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Resistance in Tomato to the Pink Form of the Potato Aphid (*Macrosiphum euphorbiae* Thomas): The Role of Anatomy, Epidermal Hairs, and Foliage Composition[1]

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Abstract. **Several characteristics of the cultivated tomato (*Lycopersicon esculentum* Mill.) and several wild relatives were explored as factors in resistance to the pink form of the potato aphid. Foliage volatiles of resistant and susceptible plants were found to be qualitatively similar but quantitatively different. Olfactometric tests revealed that the aphids did not react in any detectable way to the aroma variation conditioned by these quantitative differences. Epidermal hairs (non-glandular) of the normal genotypes were not a factor influencing degree of attack by the aphids. In the field the aphids avoided both an excessively hairy compound mutant stock *Ln-Wo*^{m} and the wild tomato relative *L. hirsutum.* However, under infestation in the laboratory the insects managed to feed on these plants. Pubescence in the normal genotype is not a factor affecting resistance. However, increase of hair density and length tends to restrict aphid feeding activity under field conditions. The presence of anthocyanin in the foliage did not inhibit aphids from feeding. No anatomical obstacles to reaching the feeding site, the internal phloem, were found in resistant accessions of the green-fruited species *L. hirsutum,* however, thick cortex in the stems might prevent aphids from reaching vascular tissue. Comparative analysis of foliage of susceptible and resistant plants revealed higher sucrose, lower quinic acid, and higher alanine and tyrosine contents and a trend toward higher total free amino-acid concentration in the former. Furthermore, susceptible plants were unique as a source of o-phosphoethanol amine.**

Recently, the pink form of the potato aphid has become an important pest of the cultivated tomato in the Sacramento Valley. This has provided an opportunity to study the nature of resistance in *Lycopersicon esculentum* to this insect. The sources of resistance in wild, red-fruited tomato species, their geographic distribution, the inheritance of this resistance, and other aspects have been studied by Geneif (6). On the basis of host plant-insect biological relationship, Beck (2) has divided plant resistance into four major groups and several sub-groups.

Several mechanisms for aphid resistance have been reported. Painter (13) mentions antibiosis. Sticky exudates from glandular hairs have also been found to provide resistance by entangling the aphids in the foliage in some wild potato species (8, 9), and in *Solanum pennellii* (7). Conversely, Clayberg (3) reported that these hairs play no role in the resistance to the potato aphid in a periclinal chimera of *pennellii* epidermis and *esculentum* core. He concluded that cell sap constituents are more likely responsible for the resistance of the former. Susceptible cultivars of pea were found to be higher in amino acids than resistant ones (1, 11). Mitler (12) analyzed the cell sap of *Salix acutifolia* susceptible to the aphid *Tuberolachnus salignus* and detected the presence of sucrose and several amino acids including alanine. Sugars and certain amino acids have been found to be important stimulants for the maintenance of feeding of several insects (2).

The present paper is concerned with the possible role of foliage components on host plant recognition or as physiological inhibitors and with the role of variation in anatomy or epidermal hairs in biophysical resistance.

Materials and Methods

Foliage volatiles. Foliage volatiles of resistant and susceptible plants were sampled using a method previously described (14, 17). The resistant plants were *L. esculentum* cv. VF36 and *L. esculentum* var. *cerasiforme* (LA1291); the susceptible plants, an anthocyaninless mutant (*are*) of 'VF36', 'Red Cherry' and *L. pimpinellifolium* (LA1342). Geneif (6) has established the reaction of these lines to this aphid by evaluation of aphid infestation. Furthermore, he has determined the inheritance of resistance to the pink potato aphid.

Olfactometric tests. Aphid response to volatiles from tomato foliage was evaluated using 2 types of olfactometer. The first type used was a Y-shaped tube of 50 mm ID and 500 mm arm length, with filter papers impregnated with volatiles of either resistant or susceptible plants in one arm and in the other arm a clean filter paper as a control. The reaction to volatiles from resistant or susceptible plants was tested with ten winged aphids reared on sugar beet leaves and 20 additional ones collected randomly from a tomato field. The second type of olfactometer used was one developed by Marsh (10) for his studies on aphid response to sex pheromones. Briefly, it consists of a tract with a perforated paper floor below which there are two compartments for the volatiles intercalated twice with powdered activated charcoal regions. The aphids are released at one end of the track and are attracted toward a light source at the other end. As they cross the volatile and the charcoal zones, the time spent and the reactions displayed are recorded. The volatile sources were filter paper impregnated with volatiles of either resistant or susceptible plants or fresh leaves of these plants. Ten winged aphids reared on sugar beet leaves and starved in plastic boxes for 12 h (110 × 110 × 30) with filter paper lining on the floor were tested for reaction to volatiles from resistant plants, and 10 other insects for reaction to susceptible plant volatiles. The experiment was repeated using 20 additional winged aphids randomly collected from tomato fields.

Epidermal hairs. F_2 progenies segregating for the hairless gene *h* (absence of non-glandular trichomes) were scored in the field for aphid infestation. Leaves and shoots of extremely hairy plants grown in the field, including the double mutant *Ln-Wo*^{m} (16) and *L. hirsutum* var. *typicum* (LA1352), were artificially infested with aphids in the laboratory. Sections of infested tissue were cytologically examined using standard microtechniques (18) to detect any feeding in the resistant

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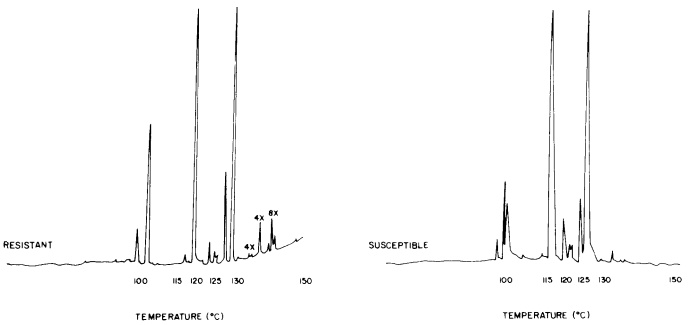

Fig. 1. Chromatograms of the foliage volatiles from the resistant lines LA1291 (left) and from the susceptible line LA1342 (right). The last group of peaks in the resistant line was magnified four to eight times to make them distinguishable.

plants.

Presence vs. absence of anthocyanin. F_2 populations, each segregating for the anthocyanin deficient genes *ag* and *ae*, were scored in the field for aphid infestation. There was a heavy natural aphid infestation in the populations. A score of zero indicated plants free of aphids and five indicated heavy infestation.

To determine any possible association between these genes and aphid reaction, χ^2 tests for independence, including the Yates correction for small samples, were performed.

Anatomical studies. Leaves and shoots of tomato plants infested with aphids were collected in the field and introduced for about one minute into a flask containing an atmosphere saturated with ether. Generally the aphids remained anchored in the tissue by their probosices. The tissues were carefully cut in small pieces and immediately fixed in 3:1 alcohol-acetic acid. Standard mitrotechnique was followed for paraffin embedding and microtome sectioning (18). Sections were cut 10 mm thick and stained with safranin-fastgreen. The resistant plants, collected from the field were infested with aphids in the laboratory for this study. The component tissues of shoot and leaf sections from resistant and susceptible plants were measured with the aid of an eyepiece micrometer. These determinations were based on three sections per plant and three measurements per section. An F test was performed to detect statistical differences in tissue thickness among the genotypes assayed. The embedded probosices of ten adult aphids were also measured in tissue sections.

Chemical analysis. Foliage of plants from the segregating progeny of the cross of resistant *L. esculentum* var. *cerasiforme* and the susceptible *L. pimpinellifolium* was collected in the field and dried in the oven for 48 hours. Samples were also taken from two other susceptible *pimpinellifolium* accessions (LA1335, LA1582). In addition, plants of the wild species *L. hirsutum* (LA1352, LA1361) and *Solanum pennellii* (LA 716, LA1277) were examined. Samples from the normal, resistant genotype and the susceptible mutant *are* of 'VF36', both growing in the greenhouse, were also taken. Four accessions of *L. peruvianum* (LA107, LA1346, LA1646, and LA 1647) growing under greenhouse conditions were similarly analyzed. For sugars and organic acid analysis, one gram of ground tissue was extracted with 100 ml 80% ethanol in a steam bath for about 30 min. The extract was filtered and washed with 100 ml benzene in a separation funnel to remove the chlorophyll. The alcoholic extract was evaporated to dryness under vacuum. The residue was dissolved in 10 ml water with 1.5 ml 1% ribose and 1 ml 1% tartaric acid added as internal standards. This solution was passed through a 10 × 20 mm AG1-X8 column, which was then washed with 60 ml water to recover the sugars, and the acids were eluted with 60 ml 6N formic acid (19). The eluates were evaporated to dryness and each redissolved in 10 ml water. One ml of this solution and 2 ml 95% ethanol were added to a 5 ml serum bottle. This solution was dried with an air stream on a hot plate at 35°C. Trimethylsilyl derivatives were prepared by adding 1 ml of the mixture hexamethyldisilazane, trimethylchlorosilane, trimethylsilylimadazole (TSIM) and pyridine (0.1:0.4:1:4) to the sugars. For the acids, the mixture did not include TSIM and was in the proportion 1:0.5:4. Four samples per plant, 2 for sugars, and 2 for organic acids, were prepared. TMS ethers were separated on a 1.52 m × 32 cm O.D. stainless steel column packed with 5% OV101 on 80-100 mesh AW DMCS treated Chromosorb W. A flame-ionization Hewlett-Packard 5700 gas chromatograph was used for the analyses. The temperature program was 150-300°C @ 8°/min. Gas flow rates were 20, 30, and 200 ml/min for H_2, N_2, and air, respectively. Peak height of the sugars relative to ribose and of the organic acids relative to tartrate was used to estimate concentrations. For amino acid analysis ½ g samples of the dry tissue were extracted under vacuum in 25 ml 3% sulfasalicylic acid. The extract was centrifuged for 10 min at 10,000 rpm at 9°C. The supernatant was filtered and stored in a 5 ml vial in the freezer until analyzed. The samples were run in a Beckman Model 121M amino acid analyzer.

The F test was performed to detect statistical differences among the genotypes assayed for the components analyzed.

Results and Discussion

Foliage volatiles. Variation in the volatile compound composition between the resistant *L. esculentum* var. *cerasiforme* and susceptible *L. pimpinellifolium* plants appears to be quantitative rather than qualitative (Fig. 1). Apparently these quantitative differences are responsible for the variation in foliage aroma between resistant and susceptible plants. These tests were repeated at least 5 times with different plants with no detectable variation within species. The aroma and volatile composition of the normal (resistant) and mutant *are* (susceptible) plants of 'VF36' and of the *cerasiforme* (resistant) accession were similar. This indicates that foliage aroma is not important in the resistance of tomato plants to the pink potato aphid. The olfactometric tests confirmed this observation.

Olfactometric tests. Biological tests with the Y-shaped olfactometer indicated that aphids do not react to the presence of foliage volatiles from the plants used in this study. The insects tested moved randomly to either branch of the tube regardless of the presence or absence of volatiles from resistant or susceptible plants. Since it is possible that the entire tube was contaminated by diffusion of the volatiles present in one of the arms, additional insects were not assayed using this method. Rather, to further test aphid response to volatiles, the more sophisticated pathway olfactometer (10) was used. Negative results were also obtained with this instrument. The 40 individuals tested did not reduce their speed when crossing the volatile zones and there was no apparent change of behavior. To assure that this indifference to volatiles was not due to a strong light attraction, the test was repeated with at least 20 more aphids without the light source. Here again, there was no apparent discrimination between odor and non-odor (charcoal) regions in the olfactometer. Conversely, with the aphid *Megoura viciae*, Marsh (10) found definite responses to sex pheromones in this olfactometer. These were manifested by reduction of walking speed, greatly enhanced rate of turning, waving of antenna with great vigor and prompt return to the pheromonal region. Since we did not detect any reaction whatsoever in the 60 individuals tested with the Y-shaped tube, we did not consider necessary further testing with these devices. Furthermore, limited tests performed to determine any effects of volatiles from resistant or susceptible plants on the aphid fecundity were also negative. Thus, our results indicate that foliage volatiles of the susceptible and resistant tomato plants tested neither attract nor repel the pink potato aphid – results which agree with Beck's

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Table 1. Leaf thickness in micrometers of normal (aphid resistant) and mutant *are* (susceptible) plants of 'VF36'.

Plant	Section no.	Palisade cells	Spongy parenchyma	Total
Normal	1	27	43	83
(Resistant)	2	25	49	85
	3	23	52	91
are	1	43	75	147
(Susceptible)	2	53	87	169
	3	55	85	153
F values		42.47**	57.73**	100.23**

(2) conclusions.

Epidermal hairs. Preliminary field observations suggested that the presence of epidermal hairs (non-glandular) in normal genotypes of the tomato cultivars was not associated with resistance to the pink potato aphid. To confirm this observation, three F_2 families segregating for the hairs-absent gene (*h*) were scored for degree of aphid infestation under field conditions. No significant association between parameters was obtained (χ^2 = 0.8) for pooled data from the three F_2 populations (184 plants scored). It appears that epidermal hairs of normal genotypes are not a biophysical barrier to aphid feeding. To pursue this matter further, the following extremely hairy plants were artificially infested in the laboratory. We used the compound mutant stock *Ln-Wo*^{m} with extremely long and thick epidermal hairs but lacking glandular hairs, and the wild tomato species *L. hirsutum* var. *typicum* with long epidermal hairs and a dense population of glandular trichomes. Even under field conditions of heavy infestation, aphids were not found on these plants. The purpose of the experiment was to determine whether the extreme hairiness might prevent the aphids from reaching the plant tissue for feeding. Evidence that this is not the case was the presence of a proboscis embedded in the infested tissue of *Ln-Wo*^{m} in the laboratory tests. Further evidence of feeding on *Ln-Wo*^{m} and *hirsutum* was the secretion of honeydew droplets when gentle pressure was applied to the feeding insects. No attempt was made to calculate the rate of feeding success by the aphids in these plants, but usually of 10 aphids populating a shoot or leaf of the mutant plants, one or two were found feeding while the rest moved about. Thus, despite the dense population of long hairs, the aphids managed to find areas where their probocises could penetrate the leaf and reach the phloem for feeding purposes. It appears that these insects avoid plants with extreme hairiness.

Table 2. Thickness in micrometers of several tissues in the stems of resistant and susceptible plants.

Plant	Section no.	Epidermis	Cortex	Vascular bundles
Normal				
'VF36'	1	17	243	179
(Resistant)	2	17	253	167
	3	19	273	183
are				
'VF36'	1	17	280	196
(Susceptible)	2	17	293	212
	3	17	280	189
F values		1.0	8.12*	7.40
LA1291	1	13	227	193
(Resistant)	2	11	223	173
	3	11	191	167
LA1342	1	13	123	120
(Susceptible)	2	12	128	116
	3	15	176	117
F values		2.27	12.25*	56.94**

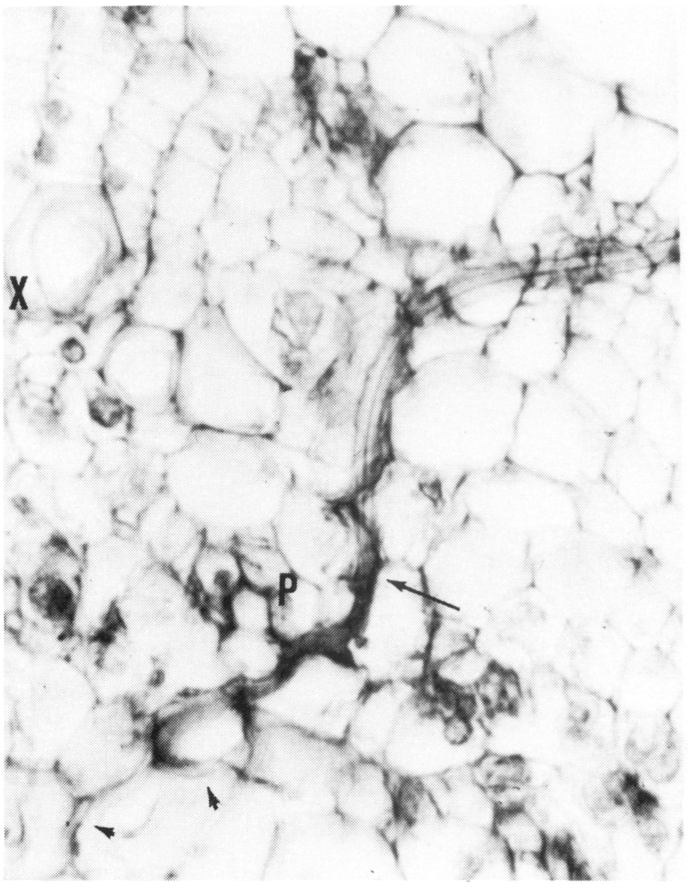

Fig. 2. Cross section of stem of LA1342 with an embedded aphid proboscis with its tip directed toward the phloem (arrow). Associated salivary tracts continued toward the pith (arrow heads) (×300). P = phloem, X = xylem.

Presence vs. absence of anthocyanin. Previous studies by Geneif (6) revealed extreme susceptibility of the anthocyanin-free mutant *are,* and, in contrast, resistance in another anthocyaninless mutant (*al*). These results dissociate resistance from the presence of anthocyanin *per se.* We confirmed his findings in the following test. To determine whether the lack of anthocyanin was a factor influencing the susceptibility to the aphids, two additional mutants also blocking anthocyanin synthesis (*ag* and *ae*) were scored for infestation in segregating F_2 populations. For both genes, infestation was independent of the presence or absence of anthocyanin (χ^2 = 0.01 for *ag,* 53 plants scored; χ^2 = 2.86 for *ae,* 76 plants scored). The aphid population was heavy during the scoring, making the possibilities of plant escapes unlikely. Therefore, anthocyanin probably has no adverse biochemical influence on the aphids. The susceptibility of the mutant *are* may be due to a favorable nutritional status.

Anatomy. The leaves of the susceptible mutant *are* are significantly thicker than those of the resistant isogenotype. This difference was reflected in thicker epidermis, palisade layer, and spongy parenchyma (Table 1). Similarly, a significantly greater thickness was observed in the stem cortex of *are* (Table 2), but differences in epidermis and vascular tissue dimensions were not significant. Conversely, the cortex and vascular bundles of the susceptible *L. pimpinellifolium* (LA1342) were significantly smaller than those of the resistant *L. esculentum* var. *cerasiforme* (LA1291) (Table 2). When aphid probosces were found in the sections, the tips were localized in the internal phloem in most of the 30 observed cases (Fig. 2). The mean penetration of the proboscis is 385 μ, whereas the mean depth of the internal phloem is 320 μ, and never approxi-

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Table 3. Percent sugars in resistant and susceptible plants.

Reaction	Plant[z,y]	Fructose	Glucose	Inositol	Sucrose
Resistant	LA1291-1	0.90	1.80	1.56	3.32
	LA1291-2	0.81	1.44	1.56	2.49
	S4-49	0.39	0.56	2.04	5.10
	S9-2	0.54	0.64	1.62	5.13
	S9-44	1.58	1.81	1.98	3.96
	S9-45	1.14	3.51	2.97	6.03
	Normal VF36-1	3.83	7.40	2.84	1.86
	Normal VF36-2	1.17	2.99	1.50	4.71
	$\bar{x}$	1.30	2.51	2.01	3.61
Susceptible	LA1342-1	1.08	1.37	2.01	6.75
	LA1342-2	0.96	1.29	4.19	5.04
	S4-3	0.80	0.99	2.19	6.62
	S81	0.51	0.56	1.71	3.27
	LA1335-1	2.01	2.55	7.14	15.39
	LA1582-1	1.43	1.41	2.12	7.92
	LA1342-3	1.23	1.77	1.65	8.18
	are VF36-1	2.94	1.58	2.55	6.63
	are VF36-2	1.32	2.96	1.89	6.33
	$\bar{x}$	1.36	1.61	2.82	7.34

[z]Plants preceded by S are F_3 segregants of the cross LA1291 x LA1342.
[y]Normal and *are* VF36 and LA1342-3 grown under greenhouse conditions, free of aphids.

Table 4. Percent organic acids in resistant and susceptible plants.

Reaction	Plant[z,y]	Malic	Citric	Quinic
Resistant	LA1291-1	0.78	0.26	0.48
	LA1291-2	0.89	0.59	0.34
	S4-49	0.97	0.36	0.58
	S9-2	1.04	0.31	0.30
	S9-44	1.33	0.33	1.10
	S9-45	1.68	0.18	0.88
	Normal VF36-1	0.54	0.05	0.31
	Normal VF36-2	0.96	0.18	0.26
	$\bar{x}$	1.02	0.28	0.53
Susceptible	LA1342-1	1.08	0.76	0.28
	LA1342-2	0.50	0.48	0.44
	S4-3	0.72	0.45	0.52
	S8-1	0.90	0.36	0.28
	LA1335-1	0.94	0.45	0.30
	LA1582-1	2.53	0.77	0.26
	LA1342-3	0.56	0.15	0.24
	are VF36-1	0.80	0.06	0.05
	are VF36-2	0.97	0.12	0.33
	$\bar{x}$	1.00	0.40	0.30

[z]Plants preceded by S are F_3 segregants of the cross LA1291 x LA1342.
[y]Normal and *are* VF36 and LA1342-3 were grown under greenhouse conditions and free of aphids.

mates the former value in these lines. Thickness of intervening tissues in either resistant or susceptible red-fruited lines is therefore not large enough to constitute a biophysical barrier to prevent the aphid proboscis from reaching internal phloem. In some instances, furthermore, in the infested stems the branched salivary tracks penetrated as deep as the pith (Fig. 2), but the proboscis associated with these tracks terminated in the phloem. These observations suggest that this aphid biotype, as others (5), probes the tissues in order to find the phloem.

Once it had been determined that the pink potato aphid feeds in the phloem, we proceeded to make chemical analyses of some of the compounds normally found in this vascular tissue.

Composition. The sugars found in tomato foliage, fructose, glucose, inositol, and sucrose, varied among the plants tested (Table 3). Concentration of fructose, glucose, or inositol did not vary significantly among resistant and susceptible plants; but sucrose concentration was significantly higher in susceptible plants ($F = 8.37^*$, 1 and 15 d.f., arc sine transformation). The sucrose differences were significant, even after excluding from the statistical analysis the plant with the highest sucrose values (LA1335-1). The rest of the sugars – especially fructose and glucose – tended to be lower in concentration in susceptible plants.

The major organic acids found in tomato foliage were malic,

Table 5. Free amino acid composition in resistant and susceptible plants.

	Concn (μM/g of dry tissue)							
	Resistant (normal)				Susceptible (*are*)			
Amino acid	VF36-2	LA1291-2	S9-2	S9-44	VF36-2	LA1342-2	LA1335-2	S8-1
Aspartic acid	0.73	2.08	3.45	2.54	2.09	2.16	3.24	2.80
Threonine	0.92	2.62	2.06	3.06	2.60	3.04	2.38	8.76
Serine	1.00	3.04	3.55	6.00	2.96	4.26	4.38	4.98
Asparagine	0.58	1.44	2.14	2.90	1.65	3.90	2.77	3.07
Glutamic acid	0.34	1.17	2.40	2.76	0.61	2.20	1.60	4.36
Glutamine	2.62	4.60	10.81	18.42	6.84	6.96	11.40	10.86
Proline	3.86	15.32	34.90	46.30	9.88	11.54	32.84	34.58
Glycine	0.74	1.62	3.70	3.80	0.95	3.46	2.28	1.15
Alanine**	5.96	11.60	11.58	11.74	21.96	24.82	17.50	23.94
Valine	1.94	5.71	7.34	4.48	6.68	7.02	5.50	10.70
Methionine	0.12	0.29	0.80	0.24	0.22	0.00	0.14	1.28
Isoleucine	1.38	3.92	2.28	3.34	4.09	5.52	3.32	6.02
Leucine	1.33	5.39	2.55	3.90	4.03	7.18	4.30	8.64
Tyrosine*	0.93	2.61	2.09	1.67	2.88	3.84	2.36	3.94
ϕ-Alanine	0.89	2.88	1.84	2.20	4.84	3.16	2.08	4.70
γ-Amino butyric	19.18	58.50	35.22	27.25	39.93	61.40	54.26	63.56
Ethanol amine	1.40	4.76	3.16	4.54	3.71	1.79	3.74	2.81
Lysine	1.38	3.78	2.16	3.82	3.91	5.40	2.74	12.23
Histidine	1.17	1.23	0.82	1.82	2.88	1.64	0.91	3.06
Arginine	0.90	2.70	1.70	2.56	2.58	4.33	2.23	3.96
Tryptophan	0.50	1.34	0.70	1.10	1.96	0.35	0.40	1.85
O-phosphoethanolamine	0.00	0.00	0.00	0.00	0.54	0.76	0.95	0.20
TOTAL	47.87	136.60	135.25	154.44	127.79	164.73	161.32	217.45

**Significant differences among lines at the 1% level.
*Significant differences among lines at the 5% level.

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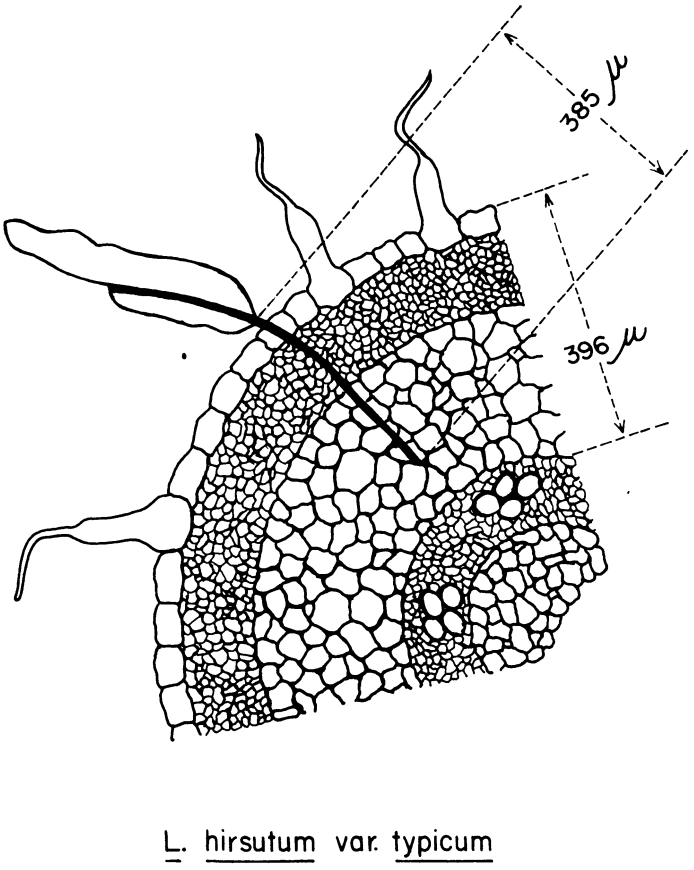

Fig. 3. Cross section of the stem of *L. hirsutum* var. *typicum* showing the buccal parts of an aphid with its proboscis embedded in the cortex. The proboscis is not sufficiently long to reach the phloem.

citric and quinic. Although the concentrations of these acids were similar in the resistant and susceptible plants, a trend toward higher concentration of quinic acid was found in the former (Table 4). The F value (4.13, 1 & 15 d.f., arc sine transformation), although not significant at the 5% probability level, was significant at 10% level.

Total free amino acid content in foliage tended to be higher in susceptible than in the resistant plants (Table 5). Significantly higher concentrations of alanine (F = 29.92**, 1 & 6 d.f.) and tyrosine (F = 7.52*, 1 & 6 d.f.) were found in the susceptible plants. Moreover, O-phosphoethanol amine was found only in the susceptible plants. Alanine has been reported to be a feeding stimulant for the corn borer (2). Alanine and tyrosine are known to be essential to the diet of *Myzus persicae* (4).

A relationship might possibly exist between sucrose, quinic acid, free amino acid concn, and aphid reaction. Generally, resistant plants are also high in quinic acid. Susceptible plants are usually high in sucrose and low in quinic acid, but the exceptionally susceptible S8-1 was very low in both but was high in total free amino acids and was relatively high in alanine and tyrosine. The exceptionally resistant plants S9-2 and VF36-2 were low in total free amino acids and in alanine and tyrosine.

These data suggest that less than 4% sucrose or more than 0.55% quinic acid or both contribute to resistance in tomato plants to the pink potato aphid. Low concn of alanine and tyrosine, and perhaps a lack of O-phosphoethanol amine, may also contribute to aphid resistance. These findings indicate that susceptible plants favor the reproduction and growth of aphids by supplying necessary nutrients. Quinic acid may act as a deterrent or antibiotic agent. Results of our analyses of the highly susceptible *Capsella bursa-pastoris* (6.55% sucrose and only traces of quinic acid) are compatible with this suggested role of sucrose and quinic acid. We found the pink potato aphid over-wintering in active form on this weed.

Primitive species. For the wild tomato relative *Solanum pennellii,* a sticky exudate released from glandular hairs (7) and possibly the cell sap constituants (3) have been reported responsible for resistance to the potato aphid in certain accessions. Gentile and Stoner (7) found all tested accessions of *L. peruvianum* resistant to the same aphis and suggested that an antibiotic agent is responsible. We have analyzed several accessions of *L. hirsutum, L. peruvianum,* and *Solanum pennellii* for sugars and organic acid content and the data suggest that these components are not responsible for their resistances. It is possible that the cortex in stems of *L. hirsutum* (LA1352) contributes to its resistance. In these plants the thickness of tissue that had to be penetrated to reach the vessels in the young stems is about 396 μ. The average proboscis length of the pink aphis is 385 μ (Fig. 3). Vascular tissue may, nevertheless, be reached rapidly in the leaves. In any event, the source of food would probably be less accessible in these than in susceptible plants. The extreme hairiness of *L. hirsutum* may add to its resistance. In the case of *S. pennellii,* the role of glandular hairs is controversial (3, 7). Although plants of this species are resistant under field conditions, we were not able to analyze this resistance.

This study indicates that foliage volatiles probably do not play a role in antibiosis or hostplant recognition by the pink form of the potato aphid nor affect infestation. Stem anthocyanin appears not to be a physiological inhibitor for this pest. Epidermal hairs of normal genotypes are not a biophysical barrier interfering with aphid feeding, but epidermal hairs of extremely pubescent plants appear to result in a non-preference reaction under field conditions.

Nutritional composition of the foliage of tomato plants, particularly sugars and free amino acids, may play an important role in resistance. Furthermore, higher concentrations of quinic acid may act as an antibiotic agent or at least as a deterrent. Biophysical barriers in leaf and stem anatomy that might impede aphid feeding were not found in resistant lines of the red-fruited tomato species. They may, nevertheless, be a factor in some accessions of *L. hirsutum.* Thus we conclude that low nutrient content, high quinic acid, and thick cortex may all act as antibiotic agents. The insects will thrive neither on plants lacking necessary nutrients for their development and reproduction nor on plants where they are impeded from reaching food sources.

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Seasonal Sugar Concentration in Two Peach Cultivars Differing in Cold Hardiness[1]

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Abstract. **Levels of soluble sugars in bark, leaves, leaf buds and flower buds of 2 cultivars of peach (*Prunus persica* (L.) Batsch) differing in cold hardiness were compared throughout the year. Thirteen sugars – galactose, glucose, fructose, xylose, stachyose, sucrose, raffinose, rhamnose, maltose, trehalose, arabinose, ribose and mannose – were present in measurable and variable concentrations. In general, oligosaccharides accumulated, particularly in the bark, during fall and winter, whereas monosaccharides accumulated during periods of active growth. These data do not show significant differences between the 2 cultivars regarding the accumulation of these sugars and cold hardiness.**

Earlier reports by the authors (7, 8) indicate that some correlation exists between the levels of soluble sugars in peach cultivars and winter hardiness. More recent literature also indicates such correlations in apple (18); stone fruits including peach (1, 9); citrus (10, 14); wheat (4) and pine (17). Some correlations between certain sugars, either individually or in groups, and winter hardiness have also been reported (1, 4, 10, 18). Sugars and sugar alcohols were reported by Sakai (13) to be most effective among the 60 compounds used in preventing freezing injury of cabbage cells frozen in suspending medium and subjected to slow cooling and rewarming. In peach cultivars, however, little is known except that fructose, glucose, and sucrose commonly occur throughout the season in peach tissue; and raffinose and stachyose may appear during the winter (12).

Materials and Methods

Two peach cultivars, 'Lizzie' (cold hardy) and 'Loring' (cold tender), were selected for this study according to criteria described earlier (8). Trees were planted in a greenhouse in holes 0.6 m diam × 1.2 m deep lined with black plastic and filled with a 2 soil:1 perlite:1 peat mixture (v/v). To each m^3 of this soil mix were added 15 kg superphosphate, 3 kg 5N-4.3P-8.3K fertilizer, and 3 kg dolomite. To expose trees to prevailing outside temp, the greenhouse was provided with movable side panels which were left open except when killing winter temp were predicted. Each cultivar was represented by 12 trees in a randomized complete block design with 3 replications, each consisting of 4 trees. Starting when trees were 3 years old, samples were collected on the 1st and 15th day of each month, with unbranched shoots collected from Jan. 1 through Dec. 15, mature leaves (mid-shoot) from March 1 through Nov. 1, leaf buds from Nov. 15 through Dec. 15 and flower buds from Nov. 1 through April 1. All samples were collected between 8 and 10 AM and immediately frozen. Leaf and flower buds were dissected from the frozen shoots. The bark was then dissected from the wood of the partly thawed shoots. Bark, leaf and bud samples were lyophilized, ground and stored in desiccators at 5°C. Sugars were extracted from 250 mg samples by shaking in 25 ml 0.1 M H_3BO_3 at pH 8 (regeneration buffer in the analytical procedure). Interfering phenolic compounds were precipitated with lead acetate and potassium oxalate (16). A standard stock solution of sucrose, raffinose, stachyose, maltose, rhamnose, mannose, fructose, galactose, glucose, trehalose, cellobiose, arabinose, sorbose and lactose (internal standard) was prepared by dissolving 125 mg of each sugar in 250 ml 0.1 M H_3BO_3 at pH 8 and stored in a freezer. From the stock solution a working standard was prepared to contain 50 μg/ml of each sugar. A separate internal standard was similarly prepared to contain 50 μg/ml of lactose. Individual sugars were determined on an Auto-Analyzer system in which sugar-borate complexes were formed and chromatographed on a Dowex I, borate-form, anion exchange column; the eluted bands were measured colorimetrically as sugar-orcinol complexes (6, 15). A 1 ml aliquot of each extract and 0.2 ml lactose standard were placed on the column and eluted with a NaCl-H_3BO_3 gradient starting with 0.1 M H_3BO_3 at pH 8 and ending with 0.2 M H_3BO_3 + 0.2 M NaCl at pH 9.5. The eluate and 0.1% orcinol reagent in 70% (v/v) H_2SO_4 were mixed, heated to 95°C and the color measured automatically at 420 nm.

Results and Discussion

Thirteen soluble sugars, in measurable but variable concn,

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