV trichome densities on *NNH* plants in the March test ($r = -0.464$; $P = 0.015$; $n = 27$) and across seasons (March and August tests; $r = -0.291$, $P = 0.024$, $n = 60$) suggest that the secretions of these trichomes or traits linked to the density of type IV trichomes contribute to the resistance. Type IV trichome densities have been correlated with spider mite resistance in previous studies, but causality has not been established (Carter and Snyder, 1985, 1986; Good and Snyder, 1988; Weston et al., 1989).

On the basis of GC analysis, the hexane surface extracts

contained a large number of compounds other than sesquiterpenes that may contribute to resistance. These may have included minor secretions of the type VI trichomes and secretions of the type IV trichomes. Others were evidently components of the leaf surface waxes. Correlations between the areas of the 25 major peaks and *S. exigua* survival in the January test were all nonsignificant, and this analysis was not repeated in the March and August tests.

CONCLUSIONS

The topical toxicities of sesquiterpenes, including the dominant sesquiterpene zingiberene from accessions of *hir*, are equivalent to those of the methyl ketones known to condition resistance in *L. hirsutum* f. *glabratum*. This and the fact that their removal reduces the antibiosis to *S. exigua* in *hir* in PI 126445 suggest that breeding sesquiterpene secretion into commercial tomatoes could confer resistance to *S. exigua* and possibly other tomato pests. Unfortunately, in the F_2 and backcross populations examined in the present study, concentrations of sesquiterpenes on the leaf surface were very low, and it is not possible to assess thier potential, if expressed at higher concentrations, for conferring resistance in an *L. esculentum* background. Different breeding schemes or much larger populations may be required to produce high-sesquiterpene *L. esculentum* plants.

Nevertheless, foliar antibiosis to *S. exigua* was high in some individual *NNH* plants. Although this resistance is apparently produced by other trichomal or lammellar factors we have not identified, additional study of PI 126445 and lines produced from it appears warranted for the development of resistance to *S. exigua*.

ACKNOWLEDGMENT

We thank C. D. Carter for providing seed and plant material, W. G. Carson and S. Williams for technical assistance, and M. Berdegue, W. G. Carson, C. D. Carter, M. M. Diawara, R. Katchadorian, J. R. McFerson, J. C. Snyder, and three anonymous reviewers for helpful comments on earlier drafts of the manuscript. The research was partly supported by The California Tomato Board.

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Received for review April 13, 1993. Revised manuscript received September 2, 1993. Accepted December 6, 1993.[⊗]

[⊗] Abstract published in *Advance ACS Abstracts*, January 15, 1994.