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 x MSU 72-279 | .83 | .74 | NS |
| Bulgaria 12 x Earliana | 1.75 | 1.95 | NS |
| Bulgaria 12 x PI 344102 | 2.90 | 2.92 | NS |
| PI 344102 x MSU 72-279 | .76 | 1.33 | ** |
| Utah 737 x MSU 72-279 | .78 | 1.14 | ** |
| Utah 737 x 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' x 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 x MSU 72-279 and PI 344102 x 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.

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# Acidity and Total Soluble Solids in *Citrus* Hybrids and Advanced Crosses Involving Acidless Orange and Acidless Pummelo[1]


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*Additional index words.* plant breeding, mandarin hybrids



*Abstract.* **Titratable acidity and total soluble solids were measured in $F_1$ 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 $F_2$ 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 $F_1$ 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


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Table 1. Range of titratable acidity and total soluble solids among parent cultivars during several seasons, at Riverside, Calif.[z]

| Parent | Mean titratable acidity (%) | Mean total soluble solids (%) |
|---|---|---|
| Acidless pummelo | 0.1-0.2 | 12.3-12.6 |
| Acidless orange | 0.1-0.2 | 11.0-14.0 |
| Clementine mandarin | 0.8-1.2 | 12.0-14.0 |
| Frua mandarin | 1.1-1.3 | 10.6-13.3 |
| Kincy mandarin | 1.1-1.2 | 10.0-13.0 |
| Kinnow mandarin | 1.2-1.5 | 15.0-17.0 |
| Wilking mandarin | 1.1-1.5 | 12.0-16.0 |
| Dweet tangor | 1.2-1.3 | 13.5-15.3 |
| Temple tangor | 1.1-1.3 | 11.0-13.0 |
| Sukega grapefruit hybrid | 2.4-2.6 | 11.0-14.0 |
| Seedy white grapefruit | 1.8-2.2 | 11.0-12.5 |

[z]Lowest and highest values obtained between 1964 and 1970, during the season of use of each parent. Not all parents were sampled in every year.

*Citrus* cultivars. The acidless pummelo imparted much lower average acidity levels to its hybrid progenies than did any of 4 medium-acid pummelos; however, none of the hybrids was entirely acidless. Total soluble solids averaged essentially as high in the progenies of the acidless pummelo as in those with the acid ones and thus solids-to-acid ratios were usually much higher in the former group, resulting in individuals with early seasons of use.

New $F_1$ populations and some advanced crosses involving the acidless pummelo, and in addition, several $F_1$ populations with an acidless orange as 1 parent have been obtained during the last several years. The behavior of these progenies with respect to titratable acidity and total soluble solids is reported here.

## Materials and Methods

The parental cultivars used in this study were part of the collections at the Citrus Research Center, Riverside. The acidless pummelo, CRC 2240, [*Citrus grandis* (L.) Osbeck] was introduced from the Orient in about 1930. Two accessions of acidless sweet orange [*C. sinensis* (L.) Osbeck] were used, CRC 950 from Brazil and CRC 371 from Florida. Their horticultural characters are very similar and they are hereafter referred to as the acidless orange. Other parents were 'Clementine' mandarin (*C. reticulata* Blanco); 'Frua', 'Kincy', 'Kinnow', and 'Wilking' mandarin (*C. reticulata* × 'King' tangor); 'Dweet', 'Temple', and an unnamed tangor (*C. reticulata* × *C. sinensis*); a seedy white grapefruit (*C. paradisi* Macf.); and 'Sukega' (*C. paradisi* × *C. sinensis*).

The hybrid populations were produced at Riverside and were field-planted between 1957 and 1966. Nearly all were seedling trees on their own roots. Three locations were involved, Lindcove, in the southern San Joaquin Valley; Riverside, in the inland Los Angeles Basin; and Tustin, at a more coastal location 35 miles from Riverside. Average time of citrus ripening at these locations is in the order listed and this was taken into account in sampling. Climatic effects on maturity varied slightly from year to year, but no major distortions occurred. Hybrids with the pummelo were produced a few years earlier than those with the orange, therefore testing was also carried out earlier. The backcross progenies were the youngest and were sampled in only 1 year. Not all trees in a population fruited in every year; the 1 largest sample of trees tested from each population is indicated in Table 2. Individual fruit samples consisted of 8 to 10 representative fruits. Titratable acidity and total soluble solids were measured with an automatic titrator and an Abbe 3L refractometer, respectively. The terms acid, acids, acidless or acidity refer to titratable acidity and solids or soluble solids refer to total soluble solids throughout this report.

Statistical analyses were carried out according to Snedecor (6). Duncan's multiple range test (Table 3) was based on an analysis of variance in which the different crosses were considered as treatments, and the members of each individual cross were replicates. Such replicates are not genetically identical, but are postulated to be more similar in their genetic effects than are the average effects of separate crosses.

## Results

Table 1 shows the range of acidity and soluble solids among the parent cultivars over several years. The acidless parents at no time had more than 0.1 to 0.2% apparent titratable acidity, and even that may be due to other reactive substances. The other parents had from 0.8 to 2.6% acid, with the grapefruit types being highest. Total soluble solids were not widely different in any parent, except that the 2 mandarins, 'Kinnow' and 'Wilking', sometimes had very high solids, as was already known. One parent listed in Table 2, a 'Ruby' × 'Dancy' hybrid, was not tested but is known to have midseason maturity and moderate acidity and soluble solids.

Tritable acidity and total soluble solids data for the hybrid populations are shown in Table 2. The range of mean acidities for all samples was 0.9 to 1.5%, and the overall mean was 1.1% among 5 crosses with acidless pummelo (Section I). The mean was again 1.1% for the 1 largest sample of trees from each cross. Distribution of acidity values among 3 levels was similar among all samples, except that crosses with grapefruit and with 'Sukega' had more higher-acid individuals. Overall means showed only 34 acid values higher than 1.6% out of a total 332 tests. Acidities averaged much higher among the 6 progenies involving acidless orange (Section II), with a range from 1.3 to 2.6%, an overall mean of 2.0%, and a mean of 2.1 for the largest samples. The distribution of acidities among 3 levels showed only 26 tests below 1.0%, out of a total of 695.

Total soluble solids were not as widely different as titratable acidity between the 2 groups of crosses. The overall mean was 11.6% solids for all tests involving acidless pummelo, and the mean of the largest samples was 11.3%. The overall mean was 12.6% for the acidless orange crosses and the mean of the largest samples was 12.7%.

The largest samples of trees from all progenies in both Sections were statistically analyzed (Table 3). Mean differences in both acid and solids percentages, between Section I and Section II, were significant at the 0.1% point by the "t" test. Duncan's multiple range test, applied to the largest samples from both sections taken together, showed separations among both titratable acidity and total soluble solids. Subgroups II-4 and II-5 were significantly higher in acid than all others, while I-2 and I-5 were among the lowest. All subgroups with acidless pummelo were lower in acid than any of those involving acidless orange.

Separations with respect to soluble solids were much less consistent. The 3 statistically highest percentages occurred among acidless orange progenies, while the 2 lowest were among the acidless pummelo progenies, but there were several points of overlap. Acidless orange imparted higher total soluble solids to its hybrids on the average than did acidless pummelo, but there also appeared to be specific combining effects due to the acid parents. Thus progenies II-1 and II-5, with high solids, both had 'Wilking' as a parent. This cultivar attains very high total soluble solids and has imparted high solids to its hybrids in other crosses. Conversely, progenies involving grapefruit and 'Sukega' averaged lower in solids, as do those parents.

Correlation coefficients between titratable acidity and total soluble solids for each progeny (Table 3, column 5) were nonsignificant in 9 of 11 cases. There was significance at 5% in I-2 and I-3; however, these were the 2 progenies with the smallest populations. There is thus little evidence for close genetic inter-

Tabld 2. Titratable acidity and total soluble solids of citrus hybrids with acidless pummelo or acidless orange as one parent.

| Location and season[z] | Acid parent | No. trees sampled[x] | Distribution: Samples with % acidity <1.0 | 1.0 | >1.6 | Mean titratable acidity (%) | Mean total soluble solids (%) |
|---|---|---|---|---|---|---|---|
| | | *I. Hybrids with acidless pummelo* | | | | | |
| Riverside | | | | | | | |
| 1965 | Temple | 43 I-1[w] | 9 | 34 | 0 | 1.1 | 12.4 |
| 1966 | | 35 | 7 | 28 | 0 | 1.1 | 11.5 |
| 1966 | Wilking | 16 | 7 | 8 | 1 | 1.1 | 12.2 |
| 1967 | | 18 | 7 | 10 | 1 | 1.0 | 13.3 |
| 1968 | | 20 I-2 | 12 | 7 | 1 | 0.9 | 12.0 |
| 1966 | Sukega | 21 | 5 | 14 | 2 | 1.2 | 10.3 |
| 1967 | | 26 I-3 | 2 | 18 | 6 | 1.3 | 11.2 |
| 1966 | Seedy | 50 I-4 | 15 | 29 | 6 | 1.1 | 10.5 |
| 1967[y] | white | 28 | 7 | 16 | 5 | 1.3 | 11.6 |
| 1967 | grapefruit | 33 | 3 | 18 | 12 | 1.5 | 12.2 |
| Tustin | | | | | | | |
| 1968 | Ruby x Dancy | 42 I-5 | 21 | 21 | 0 | 0.9 | 10.2 |
| Totals and means: | | | | | | | |
| All samples | | 332 | 95 | 203 | 34 | 1.1 | 11.6 |
| Largest no. of trees, each cross | | 181 | 59 | 109 | 13 | 1.1 | 11.3 |
| | | *II. Hybrids with acidless orange* | | | | | |
| Riverside | | | | | | | |
| 1967[y] | Wilking | 34 | 0 | 1 | 33 | 2.4 | 12.6 |
| 1967 | | 29 | 0 | 5 | 24 | 2.2 | 13.9 |
| 1968[y] | | 37 | 0 | 0 | 37 | 2.6 | 14.1 |
| 1968 | | 33 | 0 | 0 | 33 | 2.2 | 13.6 |
| 1971 | | 39 II-1 | 0 | 6 | 33 | 2.1 | 13.3 |
| Tustin | | | | | | | |
| 1969[y] | Temple | 28 II-2 | 2 | 12 | 14 | 1.9 | 11.9 |
| 1969 | | 22 | 2 | 13 | 7 | 1.5 | 12.9 |
| 1971 | | 23 | 7 | 9 | 7 | 1.3 | 11.2 |
| 1969 | Clementine | 41 | 2 | 20 | 19 | 1.6 | 12.1 |
| 1970 | | 42 II-3 | 0 | 22 | 20 | 1.6 | 11.5 |
| 1971 | | 39 | 5 | 23 | 11 | 1.4 | 11.5 |
| 1969[y] | Kincy | 37 II-4 | 1 | 4 | 32 | 2.6 | 11.5 |
| 1969 | | 36 | 1 | 12 | 23 | 2.0 | 12.7 |
| 1970 | | 35 | 2 | 12 | 21 | 1.8 | 10.6 |
| 1971 | | 34 | 2 | 16 | 16 | 1.7 | 11.0 |
| Lindcove | | | | | | | |
| 1969 | Wilking | 38 | 1 | 8 | 29 | 2.2 | 12.2 |
| 1970 | | 43 II-5 | 0 | 3 | 40 | 2.6 | 14.4 |
| 1969 | Clementine | 33 | 1 | 15 | 17 | 1.7 | 12.8 |
| 1970 | | 40 II-6 | 0 | 9 | 31 | 2.0 | 13.8 |
| 1971 | | 32 | 0 | 11 | 21 | 1.9 | 14.6 |
| Totals and means: | | | | | | | |
| All samples | | 695 | 26 | 201 | 468 | 2.0 | 12.6 |
| Largest no. of trees, each cross | | 229 | 3 | 56 | 170 | 2.1 | 12.7 |

[z]One sampling was made at midseason for each population in each listed year, except as indicated.

[y]An additional, early-season sampling within the season.

[x]Not all trees bore fruit in all years.

[w]Identifies single largest samples analyzed in Table 3.

dependence between the 2 components. Many previous studies with citrus (3, 5) lead to the same conclusion.

One $F_2$ and 2 "backcross" populations involving acidless pummelo were also examined (Table 4). All trees of the $F_2$ (acidless pummelo x 'Kinnow', selfed) which fruited during 3 seasons were tested. Twelve had essentially acidless fruit and 4 others had acidity below 1.0% among 40 individuals. Many of the 12 were tested in all 3 seasons, and were consistent in their lack of titratable acidity. Their titers were indistinguishable from that of the acidless pummelo, and were set sharply apart from the remainder of the population. Eight trees had acidities above 1.6% while, in contrast, only 1 was above 1.6% among 105 $F_1$ trees of Table 2 involving comparable acid parents, items I-1, I-2, and I-5.

Table 3. Statistical analyses of selected samples from Table 2.[z]

| Subgroup samples | No. trees sampled | Mean titratable acid (%) | Mean total soluble solids (%) | Correlation coefficient (r) within subgroups |
|---|---|---|---|---|
| | *I. Hybrids with acidless pummelo* | | | |
| I-1 | 43 | 1.0 DE[y] | 12.4C | 0.24NS |
| I-2 | 20 | 0.9E | 12.0CD | .55*[x] |
| I-3 | 26 | 1.3D | 11.2E | .40* |
| I-4 | 50 | 1.1DE | 10.5F | .15NS |
| I-5 | 42 | 0.9E | 10.2F | .18NS |
| | Mean | 1.1 | 11.3 | |
| | *II. Hybrids with acidless orange* | | | |
| II-1 | 39 | 2.1B | 13.3B | .23NS |
| II-2 | 28 | 1.9BC | 11.9CD | .09NS |
| II-3 | 42 | 1.6C | 11.5DE | −.20NS |
| II-4 | 37 | 2.6A | 11.5DE | .12NS |
| II-5 | 43 | 2.6A | 14.4A | .01NS |
| II-6 | 40 | 2.0B | 13.8AB | .16NS |
| | Mean | 2.1 | 12.7 | |
| Mean difference, II minus I | | 1.0***[w] | 1.4***[w] | |

[z]Includes the one largest sample of trees from each cross, at each location, irrespective of year.

[y]Mean separations within columns, among all subgroups, by Duncan's multiple range test, 1% level.

[x]Significant at 5% level.

[w]Means II minus I within columns significant at .001 level.

The 2 backcross populations, (pummelo x mandarin hybrid) x mandarin hybrid, had no acidless members among 42 trees. Four had about 0.4% acid, and 4 were above 1.6%. Means and ranges of soluble solids were rather similar in all 3 populations. They were also not very different from the overall values in the pummelo $F_1$ populations. As with the $F_1$'s there is little indication of correlation between acid and solids levels in these populations.

## Discussion

The acidless pummelo in this study and the earlier one (7) markedly reduced the average acidity levels of its $F_1$ progenies and undoubtedly contributed to the segregation of acidless individuals in the $F_2$. Twelve acidless individuals out of 40 is highly suggestive of single recessive gene action, even though the considerable range of acidities among the other members – and among many other citrus crosses which have been studied – demonstrates that inheritance of acidity is usually quantitative. Pummelo also influenced the occurrence of many low and medium-acid individuals in the backcrosses to mandarin hybrids. However, the early-maturing nature of the backcross parents, 'Frua' and 'Clementine', must also have played an important part.

The acidless orange, in contrast, did not impart low acidity to its $F_1$'s. The majority of its individual hybrids were more acid than their acid parents during their main seasons of use, and the mean acidity levels within crosses were nearly always higher than the means of the parents. It appears that the genetic basis for acidlessness is different in the two acidless cultivars. A factor controlling low acidity was transmitted to the sexual progeny of the pummelo, indicating that it was present in histogenic Layer II which forms the gametes. The lack of transmittance from the orange suggests that the factor may be present only in Layer I, which takes part in juice vesicle formation but does not form gametes. A similar explanation has been proposed as the basis for color changes in the pigmented grapefruits (2). One bud progeny tree from the acidless orange

Table 4. Titratable acidity and total soluble solids of $F_2$ and "backcross" populations with acidless pummelo as a grandparent.

| Location & (season) | Cross | Trees sampled (no.) | Distribution: Samples with % acidity 0.1 | 0.4 | 0.5-0.9 | 1.0-1.6 | >1.6 | Total soluble solids (%) Mean | Range |
|---|---|---|---|---|---|---|---|---|---|
| Tustin[z] (1969, 1970, 1975) | (Acidless pummelo × Kinnow) selfed | 40[y] | 12 | 0 | 4 | 16 | 8 | 10.9 | 8.9-14.4 |
| Riverside (1975) | (Acidless pummelo × Frua) × Clementine | 27 | 0 | 4 | 10 | 12 | 1 | 11.9 | 9.1-14.2 |
| Riverside (1975) | (Acidless pummelo × Dweet) × Frua | 15 | 0 | 0 | 4 | 8 | 3 | 10.1 | 8.5-13.1 |

[z]One sampling was made each year.

[y]Data are for 40 different trees sampled in 1 or more years.

has consistently produced acid fruit at Riverside, while a sister progeny tree has remained acidless (J. W. Cameron, unpublished). This behavior is also suggestive of chimerism. Inheritance involving a cytoplasmic factor for acidlessness appears unlikely in the pummelo, since it was used as seed parent in some crosses and as a pollen parent in others. However, the acidless orange was always used as a pollen parent, so that the possibility of cytoplasmic involvement is not ruled out. The general absence of correlation between acid levels and solid levels found here extends the evidence that these 2 groups of compounds are inherited essentially independently.

Our progenies with acidless pummelo have included numerous individuals with good characters, including large size, earliness, and good flavor. The present crosses with 'Wilking' in addition to the 'Chandler' released in 1961 (1) have been outstanding, as are certain early-maturing triploid hybrids.

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# Variations in Susceptibility of Apple Stems to Attack by Pine Voles[1]


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*Abstract.* **Caged feeding tests of 77 *Malus* clones, representing 15 species and hybrid species, revealed 9 cultivars apparently less susceptible to feeding by pine voles than 'Golden Delicious'. *Malus* X *sublobata* PI 286613 shoots were attacked least; other cultivars of special promise include 'Charlotte', 'Hucker No. 1', 'N.Y. 11928', 'Robusta 5', 'Sissipuk', and 'Ivory's Double Vigour'.**


Apple cultivars on seedling rootstocks and on some clonal rootstocks have been reported to vary in susceptibility to vole injury (4, 8). Many fruit growers in the eastern USA have observed that 'Delicious' and 'Golden Delicious' trees are very susceptible to pine vole injury and 'Stayman' trees are much more resistant. Toenjes (8) reported that 'Virginia Crab' was less susceptible than other clones when compared in a group test of *Microtus pennsylvanicus* Ord in outside mulched plot areas. Cummins (4) characterized 'Hibernal' rootstocks as very attractive to meadow voles.

Rootstock resistance to vole attack could greatly reduce the annual labor, chemical and equipment costs for cultural and/or toxicant vole control methods (1, 2, 5, 6, 7). We examined 77 clones in 1974-76 to identify resistant taxons which could be used as parents in breeding improved rootstocks. We also sought preliminary information on transmission of vole resistance to seedlings.

### Materials and Methods

Most of the plant material in these experiments was collected


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