THE HORTICULTURAL SIGNIFICANCE OF NUCELLAR EMBRYONY IN CITRUS[1]

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HISTORICAL SKETCH

During the last ten years, the effects of nucellar embryony in citrus have become of greatly increased interest to citrus pathologists and horticulturists throughout the world. This interest is related partly to the number and severity of virus diseases now known to affect citrus, partly to the difficulty of replanting citrus in old citrus soils in some areas, and partly to the problem of the physiological changes which acompany asexual seed reproduction. The favorable characteristics of properly selected nucellar seedling lines are at present leading to their widespread use in plantings in California.

We propose to review briefly the historical and biological aspects of our subject, and to point out some recent evidence on the behavior of nucellar citrus lines in California.

Eduard Strasburger in 1878 (*12*) was the first to establish the nucellar and thus asexual origin of the extra embryos in citrus seeds. As a result, it became clear that such embryos should regularly repeat the genetic type of their seed parent.

In the United States, in 1893, W. T. Swingle and H. J. Webber began long-continued studies of citrus, which resulted in many important observations on the behavior of nucellar seedlings. In 1932, Webber (*15*) emphasized the importance of nucellar embryony to the production of uniform citrus rootstocks, as had Toxopeus (*14*) in Java. It is today well recognized that nucellar seedlings are highly uniform and that in this they often differ markedly from associated gametic seedlings, which are usually variable, even from selfing. At fruiting, the two types can almost invariably be distinguished from each other. Most citrus varieties produce moderate to very high proportions of nucellar embryos. Some, including the shaddocks, *Citrus grandis* (Linn.) Osbeck, produce none.

Swingle (*13*), in 1932 and, earlier, in an address at the University of California Citrus Experiment Station, was probably the first to point out clearly the presence of juvenile characteristics in citrus. He discussed them as an essential feature of embryo formation and evidently did not consider the related problem of elimination of virus diseases by seed reproduction.

Following Swingle's address, trials of young nucellar lines and of own-rooted seedlings, in comparison with old-line trees, were conducted at the University of California at Riverside and at Los Angeles. Reports published in 1938 by Frost (*4*) and by Hodgson and Cameron (*9*) emphasized the differences among lines in thorniness, tree habit, and tendency to fruit. Frost pointed out that repeated cell division, rather than age *per se*, is the important feature in reducing thorniness. A comprehensive, general dis-

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cusion of nucellar embryony and young nucellar lines was published by Frost in 1943 (*5*).

H. S. Fawcett, who identified psorosis as a virus disease in 1933 (*3*), early realized the importance of the fact that it might not pass through the seed. He grew seedlings from psorosis-infected Valencias and established nucellar lines of the Cutter Valencia, which are still under trial in California.

L. D. Batchelor, in conjunction with his studies of lemon strains, made the first extended trials of the Frost nucellar Eureka and demonstrated its superiority over the old line (*1*). Later, in 1952, Cameron and Soost (*2*) and Frost (*6*) reported results of comparisons between nucellar and old-line trees of some ten varieties budded 22 years earlier. These results emphasized the generally increased vigor and yield of nucellar lines and also indicated the usual genetic similarity of a nucellar line to its parent old line in the horticultural characters measured. Certain exceptional differences will be considered later in this paper.

Oberholzer and Hofmeyr in 1955 (*11*) presented a comprehensive review of virus and senility problems of citrus in South Africa. They consider nucellar seedling lines to be potentially promising in that country, although still in an experimental stage.

PRESENT INFORMATION

Nucellar Embryony and Virus Diseases. Most of the known virus diseases in citrus are eliminated in the process of nucellar embryony. This fact is of course of great importance to horticulturists. Since another paper in this volume deals with this subject in detail, we wish only to point out examples of the horticultural behavior of certain nucellar lines derived from diseased old lines. Two old-line Frost Valencia trees planted at the Citrus Experiment Station 24 years ago carry psorosis and are in poor condition today. Frost nucellar Valencias derived from the original old clone and of the same age from budding as the two old-line propagations are vigorous and productive. Young budded trees of the Cutter nucellar Valencia, 24 years from seed, are beginning to yield satisfactorily. The old line carries psorosis and would not be acceptable for propagation.

Two old-line Frost Eureka lemon trees, 27 years from budding, have long shown severe bark shelling, which is not known to be caused by virus. Two nucellar Frost Eurekas, also 27 years from budding, and 42 years from seed, had until 1948 shown no bark shelling. One of them now has slight lesions which may be the initial stages of shell bark. About ten trees each of a later-budded generation of these two lines were planted by L. D. Batchelor in 1942. At 15 years of age, all the old-line trees are now showing bark shelling, while no shelling has occurred on the nucellar-line trees.

Recognized Juvenile Characters. The existence of certain juvenile characters in citrus is well established. These characters include thorniness, upright habit of growth, slowness in fruiting, and early alternate bearing. They occur so generally in citrus seedlings, and decrease so systematically in later-budded generations (although not always at the same rate in different varieties), that they can scarcely be attributed simply to elimination of viruses.

Thus trees budded from young seedlings may be highly thorny, but in later propagations thorniness is reduced, especially by the use of budwood taken from high positions in a tree. Slowness in flowering and fruiting is typical of the great majority of seedlings. Furr, Cooper, and Reece (*8*) performed grafting and ringing experiments with young seedlings in an attempt to induce flowering. Only occasionally could a seedling as young as three years of age be made to flower; such flowering, when it occurred, was at the tips of branches farthest from the roots.

Frost (*6*) found that among 85 three-year-old budlings of 15 varieties from young lines which were 16 to 18 years from seed, only nine bore any fruit. Of these nine, seven were from "high" budwood. Among 82 old-line budlings, in contrast, 65 carried fruit. Additional data on the early orchard behavior of some trees from high and low budwood are shown in table 1. In the fourth and fifth years after planting, yields of nucellar Lisbon lemon trees from high budwood were more than twice as great as those from low budwood. In the sixth and seventh years, yields were more nearly equal.

The differences in yield of old-line and nucellar Lisbon lemon trees and old-line and nucellar Eureka lemon trees in this same period are shown in table 2. Beginning with the earliest crops of this planting, the nucellar Eureka regularly outyielded its old line. The nucellar Lisbon, however, did not equal the yield of its old line in any of these years. The nucellar Lisbon data are the averages of those in table 1.

Long-term Yield Behavior. Older orchard trees of most of the longer-established nucellar lines that we have studied have shown markedly higher yields than trees of the compared old lines. This is usually correlated with larger tree size in the nucellar lines. Higher yields were shown in nine out of ten varieties discussed in 1952 (*2*). However, the trees of the nucellar Frost Lisbon, referred to above, still showed a 7 per cent deficiency in total yield up to 1952, as compared to the old line. Since 1952, the yield of these trees has almost exactly equaled the yield of the old line. The yields in boxes per tree per year are: nucellar line, 5.75; old line, 5.70.

Additional evidence of the satisfactory yield potential of the Frost Lisbon lemon is shown in table 3. In a recent planting at Corona, California, trees of this line have yielded as well during the first four years of fruiting as have comparable trees of a

Table 1. EARLY YIELDS OF NUCELLAR LISBON LEMON TREES FROM HIGH AND LOW BUDWOOD*

Budwood	Tree No.	Years after planting: 4	5	6	7
		Yield, in pounds per tree			
High	1	57	197	267	357
	2	33	236	203	293
Low	3	10	68	239	198
	4	13	124	267	331

* For the seasons 1937–1940. This line 20 years old from seed in 1937.

Table 2. YIELDS OF YOUNG TREES OF OLD-LINE AND NUCELLAR EUREKA AND LISBON LEMONS*

Variety	Line†	Years from seed in 1937	Years after planting: 4	5	6	7	Total
			Yield, in pounds per tree				
Eureka	Old	Many	50	72	307	260	689
	Nucellar	22	84	238	354	350	1026
Lisbon	Old	Many	109	176	263	352	900
	Nucellar	20	28	156	244	295	723

* For the seasons 1937–1940.
† Number of trees: nucellar Lisbon, 4; others, 2 each.

vigorous old line called the Prior Lisbon. The Frost Lisbon trees are on sweet orange rootstock, while the Prior Lisbon trees are on Sampson tangelo, but this should not seriously affect the comparison.

The Frost nucellar Washington Navel (Nucellar Line No. 1) also seems to be showing satisfactory early-yield behavior. In a planting at the McMaster Ranch in Tulare County, a group of five-year-old trees of this line yielded slightly more in 1957 than did five- and six-year-old trees of a selected old line in adjacent rows. For the 1958 crop there is a considerably heavier set of fruit on the nucellar-line trees than on the old-line trees.

Strain tests of Valencia orange have recently been established in Ventura County by W. P. Bitters. Table 4 shows the 1956 and 1957 yields of five lines. An old-line Valencia called Sespe XI, the old-line Campbell (derived from seed about 87 years ago), and the Frost nucellar Valencia No. 1 (42 years from seed) all yielded about equally in these two years. In contrast, young nucellar lines of the Cutter and Campbell Valencias, respectively only 24 and 19 years removed from seed, still showed an extreme alternation in yield, which reflects their juvenile condition. In a similar planting at the University of California Citrus Experiment Station, these two lines also showed this alternation.

The sum total of these yield data are encouraging with respect to the behavior of older nucellar lines. They show that young budded trees of several of these lines are coming into bearing as early as do old lines.

Fruit Characteristics. In 1952 (*2*) we stated that among the older nucellar lines we still found some indications of the thicker fruit rinds and coarser flesh texture which often reflect the juvenile condition. These characters are being studied as new plantings begin to fruit. In the comparison of Washington Navel lines at the McMaster Ranch, discussed above, a slightly coarser pebbling of the rind and slightly more loose-

Table 3. YIELDS OF A RECENT COMMERCIAL PLANTING OF FROST LISBON AND PRIOR LISBON LEMONS*

Line†	No. of trees	Years after planting				Total
		2	3	4	5	
		Yield, in field boxes per tree				
Frost nucellar	1020	0.02	0.35	1.96	3.90	6.23
Prior old line	539	0.07	0.61	1.65	3.75	6.08

* Data from Jameson Ranch Company, Corona, California, for the period 1953–1957.
† Rootstocks: sweet orange for the Frost Lisbon; Sampson tangelo for the Prior Lisbon.

Table 4. YIELDS OF YOUNG TREES OF OLD-LINE AND NUCELLAR VALENCIA ORANGES*

Line†	Years from seed in 1957	Yield, in pounds per tree	
		1956	1957
Sespe XI	Many	162	258
Campbell	87	169	252
Frost nucellar	42	144	257
Cutter nucellar	24	227	64
Campbell nucellar	19	271	72

* Planted in 1949 in Ventura County. (Data from W. P. Bitters.)
† Twelve to 28 trees of each, on sweet orange rootstock.

ness of core were observed in the nucellar-line fruit than in the unrelated old line. Rind thickness, in samples of 160 fruits each, averaged 5.4 mm for the old line and 5.8 mm for the nucellar line. In comparisons of this kind, it is difficult to determine whether such differences are related to the age of the line from seed or to actual genetic variations among lines.

Other characteristics of nucellar lines also appear to be long-sustained physiological effects of rejuvenation. Lower seed number is one of these. Hodgson and Cameron (*9*), Frost (*4*), and Hu and Cameron (*10*) all reported that young nucellar lines of certain oranges had fewer seeds than the parent lines. Among seven varieties considered by us in 1952, the nucellar lines of at least two were still showing lower seediness than the parent lines. Those lines were then about 35 years removed from seed. Since then, a two-tree comparison has been continued with one variety, the Marsh grapefruit. Table 5 shows that the nucellar Marsh tree has maintained somewhat lower seed numbers in each year.

Table 5. SEEDINESS IN AN OLD-LINE AND A NUCELLAR MARSH GRAPEFRUIT TREE*

Line	Seeds per fruit†				
	1949–1951	1954	1955	1956	1957
Old	4.6	3.2	4.1	5.0	3.0
Nucellar	3.0	2.6	2.2	3.6	2.7

* Planted in 1933 on sour orange stock.
† Sixty or more fruits per sample.

Navel structure is another character which has shown a persistent difference in old and nucellar lines. In all cases known to us, the navel has averaged smaller in nucellar-line fruit. Years ago W. T. Swingle observed that this structure was small, although not absent, in populations of Washington Navel seedlings which he obtained. Frost (*4*) reported in 1938 that in both the Washington Navel and another navel variety called the Ruvel, the average size of navel was considerably smaller in nucellar lines than in old lines. In 1951, measurements from 18-year-old, budded trees of these same lines showed that this difference still persisted. Oberholzer and Hofmeyr (*11*), in South Africa, have also reported that a nucellar navel orange line which originated there in about 1920 shows navel apertures only about half as large as those of fruit of adjacent old-line trees.

During the present season, data were taken on navel-structure size in fruits from the Washington Navel comparison at the McMaster Ranch. Table 6 shows that the internal

Table 6. SIZE OF NAVEL STRUCTURE IN OLD-LINE AND NUCELLAR WASHINGTON NAVEL ORANGES, 1957*

Line	Tree No.	Navel structure		
		Length	Width	External opening
		mm	*mm*	*mm*
McMaster old line	1	18.8	18.9	8.2
	2	23.5	20.3	5.8
Frost nucellar	3	14.9	15.0	5.3
	4	10.0	13.7	7.3

* Trees planted in 1951, in Tulare County, on sweet orange stock. Data based on 20 fruits per tree.

size of the navel was smaller in the Frost nucellar line than in the McMaster old line, although the external openings were about equal.

These reductions in navel-structure size and in seed number are probably related to the over-all, lesser tendency of nucellar lines to reproduce during the earlier part of their life histories.

Genetic Variation. In conclusion, we must emphasize the relation of genetic variations to nucellar embryony. These variations within varieties are recognized as being of frequent occurrence. The majority of them are unfavorable, and it is often of importance to eliminate them in both the budded and the nucellar progeny of a variety. If a favorable variation occurs, it is useful to be able to propagate it in vigorous form by means of nucellar seedlings.

As a case in point, we should like to cite a long-term study of nucellar lines in Satsuma, recently reported (7). Two nucellar Satsuma lines derived from a single seed parent tree, both show larger tree and leaf size and greater yield than the parent line. Fruit shape and tree habit have been significantly different, statistically, between the two nucellar lines. Fruit coloring has been significantly earlier in line 1 than in the old line. Soluble solids have been significantly higher in both young lines than in the parent.

We have interpreted these results to be partly effects of nucellar embryony and partly effects of mutations perpetuated as nucellar variations. Neither the parent nor the nucellar lines carry tristeza, or show symptoms of the dwarf disease of Satsuma described in Japan. However, other unrecognized diseases may still be found to be related to this system of character differences.

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