University of California Strawberry Breeding

Hedrick (1925, p. 355) states in the introduction to the strawberry sections of *The Small Fruits of New York*

“The Strawberry has remarkable powers of adapting itself to climates and soils. In consequence it is found in one species or another in almost every part of the globe. But in general the many species are lovers of cool climates and of dry, loose, warm soils. Under culture strawberries belong distinctly to cold climates. In tropical and sub-tropical countries, the plants grow but languidly, refuse to bear abundantly, and the fruits are deficient in size, color, flavor, and the delicate fragrance from which the strawberry derives its generic name *Fragaria*. The plants are most luxuriant, and the fruits are most pleasing to eye and palate where greatest hardihood to cold is required. Wild or cultivated, strawberries are little esteemed to warm countries. Accordingly, they are valued most, and came to their present high estate as cultivated plants in the colder parts of the temperate zones, especially in Europe and North America, to whose peoples they owe domestication.”

Most of the above statements were true at that time because the breeding of strawberries for adaptation to warmer (subtropical) environments that was to be carried out at the Univ. of California was only about to begin (1926) and ‘Lassen’, the first cultivar truly adapted to southern coastal California, was not to be released until 1945 (H.E. Thomas and E.V. Goldsmith, 1945).

While California yields per unit area were the highest in the nation prior to World War II, they were only ≈ 1 to 2 t higher than those of the highest-yielding other states, a relatively insignificant difference (Tables 1 and 2).

California strawberry production was effectively terminated for the duration of World War II, starting in 1942, and was not resumed until the return of the Japanese-descended farmers after the war ended. Post-World War II yields in California more than tripled prewar yields, and commercial strawberry production has been dominated by California ever since (Tables 3 and 4). Excluding California, average yields over all other states did not increase during 1949-54 (Table 3). The principal reason for the large increase in postwar yield was the development and re-

lease of the Univ. of California strawberry cultivars.

The Univ. of California Strawberry Breeding Program was started in 1924-26 by A.G. Plakidas, a U.C. Berkeley pathologist, and continued by W.T. Home in a successful effort to identify virus-tolerant material that might be useful in breeding (Wilhelm and Sagen, 1974).

H.E. Thomas and E.V. Goldsmith, also of the Dept. of Plant Pathology, Berkeley,

followed up on the Plakidas virus tolerance work and, in addition, bred for adaptation to coastal California (subtropical) growing conditions and released the five original university cultivars in 1945 (Table 5), after which they left the university to conduct a successful private breeding program.

Of the five 1945 releases, ‘Shasta’ was highly successful in central coastal California for ≈ 30 years and ‘Lassen’ in southern California and in central California for ≈ 20

Table 1. Production, hectareage, and yield of the 20 leading strawberry-producing states in 1919 (from Hedrick, 1926, D. 369).

State	U.S. strawberry production					
	Crop		Area		Yield	
	%	Rank	%	Rank	t·ha ⁻¹	Rank
Tennessee	7.4	1	9.1	1	2.0	19
Missouri	7.3	2	7.2	2	2.5	8
Michigan	7.1	3	6.7	4	2.6	7
Arkansas	6.5	4	7.0	3	2.3	15
California	6.1	5	4.2	8	3.6	1
Maryland	5.1	6	5.9	5	2.1	17
New York	4.8	7	4.1	9	3.0	4
New Jersey	4.2	8	4.7	6	2.9	6
Pennsylvania	4.1	9	3.4	12	3.0	3
Ohio	4.0	10	3.5	11	2.9	5
Illinois	3.9	11	4.2	7	2.3	14
Iowa	3.7	12	3.7	10	2.5	10
Washington	3.6	13	2.6	17	3.5	2
Louisiana	3.0	14	3.4	13	2.2	16
Wisconsin	2.9	15	3.1	14	2.4	13
Indiana	2.4	16	2.8	16	2.1	18
Oregon	2.3	17	2.3	18	2.5	11
Minnesota	2.3	18	2.3	19	2.5	9
Delaware	2.3	19	2.9	15	1.9	20
North Carolina	2.1	20	1.8	20	2.5	12
Total	85.6		84.4		Mean 2.6	

Table 2. Production, hectareage, and yield of the 20 leading strawberry-producing states in 1941 (Federal-State Market News Service, 1955).

State	U.S. strawberry production					
	Crop		Area		Yield	
	%	Rank	%	Rank	t·ha ⁻¹	Rank
Arkansas	12.4	1	11.4	2	3.2	6
Louisiana	10.8	2	13.2	1	2.4	14
Oregon	10.8	3	7.9	3	4.0	3
Michigan	6.6	4	6.0	5	3.3	7
Washington	6.5	5	4.2	7	4.6	2
Tennessee	6.5	6	6.3	4	3.0	10
California	6.1	7	3.5	10	5.0	1
North Carolina	5.1	8	3.9	8	3.8	4
Wisconsin	3.4	9	3.1	13	3.2	8
New York	3.3	10	3.0	14	3.2	9
Ohio	3.2	11	2.6	16	3.6	5
Florida	3.1	12	3.2	11	2.8	11
Kentucky	2.6	13	3.9	9	2.0	17
Virginia	2.3	14	4.2	6	1.6	20
Alabama	2.2	15	2.3	17	2.8	12
Maryland	2.2	16	2.9	15	2.2	16
Missouri	1.9	17	3.2	12	1.8	19
Pennsylvania	1.9	18	1.9	20	2.8	13
New Jersey	1.7	19	2.1	19	2.4	15
Indiana	1.5	20	2.2	18	2.0	18
Total	94.1		91.0		Mean 2.9	

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years (Table 6). Of the others, 'Dormer' became an important cultivar in Japan, but was never used elsewhere.

A. Etter (1887-1950), a private breeder from Ettersburg, Calif., must be credited with developing important breeding stock that led, in part, to the development of the UC cultivars; in particular, to virus resistance and adaptation to relatively warm southern coastal conditions, via 'Lassen'. In retrospect, Etter's most important contribution was the breeding of derivatives from California *Fragaria chiloensis*, perhaps the most important of which was a hybrid between an *F. chiloensis* plant that he collected from Cape Mendocino (not far from Ettersburg) and an unknown cultivated octoploid ($2n = 56$) that he, by mistake, assumed to be *F. vesca* (diploid 'Alpine', $2n = 14$). This important hybrid was 'Ettersburg 121'.

In commenting about the great vigor of 'Ettersburg 121', Etter (1919) said,

"In general, it would seem to favor poor land to do its best. I have seen 121's growing on land too poor to grow wild grass and weeds, and producing bountiful yields while in the same climate and locality where they were on rich land they simply indulged in riotous living and did nothing worthwhile."

We note that great or even excessive vigor is typical of California *F. chiloensis* cultivar hybrids. 'Ettersburg 121' is the hybrid that was the direct ancestor of 'Lassen', released by Thomas and Goldsmith in 1945. 'Lassen' was characterized by superior adaptation and was the only cultivar of the original five that was derived directly from California *F. chiloensis*.

According to Thomas and Goldsmith (1945), the double-cropping trait was derived for the most part from the 'Nich Ohmer' parentage of the original five cultivars. In this regard, it is worth noting that, of the five originals, only 'Dormer' failed to have the double-cropping trait and that it has the lowest percentage of 'Nich Ohmer' ancestry (Table 5).

'Lassen', the best-adapted of the original five, has the broadest ancestral base (Table 5) and tolerates extreme inbreeding (successful selfing) the best of the five. In contrast, 'Shasta', the other originally successful cultivar of the five, had a relatively narrow ancestral base and tolerates extreme inbreeding the least successfully of all. In fact, it is difficult to impossible to maintain self-pollinated lines of 'Shasta'. They lack vigor to the point that they tend to die in the second generation.

Bringhurst and Voth bred the successful cultivars that have subsequently replaced 'Lassen' and 'Shasta' in California, starting with 'Fresno' and 'Tioga' and continuing successively through 'Douglas', 'Pajaro', 'Chandler', and 'Selva' (Table 6).

'Lassen' has been the most important ancestral cultivar in the development of these California-bred cultivars, apparently stabilizing at $\approx 20\%$ to 25% of the ancestry (Table 7). 'Shasta' has been a relatively poor ancestor and the only reason it appears in the

Table 3. Production, hectareage, and yield of the 20 leading strawberry-producing states in 1949-1954 (Federal-State Market News Service, 1956).

State	U.S. strawberry production					
	Crop		Area		Yield	
	%	Rank	%	Rank	t·ha ⁻¹	Rank
California	27.4	1	6.5	7	15.5	1
Oregon	12.3	2	12.6	1	3.7	5
Washington	8.1	3	6.9	6	4.4	2
Michigan	7.8	4	7.6	5	3.8	4
Louisiana	5.8	5	9.0	3	2.6	14
Arkansas	5.5	6	11.0	2	1.8	20
Tennessee	5.0	7	7.8	4	2.3	16
New York	3.5	8	3.3	12	4.0	3
Florida	2.5	9	3.7	8	2.5	15
Virginia	2.2	10	3.5	10	2.6	13
New Jersey	2.2	11	2.4	13	3.5	6
Missouri	2.0	12	3.6	9	2.1	19
Kentucky	2.0	13	3.5	11	2.1	18
North Carolina	1.4	14	1.8	15	2.8	11
Ohio	1.3	15	1.7	16	2.9	9
Maryland	1.2	16	1.4	19	3.3	8
Wisconsin	1.2	17	1.4	20	3.3	7
Oklahoma	1.1	18	2.0	14	2.2	17
Indiana	1.1	19	1.4	18	2.9	10
Pennsylvania	1.0	20	1.5	17	2.7	12
Total	94.6		92.6		Mean 2.9 ^a	

^aDoes not include California.

Table 4. Production, hectareage, and yield for the commercial U.S. strawberry-producing states in 1987 (Federal-State Market News Service, 1987).

State	U.S. strawberry production					
	Crop		Area		Yield	
	%	Rank	%	Rank	t·ha ⁻¹	Rank
California	74.0	1	37.7	1	54.9	1
Florida	9.9	2	11.0	3	25.1	2
Oregon	8.4	3	17.5	2	13.4	3
Washington	2.2	4	5.6	5	10.7	4
New York	1.4	5	6.3	4	6.3	7
Michigan	1.2	6	4.9	6	6.7	6
Ohio	0.7	7	3.1	8	5.8	9
Pennsylvania	0.5	8	2.9	9	4.7	11
North Carolina	0.4	9	4.7	7	2.5	13
Wisconsin	0.4	10	2.6	10	4.0	12
Louisiana	0.4	11	1.3	12	8.1	5
New Jersey	0.4	12	1.8	11	5.8	8
Arkansas	>0.1	13	0.4	13	5.6	10
Mean					6.6 ^a	

^aDoes not include California and Florida.

Table 5. Ancestry of the original Univ. of California cultivars, given in percentages.

Ancestor	Cultivar				
	Lassen	Shasta	Donner	Sierra	Tahoe
	Percent				
Nich Ohmer	25.0	25.0	12.5	50.0	25.0
Howard 17	18.7	37.5	12.5	25.0	---
Marshall ^a	18.7	6.2	25.0	6.3	12.5
Missionary	12.5	---	6.2	---	---
Fendall	9.4	---	---	---	---
Royal Sovereign	6.3	31.3	6.2	18.7	---
<i>F. chiloensis</i>	4.7	---	---	---	---
Redheart	---	---	25.0	---	---
Narcissa	---	---	---	---	50.0
Unknown	4.7	---	12.5	---	12.5

^aIncludes 'Banner' as 'Marshall'.

Table 6. Important or potentially important Univ. of California strawberry cultivars, type—day-neutral (D-N) or short-day (S-D) and period of use.

Cultivar	Type	Parent		Use period
		Female	Male	
<i>Bred by Thomas and Goldsmith, Dept. of Plant Pathology, Berkeley, 1929-45</i>				
Lassen	S-D	CA21-9	CA161-1	1945-64
Shasta	S-D	CA67-5	CA177-21	1945-74
<i>Bred by Bringhurst and Voth, Dept. of Pomology, Davis, 1953-present</i>				
Fresno	S-D	Lassen	CA42.8-16	1961-78
Tioga	S-D	Lassen	CA42.8-16	1964-84
Tufts	S-D	CA46.5-1	Tioga	1972-84
Aiko	S-D	CA46.5-1	CA59.51-11	1975-88
Douglas	S-D	Tufts	CA64.57-108	1979-present
Pajaro	S-D	CA63.7-101	Sequoia	1979-present
Chandler	S-D	Douglas	CA72.361-105	1983-present
Parker	S-D	Douglas	CA71.98-605	1983-present
Selva	D-N	CA70.3-117	CA71.98-605	1983-present
Muir	D-N	CA70.3-117	CA71.98-605	1987-present
Oso Grande	S-D	Parker	CA77.3-603	1987-present
Irvine	D-N	Muir	Douglas	1988-present

Table 7. 'Lassen', 'Shasta', and *F. virginiana glauca* ancestry of second group of important Univ. of California short-day-type cultivars and first group of day-neutrals.

Cultivar	Seed (year)	Release (year)	Ancestry (%)		
			Lassen	Shasta	<i>F. virginia glauca</i>
Short-day					
Tioga	1953	1964	50.0	0	0
Tufts	1963	1972	25.0	0	0
Aiko	1963	1975	31.2	0	0
Pajaro	1971	1979	12.2	0	0
Douglas	1972	1979	31.2	0	0
Chandler	1977	1983	25.0	0	0
Parker	1977	1983	21.9	0	0
Oso Grande	1981	1987	26.6	0	0
Day-neutral					
Fern	1972	1983	15.6	3.1	3.1
Selva	1975	1983	14.1	3.1	3.1
Muir	1975	1987	14.1	3.1	3.1
Mrak	1975	1987	17.2	3.1	3.1
Yolo	1975	1987	7.8	3.1	3.1
Irvine	1982	1988	22.7	1.6	1.6
Seascape	1983	1989	22.7	1.6	1.6
Capitola	1983	1989	23.8	1.6	1.6

pedigrees at all is because it was used in the original hybridization with *F. virginiana glauca* that gave rise to the California day-neutral cultivars presently in use or under test, principally 'Selva'. It is unlikely that further infusions of 'Shasta'-derived genes will occur. They are systematically being eliminated at the same rate as those from *F. virginiana glauca*.

Much of the statement cited above (Hedrick, 1925) is now obsolete because of the success of the Univ. of California Strawberry Breeding Program. The effect of this program has been felt world-wide, because the California cultivars now dominate production in subtropical and even tropical areas wherever strawberries are grown. Furthermore, it is likely that progress in breeding will continue in the Univ. of California program. Gains in morphological and physiological traits, including yield, fruit quality, and disease and pest resistance, are anticipated (Bringhurst and Voth, 1989).

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