

exudation rate in the 15 min period immediately after detopping, whereas those detopped during the first 45 min interval decreased in exudation rate. This recovery also probably reflects gradual compensation by an NH_4 detoxification mechanism whose sustained activity required the intactness of the plant.

Another result of successive collections of exudate from the same plant is a significantly increased exudate concn of cations above that found in the first 15 min collection. A likely explanation for this result exists for both NO_3 and NH_4 treatments. In the case of a transition to NH_4 , H_2O uptake and movement in the xylem was inhibited almost immediately, whereas a significant drop in divalent cation concn (intact plant function) was not seen before 1.5 hr (Fig. 5). In the case of the NO_3 treatments, cations continued to be taken up by the root, independent of H_2O flux, whereas the effect of detopping was a progressive loss of exudation ability. In either case, the sluggish acropetal movement of H_2O resulted in an accumulation of cations in the xylem sap.

The results of the present investigation suggest that short-time root exudation responses of the order of sec obtained under controlled-environment conditions would be a valuable tool to determine whether the primary action of NH_4 involves an increase in root resistance or a decrease in driving force for H_2O uptake.

Literature Cited

1. Archibald, R. M. 1943. Quantitative microdetermination of ammonia in the presence of glutamine and other labile substances. *J. Biol. Chem.* 151:141-148.
2. Barker, A. V. and R. J. Volk. 1964. Determination of ammonium amide, amino, and nitrate nitrogen in plant extracts by a modified Kjeldahl method. *Anal. Chem.* 36:439-444.
3. Bennet, W. F., J. Pesek, and J. J. Hanway. 1964. Effect of nitrate and ammonium on growth of corn in nutrient solution sand culture. *Agron. J.* 56:342-345.
4. Claasen, Maria Elena Torre de, and G. E. Wilcox. 1974. Effect of nitrogen form on growth and composition of tomato and pea tissue.

- J. Amer. Soc. Hort. Sci.* 99:171-174.
5. Clark, H. E. 1936. Effect of ammonium and nitrate nitrogen on the composition of the tomato plant. *Plant Physiol.* 11:5-24.
6. Hoff, J. E., G. E. Wilcox, and C. M. Jones. 1974. The effect of nitrate and ammonium nitrogen on the free amino acid composition of tomato plants and tomato fruit. *J. Amer. Soc. Hort. Sci.* 99: 27-30.
7. Jackson, M. L. 1958. Soil Chemical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.
8. Kafhafi, J., J. Walderstein, and S. Feigenbaum. 1971. Effect of potassium nitrate and ammonium nitrate on the growth, cation uptake, and water requirement of tomato grown in sand culture. *Israel J. Agr. Res.* 21:13-20.
9. Kirkby, E. A. and K. Mengel. 1967. Ionic balance in different tissues of the tomato plant in relation to nitrate, urea, or ammonium nutrition. *Plant Physiol.* 42:6-14.
10. Maynard, D. N., A. V. Barker, and W. H. Lachman. 1966. Ammonium-induced stem and leaf lesions of tomato plants. *Proc. Amer. Soc. Hort. Sci.* 88:516-520.
11. ———, ———, and ———. 1968. Influence of potassium and the utilization of ammonium by tomato plants. *Proc. Amer. Soc. Hort. Sci.* 92:537-542.
12. Prianishnikov, D. N. 1929. Zur Frage nach der Ammoniakernahrung hoherer Pflanzen. *Biochem. Z.* 207:341-349.
13. Quebedeaux, B. and J. L. Ozbun. 1973. Effects of ammonium nutrition on water stress, water uptake, and root pressure in *Lycopersicon* in plant extracts. *Anal. Chem.* 25:1528-1529.
14. Varner, J. E., W. A. Bulen, S. Vanecko, and R. C. Burell. 1953. Determination of ammonium, amide, nitrite, and nitrate nitrogen in plant extracts. *Anal. Chem.* 25:1528-1529.
15. Weissman, G. S. 1964. The effect of ammonium and nitrate nutrition on protein level and exudate composition. *Plant Physiol.* 39: 947-952.
16. Wilcox, G. E. and J. E. Hoff. 1974. Grass tetany: an hypothesis concerning its relation with ammonium nutrition of spring grasses. *J. Dairy Sci.* 57:1085-1089.
17. ———, ———, and C. M. Jones. 1973. Ammonium reduction of calcium and magnesium content of tomato and sweetcorn and influence on incidence of blossom end rot of tomato fruit. *J. Amer. Soc. Hort. Sci.* 98:86-89.

J. Amer. Soc. Hort. Sci. 102(2):196-198. 1977.

Combining Ability of Three *Lycopersicon* Species for Resistance to *Corynebacterium michiganense*¹

Jan de Jong² and S. Honma³

Michigan State University, East Lansing, MI 48824

Additional index words. heritability, disease resistance, tomato breeding

Abstract. Estimates of heritability and general and specific combining ability for resistance of tomato to *Corynebacterium michiganense* (E. F. Sm.) H. L. Jens. were made, using a half diallel with 6 parental entries. Both the general and the specific combining abilities of the parents differed. Additive variation accounted for 74% (narrow sense heritability) of the total variation, suggesting that a large part of the observed variation is fixable in true-breeding strains.

Infection of tomato crops with *Corynebacterium michiganense*, the causal organism of bacterial canker, results in variable losses. Severity of the disease ranges from occasional wilting to death of the plant. Some of the common symptoms, all of

which may or may not be present on the infected plants, are: unilateral wilting of leaves, death of growing points, wilting of the plants and formation of stem cankers. Resistance has been reported in the *Lycopersicon pimpinellifolium* and *L. hirsutum* (1, 6, 8). In *L. esculentum*, the cultivar 'Bulgaria 12', from a hybrid with *L. pimpinellifolium*, has been reported to be resistant (3) but it is small fruited and unacceptable in the U.S.

The purpose of this study was to determine the inheritance of bacterial canker resistance to facilitate selection of parents for use in breeding populations and to interpret the results in terms of possible breeding procedures.

¹Received for publication September 3, 1975. Michigan Agricultural Experiment Station Journal Article No. 7363.

²Present address: Institute for Horticultural Plant Breeding, P.O. Box 16, Wageningen, The Netherlands.

³Department of Horticulture. The authors thank Dr. B. D. Thyr for providing the seed of Utah 737 and PI 344102 and H. J. Heinz Co. for making the isolate of *Corynebacterium michiganense* available to us.

Table 1. F₁ hybrid and parental mean values for resistance to *C. michiganense* (isolate H).

Parents	Bulgaria 12	MSU 72-279	Earliana	PI 344102	Utah 737	PI 251305
Bulgaria 12	2.88a ^z					
MSU 72-279	.74g	.0h				
Earliana	1.95dc	.05h	.0h			
PI 344102	2.90a	1.33e	2.29cb	3.0a		
Utah 737	2.98a	1.14ef	2.24c	3.0a	2.93a	
PI 251305	2.69a	.48g	2.69a	2.83a	2.62ab	2.69a

^zMean separation by Duncan's multiple range test, 5% level [LSD 5% = 0.33; LSD 1% = 0.44].

Materials and Methods

Six tomato accessions were used in a half-diallel crossing scheme:

- PI 344102 (*L. pimpinellifolium*, (Jusl.) Mill.) resistant
- 'Utah 737' (*L. pimpinellifolium*) resistant
- 'Bulgaria 12' (*L. esculentum*, Mill.) resistant
- 'Earliana' (*L. esculentum*) susceptible
- 'MSU 72-279' (*L. esculentum*) susceptible
- PI 251305 (*L. hirsutum*, Humb. & Bonpl.) resistant

With the exception of *L. hirsutum*, all material was selfed 1 generation prior to hybridization. A single plant, multiplied vegetatively, of each parent was then used for crossing in the 6-parent half diallel. Crosses cannot be made on *L. hirsutum* as a seed parent (7); therefore all crosses with this genotype were made with *L. hirsutum* as the pollen parent. To test for maternal effects 6 of the crosses were compared with their reciprocal combinations.

Seeds were planted in vermiculite, and seedlings were transplanted 14 days later into flats. Due to the slow growth of *L. hirsutum*, it was necessary to sow these seeds 3 days earlier than seed of the other progenies. Tests for resistance were conducted in the greenhouse at 19°C or higher. Stem inoculation with isolate H of the bacterium was used for this study (2). Two to 3 weeks after transplanting, the seedling tops were clipped off 1 cm above the cotyledons and a drop of inoculum was applied directly on the clipped stem. However, because of their small size and narrow cotyledons, seedlings of the accessions of *L. pimpinellifolium* were clipped above the first true leaf, while the tops of *L. hirsutum* were clipped above the second true leaf.

The experimental design consisted of 6 randomized blocks. For each block, 7 seedlings of each progeny were planted in a row with the seedlings spaced at intervals of 4.7 cm. To verify the uniformity of inoculation, one row of the susceptible cultivar Earliana was planted every 9 rows.

Plants were rated for disease development several times during the experiment using the following scale: 0 = the growing point has succumbed to the disease. 1 = extensive wilting, large cankers or stunted growth. 2 = plant approaches normal size, but shows wilting. 3 = healthy seedlings with no apparent symptoms of the disease. The final score, taken at the time when the disease rating of successive weeks did not change, was used for the analysis.

Table 2. Combining ability analysis of variance, with parents included, of tomato accessions for resistance to *C. michiganense* (isolate H.).

Source	df	MS
GCA	5	4.45
SCA	15	.18
Error	100	.014

h^2 (narrow-sense heritability) = 0.74.

Table 3. General and specific combining ability of tomato accessions and their hybrids for resistance to *C. michiganense* (isolate H).

Variable	Bulgaria 12	MSU 72-279	Earliana	PI 344109	Utah 737	PI 251305
<i>General combining ability</i>						
	.40	-1.26	-.57	.57	.50	.36
LSD (1%)=	.45					
<i>Specific combining ability</i>						
Bulgaria 12	.10					
MSU 72-279	-.38dc ^z	.54				
Earliana	.15bc	-.09	-.82			
PI 344102	-.04bcd	.05bcd	.32b	-.11		
Utah 737	.10bc	-.07bcd	.34b	-.04bcd	-.05	
PI 251305	-.04bcd	-.60e	.93a	-.07bcd	-.22de	0.0

^zMean separation by Duncan's multiple range test, 5% level.

LSD (parents) 5% = .23; 1% = .31

LSD (hybrids) 5% = .31; 1% = .41

The data were statistically interpreted by means of variance analysis. The genotypic variance was partitioned into variances due to the general (gca) and specific (sca) combining ability according to Garretsen and Keuls (5). The estimates of the gca and sca effects were tested with Duncan's multiple range test.

Results and Discussion

Mean values for F₁ hybrids and parents are in Table 1. Table 2 partitions the genetic variance. Both the general and specific combining ability effects were significant at the 1% level (Table 3).

It is notable that MSU 72-279 and 'Earliana' are susceptible themselves, but their progenies resulting from crosses with resistant plants differed in resistance. Also the gca of 'Earliana' is higher than that of MSU 72-279. Presumably the R-genes of the resistant accessions are better expressed in 'Earliana' than in the MSU 72-279 genotype. It is also possible that a less severe inoculation method or inoculation with a less virulent strain might better show the differences between the selfs of these 2 cultivars. A general observation was that 'Earliana' showed symptoms somewhat later than MSU 72-279, but this was not reflected in the final score. Differences in susceptibility between cultivars of *L. esculentum* have been reported (2).

As resistance to the bacterium is to be derived from accessions used in this study, it was of interest to estimate the heritability of the resistance in this material (Table 2). The additive portion of the genetic variance, when analyzed with the selfs is about 3 times the non-additive portion with a narrow sense heritability (of progeny means) of .74 (Table 2). When analyzed without the selfs the narrow sense heritability increases to .91. This increase is due to the smaller sca component in the genetic variance and indicates that most of the sca effects were due to deviation of the selfs from the expected means. The conclusion from this analysis is that the genetic variation of the F₁'s is mainly additive and thus fixable in true breeding strains. Epistatic effects are assumed to be negligible.

It was shown that MSU 72-279 differed from 'Earliana' in its reaction to *C. michiganense*. This difference is not expressed in the selfs but it is very pronounced in the F₁'s when crossed to the resistant accessions. As these genetic effects are fixable it is important to use parents in a breeding program that will maximize the resistance level in the progeny. We therefore suggest evaluating susceptible parents by testcrossing to resistant cultivars. Depending on the aim of the project the susceptible parent can be used as the recurrent parent if resistance needs to be incorporated in an existing line. Otherwise crosses between selected F₁'s should be made to improve fruit size.

The resistant parent should preferably by 'Bulgaria 12' as this cultivar combines good resistance with reasonable fruit size

Table 4. Mean values for resistance to *Corynebacterium michiganense* for progenies of 6 crosses and their reciprocals.

Cross	Mean value for resistance		Significance
	Cross as given	Reciprocal	
Bulgaria 12 × MSU 72-279	.83	.74	NS
Bulgaria 12 × Earliana	1.75	1.95	NS
Bulgaria 12 × PI 344102	2.90	2.92	NS
PI 344102 × MSU 72-279	.76	1.33	**
Utah 737 × MSU 72-279	.78	1.14	**
Utah 737 × PI 344102	2.98	3.00	NS

**Significantly different at 1% level.

and a gca comparable to the other resistant accessions.

Reciprocal differences. Means, for resistance to isolate H, of the progenies of crosses from which reciprocals were made are in Table 4. No difference was observed between 'Bulgaria 12' × PI 344102 and its reciprocal. Hybrids of 'Bulgaria 12' with susceptible cultivars MSU 72-279 and 'Earliana' also do not differ from their reciprocals. In the crosses of MSU 72-279 with Utah 737 and with PI 344102, a higher degree of resistance was noted with MSU 72-279 as the seed parent.

At the time of inoculation, the seedlings of the crosses Utah 737 × MSU 72-279 and PI 344102 × MSU 72-279 were considerably smaller than those of the reciprocals probably

because Utah 737 and PI 344102 have smaller seeds and therefore smaller embryos and cotyledons. As the resistance of seedlings increases with their size (4), it may explain why the smaller seedlings of these crosses are more susceptible than the larger reciprocals.

Literature Cited

1. Ark, P. A. 1944. Studies on bacterial canker of tomato. *Phytopathology* 34:394-400.
2. de Jong, Jan and S. Honma. 1976. Evaluation screening techniques and determination of criteria for assessing resistance to *Corynebacterium michiganense*. *Euphytica* 25:405-414.
3. Elenkov, E. 1965. Die Selektion von Tomaten auf Resistenz gegen die Bakterienwelke. *Int. Z. Landwirt.* p. 594-597.
4. Forster, R. L. and E. Echandi. 1973. Relation of age of plants, temperature, and inoculum concentration to bacterial canker development in resistant and susceptible *Lycopersicon* spp. *Phytopathology* 63: 773-777.
5. Garretsen, F. and M. Keuls. 1973. Analysis of genetic variation in an incomplete diallel cross. Proc. Eucarpia Conf. Biometrics, Hannover. p. 24-35.
6. Hassan, A. A., D. L. Strider, and T. R. Konsler. 1968: Application of cotyledonary symptoms in screening for resistance to tomato bacterial canker and in host range studies. *Phytopathology* 58:233-239.
7. Martin, F. W. 1961. Complex unilateral hybridization in *Lycopersicon hirsutum*. *Proc. Nat. Acad. Sci.* 47:855-857.
8. Thyr, B. D. 1968. Resistance to bacterial canker in tomato and its evaluation. *Phytopathology* 58:279-281.

J. Amer. Soc. Hort. Sci. 102(2):198-201. 1977.

Acidity and Total Soluble Solids in *Citrus* Hybrids and Advanced Crosses Involving Acidless Orange and Acidless Pummelo¹

James W. Cameron and Robert K. Soost²

Citrus Research Center, University of California, Riverside, CA 92521

Additional index words. plant breeding, mandarin hybrids

Abstract. Titratable acidity and total soluble solids were measured in F₁ hybrid citrus populations involving an acidless pummelo [*Citrus grandis* (L.) Osbeck] and an acidless orange [*Citrus sinensis* (L.) Osbeck] respectively, as one parent. Three advanced crosses were also studied. Crosses of the pummelo with 5 medium acid cultivars produced no acidless individuals but many with low to medium acidity and a few with acidities above 1.6% in their main seasons of use. The overall mean titratable acidity was 1.1%. Crosses of the acidless orange with 4 medium-acid cultivars produced only a few low to medium-acid individuals, and many with acidities above 1.6%; the overall mean acidity was 2.0%, significantly higher than with the pummelo. Mean levels of total soluble solids had a range which was similar between the 2 types of crosses, although the overall mean was significantly higher in the orange crosses. There were significant correlations between acid and total soluble solids levels in only 2 out of 11 progenies among all of the crosses.

Twelve of 40 individuals were essentially acidless in an F₂ population involving the acidless pummelo as a grandparent. There were no acidless individuals, but there were many moderately-acid ones in 2 populations of acidless pummelo hybrids backcrossed to acid cultivars. These proportions suggest simple inheritance for the acidless character of the pummelo. In contrast, the high acid levels of the F₁ populations with acidless orange imply a different basis for the latter's lack of acidity.

Most edible cultivars of *Citrus* have moderate or sometimes high levels of titratable acidity in the juice during their main seasons of use. Sweet oranges and mandarins, for example, commonly have acidities near 1 to 1.5% at maturity; grapefruit often average somewhat higher. Hybrids among such cultivars

show a wide range of acidities, usually reflecting some relationship to parentage but seldom indicating consistent or simply-inherited effects. Cultivars which are essentially acidless also exist among several *Citrus* taxa, including the orange, lemon, lime, and pummelo (4). These have practically no titratable acid throughout early to late maturity and their taste is insipid to sweet, depending upon their content of sugar.

The present authors (7) studied the effects of an acidless pummelo, and several acid ones, on the titratable acidity and total soluble solids of their hybrids with moderately acid

¹Received for publication September 20, 1976.

²We thank R. H. Burnett for assistance in collecting the data, and C. K. Huszar, Department of Statistics, for the statistical analyses.