Tolerance to Melon Aphid in *Cucumis melo* L.[1]

G. W. Bohn[2], A. N. Kishaba[3], J. A. Principe[2], and H. H. Toba[3,4]
U. S. Department of Agriculture, Agricultural Research Service

Abstract. Resistance to the western biotypes of *Aphis gossypii* Glover in *Cucumis melo* L. breeding line LJ 90234 (inbred of P.I. 371395 from India) included tolerance expressed as freedom from curling of leaves following aphid infestation. The flat and curled phenotypes in progenies from a cross of this line with cv. PMR 45 were differentiated by a single gene, melon aphid tolerance (*Ag, Aphis gossypii* tolerance) with flat leaves dominant. Tolerance expressed as nearly normal ht of F_1 and some F_2 plants following mass infestation appeared to be less simply inherited. Its measurement was masked by inherent variation in growth rate and environmental factors including variation in insect attack.

LJ 90230, selected from P.I. 161375 from Korea, was stunted by the aphid but its leaves remained free from curl. F_2 hybrids from the cross 90234 x 90230 were free from curl but they varied in stunting after aphid attack. Single-peaked distribution curves for ht suggested complex inheritance of tolerance. LJ 90254, selected from P.I. 255478 from Korea, possessed tolerance to aphids expressed as freedom from stunting and curling. F_2 plants from the cross 90234 x 90254 were free from curl but varied in ht after aphid attack. The single-peaked distribution curves suggested complex inheritance of tolerance.

We have reported resistance of muskmelon (*Cucumis melo* L.) breeding line LJ 90234[5] to western biotypes of the melon aphid (*Aphis gossypii* Glover) (4), and briefly described the complex nature of that resistance (1). Observations on several thousand hybrid plants tested in the greenhouse or field indicated that resistance included nonpreference, apparent tolerance, and antibiosis as described by Painter (5). The 3 types of resistance are defined by the nature of the animal parasite-plant host interaction. Either nonpreference or antibiosis can affect ratings for tolerance; for example, failure of the insects to attack and feed on the host because of nonpreference could result in falsely high ratings for host tolerance. Tests designed to measure the 3 effects require different techniques and procedures and are not readily combined. We report here the results of greenhouse tests designed to minimize effects of nonpreference and antibiosis in order to emphasize and measure tolerance of the host to the parasite.

Materials and Methods

Highly resistant plants of muskmelon 90234[6] were crossed with susceptible 'PMR 45' and, also, with moderately resistant 90230 (selected from P.I. 161375 from Korea) and 90254 (selected from P.I. 255478 from Korea). F_1 plants were self-pollinated in greenhouses at La Jolla; and those from 'PMR 45' x 90234 were backcrossed to susceptible cultivars. Parents, hybrids, and susceptible checks were tested in 3 mass infestation trials similar to Ivanoff's (3) with the Western Biotype D of *Aphis gossypii* Glover (4) in greenhouses at Riverside during 1970.

Seven 8-plant rows were planted in each 45.7 cm square, soil-filled flat; 4 susceptible nurse plant rows were alternated with 3 test rows; and the 3 test rows were split to test 4 plants of each of 6 entries in each flat. The 6 entries were randomized in each of 24 to 32 flats in each test. The flats were randomized in each of 4 blocks on benches in a whitewashed greenhouse with smog filters and automatic equipment which maintained temperatures from 21°C at night to 30°C during the day. The flats were watered daily with full nutrient solution (2).

Flats for noninfested controls were removed to an adjacent, duplicate greenhouse when emergence was completed. Treated flats were then infested by distributing aphids along both sides of each of the 8 rows. Plants in the 3 tests were rated 9, 8, and 13 days, respectively, after infestation.

Emergence counts were recorded daily. Plant ht was measured at the end of tests of 90234 x 90230 and 90234 x 90254 populations. Height was measured at infestation and at the end of the 'PMR 45' x 90234 test. Leaf curl severity, descreasing with number increase, was recorded on an arbitrary 1 to 9 scale. The curl response was studied, also, in additional B_1 and in B_2 and B_3 progenies from the 'PMR 45' x 90234 cross in 2-stage tolerance plus antibiosis tests used in the breeding program.

Data were studied by analysis of variance, correlation, and Chi-square techniques (6).

Results

'PMR 45' x 90234. Seedlings of most entries emerged within 6 to 7 days. F_1 hybrids and 90234 emerged faster than 'PMR 45', which was variable. F_2 and backcross$_1$ (B_1 to susceptible parent) progenies emerged nearly as fast as 90234.

Large numbers of aphids placed in the flats when emergence was completed caused severe leaf curl, severe stunting, and necrosis of susceptible plants, some of which were dead 9 days after infestation. Aphids moved from dying and dead plants to resistant plants, which were thus exposed to severe infestation during the first half of the test period and to extremely severe infestation during the last half. The resistant plants tolerated this severe exposure which minimized nonpreference and antibiosis effects. Their leaves remained flat and they appeared only slightly less robust than control plants although large numbers of aphids survived on them.

Curl. Most leaves on noninfested control plants were flat (Class 9). Occasionally a leaf or 2 on a plant was slightly curled by crowding (Classes 8 and 7). Only rarely was a control plant leaf curled enough to be rated 6. The control plants of the

---

[1]Received for publication September 25, 1972.

[2]Research Geneticist and Research Technician, Plant Science Research Division, La Jolla, California.

[3]Research Entomologists, Entomology Research Division, Riverside, California.

[4]We gratefully acknowledge the assistance of Thomas Gibson and Sharon Schureman, Agricultural Research Technicians, with all aspects of the resistance tests; and valuable suggestions on the manuscript by R. E. Foster, W. M. Epps, H. M. Munger, and R. W. Robinson.

[5]LJ, for 5-digit La Jolla progeny numbers, is hereinafter omitted.

[6]A resistant selection from P.I. 371395, the renumbered *Cucumis melo* fraction of P.I. 175111 from India, which contained, also, *C. sativus* L.

susceptible parent 'PMR 45' had a greater tendency to curl naturally than did those of the resistant parent, 90234. They averaged 7.6 and 8.6 on the 9-class scale, respectively.

The infested plants of 90234, mean 8.3, were curled little more than the controls. In contrast, most leaves of 'PMR 45' (and the 'Hale's Best' nurse plants) were tightly curled and stunted and plants averaged 3.2. The ranges of curl severity on control and infested susceptible plants were nearly discontinuous.

Control and infested plants of the F_1 hybrids performed alike with curl averages of 8.1 and 8.0. The observations clearly demonstrated dominance of genes for tolerance expressed by freedom from curling of leaves following aphid infestation.

The distributions of infested F_2 and B_1 populations were nearly discontinuous with peaks at classes 4 and 8. If plants in classes 7 to 9 were combined as a flat-leaved, tolerant group in each population, and classes 1 to 6 were combined as a curled, susceptible group, the segregations fitted those expected on the hypothesis that the noncurling response was dependent on a single gene, *Ag,* dominant to its aphid curl allele, *ag* (Table 1). B_1 progeny 2 contained a significant excess of tolerant plants, causing a significant Chi-square value for heterogeneity (Table 1). However, F_2 progeny 2, obtained by selfing the same resistant parent plant, yielded the numbers expected on a single gene pair hypothesis. It seems likely, therefore, that the aberrant ratio resulted from sampling error in small (48-plant) populations. We concluded that a single gene pair *Ag/ag* controlled the flat-curl tolerance responses in all tested populations.

The hypothesis was supported by segregation of flat and curl phenotypes in equal numbers in subsequent 2-stage mass tolerance and caged antibiosis tests of progenies from successive backcrosses (B_1, B_2, and B_3) to susceptible cultivars (Fig. 1 and Table 2). 'PMR 45' and other susceptible cultivars used as recurrent parents in backcross progenies yielded similar results, so the data were combined for brevity.

Height. 90234 emerged and grew much faster than 'PMR 45', which was more variable in ht increase with or without aphids (Table 3). Mean ht of all populations was reduced by aphid infestation but ht of resistant plants was reduced less than that of suscepts (Table 3). The differences in plant size at infestation and in subsequent growth rate within populations in both control and infested flats prevented lucrative analysis of the raw ht increase data, or of data adjusted for differences in population and flat means. However, relatively low correlation in F_2 (r = 0.19, 0.39, and 0.41 for 3 families) and B_1 (r = 0.41, 0.53, and 0.58) in contrast with high correlation in 'PMR 45' (r = 0.75 and 0.77 in 2 test groups) suggested that genetic controls for tolerance to curl and stunting by aphids were not identical. F_2 and B_1 frequency curves for ht and for ht increase during infestation had single broad peaks suggesting complex inheritance of growth sensitivity to aphid attack or gross environmental effects.

90234 x 90230. Plants of 90234 and the hybrid populations emerged promptly; those of 'Hale's Best Jumbo' ('HBJ') and 90230 emerged more slowly and erratically (Table 4). A few plants of 90230 had just emerged or had not emerged at infestation; all others had well expanded cotyledons and slightly enlarged first leaf.

Curl. Controls remained vigorous with flat leaves (Fig. 2). The aphids caused severe curling and stunting of the susceptible nurse and check plants within 5 days. The infestation was so severe that the nurse 'PMR 45' and check 'HBJ' plants were extremely curled, stunted, and necrotic after 13 days exposure (Table 4). Some of those plants were dead so that all remaining test plants were exposed to large numbers of migrating aphids.

In contrast to the infested cultivars, both cotyledons and true leaves of 90230 and 90234 and their hybrids were free from typical aphid induced curl at both 5 and 8 days after infestation (Fig. 3). Their means were in the high range of acceptable performance only slightly lower than means of noninfested controls (Table 4). Some infested plants of 90230,

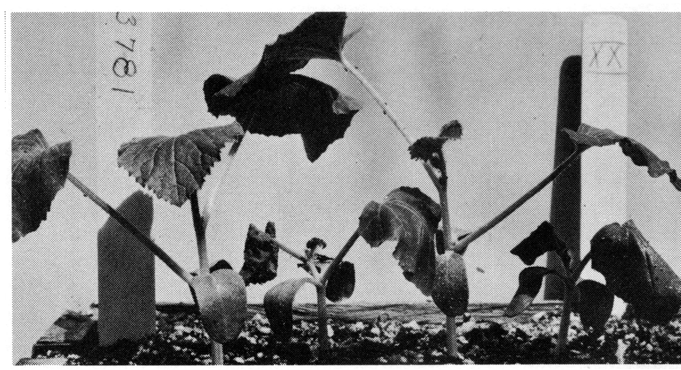

Fig. 1. B_1 to 'PMR 45' from the cross 'PMR 45' x 90234. Alternate tolerant and susceptible plants after 9 days exposure to mass infestation by aphids. Curl classes 7, 3, 8, 3.

Table 1. Tolerance to aphid attack in hybrids from the cross 'PMR 45' x 90234.

Population	Controls No. of plants Flat	Controls No. of plants Curled	Aphid-infested No. of plants Flat	Aphid-infested No. of plants Curled	X^2 1 gene pair
90234	16	0	47	0	
'PMR 45'	28	1	2	91	
F_1-1	15	1	48	0	
F_1-2	16	0	48	0	
F_1-3	16	0	48	0	
F_1-Total	47	1	144	0	
F_2-1	15	0	39	9	1.00
F_2-2	10	2	23	11	0.98
F_2-3	12	0	26	7	0.21
F_2-Total	37	2	88	27	0.14
Heterogeneity 2 df					2.04
B_1-1 (F_1 x 'PMR 45')	16	0	26	22	0.33
B_1-2 (F_1 x 'PMR 45')	16	0	31	17	4.08*
B_1-3 (F_1 x 'PMR 45')	16	0	19	29	2.08
B_1-Total	48	0	76	68	0.44
Heterogeneity 2 df					6.06*
$B_1$2 3:1			31	17	2.78

*Indicates significant value at the 5% level.

Table 2. Segregation of flat and curled leaf plants in progenies from successive backcrosses to susceptible muskmelon cultivars[z] from the cross 'PMR 45' x 90234. Riverside 1970-71.

Generation	Progenies no.	Plants no.	Flat no.	Curled no.	
B_1[z] to susc.	10	499	234	265	1.93 NS[y]
B_2 to susc.	13	374	176	198	1.29 NS
B_3 to susc.	20	464	241	223	0.70 NS
B_3 to susc.	30	713	342	371	1.18 NS
Sum					5.10
Good fit 1:1	73	2050	993	1057	2.00 NS
Heterogenity 3 df					3.10 NS

[z]All cultivars used in the successive backcrosses (B_x) yielded similar results; the data were pooled for each generation.
[y]NS, nonsignificant.

Table 3. Means and variability for plant ht increase during 9 days infestation by aphids in muskmelons from the cross 'PMR 45' x 90234. Riverside, 1970.

Population	Controls Plants no.	$\bar{x}$ cm	CV	Infested[z] Plants no.	$\bar{x}$ cm	CV
LJ 90234	16	14.3a	21	47	10.0a	22
F_1 combined	48	16.4a	14	144	11.0a	25
F_2 (combined)	39	13.1a	30	115	8.3b	36
B_1 to 45 (combined)	48	12.4ab	29	144	6.1b	46
PMR 45	27	8.3b	35	93	3.5c	54

[z]Within columns means followed by the same letter did not differ at 5% by Duncan's multiple range test (6).

90234, and the hybrid populations showed slight curling, but none showed tight leaf rolling typical of susceptible plants. Similar mild curvature occurred from contact or shading in some noninfested control plants. Frequency distributions were normal, yielding single peaked curves for all populations. They were nearly identical in parental, F_1, and F_2 populations, with means much higher than that of the infested susceptible 'HBJ' check. Obviously, 90230 as well as 90234 lacked the gene *ag* for leaf curling response to Western Biotype D of *A. gossypii.*

Table 4. Mean emergence time, leaf curl, and adjusted plant ht[z] in muskmelon populations from the cross 90234 x 90230 noninfested and infested 13 days with melon aphids. Riverside, May 1970.

Population	Emergence time all flats $\bar{x}$ days	CV	Leaf curl rating Non infested[y] $\bar{x}$ 1-9	Infested[x] $\bar{x}$ 1-9	CV	Plant ht Noninfested[y] $\bar{x}$ cm	Infested[x] $\bar{x}$ cm	CV
90234	4.4b	15	7.5	7.0a	14	14.7	10.1a	18
F_1	4.7b	14	8.7	7.3a	12	12.8	9.0a	20
F_2-1	4.7b	15	9.0	6.8a	16	9.0	6.8b	30
F_2-2	4.7b	14	7.7	7.2a	14	11.2	5.5b	27
90230	6.8a	28	9.0	7.4a	14	8.8	2.6c	31
'HBJ', susc.	5.6a	32	7.3	1.0b	0	12.9	2.4c	53
Midparent	5.6			7.2			6.3	

[z]Height adjusted to remove variation due to replications.

[y]Within columns means followed by the same letter did not differ at 5% by Duncan's multiple range test (6).

[x]Means of 4 noninfested and 92 infested plants.

Plant height. Without aphids, plants of all entries in the check flat grew vigorously and averaged 12.5 cm tall 21 days after planting. Parent 90230 grew more slowly than other entries and produced more slender and delicate plants (Table 4). F_2-1 also grew slowly but the plants were robust.

Plants of 90230 were obviously stunted by the aphids. They were little larger than those of 'HBJ' after 13 days exposure to aphids (Table 4). Although flat-leaved and green, the plants were slightly wilted and nonthrifty in appearance. In contrast, plants of 90234 and the F_1 hybrid were turgid and nearly as large and robust as those in the noninfested flat. Means for the 2 F_2 families were intermediate and close to the midparent mean (Table 4). The means demonstrated a genetic difference between the parents in tolerance expressed by differences in stunting by aphids. The F_2 populations, however, were not more variable than 90230, itself. Since both parents were *Ag/Ag,* other genes caused the differences in growth of plants under aphid attack. The similarity of the F_1 mean to that of 90234 demonstrated dominance of the factor or factors for freedom from stunting. Again, F_2 and B_1 frequency distributions, yielding normal curves with single broad peaks. suggested that tolerance expressed by growth differences during aphid attack was not simply inherited. This was supported by the infrequent occurrence, 7%, of F_2 plants as short as the tallest 90230 plant in the same flat.

Fig. 2. Noninfested plants 18 days after planting; test rows bordered by nurse rows. Front test plots: F_1 90235, parent 90230, F_2 90292. Back: parent 90234, F_2 90291, HBJ 6827.

90234 x 90254. Most populations emerged with good uniformity in an average of 5.4 days after planting (Table 5). F_2-1 and 'HBJ', the populations slowest to emerge, were also the most variable in rate of emergence with larger coefficients of variation. The causes of this variation are unknown.

Curl. Slight, random leaf curl was caused by crowding in all populations in the absence of aphids (Table 4). In the infested house, aphids caused extreme leaf curl in the susceptible check 'HBJ'. Such leaf curl did not occur in 90234, 90254, or their hybrids (Table 4). Therefore, 90234 and 90254 lacked the gene *ag* causing susceptibility to leaf curl by the Western Biotype of *A. gossypii.*

Height. Without aphid infestation plants of all entries grew vigorously and achieved an average height of 8.6 cm 19 days after planting (Table 4). Infested plants, except the susceptible 'HBJ', grew nearly as well. 'HBJ' was severely stunted by aphids (Table 4) and some plants were killed. The resistant 90234 and

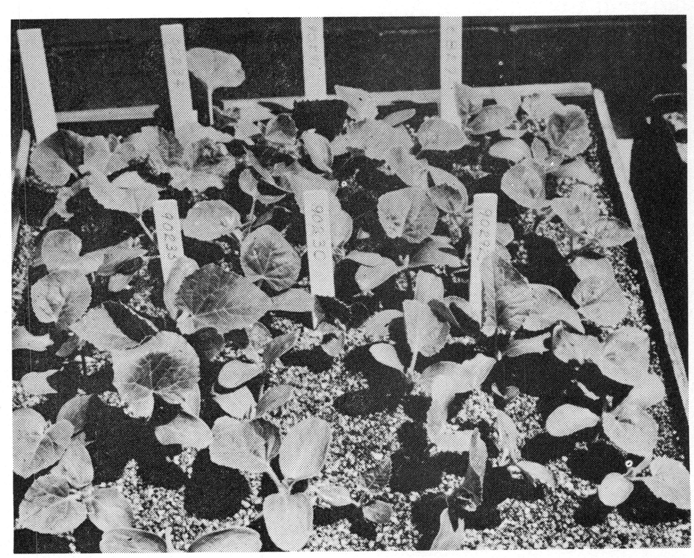

Fig. 3. Plants 18 days after planting, infested 5 days with aphids; test rows bordered by nurse rows. Front test plots: HBJ 6827, F_1 90235, F_2 90292. Back: parent 90234, parent 90230, F_2 90291.

Table 5. Mean emergence time, leaf curl, and adjusted plant ht[z] in muskmelon populations from the cross 90234 x 90254 noninfested and infested 8 days with melon aphids. Riverside, June 1970.

	Emergence time All flats		Leaf curl ratings[y]				Plant height			
			Noninfested[x]		Infested[x]		Noninfested[x]		Infested[x]	
Population	$\bar{x}$ days	CV	$\bar{x}$ 1-9	CV	$\bar{x}$ 1-9	CV	$\bar{x}$ cm	CV	$\bar{x}$ cm	CV
90234	5.1	9	8.0a	13	8.1a	10	10.1a	18	9.0ab	30
F_1	5.4	4	8.6a	8	8.4a	9	10.8a	24	10.1a	27
F_2-2	5.1	6	8.6a	7	8.1a	11	10.4a	23	7.6bc	34
F_2-1	6.2	17	8.4a	8	8.1a	11	7.5b	34	7.2bc	42
90254	5.3	12	8.9a	5	8.6a	7	7.0b	26	5.5c	38
'HBJ'	5.8	16	8.4a	10	2.0b	0	6.5b	28	3.1d	32
Midparent	5.2		8.5		8.4		8.6		7.3	

[z]Height adjusted to remove variation due to replications.

[y]Within columns means followed by the same letter did not differ at 5% by Duncan's multiple range test (6).

[x]Means of 16 noninfested plants and an average of 94 infested plants.

its F_1 hybrid with 90254 were stunted very little. Aphids caused stunting of a few plants of 90254 and the F_2-2 population. The apparent lack of stunting in 90234 its F_1 hybrid with 90254, and the F_2-1 population indicate that 90234 and at least some plants of 90254 lacked genes that cause susceptibility to severe stunting by aphids in curling American cultivars and in noncurling 90230 from Korea.

Discussion

Tests for tolerance to aphids cannot be made entirely free from nonpreference and antibiosis effects. It was not practicable to determine the relative amounts of insect feeding on different plants. However, with the mass infestation methods we used, many aphids were present on resistant plants throughout the tests, and they were able to grow and reproduce on them (1, 4). We judged that sufficient aphid feeding occurred on resistant as well as susceptible plants to indicate that the reported differences in tolerance were real, and did not result from nonpreference or antibiosis.

Freedom from the leaf curl effect of melon aphids is a valuable economic character to transfer into muskmelon cultivars because it maintains leaves in a functional state for the absorption of light and CO_2. It may also, by exposure, increase the effectiveness of natural control by parasites and predators, and artificial control by insecticides.

Absence of the leaf curl effect on a muskmelon from India and 2 from Korea suggests that those cultivars may have origins different from those of American cultivars, and that additional sources of tolerance to melon aphids may be found in the Far East.

The occurrence of stunting in 90230 in the absence of leaf curl demonstrated that the stunting effect of the aphid on muskmelons is at least partly independent of its leaf curling effect. Therefore, tolerance selection in populations showing both effects should be based on flat leaves and plant vigor.

The 3 tolerant parents reported here differed in many plant and fruit characters. They differed, also, in antibiosis to the aphid. In a typical antibiosis test, similar to those reported (4), of 16 plants, each, of 90230, 90234, and 90254 yielded average aphid populations 29, 22, and 48% as numerous as those on 'PMR 45'. Variation occurred within each parent line, but the highly tolerant 90254 was significantly less antibiotic to aphids than the other 2. Those observations supported the view that resistance with a broader genetic base might be gained from complex hybrids combining all 3 sources of resistance.

Literature Cited

1. Bohn, G. W., A. N. Kishaba, and H. H. Toba. 1972. Mechanisms of resistance to melon aphid in a muskmelon line. *HortScience* 7:281-282.
2. Hoagland, D. R., and D. I. Arnon (revised by D. I. Arnon). 1950. The water culture method for growing plants without soil. *Calif. Agr. Expt. Sta. Circ.* 347:1-32.
3. Ivanoff, S. S. 1945. A seedling method for testing aphid resistance, and its application to breeding and inheritance studies in cucurbits and other plants. *J. Hered.* 36:357-361.
4. Kishaba, A. N., G. W. Bohn, and H. H. Toba. 1971. Resistance to *Aphis gossypii* in muskmelon, *Cucumis melo*. *J. Econ. Entomol.* 64:935-937.
5. Painter, R. H. 1951. Insect resistance in crop plants. 520 p. The MacMillan Co., New York.
6. Steel, R. D. G., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc. New York. 481 p.