HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY
THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION

Volume 39, Number 20 · July, 1969

Tree and Fruit Characters of *Citrus* Triploids from Tetraploid by Diploid Crosses

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Tree and fruit characters of citrus triploids from six crosses involving tetraploid grapefruit and tetraploid lemon as seed parents, and five diploid varieties as pollen parents, are described. A high percentage of the triploids have maintained good vigor but only about one-third have yielded well. Seed numbers typically have been low. Percentages of total soluble solids were generally intermediate as compared with the parents. Percentage of acid was usually high, being strongly influenced by the tetraploid parents. Leaf thickness and shape were usually intermediate, but sometimes approached the tetraploid parents. A few of the triploids have fruit and tree characteristics desired in a satisfactory variety, but, partly because of their high acidity, none has been released.

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INTRODUCTION

THE BASIC HAPLOID CHROMOSOME NUMBER in *Citrus* and its closely related genera is 9; nearly all varieties are diploid, with a 2n number of 18. Forms with higher chromosome numbers have been known for some time, however, both from spontaneous occurrence and as the result of early breeding programs. Longley (1925) found that the Hongkong wild kumquat (*Fortunella hindsii* Swingle) is tetraploid, and he showed (1926) that a hybrid, obtained by W. T. Swingle, between it and a diploid citrus form is triploid. Frost (1925, 1926, 1943) obtained spontaneous tetraploids as apomictic seedlings from several diploid varieties, as did Lapin (1937). Nakamura (1942) reported two cases of tetraploidy among a large number of citrus types examined. Both Frost and Lapin obtained, in addition, spontaneous triploid hybrids from crosses between diploid parents. A few aneuploids and higher euploid numbers have also been reported (Lapin, 1937; Krug, 1943; Krug and Bacchi, 1943).

The autotetraploid chromosome level in citrus is usually physiologically unfavorable, but there is evidence that triploidy would hold more promise. Bacchi (1940) and Krug and Bacchi (1943) reported that the large-fruited Persian lime and the very similar Bearss lime are triploid. These forms are vigorous and, despite nearly complete seedlessness, are fruitful.

Frost (1943) reported the production of hybrid triploid seedlings from controlled crosses of tetraploids by diploids; later studies of these hybrids are the subject of this paper. Russo and Torrisi (1953) obtained triploids from crosses of diploid lemon by tetraploid lemon pollen parent, and Tachikawa, *et al.* (1961) obtained several triploids from crosses in which a tetraploid Natsudaidai was sometimes the seed parent and sometimes the pollen parent.

The spontaneous triploids obtained by Frost (1943) were, as described later, relatively vigorous and few-seeded Since it was recognized that the sterility of citrus triploids could provide seedlessness in new varieties, studies of triploids and other citrus polyploids have been continued and expanded by the present authors (see also Cameron and Soost, 1969).

MATERIALS AND METHODS

The older *Citrus* forms referred to in this paper, including diploids and tetraploids, are: *C. sinensis* Osbeck, vars. 'Ruby,' 'Paperrind,' 'Trovita,' 'Washington' navel, and a seedy sweet seedling; *C. reticulata* Blanco, vars. 'Cleopatra,' 'Dancy,' 'Owari' (?) satsuma, and 'Willowleaf'; *C. paradisi* Macf.,

[1] Submitted for publication October 7, 1968.

vars. 'Hall's Silver,' 'Imperial,' 'Marsh,' 'Royal,' and a white seedy selection; *C. limon* (L.) Burm. F., var. 'Lisbon'; C. sinensis × *C. reticulata* (?), vars. 'King'; King × Willowleaf, var. 'Kinnow'; King × 'Mediterranean Sweet' orange, var. 'Ruddy'; and a lemon hybrid, King × *C. limon.* 'Troyer' citrange rootstock is a hybrid between *C. sinensis* and *Poncirus trifoliata* (L) Raf. The 'Persian' or 'Bearss' lime is a triploid of uncertain origin. The autotetraploid forms were those obtained as nucellar seedlings by Frost (1943). The triploid hybrids from controlled pollination were obtained by Frost, mostly in 1939, from tetraploid seed parents.

Tree vigor classifications were based on a graded scale which included size, foliage density, leaf color, and absence of dieback. Trunk cross-section areas were calculated from circumferences measured 3 inches above the bud union for budded trees, and 9 inches above ground for seedling trees. Yield ratings were based on careful estimates of crop-per-unit area of tree at early fruit maturity. "Moderate to high" yields represent from 100 to 200 lbs of fruit on the 4- to 11-year-old seedling budlines concerned. For seed counts, full-size fruits from all sides of the tree were used; all well-developed seeds and large empty seedcoats were included in the counts, but rudimentary seedcoats were not. Total soluble solids and acid in the juice were measured by refractometer and titration (Soost and Cameron, 1961).

Leaf thickness and shape were determined on samples of 20 mature, sound leaves, usually from a single-growth flush. Thickness was measured near the center of the leaf, avoiding the midvein and prominent secondary veins, by use of a caliper graduated in hundredths of millimeters. The firm texture of the citrus leaf permits reproducibility of this measurement to within about 5 per cent. Leaf length and width (excluding the petiole) were measured by flattening the leaves on a grid graduated in millimeters.

Chromosome counts were made from young meristematic shoot tips. The tips were fixed for 48 hours in 3:1 alcohol-acetic acid, washed in water, trimmed of excess tissue, and hydrolyzed in 3.5 per cent HCl at 60° C for about 6 minutes. They were then stained in 1 per cent acetoorcein for at least 12 hours and later smeared in the same stain.

RESULTS AND DISCUSSION

Characters of older tetraploid selections and spontaneous triploid hybrids

A series of autotetraploid citrus forms, obtained as apomictic seedlings by Frost (1943) has been maintained at Riverside for many years. Some of them are the seed parents of the triploids discussed later. Table 1 indicates the condition of these tetraploids at 30 to 35 years after planting. Most of them have been smaller and weaker than diploids of the same variety; the tetraploid grapefruits, however, have been more vigorous than the others.

The leaves of tetraploids are characteristically broader and thicker than those of diploids. Tetraploids generally show more dieback than diploids, and in the weakest varieties such as King and Dancy some trees have died. Yields of most tetraploids are low, and fruit quality is usually poor. Furusato (1953) reported that young tetraploid seedlings of four *Citrus* species had a thicker main root and fewer lateral roots than diploids. Mukherjee and Cameron 1958 found tetraploid *Poncirus* seedlings used as rootstocks gave erratic results. Tetraploids, in themselves, have little promise for tree and fruit production.

Among the spontaneous hybrid triploids obtained by Frost (1943) seven were maintained in duplicate as budded orchard trees, from 1931 to 1967. These selections involved orange, grapefruit, and mandarin parentage, and they showed a much higher average level of vigor than the tetraploids. Over the period 1950–1955, three of these triploid selections averaged moderate to high yields of fruit while four had very poor yields. All had nearly seedless fruit. None had enough good characters to become a successful variety, but their behavior strengthened the indication of the value of triploidy in the development of citrus varieties.

Characters of triploids from controlled crosses in a primary trial

Triploid hybrids from controlled pollination were grown as a first-budded generation in a close-planted field trial. Data on vigor and yield of these trees are shown in table 2. Among 91 individuals from six crosses, 70 maintained moderate to high vigor for a 15-year period, until the planting was removed in 1958. These vigorous hybrids were rather evenly distributed among crosses and they constituted at least as high a proportion of the total as is commonly found among crosses between diploid parents. Tree-by-tree yield estimates were obtained from 1952 through 1955, when the trees were 8 to 12 years from planting. Only 15 trees averaged moderate to high yields, relative to tree size. This is a lower proportion than is usually found among diploid hybrids of a similar age from seed, but variation in the vegetative, juvenile stage among citrus forms is great, and the crowded plantings was not favorable to heavy yields.

Seed numbers per fruit were determined in two seasons for all trees from which fruits were available (table 3).

TABLE 1

IDENTITY AND CONDITION OF 30 TO 35-YEAR-OLD TETRAPLOID CITRUS TREES OF SEVERAL VARIETIES AT RIVERSIDE, CALIFORNIA, IN 1963*

Variety or selection	Number of trees†	Condition, relative to nucellar diploids‡	
		Size	General vigor
Grapefruit			
Hall's Silver	4	smaller	nearly equal
Imperial	1	equal	equal
Royal	2	nearly equal	equal
Seedy white	3	smaller	slightly poorer
Lemon			
Lisbon	5	much smaller	poorer
Orange			
Paperrind	4	much smaller	slightly poorer
Ruby	3	much smaller	slightly poorer
Seedy sweet	2	much smaller	slightly poorer
Washington navel	1	much smaller	much poorer
Mandarin			
Dancy	1	much smaller	much poorer
King	7	smaller	much poorer
Willowleaf	2	much smaller	much poorer
Satsuma	2	smaller	slightly poorer

* Data listed also in Cameron and Frost (1968).
† Includes repropagations on various rootstocks, and some original seedling trees. All selections originally obtained as spontaneous nucellar tetraploids.
‡ Comparisons based on trees of the same age on the same rootstock.

These were not always the same trees, so that a total of 58 different hybrids is included. Seed numbers were very low in nearly every hybrid. The range among all trees was from 0 to 7.8 seeds per fruit, but only 4 hybrids averaged more than 4.0 seeds. The crosses with tetraploid seedy grapefruit clearly tended to have higher seed numbers than those with tetraploid Lisbon lemon. The low seed numbers are in sharp contrast to the seediness of the parental varieties which, except for the low-seeded Trovita orange, averaged from 14 to 33 seeds per fruit in 1958.

Characters of the triploids in the secondary trial

1960, 85 repropagated hybrids from the primary trial were planted in a secondary field trial, at 10 × 24 ft spac-

TABLE 2

VIGOR AND YIELD BEHAVIOR OF TRIPLOID HYBRIDS IN PRIMARY AND SECONDARY TRIALS, AND VIGOR OF RELATED DIPLOID VARIETIES

Cross	Vigor and yield in first trial*			Vigor and yield in second trial‡				
	No. of trees	No. with moderate to high vigor,† 1958	No. with moderate to high yield, 1952–55	No. of trees	No. with high vigor, 1968	Trunk cross-section areas in 1966		No. with moderate to high yield, 1964–68
						Range	Mean	
						cm^2	cm^2	
4n seedy white grapefruit seed parent								
× 2n Dancy tangerine	11	9	4	10	6	82–136	109	4
× 2n Kinnow mandarin	17	11	4	13	8	103–132	119	4
4n Lisbon lemon seed parent								
× 2n Trovita orange	32	20	4	28	21	89–146	118	6
× 2n Ruddy tangor	7	6	1	11	7	86–161	117	3
× 2n Kinnow mandarin	17	17	1	17	14	89–142	109	6
× 2n lemon hybrid	7	7	1	6	4	129–147	138	0
Totals	91	70	15	85	60			23
Related diploid varieties								
2n Marsh grapefruit								
on own roots				4		105–151	129	
on Troyer citrange				4		115–132	121	
2n Lisbon lemon								
on own roots				4		110–139	124	
on Cleopatra mandarin				4		111–133	122	
2n Kinnow mandarin								
on own roots				4		66–75	72	
on Troyer citrange				4		76–90	82	

* Planted in 1944 on sweet orange rootstock, at 10 × 12 ft spacing.
† Based on size, density, and leaf color, on a scale from 1 to 5, and relative to vigorous diploid varieties.
‡ Triploids planted in 1960 on Cleopatra mandarin rootstock, at 10 × 24 ft spacing. Diploid varieties on own roots planted in 1960; those on rootstocks planted 1961: all at 10 × 24 ft spacing, in a plot adjoining the triploids.

ing. Data on this trial were taken up until 1968.

Vigor, yield, and seed numbers. Table 2 indicates the vigor and yield behavior of the repropagated hybrids, and some related diploids. A vigor classification made in 1968, by the same criteria used in the primary trial, indicated that about 60 of the 85 hybrids were of high vigor 8 years after planting. In 1966, trunk cross-section areas of these 60 trees averaged from 109 to 138 cm^2, by crosses; only 9 of the 60 had cross-sections smaller than 100 cm^2. In comparison, 4-tree plots of the related diploid Marsh grapefruit and Lisbon lemon, both vigorous varieties and growing in an adjoining planting, had cross-section areas averaging from 121 to 129 cm^2. The parental diploid Kinnow has been slower-growing, and averaged only 72 and 82 cm^2. One plot of the diploid Lisbon and all of the triploids were on Cleopatra mandarin rootstock, which has frequently shown bud-union irregularities in California. Some of the present trees have shown overgrowth of the scion at the bud union, but not to a degree which would invalidate the comparisons. The overall data of table 2 support the earlier evidence that vigorous triploid selections can often be obtained from *Citrus* crosses.

Yield data were taken in the secondary trial for the period 1964 through 1968. Twenty-three of the 85 trees averaged moderate to high yields (table 2), an appreciably higher proportion than had done so in the primary trial. Seed numbers were determined in several years, and were always low. Among 43 trees with adequate fruit in 1965, average seed numbers per fruit ranged from 0.0 to 6.2 (table 3). Three trees had an average greater than 4 seeds per fruit. As in the primary trial, seed numbers were especially low in the hybrids having tetraploid lemon as a parent.

Soluble solids and acidity of the juice. Data on total soluble solids and acidity of the fruits were taken in several years. The data for 1965 (table 3) are representative. Soluble solids averaged higher in the hybrids with tetraploid grapefruit than in those with tetraploid lemon, while acidity was much higher in the lemon hybrids. This is in agreement with the characters of the tetraploid parents. Since the diploid parents (except for the diploid lemon hybrid) characteristically have relatively high soluble solids and moderate acidity (table 3), the behavior of the progenies indicates a marked effect of the tetraploid parents, which contributed two of the three sets of chromosomes. At the date measured, none of the 27 individual lemon hybrids had an acid percentage nearly as low as their nonlemon parents, and only one of the 16 grapefruit hybrids was as low in acid (1.50 per cent) as the Dancy or Kinnow parents.

At Riverside, the fruits of the diploid parents reach market maturity between January and March. Later in the season, soluble solids can increase somewhat, while acidity gradually decreases; this pattern of behavior is typical of most citrus varieties (Soost and Cameron, 1961). Nearly all of the hybrids in the present study also ripened between January and March, as judged by physical characters including rind color, juiciness, the begining of softening or puffing, and drop. A few of the lemon hybrids only, still showed partly green rinds in March. It was clear from these observations that the high acidities of the triploids were characteristic of these hybrids, and were not due simply to immaturity of the fruit.

Many other fruit characters were evaluated in the hybrids, and the range of variation found was similar to that already known in diploid crosses. Some individuals have had good fruit size and shape, satisfactory rind and flesh colors, and juicy and fine-textured flesh (fig-

TABLE 3

SEED NUMBERS AND JUICE COMPOSITION OF TRIPLOID VARIETIES AND THEIR PARENT VARIETIES IN PRIMARY AND SECONDARY TRIALS

Cross	Primary trial 1952: No. of trees	1952: Seed numbers per fruit*: Range among trees	1952: Mean per tree	Primary trial 1958: No. of trees	1958: Seed numbers per fruit*: Range among trees	1958: Mean per tree	Secondary trial 1965: No. of trees	1965: Seed numbers per fruit*: Range among trees	1965: Mean per tree	Juice composition, Secondary trial†: Soluble solids (range)	Acid (range)
										per cent	*per cent*
4n seedy white grapefruit seed parent											
× 2n Dancy tangerine	8	0.3–7.8	4.5	9	0.3–5.0	2.4	6	0.0–6.2	3.1	11.1–12.3	2.1–2.7
× 2n Kinnow mandarin	9	0.0–6.1	2.9	11	0.3–3.3	2.0	10	0.3–4.7	2.7	12.1–14.5	1.5–3.3
2n Lisbon lemon seed parent											
× Trovita orange	9	0.0–1.4	0.5	13	0.0–3.0	0.6	13	0.0–0.3	0.1	8.0–12.1	3.6–6.4
× 2n Ruddy tangor	3	0.1–1.0	0.6	3	0.1–1.7	0.6	5	0.0–1.3	0.5	8.3–10.8	3.4–4.4
× 2n Kinnow mandarin	7	0.3–4.0	1.7	11	0.1–1.0	0.4	7	0.3–2.9	1.4	9.3–11.1	3.7–6.1
× 2n lemon hybrid	1	...	0.2	4	0.8–2.0	1.3	2	0.0–0.5	0.3	8.7–8.8	5.1–6.2
Totals and ranges	37	0.0–7.8		51	0.0–5.0						
Parent varieties										(*Mean*)	(*Mean*)
4n seedy white grapefruit						30				10.2	2.1
4n Lisbon lemon						20				8.0	5.2
2n Dancy tangerine						16				14.9	1.6
2n Kinnow mandarin						23				13.3	1.6
2n Trovita orange						8				11.8	0.9
2n Ruddy orange						14				11.0	1.8

* Seed numbers determined from samples of 20 fruits in 1952 and 1965, and 10 fruits in 1958.
† Data for triploids and tetraploid parents taken in March, 1965. Data for diploid parents are averages of February to March values in various years.

TABLE 4

LEAF CHARACTERS AND CHROMOSOME COUNTS OF TRIPLOID HYBRIDS IN THE SECONDARY TRIAL, AND LEAF CHARACTERS OF THE PARENTS*

Cross	No. of trees	Leaf thickness		Leaf shape index (length/width)		No. of trees verified triploid by chromosome counts†
		Range among trees	Mean per tree	Range among trees	Mean per tree	
		mm	*mm*			
4n seedy white grapefruit						
× 2n Dancy tangerine	10	0.35–0.44	0.38	1.22–1.51	1.41	2
× 2n Kinnow mandarin	11	0.33–0.42	0.37	1.45–1.82	1.60	9
4n Lisbon lemon						
× 2n Trovita	11	0.33–0.42	0.38	1.36–1.92	1.53	7
× 2n Ruddy tangor	11	0.33–0.40	0.36	1.47–1.89	1.59	5
× 2n Kinnow mandarin	11	0.33–0.37	0.35	1.41–1.93	1.64	14
× 2n lemon hybrid	6	0.32–0.38	0.35	1.53–1.60	1.56	..
Parent varieties						
4n seedy white grapefruit	2	0.43–0.46	0.45	1.40–1.40	1.40	
4n Lisbon lemon	2	0.43–0.44	0.44	1.39–1.47	1.43	
2n Dancy	2	0.27–0.28	0.28	1.84–2.01	1.93	
2n Kinnow	2	0.25–0.26	0.26	2.20–2.29	2.25	
2n Trovita	2	0.30–0.30	0.30	2.00–2.08	2.04	
2n Ruddy	2	0.26–0.28	0.27	1.88–1.92	1.90	
2n lemon hybrid	2	0.24–0.25	0.25	1.82–1.92	1.87	

Probability values (P) for differences of means

	Leaf thickness	*Leaf shape index*
4n parents minus 2n parents	<0.01	<0.01
4n parents minus 3n progenies	<0.01	0.04
2n parents minus 3n progenies	<0.01	<0.01

* Leaf data taken in 1964, chromosome data in 1966. Diploid parents were located in nearby plantings.

† Not all hybrids were examined. No tree was proven to be other than triploid, but in some cases chromosome numbers of 26 or 28 could not be ruled out. Six of the 14 hybrids of 4n Lisbon × Kinnow were different ones than those measured for leaf characters.

ures 1 and 2). One hybrid (4n grapefruit × 2n Kinnow) may be a satisfactory variety if grown in areas conducive to lower acidity.

Leaf thickness, leaf shape, and chromosome numbers. Leaf thickness and shape are useful characters for the diagnosis of polyploidy in citrus. Frost (1925, 1943) and others have found that citrus autotetraploids commonly have broader and thicker leaves than diploids of the same variety. Triploids show a similar tendency, but can be more variable when they arise from diverse parents. Nearly all the triploids in the present study were first tentatively identified as polyploids by their leaf characters. In 1964, leaf data were taken on a random group of hybrids from each cross in the secondary trial, and from the parent varieties (table 4). For leaf thickness, the means for the two tetraploid parents were 0.44 and 0.45 mm, while the means among the diploid parents ranged from 0.25 to 0.30 mm. For leaf-shape ratios, the means for the tetraploids were also clearly different from those of the diploids. For both measurements the differences were significant at P values of 0.01.

The means of the hybrids, by crosses, were nearly always intermediate for leaf thickness, although a few individuals had leaves as thick as their tetraploid parent. Leaf-shape ratios, by crosses, were also mostly intermediate, except for hybrids of tetraploid grapefruit × Dancy, which had unusually short, broad leaves. The differences between tetraploids and triploids, and between diploids and triploids, as groups, were statistically significant.

Somatic chromosome counts of many of the hybrids were made from smears of young shoot tips. Exact counts are often difficult to obtain by this method, but the 37 individuals studied from among five crosses were all found to be either exact or nearly exact triploids (table 4). No cases of aneuploid plants with numbers approaching diploidy or tetraploidy were proven in this group. It is possible that some weak hybrids, not repropagated in the secondary trial, may have been aneuploids.

Tachikawa, et al. (1961) reported the occurrence of both triploid hybrids and tetraploid hybrids from crosses where the seed parent was diploid and the pollen parent was the tetraploid. In a recent study (Cameron and Soost, 1969) we have obtained many unexpected tetraploid hybrids from crosses made in this way. We have postulated that a doubling of the haploid egg chromosome set, together with functioning of diploid male gametes, may account for their occurrence.

SUMMARY

Tree and fruit characters of citrus triploids from six crosses involving tetraploid grapefruit and tetraploid lemon as seed parents, and five diploid varieties as pollen parents, are described. In a primary field trial at close spacing, about 70 out of 91 hybrids showed satisfactory vigor, but only 15 gave high yields of fruit. Seed numbers were consistently low in almost all of these trees. Among 85 repropagated hybrids in a secondary trial at wider spacing, 60 have maintained good vigor up until 1968 (8 years after planting) and about 23 have yielded well. Seed numbers have remained low, usually fewer than 5 seeds per fruit, despite the proximity of other varieties with fertile pollen. Hybrids with tetraploid lemon as seed parent have averaged definitely lower in seed numbers than those with tetraploid grapefruit. Percentages of total soluble solids in the fruits of these hybrids were generally intermediate as compared to the parent varieties, and were within the range commonly found in diploid crosses. Percentage of acid, however, was usually high, being strongly influenced in the direction of the tetraploid parents, which contributed two of the three sets of chromosomes. Leaf thickness in the tetraploid parents was significantly greater than in the diploids, and ratios of length to width of the leaves were significantly smaller. The triploids were usually intermediate in these leaf characters, but they sometimes reached the values found for the tetraploids. Chromosome counts of 37 of the hybrids indicated that all are apparently exact or nearly exact triploids. Studies reported elsewhere show that when the pollen parent rather than the seed parent is the tetraploid, tetraploid hybrids and other ploidy levels can ocur in the progenies. Some of the triploids have had many of the fruit characters desired in a satisfactory variety, but partly because of their high acidity none has as yet been officially introduced.

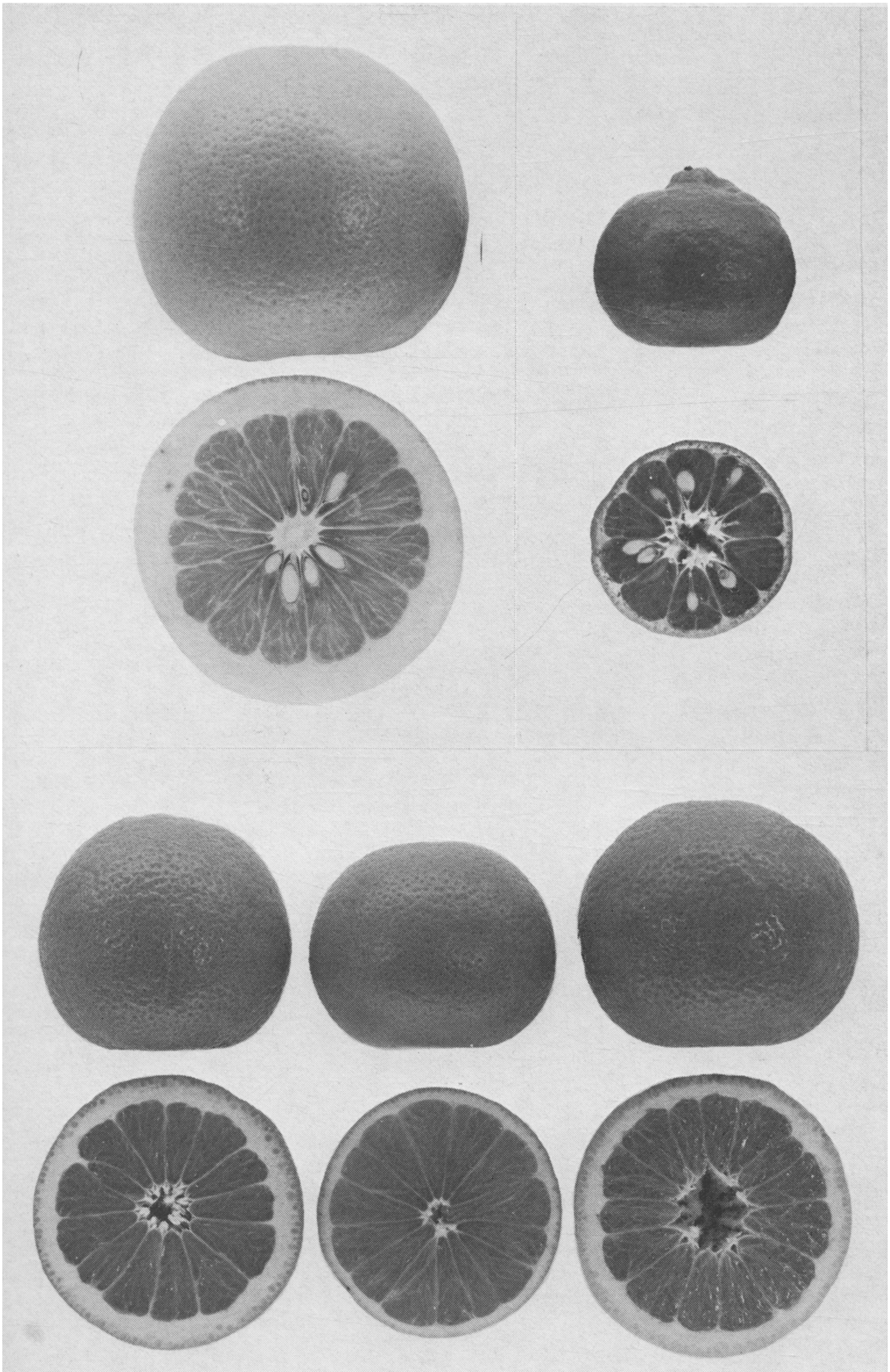

Fig. 1. *Top:* Whole and cut fruits of the parents. *Left:* tetraploid seedy white grapefruit; *right:* diploid Dancy tangerine. Note numerous seeds in both. *Bottom:* Whole and cut fruits of three selected triploid hybrids of these parents, showing lack of seeds and generally good physical characteristics. All × 0.4.

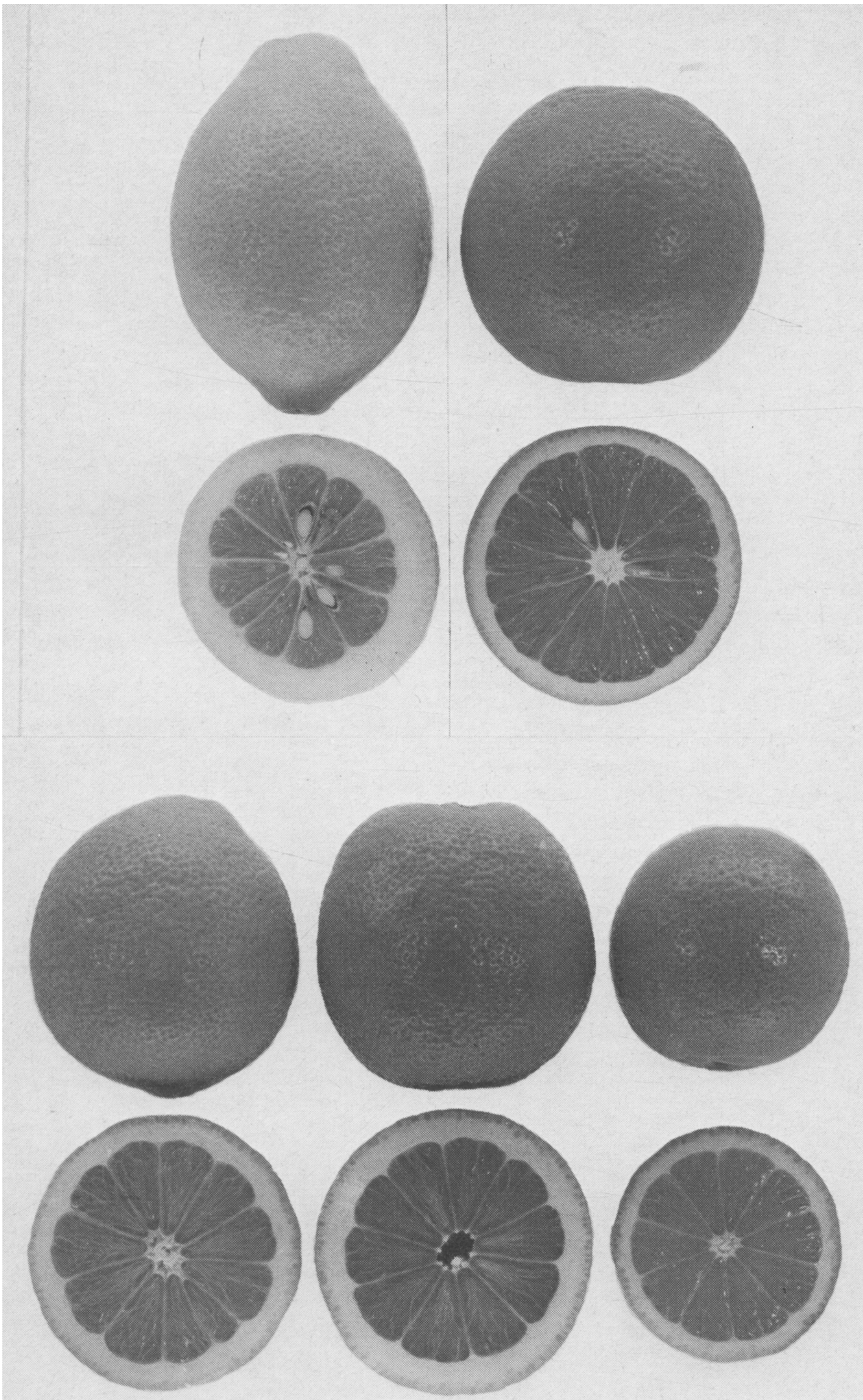

Fig. 2. *Top:* Whole and cut fruits of the parents. *Left:* tetraploid Lisbon lemon; *right:* diploid Trovita orange. Note seeds in both parents. *Bottom:* Whole and cut fruits of three selected triploid hybrids of these parents, showing lack of seeds and generally good physical characteristics. All × 0.4.

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