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INBREEDING AND HETEROSIS AND THEIR RELATION TO THE DEVELOPMENT OF NEW
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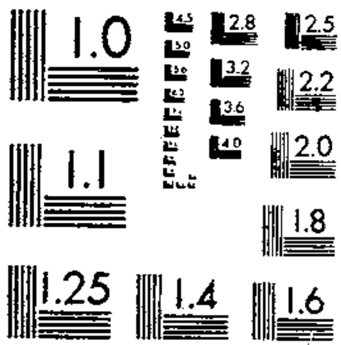

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Inbreeding and Heterosis and Their Relation to the Development of New Varieties of Onions[1]

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CONTENTS

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CROSSING INBRED AND MALE-STERILE LINES TO DEVELOP BETTER ONIONS

Onion (*Allium cepa* L.) is one of the oldest cultivated crops, but little has been known about its breeding behavior. In 1922, breeding studies were begun by the California Agricultural Experiment Station, and in 1936 the work was established on a cooperative basis between that station and the United States Department of Agriculture as a part of its cooperative onion-breeding program with various States. The objective of this program is the development of resistant high-yielding varieties adapted to certain regions and for certain purposes. New breeding methods have been developed to facilitate pollination, and inbreeding has been conducted to determine its influence on vigor and to isolate good homozygous lines for use in breeding. These lines have been used to introduce valuable genes into commercial varieties and to determine their value in the production of hybrid seed.

Shortly after the breeding program was begun in this country Kotowski (*7*)[2] published the results of his study of the effects of one generation of inbreeding on onions. He found that bulbs from open-pollinated seed averaged 137 gm. in weight, whereas those from selfed seed of the same plant averaged only 120 gm. Subsequent analysis of these data by the authors of this paper revealed that the difference was highly significant.

In 1937 Jones and Emsweller (*5*) presented preliminary data comparing bulb yields of hybrids and parents when a male-sterile clonal line of Italian Red 13–53 and various male-fertile varieties were used. In most crosses the mean weight of the hybrid bulbs was much greater than that of either parent. The percentage of hybrid plants bolting was much less than that of those of the pollen parent. These studies on hybrid vigor have been continued, and the results obtained are presented as part of this bulletin.

In further studies with this male-sterile line of Italian Red 13–53, Jones and Clarke (*2*) observed that when it was crossed with male-fertile plants three types of breeding behavior were present in the F_1, some progenies being entirely male-fertile, others being entirely male-sterile, and others producing both male-fertile and male-sterile in a ratio of 1 to 1. This type of behavior was explained by assuming that the male-sterile condition results from an interaction between a recessive nuclear gene and a nonnuclear, or cytoplasmic, factor.

The results of the studies reported in this bulletin may be summarized as follows:

From 1922 to 1934 six varieties of onions were inbred one to six generations. Some years certain inbred lines yielded as much as the commercial parent, but in general weight became less with inbreeding. Usually the loss in weight was greatest in the first generation of inbreeding. Many inbred lines of onions that were superior to the commercial parent in many characters except vigor were isolated. These characters included bolting habit, keeping quality, and uniformity of size, shape, and color. These results indicate that the probability of developing good high-yielding commercial lines by inbreeding is remote, but that superior lines can be isolated for hybridization purposes.

Vigor of onions can often be greatly increased by crossing male-fertile inbreds, but quantity production is not feasible because of the necessity of emasculation.

A male-sterile clonal line of Italian Red 13–53 has been used experi-

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[2] Italic numbers in parentheses refer to Literature Cited, p. 28.

mentally as the female parent in crosses with various male-fertile inbred varieties. Its use in the production of hybrid seed, however, is rather limited. Some of the hybrids were more vigorous and bolted less than the pollen parent. The hybrid Italian Red 13-53 × Lord Howe Island has been introduced as California Hybrid Red No. 1 by the California Agricultural Experiment Station and the United States Department of Agriculture.

By backcrossing, the male-sterile character of Italian Red 13-53 has been incorporated into a number of commercial varieties so that this character can be perpetuated in the seed. Backcross populations of crosses between male-sterile and certain male-fertile lines are always 100 percent male-sterile. The latter can be used in combination with desirable pollen parents for the production of hybrid seed.

WHAT GROWERS SHOULD KNOW ABOUT ONION INBREDS AND HYBRIDS

The results of inbreeding show that in general a gradual loss of vigor is to be expected with inbreeding and that the chances of obtaining improved varieties from inbreeding alone are rather remote. Methods of improvement that increase rather than decrease vigor must be adopted.

In the production of hybrid seed inbreeding becomes an integral part of the program. As a rule most lines are sufficiently uniform after two generations of inbreeding, but if inbreeding is continued, most of the lines become rather weak and are difficult to propagate. This is especially true of white varieties. After about two generations of inbreeding the plants can be massed to prevent further loss of vigor.

Crosses between male-fertile inbred onion varieties usually showed greatly increased vigor when compared with the parents and great uniformity in size, shape, and color of the bulbs and in many other characters. These crosses between male-fertile plants showed great inherent possibilities in the production of hybrid seed. However, as emasculation is necessary, quantity production of hybrid seed from crossing male-fertile varieties is not practicable.

The disadvantage of emasculation is not present when a male-sterile line, such as Italian Red 13-53, is available as a female parent. This male-sterile clonal line, which is increased by bulbils produced in the seed head, is now being used to a limited extent in the production of hybrid seed. Its use, however, is limited to the production of mild red types. Being a poor storage onion, it cannot be used in the production of hybrid seed of the storage types.

The male-sterile character found in Italian Red 13-53 has now been incorporated in practically all important commercial varieties and is perpetuated through the seed rather than in clones. This not only makes possible the combining of those lines that are resistant to the attack of various insects and diseases but also provides a method of obtaining the expression of the maximum amount of vigor. The production of hybrid seed opens up an almost unlimited field for the production of improved onion varieties.

MATERIALS AND METHODS

The varieties of onions used most in the early studies on inbreeding and hybridization were those important in California, although some attention was given to most of the commercial varieties. Most of the varieties have been characterized recently by Magruder and others (*8*). The intermediate varieties, such as Red 21 (California Early Red), Stockton Yellow Globe, and Italian Red, were used extensively. These are called intermediate because they mature after the early varieties and before the late ones. Because of its importance in California, Australian Brown was the chief storage variety used. At the time these studies were begun Yellow Danvers Flat was being used as a dry set variety, but in recent years it has been replaced almost entirely by Ebenezer. The yellow globe types, as well as Sweet Spanish, were also used to some extent. The early varieties used were Early Grano, Lord Howe Island, Yellow Bermuda, and Crystal Wax. The male-sterile clonal line Italian Red 13–53 has been used very extensively in the development of male-sterile lines for the production of hybrid seed. It has also been used in breeding for resistance to downy mildew, caused by *Peronospora destructor* (Berk.) Casp. (*6*), and to purple blotch, caused by *Alternaria porri* (Ell.) Cif.

The methods for selfing described by Jones and Emsweller (*3, 4*) were modified from time to time as better techniques were developed. In the earlier years self-pollination was accomplished chiefly by enclosing the flower head in a manila paper bag and tapping it once or twice each day to distribute pollen. This method, however, did not always provide sufficient quantities of seed for testing; so in recent years all selfing has been done by the use of flies. In the greenhouse at Beltsville, Md., single heads to be self-pollinated were enclosed in 2-pound permeable cellophane bags. When two or more heads of a plant were used they were enclosed in small cloth cages. Flies were added to do the pollinating in both the cellophane bags and the cloth cages. The latter, however, have proved to be more satisfactory in the greenhouses at Beltsville and are now being used almost exclusively.

Most first-generation inbred lines were discarded because of various defects. The data on inbreeding included herein were obtained from lines that had been rather rigidly selected as breeding parents or as potential varieties.

In the earlier studies on hybrid vigor the male-sterile character was not available, and crosses were made between self-fertile varieties. Emasculation was not practiced, but the plants to be crossed were grown under cloth cages with flies introduced to do the crossing. When this method was used considerable selfing occurred, but the hybrids could be recognized when the bulbs matured. In later crosses between self-fertile varieties, however, the flowers were emasculated, and consequently the hybrid and selfed seed could be planted separately. A limited supply of hybrid seed was also obtained by enclosing the male-sterile clonal line Italian Red 13–53 under cloth cages with male-fertile plants and later by alternating rows of male-sterile and male-fertile plants in the open.

The intermediate varieties were seeded in a field nursery at Davis, Calif., in late August or early September, and the seedlings were transplanted in the late fall or early winter. Early varieties were usually seeded at the same time or somewhat later than the intermediate ones. Late or storage varieties were usually seeded in coldframes in November or December and transplanted in early spring. In 1929 the late types were seeded directly in the field, but that was the only year when this procedure was followed because it prevented the economical use of small quantities of seed and made impossible a uniform spacing of plants in the row.

On sedimentary soils requiring surface irrigation the plants were usually set on raised beds. These were 3 feet from center to center, and the two rows on the bed were 12 inches apart. On subirrigated muck soils where level cultivation was practiced the rows were spaced 15 inches apart. The large-bulb types, such as Red 21, Italian Red, Stockton Yellow Globe, and Sweet Spanish, were spaced 4 inches apart in the row. The smaller varieties, such as Yellow Danvers Flat and Australian Brown, were spaced 3 inches apart. Irrigation was usually necessary during the late spring and summer.

The system of pedigree numbering is one commonly used. The first number of a pedigree indicates the variety; for example, the number 13 was assigned to Italian Red. The pedigree 13–52–9–6–S_2 denotes five generations of inbreeding. The second number indicates that it was the fifty-second plant of the original lot selected for inbreeding; the third number indicates that it was the ninth plant of the 13–52 inbred population selected for further inbreeding; the fourth number indicates that it was the sixth plant of the 13–52–9 inbred population selected for further inbreeding. To avoid long pedigrees the number of selfings after three generations is indicated by S and a subnumeral. When selected bulbs of an inbred line were massed for seed increase the letter m was inserted after the pedigree.

The bulb weights of inbred lines and hybrids were usually compared by intermingling, planting in adjacent rows, or planting in replicated plots and weighing the bulbs individually. In order to obtain sufficient seed for four or five replicates for yield tests the best individuals of an inbred population were usually massed under cloth cages. This massed seed is consequently not a true inbred line but is simply the result of interpollinations within an inbred population. At first the plots for the yield tests were replicated systematically, but in later years they were randomized. Besides transplants, dry sets of the Yellow Danvers Flat variety were also used for planting the plots to compare the vigor of inbred lines and the commercial parent. Dry sets were grown at Davis, Calif. They were harvested, stored, and graded to a uniform size, and at planting they were set in shallow furrows. Spacing was the same as for green seedlings.

Onion bulbs were always stored in shallow slat-bottom trays in a warehouse where the storage conditions fluctuated with the weather.

The standard errors of the coefficients of variability were calculated from the tables published by Brown (*1*).

EFFECTS OF INBREEDING ON VARIOUS CHARACTERS

Bulb Weight and Yield

YELLOW DANVERS FLAT

Plants of the Yellow Danvers Flat variety of onion were selfed in 1923, and the progenies were grown in 1924. Line 1–10 was one of the best; the 337 bulbs had a mean weight of 32.9 gm. Another line, 1–22, had a population of 383 bulbs with a mean weight of 29.7 gm. A number of the best bulbs of these two lines were selected and selfed in 1925, and the progenies were grown in 1926. Line 1–10–25 produced the heaviest bulbs (table 1). Most of the lines derived from 1–10 had heavier bulbs than those from 1–22, and the difference in the mean weight per bulb between the two groups was highly significant. Inbreeding was continued for six generations, and comparisons were made among the inbreds and with the commercial strain from which the original selections were made.

In 1930 and 1931 commercial Yellow Danvers Flat was grown from transplants for comparison with five lines of 1–10 and with three others from this same variety (table 2). As indicated, all these lines had been

TABLE 1.—*Mean weight per bulb and percentage sprouted during storage of inbred lines of Yellow Danvers Flat, Davis, Calif., 1926*

Line	Bulbs stored	Mean weight per bulb	Bulbs sprouted (Dec. 12)	Line	Bulbs stored	Mean weight per bulb	Bulbs sprouted (Dec. 12)
	Number	*Grams*	*Percent*		*Number*	*Grams*	*Percent*
1-10-3...	101	46.5	15.8	1-22-1...	113	50.8	81.4
1-10-4...	247	61.0	26.7	1-22-3...	75	39.4	93.3
1-10-5...	58	72.2	19.0	1-22-6...	220	24.4	65.9
1-10-7...	243	76.4	39.3	1-22-7...	77	33.3	94.8
1-10-8...	241	75.5	51.0	1-22-9...	159	32.1	71.1
1-10-9...	199	70.4	47.2	1-22-11..	90	26.3	73.3
1-10-10..	236	66.2	26.2	1-22-12..	50	31.2	86.0
1-10-11..	210	43.2	33.8	1-22-19..	211	28.5	93.3
1-10-13..	193	50.6	34.2	1-22-20..	211	31.3	100.0
1-10-15..	93	70.3	47.1	1-22-22..	48	24.4	100.0
1-10-17..	119	59.3	3.4	1-22-26..	46	40.5	100.0
1-10-23..	54	54.6	40.7	1-22-30..	52	35.3	82.7
1-10-24..	288	62.6	84.4	1-22-32..	134	40.2	98.5
1-10-25..	420	91.3	21.8	1-22-33..	104	50.2	69.2
1-10-26..	482	61.6	5.8				
Mean..	....	64.1 ± 12.6	33.1 ± 20.3	Mean..	....	35.3 ± 8.9	86.4 ± 12.5

TABLE 2.—*Mean weight per bulb of commercial and inbred lines of Yellow Danvers Flat grown from transplants, Davis, Calif., 1930 and 1931*

Line	Generations inbred	1930		1931	
		Bulbs per plot	Mean weight per bulb	Bulbs per plot	Mean weight per bulb
	Number	*Number*	*Grams*	*Number*	*Grams*
Commercial	0	104	158	104	66
1-10-26m	2	102	177	105	78
1-10-25m	2	103	144	104	64
1-10-25-17m	3	103	124	105	55
1-10-4m	2	104	128	103	62
1-10-4-2m	3	106	96	106	53
1-24-15-2m	3	104	106	87	36
1-16-7-4m	3	100	93	102	46
1-14-10-1m	3	102	82	103	40
Difference required for significance:					
5-percent level	.	(1)	20	5.7	7.5
1-percent level	.	(1)	27	7.6	10.1

[1] No significant difference.

inbred two or three generations and then massed. In both years 1-10-26m was heavier than the commercial parent. In 1930 the difference was not significant, but in 1931 it was highly significant. Plant 1-10-26 evidently had a combination of very favorable growth factors, so that when it was selfed and the best bulbs of the inbred population were mass-pollinated the vigor surpassed that of the parent variety. The mean bulb weight of 1-10-25m was below that of the commercial in both 1930 and 1931, but in neither year was the difference significant. When 1-10-25 and 1-10-4 were inbred another generation a considerable reduction in vigor occurred. All bulb weights were considerably smaller in 1931 than in 1930, owing primarily to a very severe thrips attack.

In 1931, when the same lines of Yellow Danvers Flat were grown from dry sets (table 3), the bulb sizes were considerably larger than when they were grown from transplants. Line 1-10-26m again had much heavier bulbs than the commercial parent. There was no significant difference in weight of bulb between lines 1-10-25m and 1-10-25-17m, which had been inbred two and three generations, respectively, but there was a

TABLE 3.—*Comparison of commercial and inbred lines of Yellow Danvers Flat grown from dry sets, Davis, Calif., 1931*

Line	Generations inbred	Dry sets planted per plot	Plants per plot	Bolters per plot	Mean weight per bulb
	Number	*Grams*	*Number*	*Percent*	*Grams*
Commercial	0	287	101	48.7	140
1–10–26m	2	294	89	9.7	188
1–10–25m	2	297	88	9.0	134
1–10–25–17m	3	291	88	8.7	130
1–10–4m	2	294	98	15.3	134
1–10–4–2m	3	295	81	8.3	99
1–14–10–1m	3	298	98	31.3	104
1–16–7–4m	3	285	100	86.3	92
1–24–15–2m	3	293	85	4.0	65
Difference required for significance:					
5-percent level	.	(1)	(1)	6.4	28
1-percent level	.	(1)	(1)	8.8	38

[1] No significant difference.

significant difference in mean weight of bulb between 1–10–4m and 1–10–4–2m. In 1931, 1–24–15–2m produced the smallest bulbs—grown from transplants or from dry sets.

In 1932 a number of comparisons of bulb weights were made between lines inbred two to five generations and between certain of these inbred lines and the commercial variety (table 4). As in preceding years, 1–10–4m showed considerable loss in weight from two generations of inbreeding. When 1–10–4 was inbred three more generations one of the lines showed a highly significant loss in weight of bulb while the other did not. Bulbs of 1–10–25–17m weighed considerably less than those of 1–10–25m. When they were still further inbred, loss of weight continued; it was significant between the third and fourth generations and highly significant between the fourth and fifth. Bulbs of 1–10–11–2–S_2 weighed only about one-half as much as those of commercial. Bulbs of 1–10–26–7–S_2 weighed approximately one-half as much as those of 1–10–26m.

TABLE 4.—*Mean weight per bulb of commercial and inbred lines of Yellow Danvers Flat, Davis, Calif., 1932*

Line	Generations inbred	Bulbs weighed	Mean weight per bulb	Coefficient of variation
	Number	*Number*	*Grams*	*Percent*
Commercial	0	205	132 ± 3.1	33.8 ± 1.9
1–10–4m	2	196	**114 ± 3.0	37.4 ± 2.1
1–10–4m	2	196	111 ± 3.0	37.4 ± 2.1
1–10–4–4–S_2[1]	5	207	** 96 ± 2.2	34.0 ± 1.9
1–10–4–4–S_2[1]	5	201	106 ± 2.7	35.4 ± 2.0
1–10–25m	2	103	142 ± 4.5	32.2 ± 2.5
1–10–25–17m	3	102	*103 ± 2.8	26.4 ± 2.0
1–10–25–17m	3	102	109 ± 2.8	26.4 ± 2.0
1–10–25–17–S_1m	4	98	* 98 ± 3.2	32.9 ± 2.6
1–10–25–17–S_1m	4	98	98 ± 3.2	32.9 ± 2.6
1–10–25–17–S_2[1]	5	37	** 77 ± 3.3	26.0 ± 3.2
1–10–25–17–S_2[1]	5	83	** 83 ± 3.4	23.9 ± 3.1
Commercial	0	88	139 ± 6.5	44.0 ± 3.9
1–10–11–2–S_2	5	82	** 67 ± 3.2	43.4 ± 4.0
1–10–26m	2	103	128 ± 5.1	40.7 ± 3.3
1–10–26–7–S_2	5	105	** 68 ± 2.9	43.2 ± 3.5

* Significantly different from parent line or variety at 5-percent level.
** Significantly different from parent line or variety at 1-percent level.
[1] Sib lines.

In 1934, comparisons were made between commercial Yellow Danvers Flat and lines inbred two, three, five, and six generations (table 5). The data seem to show loss of vigor with each additional one or two generations of inbreeding, but as there was only one plot of each of the inbred lines it was impossible to determine whether or not the differences were significant.

TABLE 5.—*Mean weight per bulb of commercial and inbred lines of Yellow Danvers Flat, Davis, Calif., 1934*

Line	Generations inbred	Replicates	Bulbs per plot	Mean weight per bulb
	Number	*Number*	*Number*	*Grams*
Commercial	0	10	98	65.5
1-10-25m	2	1	98	58.4
1-10-25-17m	3	1	101	39.5
1-10-25-17-S_2m	5	1	88	38.6
1-10-25-17-S_3	6	1	100	37.4

EBENEZER

In 1930 three lines of Ebenezer which had been selfed one generation and another which had been selfed two generations were compared with two commercial strains of this variety (table 6). The inbred lines were lower yielding than the commercial, but the difference between 11-6-3m and the lower yielding commercial was not significant.

TABLE 6.—*Mean weight per bulb, yield per acre, and percentage of bulbs sprouted during storage of commercial and inbred lines of Ebenezer, Davis, Calif., 1930*

Line	Field data			Storage results	
	Bulbs per plot	Mean weight	Yield	Bulbs stored	Bulbs sprouted
	Number	*Grams*	*100-pound sacks*	*Number*	*Percent*
Commercial	106	126	313	530	18.9
Do	106	132	331	530	11.5
11-6-3m	101	124	307	521	4.6
11-208m	102	119	287	481	23.1
11-145m	101	98	241	518	5.2
11-216m	100	94	223	499	3.0
Difference required for significance:					
5-percent level	(1)	11.6	29.0	....	....
1-percent level	(1)	15.9	39.6	....	....

[1] No significant difference.

YELLOW GLOBE DANVERS

In 1929 and 1930 three commercial strains of Yellow Globe Danvers were compared with various lines inbred one and two generations (table 7). In 1929 the three commercial strains were about alike in weight of bulb and yield per acre, but in 1930 strain *a* was significantly higher yielding than the other commercial strains. Both years line 15-8m had the heaviest bulbs of the inbreds. In 1930 a significant difference in weight per bulb and yield per acre occurred between 15-8m and 15-8-2m. All inbred lines produced lower yields than the commercial strains. In some cases the differences were barely significant; in others, highly significant.

TABLE 7.—*Mean weight per bulb and yield per acre of commercial and inbred lines of Yellow Globe Danvers, Davis, Calif., 1929 and 1930*

Line	Generations inbred	1929			1930		
		Bulbs per plot	Mean weight	Yield	Bulbs per plot	Mean weight	Yield
	Number	*Number*	*Grams*	*100-pound sacks*	*Number*	*Grams*	*100-pound sacks*
Commercial *a*	0	93	151	331	102	166	402
Commercial *b*	0	90	118	317	99	157	368
Commercial *c*	0	89	150	316	105	148	366
15–8m	1	87	131	274	101	130	311
15–8–2m	2	...	...	...	101	111	266
15–68m	1	86	115	231	94	98	218
15–24–4m	2	92	103	221	98	103	238
15–83–3m	2	92	84	183	...	...	...
15–152–3m	2	...	...	...	104	108	266
Difference required for significance:							
5-percent level	.	(1)	15	37	5	13	31
1-percent level	.	(1)	20	50	7	17	41

[1] No significant difference.

The various lines alined themselves somewhat differently for mean weight per bulb and yield per acre. This is to be expected, since the order of arrangement for bulb weight depends upon one variable, while that for yield per acre depends upon two variables—stand and mean weight per bulb. Since reduced stand probably resulted from inherent weaknesses it may be assumed that yield per acre represents the better index of performance.

In 1931 the same three commercial strains were planted with four lines inbred one generation, four lines inbred two generations, and one line inbred three generations (table 8). The commercials did not vary significantly among themselves in mean weight per bulb or yield per acre. The mean bulb weight of line 15–24m was significantly lower than that of commercial *c* but not than that of *a* or *b*. The bulb weight of line 15–27m was significantly lower than that of commercial *a* and *c* but not than that of *b*. When 15–24 was inbred another generation a significant reduction in bulb weight occurred; 15–27 also lost vigor with two additional generations of inbreeding.

TABLE 8.—*Mean weight per bulb and yield per acre of commercial and inbred lines of Yellow Globe Danvers, Davis, Calif., 1931*

Line	Generations inbred	Bulbs per plot	Mean weight	Yield
	Number	*Number*	*Grams*	*100-pound sacks*
Commercial *a*	0	100	58	137
Commercial *b*	0	103	56	137
Commercial *c*	0	105	61	153
15–8m	1	104	48	119
15–68m	1	93	49	109
15–24m	1	103	52	126
15–24–3m	2	107	39	99
15–24–4m	2	101	44	107
15–27m	1	100	50	118
15–27–5–2m	3	99	43	101
15–83–3m	2	98	44	102
15–108–1m	2	106	46	115
Difference required for significance:				
5-percent level	.	6	7	19
1-percent level	.	8	10	26

AUSTRALIAN BROWN

In 1929 and 1930 three commercial strains of Australian Brown were compared with lines that had been inbred one and two generations (table 9). In 1929 the seed was sown directly in the field in early winter. The poor stands of most of the inbred lines show that they gave poor germination or were not able to withstand the rigors of winter. All the inbred lines except 5–34m were greatly reduced in weight of bulb. This line, however, was not significantly different from any of the commercial strains. In 1930, 5–34m again had the heaviest bulbs of the inbred lines, but they were significantly lighter than those of commercial *b*. Better stands and

TABLE 9.—*Mean weight per bulb and yield per acre of commercial and inbred lines of Australian Brown, Davis, Calif., 1929 and 1930*

Line	Generations inbred	1929		1930		
		Bulbs per plot	Mean weight	Bulbs per plot	Mean weight	Yield
	Number	*Number*	*Grams*	*Number*	*Grams*	*100-pound sacks*
Commercial *a*	0	98	158	106	151	379
Commercial *b*	0	96	139	102	170	413
Commercial *c*	0	101	154	106	158	397
5–34m	1	106	146	99	151	355
5–34–2m	2	99	119	100	122	289
5–31m	1	101	112	105	114	282
5–93m	1	.....	.....	108	107	262
5–87m	1	.....	.....	96	90	205
5–20–2m	2	64	113	102	122	294
5–20–1m	2	87	102	97	104	241
5–23–1m	2	60	93	.....	.....	.....
5–33–3m	2	88	92	.....	.....	.....
5–47–4m	2	60	77	.....	.....	.....
5–33–3m	2	81	59	.....	.....	.....
5–111–13m	2	.....	.....	98	75	174
Difference required for significance:						
5-percent level		13.8	19.1	4.6	15.6	38.0
1-percent level		18.4	25.5	6.2	21.0	51.1

TABLE 10.—*Mean weight per bulb and yield per acre of commercial and inbred lines of Australian Brown, Davis, Calif., 1931*

Line	Generations inbred	Bulbs per plot	Mean weight	Yield
	Number	*Number*	*Grams*	*100-pound sacks*
Commercial *a*	0	104	47.8	117
Commercial *b*	0	105	46.0	115
Commercial *c*	0	102	44.0	108
5–34m	1	105	56.3	141
5–34–2m	2	102	45.2	108
5–24m	1	104	55.2	137
5–24–1m	2	104	45.8	113
5–107m	1	104	43.8	108
5–23–1m	2	103	41.8	102
5–32–2m	2	107	40.5	103
5–31m	1	104	40.2	99
5–93m	1	101	39.2	93
5–87m	1	97	31.8	80
5–22m	1	105	32.8	81
5–46m	1	98	27.2	63
5–111–13m	2	94	26.0	58
5–111–10m	2	90	23.0	49
Difference required for significance:				
5-percent level		4.9	6.2	16.6
1-percent level		6.5	8.2	22.1

heavier bulbs made two of the commercial strains significantly higher yielding than 5–34m. Line 5–87m inbred one generation was lower yielding than other lines inbred two generations.

In 1931 the same three commercial strains of Australian Brown were compared with eight lines inbred one generation and six lines inbred two generations (table 10). Line 5–34m produced the heaviest bulbs and highest yield per acre, and when it was compared with the highest yielding commercial strain the differences in bulb weight and yield per acre were highly significant. The bulb weight and yield per acre of 5–24m were also significantly higher than any of the commercial strains. Plants 5–34 and 5–24 no doubt carried a very favorable combination of growth factors. The vigor of both of these lines was greatly reduced, however, when inbred another generation, as is shown by the performance of 5–34–2m and 5–24–1m. In each case the difference in mean weight of bulb between the one- and two-generation inbreds was highly significant.

ITALIAN RED

In 1930 four lines of Italian Red that had been inbred three generations and another line that had been inbred two generations were compared with the commercial parent (table 11). Three of these lines were not significantly different from the parent variety in weight of bulb, but the weights of two were lighter. In all five comparisons the commercial parent was the same, but the data could not be averaged because a separate plot was used for each comparison.

TABLE 11.—*Mean weight per bulb of commercial and inbred lines of Italian Red, Davis, Calif., 1930*

Line	Generations inbred	Bulbs weighed	Mean weight	Coefficient of variation
	Number	*Number*	*Grams*	*Percent*
Commercial	0	77	325 ± 17.2	46.4 ± 4.5
13–20–3–4	3	121	351 ± 8.0	21.9 ± 1.7
Commercial	0	97	358 ± 17.2	47.4 ± 4.1
13–52–9–6	3	93	359 ± 15.6	42.0 ± 3.6
Commercial	0	81	341 ± 19.1	50.5 ± 4.9
13–20–3–16	3	69	303 ± 14.0	38.3 ± 3.7
Commercial	0	101	361 ± 13.7	37.9 ± 3.0
13–20–3–13	3	47	**270 ± 10.0	28.3 ± 3.2
Commercial	0	96	249 ± 12.2	48.0 ± 4.2
13–5–4m	2	100	**157 ± 7.2	45.5 ± 3.8

** Significantly different from commercial at the 1-percent level.

In 1931 commercial Italian Red was compared with 13–5–4m and with 10 sib lines of 13–5–4–1–S_1 (table 12). All inbred lines had lighter bulbs than the commercial, and all but 1 of the differences were significant. The differences in vigor between the commercial strain and inbred lines growing in the field are shown in figure 1.

In 1932 a number of inbred lines of Italian Red were again compared with the commercial parent (table 13). For the third consecutive year the bulb weights of 13–5–4m were significantly lighter than those of the commercial variety. In 1930 (table 11) the line 13–52–9–6 produced bulbs of the same weight as the commercial; in 1932 two of the selections from this line which was inbred five generations produced bulbs that did not differ

FIGURE 1.—*A*, Commercial Italian Red; *B*, Italian Red 13-5-4-1-S_1 selfed four generations; *C*, Italian Red 13-5-4 selfed two generations, Davis, Calif., June 26, 1931.

significantly in weight from the commercial parent. The line 13-20-3m produced bulbs considerably smaller than the original variety, but a selection, 13-20-3-43-S_2, produced bulbs significantly heavier than 13-20-3m and not significantly different from the commercial parent.

TABLE 12.—*Mean weight per bulb and yield per acre of commercial and inbred lines of Italian Red, Davis, Calif., 1931*

Line	Generations inbred	Bulbs per plot	Mean weight	Yield
	Number	*Number*	*Grams*	*100-pound sacks*
Commercial	0	73	250	436
13-5-4m	2	71	197	331
13-5-4-1-S	4	78	221	407
13-5-4-1-S	4	73	201	347
13-5-4-1-S	4	77	192	351
13-5-4-1-S	4	69	180	294
13-5-4-1-S	4	68	176	286
13-5-4-1-S	4	59	175	249
13-5-4-1-S	4	69	171	280
13-5-4-1-S	4	70	168	276
13-5-4-1-S	4	68	147	242
13-5-4-1-S	4	65	126	193
Difference required for significance:				
5-percent level			31	88
1-percent level			46	

[1] Sib lines.
[2] No significant difference.

In 1934 commercial Italian Red was compared with 13-20-3m (table 14), and the latter was compared with five progeny lines that had been inbred six generations. The mean weight per bulb of 13-20-3m was only 53 percent of that of the commercial, whereas in 1932 it was 80 percent. This 13-20-3m line consistently yielded somewhat less than the commercial variety when tested still further. In certain selected lines inbred an additional four generations, vigor was maintained on a level with 13-20-3m; in other cases, however, a considerable reduction occurred. The same seed stock of 13-20-3m was used for all the comparisons shown in table 14.

TABLE 13.—*Mean weight per bulb and yield per acre of commercial and inbred lines of Italian Red, Davis, Calif., 1932*

Line	Generations inbred	Bulbs per plot	Mean weight	Yield
	Number	*Number*	*Grams*	*100-pound sacks*
Commercial	0	64	377	571
13-5-4m	2	62	268	383
13-20-3m	2	69	281	457
13-20-3-43-S_2	5	73	347	599
13-20-3-10-S_2	5	77	221	412
13-52-9-6-S_2[1]	5	71	387	684
13-52-9-6-S_2[1]	5	73	355	618
13-52-9-6-S_2[1]	5	70	305	506
13-52-9-6-S_2[1]	5	69	299	490
13-52-9-6-S_2[1]	5	77	290	532
Difference required for significance:				
5-percent level	.	(2)	64	110
1-percent level	.	(2)	73	162

[1] Sib lines.
[2] No significant difference.

TABLE 14.—*Mean weight per bulb of commercial and inbred lines of Italian Red, Davis, Calif., 1934*

Line	Generations inbred	Bulbs weighed	Mean weight	Coefficient of variation
	Number	*Number*	*Grams*	*Percent*
13-20-3m	2	...	212	....
Commercial	0	...	399	....
13-20-3m	2	74	208 ± 6.67	27.6 ± 2.4
13-20-3-45-S_3	6	79	212 ± 6.37	26.7 ± 2.3
13-20-3m	2	79	210 ± 7.40	31.1 ± 2.7
13-20-3-45-S_3	6	79	*186 ± 5.75	27.5 ± 2.3
13-20-3m	2	76	220 ± 8.10	32.5 ± 2.9
13-20-3-43-S_3	6	77	212 ± 7.03	29.1 ± 2.5
13-20-3m	2	230	213 ± 4.62	32.9 ± 1.7
13-20-3-43-S_3	6	232	**184 ± 2.97	21.4 ± 1.2
13-20-3m	2	77	225 ± 8.78	33.8 ± 3.0
13-20-3-10-S_3	6	74	**156 ± 6.04	36.6 ± 3.4

* Significantly different from 13-20-3m at the 5-percent level.
** Significantly different from 13-20-3m at the 1-percent level.

RED 21 (CALIFORNIA EARLY RED)

The variety Red 21 (*9*) is an inbred line of California Early Red released by the California Agricultural Experiment Station in 1935. The pedigree number 21-22-1m is used in table 15 rather than Red 21, in order to show relationships of two and six inbred generations. It has not been possible to compare these inbred lines with the commercial strain of California Early Red formerly grown in California because seed has not been available for some time, this variety having been replaced by the improved variety Red 21. In 1934, 21-22-1m was compared with 14 of its progenies inbred 6 generations (table 15). In 12 of the 14 comparisons there was either a significant or a highly significant difference in mean weight of bulb between 21-22-1m and the 6-generation inbreds. The fluctuation in bulb weight of 21-22-1m in the different plots is rather striking. No doubt soil variation was partly responsible, but whatever the cause the effect on the 6-generation inbreds was not so pronounced as on 21-22-1m.

Table 15.—*Mean weight per bulb of inbred lines of California Early Red, Davis, Calif., 1934*

Line	Generations inbred	Bulbs weighed	Mean weight	Coefficient of variation
	Number	*Number*	*Grams*	*Percent*
21-22-1m	2	70	162 ± 5.93	30.6 ± 2.8
21-22-1-8-S_5	6	76	157 ± 6.61	36.7 ± 3.4
21-22-1m	2	76	169 ± 5.60	29.9 ± 2.6
21-22-1-8-S_5	6	77	163 ± 6.79	36.5 ± 3.3
21-22-1m	2	78	186 ± 6.86	32.6 ± 2.9
21-22-1-8-S_5	6	78	*166 ± 6.84	36.4 ± 3.3
21-22-1m	2	76	181 ± 7.72	37.2 ± 3.4
21-22-1-8-S_5	6	64	*158 ± 6.67	33.1 ± 3.2
21-22-1m	2	80	193 ± 6.20	28.7 ± 2.4
21-22-1-8-S_5	6	77	*174 ± 7.53	38.0 ± 3.5
21-22-1m	2	77	182 ± 7.17	34.6 ± 3.1
21-22-1-8-S_5	6	75	**149 ± 6.44	38.2 ± 3.5
21-22-1m	2	150	192 ± 5.12	32.7 ± 2.1
21-22-1-8-S_5	6	150	**158 ± 3.46	27.4 ± 1.7
21-22-1m	2	74	193 ± 6.94	30.0 ± 2.8
21-22-1-8-S_5	6	75	**156 ± 5.61	31.1 ± 2.8
21-22-1m	2	77	185 ± 7.47	35.4 ± 3.2
21-22-1-8-S_5	6	77	**143 ± 6.15	37.8 ± 3.5
21-22-1m	2	74	211 ± 6.09	24.8 ± 2.2
21-22-1-8-S_5	6	81	**167 ± 4.23	22.8 ± 1.9
21-22-1m	2	72	240 ± 8.30	29.3 ± 2.6
21-22-1-8-S_5	6	64	**163 ± 6.89	33.7 ± 3.3
21-22-1m	2	153	214 ± 4.59	26.5 ± 1.6
21-22-1-8-S_5	6	123	**147 ± 3.80	28.6 ± 2.0
21-22-1m	2	77	237 ± 6.53	24.2 ± 2.1
21-22-1-8-S_5	6	77	**165 ± 5.52	28.2 ± 2.4
21-22-1m	2	152	234 ± 5.35	28.2 ± 1.7
21-22-1-8-S_5	6	143	**156 ± 3.89	29.0 ± 1.9

* Significantly different from 21-22-1m at the 5-percent level.
** Significantly different from 21-22-1m at the 1-percent level.

MEAN LOSS IN WEIGHT OF BULB FOR ALL VARIETIES TESTED

The pertinent data in tables 2 to 14 have been summarized and presented in table 16 to show the rate of loss in mean weight per bulb with continuous inbreeding. Loss of weight was most pronounced in the first inbred generation, although the lots seem to show the greatest percentage of loss between the fifth and sixth inbred generations. Only a few lines that had been inbred four, five, and six generations were available for comparison. No doubt the rate of loss would be shown to be more regular if there had been a larger number of lines available for comparison.

Table 16.—*Summary table showing loss of vigor with continuous inbreeding*

Generation inbred (number)	Comparisons	Weight in percentage of commercial strain
	Number	*Percent*
0	..	100
1	25	82.6 ± 3.25
2	45	78.2 ± 2.84
3	22	72.0 ± 3.40
4	11	70.4 ± 3.04
5	14	72.0 ± 4.56
6	6	40.0 ± 2.55

Keeping Quality

YELLOW DANVERS FLAT

In 1924 a number of Yellow Danvers Flat lines inbred 1 generation were stored until November 11. Line 1–10, with a population of 337, had 5.6 percent of the bulbs sprouted; line 1–22, with a population of 383, had 23.5 percent of the bulbs sprouted. Line 1–22 started to sprout before 1–10, and at the time of removal from storage the sprouted bulbs had much longer tops. Inbreeding within these lines continued for a number of years, unsprouted bulbs always being selected for planting. Mother bulbs from these 2 lines were selected and set in the field and the plants were selfed in 1925, and progenies were grown in 1926. Fifteen sib lines of 1–10 and 14 sib lines of 1–22 were stored until December 12. A considerable variation in the percentage of sprouting occurred (table 1) among the 1–10 sib lines. Line 1–10–17 had only 3.4 percent of the bulbs sprouted, whereas line 1–10–24 had 84.4 percent sprouted. The mean number of bulbs sprouted for the 1–10 sib lines was 33.1 percent and that for the 1–22 lines, 86.4 percent. From the storage behavior of the progenies the mother bulb 1–10 appears to have been heterozygous for length of the rest period. The 1–22 sib lines sprouted earlier and more uniformly. The difference between the 2 groups was highly significant.

By 1932 some of the progeny lines of 1–10 had been inbred for five generations. These, along with lines inbred two, three, and four generations, were compared with the commercial variety (table 17). A number of these lines were exceptionally good keepers. Line 1–10–13–3 S_2 was especially outstanding over a period of years.

Table 17.—*Percentage of bulbs sprouted during storage of commercial and inbred lines of Yellow Danvers Flat in California, 1932*

Line	Generations inbred	Replicates	Bulbs per replicate	Bulbs sprouted (Dec. 14)
	Number	*Number*	*Number*	*Percent*
Commercial	0	7	95	29.0
1–10–4m	2	3	97	15.5
1–10–4–2m	3	2	105	20.6
1–10–4–4–S_2[1]	5	3	103	26.9
Do[1]	5	3	102	** 6.1
Do[1]	5	3	98	18.7
Do[1]	5	3	102	27.2
1–10–13–3–S_2	5	2	96	** 0
1–10–25m	2	3	100	** 9.0
1–10–25–17m	3	3	101	** 4.5
1–10–25–17–5m	4	3	100	** 3.3
1–10–25–17–S_2	5	3	97	** 9.6
Do[1]	5	2	101	** 1.0
Do[1]	5	2	106	** 1.0
1–10–11–2–S_2[1]	5	3	98	** 9.8
Do[1]	5	4	102	** 9.7
Do[1]	5	2	93	22.6
Do[1]	5	2	91	** 2.2
1–10–25–6–S_2[1]	5	3	104	** 3.6
Do[1]	5	3	104	** 3.2
1–10–25–10–S_2[1]	5	3	104	** 3.5
Do[1]	5	3	106	** 9.8
Do[1]	5	3	107	* 7.5
Do[1]	5	3	105	** 3.8
Do[1]	5	3	105	** 4.1
Do[1]	5	2	102	* 8.7
1–10–25–19–S_2[1]	5	3	103	** 3.6
Do[1]	5	3	101	** 3.3
Do[1]	5	2	105	** 4.0
1–10–25–27–S_2[1]	5	2	104	** 6.7

* Significantly different from commercial at the 5-percent level.
** Significantly different from commercial at the 1-percent level.
[1] Sib lines.

AUSTRALIAN BROWN

In selecting inbred lines of the Australian Brown variety, long-keeping quality is a very important consideration, because this variety is generally used as a late-storage type. Storage data for lines inbred one, two, and three generations for 1925, 1927, and 1929 are presented in table 18. In 1925 the inbred lines 5–21 and 5–22 did not have any of the bulbs sprouted at time of removal from storage on December 12. Selections from these lines inbred two and three generations kept as well as the parent lines in 1927 and 1929. Also, a number of other lines, especially 5–34 and 5–57, had only a small percentage of bulbs sprouting. These data seem to indicate that there is no decrease in keeping quality as a result of inbreeding, because lines inbred two and three generations have kept as well as the first-generation inbreds. On the other hand, certain lines, such as 5–16 and 5–19, and selections from them were consistently poor keepers.

TABLE 18.—*Total shrinkage and percentage of bulbs sprouted during storage of inbred lines of Australian Brown, Davis, Calif., 1925, 1927, and 1929*

1925		1927				1929			
Line No.	Bulbs sprouted, by count (Dec. 12)	Line No.	Number of lines	Bulbs sprouted, by count (Nov. 28)	Total shrinkage in weight (Nov. 28)	Line No.	Number of lines	Bulbs sprouted, by count (Nov. 21)	Total shrinkage in weight (Nov. 21)
	Percent			*Percent*	*Percent*			*Percent*	*Percent*
5–16	16.8	5–16–S_1	9	11.[illegible]	22.6	5–16–S_2	11	7.5	21.2
5–19	5.3	5–19–S_1	3	21.0	36.3	5–19–S_2	11	8.3	16.7
5–20	1.4	5–20–S_1	5	2.4	12.8	5–20–S_2	9	7.2	27.9
5–21	.0	5–21–S_1	3	.0	10.0	5–21–S_2	1	.0	11.8
5–22	.0	5–22–S_1	5	.0	8.0	5–22–S_2	9	.0	14.0
5–23	4.1	5–23–S_1	2	2.7	13.1	5–23–S_2	3	.0	16.2
5–24	4.1	5–24–S_1	6	23.7	33.6	5–24–S_2m	2	6.0	40.5
5–29	22.8	5–29–S_1	5	1.7	19.7	5–29–S_2m	2	2.6	25.1
5–30	3.8	5–30–S_1	4	.0	11.0	5–30–S_2	3	.0	12.3
5–31	4.2	5–31m	1	3.5					
5–32	3.4	5–32–S_1	1	9.2	16.9	5–32–S_2	6	7.0	19.6
5–33	8.2	5–33–S_1	1	7.1	11.1	5–33–S_2	1	3.9	15.5
5–34	.4	5–34–S_1	2	.0	9.4	5–34–S_2	2	1.2	11.5
5–38	4.9	5–38–S_1	7	3.4	21.4	5–38–S_2	14	9.8	24.4
5–47	1.6	5–47–S_1	7	.7	8.9	5–47–S_2	5	6.0	22.6
5–57	.0	5–57–S_1	1	.0	8.6	5–57–S_2	2	1.7	15.8

In determining total shrinkage out of storage, only those bulbs that were neither sprouted nor rotted were weighed. This weight was compared with that of the bulbs when first placed in storage. As a rule, the least shrinkage was in those lines that had the fewest sprouted bulbs (table 18). Unsprouted bulbs lose weight from respiration, loss of moisture, and loss of the outer dry scales. The 5–24–S_1m lines were especially susceptible to fusarium rot, and the large storage losses shown by these lines in 1929 were due chiefly to this organism. Great uniformity in time of sprouting exists in the lines that have been inbred a number of generations.

From 1930 to 1932 the sprouting behavior of a number of inbred lines of Australian Brown was compared with that of the commercial strains (table 19). In 1930 the percentage of bulbs sprouting with the exception of lines 5–24–1m and 5–31m was rather low. The bulbs were removed from storage somewhat sooner in 1930 than in 1931 and 1932; this may account partly for the lower percentage of sprouting. In 1931 the percentage of bulbs sprouting in all the stored lots, with the exception of 5–22m, was very high. This poor keeping quality was due chiefly to the severe thrips attack which prevented the bulbs from maturing properly. Even under these adverse conditions, however, line 5–22m had only 2.4 percent of the bulbs sprouted. In 1932 four of the inbred lines had a smaller percentage of bulbs sprouting than the best of the commercial strains. It will be noted that certain lines were consistently good keepers.

Table 19.—*Percentage of bulbs sprouted during storage of commercial and inbred lines of Australian Brown, Davis, Calif., 1930–32*

Line	1930		1931		1932	
	Bulbs stored	Bulbs sprouted (Nov. 28)	Bulbs stored	Bulbs sprouted (Dec. 18)	Bulbs stored	Bulbs sprouted (Dec. 20)
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Commercial *a*	731	1.5	301	41.2	235	17.4
Commercial *b*	718	1.5	190	19.5	105	18.6
Commercial *c*	941	.3	...	....	767	5.5
5–34m	409	.0	...	....	174	.8
5–34–2m	506	.6	...	....	189	1.6
5–24m	...	....	614	42.0	422	9.6
5–24–1m	409	6.8	...	....	191	8.6
5–107m	...	....	414	23.7	194	15.8
5–23–1m	280	1.8	412	21.8	105	1.9
5–32–2m	...	....	427	60.2	238	10.3
5–31m	521	11.0	410	36.1	145	32.9
5–93m	513	4.9	301	30.5	400	15.6
5–87m	476	.6	387	22.2	259	11.9
5–22m	...	....	419	2.4	280	1.3
5–16m	...	....	1,029	41.0	752	15.3
5–111–10m	223	1.3	359	43.4	284	22.6
5–111–13m	601	2.0	457	43.1	161	28.7

SWEET SPANISH

Sprouting in storage was especially variable among different inbred lines of Sweet Spanish. Records are not presented, but a typical example of the difference in amount of sprouting between first-generation inbreds is shown in figure 2.

Bolting Habit

The variety Sweet Spanish tends to bolt rather readily, and inbred lines behaved about the same as the parent variety, showing that the variety is fairly homozygous for this character. Conversely, the variety Italian Red has a delayed bolting habit, and the inbred lines were uniformly nonbolting. In the variety Yellow Danvers Flat, however, the inbred lines varied considerably in their bolting behavior. Comparisons of percentages of bolting can best be made from plants grown from dry sets, as these can easily be graded to a uniform size, thus eliminating the size factor as one of the variables. The data in table 3, column 5, indicate that all the lines except one were significantly lower in percentage of bolters than the commercial parent. Line 1–16–7–4m was significantly higher than the commercial. Year after year these lines were consistently low or high in percentage of bolters when compared with the parent variety.

Uniformity of Size and Shape

Occasionally one or two generations of inbreeding produced lines of remarkable uniformity, but usually four or five generations were required. Line 21–22–1m of California Early Red, introduced as Red 21, showed

FIGURE 2.—Two lines of Sweet Spanish onion inbred one generation, showing difference in keeping quality in storage. These lines were grown in the same plot on Liberty Island, Calif., in 1935, stored in the same tray, and removed from storage at the same time.

remarkable uniformity for many important commercial characters after two generations of inbreeding. The coefficient of variation figures in table 15 show very little difference in uniformity of size when lines inbred six and two generations are compared. The same holds true for lines of Italian Red inbred two and six generations (table 14). The great uniformity of size and shape brought about in a line of Yellow Danvers Flat 1-10-11-2-S_2 by inbreeding for five generations is illustrated in figure 3.

HETEROSIS

CROSSES BETWEEN MALE-FERTILE INBRED LINES

Crosses have been made between a number of lines to study hybrid vigor in the onion. Before the male-sterile character was available, crosses were made between male-fertile plants; the results of some of these latter crosses are presented below.

Stockton Yellow 21-10 and Italian Red 13-20-3-45-S_2 were crossed by interpollinating from plant to plant so that reciprocal crossing occurred. The seed on each variety was harvested and planted separately. Thus, the hybrids between the varieties were distributed at random in the field planting. Of the progeny from the Stockton Yellow plants, 24 percent were hybrids, whereas of the progeny from the Italian Red plants, 28 percent were hybrids. Stockton Yellow bulbs weighed 242 gm. and the hybrids 775 gm., a difference of 533 gm. in favor of the hybrid (table 20). The Italian Red bulbs weighed 202 gm. and the hybrids 641 gm., a difference of 439 gm. in favor of the hybrids. The hybrid bulbs could be distinguished from the Stockton Yellow parent by their red color and globe shape and from the Italian Red parent by their globe shape (fig. 4).

TABLE 20.—*Comparison of selfed lines of Stockton Yellow and Italian Red onions and their hybrids, Davis, Calif., 1932*

Variety or hybrid	Pedigree	Population	Mean weight per bulb	Coefficient of variation	Polar equatorial ratio
		Number	*Grams*	*Percent*	
Stockton Yellow × Italian Red	21-10 × 13-20-3-45-S_2	76	775 ± 27.7	31.2 ± 2.8	0.775
Stockton Yellow	21-10	244	**242 ± 8.0	51.8 ± 2.9	** .679
Italian Red × Stockton Yellow	13-20-3-45-S_2 × 21-10	79	641 ± 25.9	35.9 ± 3.2	.807
Italian Red	13-20-3-45-S_2	203	**202 ± 7.0	49.5 ± 3.0	**1.775

** Significantly different from hybrid at the 1-percent level.

The hybrids growing among the Stockton Yellow 21-10 plants averaged 134 grams heavier than those growing among the Italian Red 13-20-3-45-S_2 plants. The difference in the mean weight of hybrid bulbs between the two adjoining blocks may have been due in part to soil heterogeneity but was probably due chiefly to a difference in competition between the selfs and the hybrids. The 21-10 plants were in the proper stage for harvest on July 2 and the hybrid plants on July 12, a difference of 10

FIGURE 3.—Yellow Danvers Flat 1-10-11-2-S_2 (inbred five generations). Note uniformity of size and shape resulting from inbreeding.

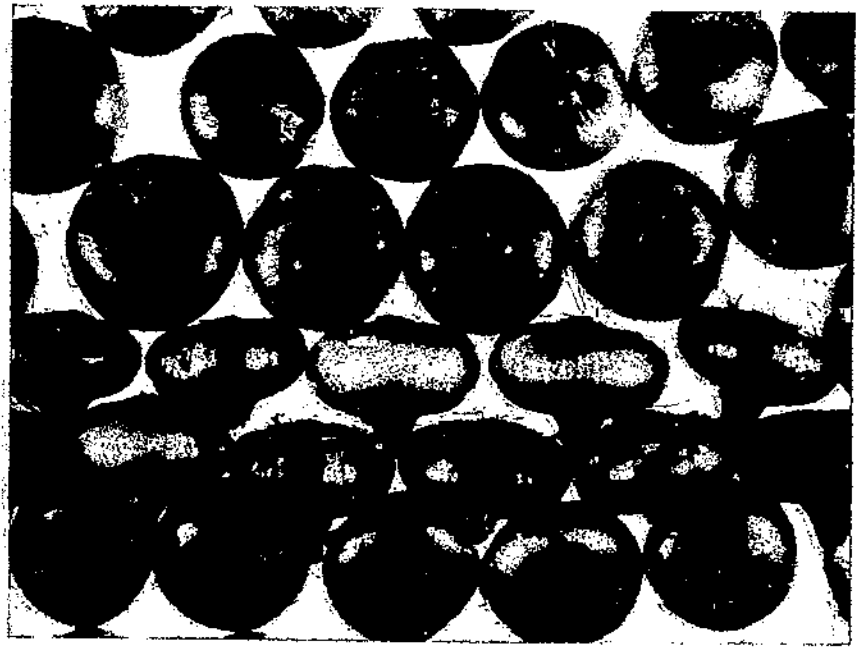

FIGURE 4. A, Stockton Yellow 21-10; B, Italian Red 13-20-3-45-S_2; C, F_1.

days in time of maturity. The 13-20-3-45-S_2 bulbs matured later than the hybrid bulbs, and for this reason competition for the latter was much more severe.

The bulbs of both parents and the hybrids were measured in two diameters—polar and equatorial—by the use of a sliding micrometer; the results are presented as the polar-equatorial ratio (table 20). The bulbs of the Stockton Yellow are oblate in shape, whereas those of Italian Red are torpedo- or bottle-shaped. The F_1 is a slightly flattened globe, intermediate between the two parents (fig. 4).

Giant White Italian Tripoli 27-5 and Red 21 (21-22-1-8-S_2) were also crossed by interpollinating. The seed from each variety was harvested and seeded separately, and the seedlings were transplanted separately. Of the plants from the 21-22-1-8-S_2 lot, 68 percent were hybrids, and of those from the 27-5 parents, 28 percent were hybrids. As there was no significant difference in the mean weight per bulb of the hybrids of the reciprocal crosses, the data for the two lots of hybrids were combined (table 21). In this cross the white bulb color was incompletely dominant; the hybrids had a pinkish tint, especially in the neck region, which made it possible to identify them.

In two other crosses, Italian Red 13-20-3-45-S_2 × Stockton Yellow Globe 36-34-45 (table 21) and Italian Red 13-52-9-6-S_2 × Italian Red 13-20-3-45-S_2 (table 21), the differences between the hybrid and the parents were highly significant. In both of these crosses the female parent was emasculated, and the hybrid and selfed seed were harvested and planted separately.

In certain other crosses the hybrid was not significantly heavier than both parents. In the cross Stockton G36 × Yellow Globe Danvers 15-108-1 the hybrid was heavier than the Yellow Globe Danvers parent but lighter than the Stockton G36 parent (table 22). In the cross Stockton Yellow 21-10 × Red 21, the bulbs of the hybrid were significantly heavier

TABLE 21.—*Comparison of various selfed lines of onions and their hybrids, Davis, Calif., 1934*

Variety or hybrid	Pedigree	Population	Mean weight per bulb	Coefficient of variation
		Number	*Grams*	*Percent*
Giant White Italian Tripoli × Red 21	27-5 × 21-22-1-8-S_2	71	225 ± 6.69	25.6 ± 2.2
Giant White Italian Tripoli	27-5	53	** 43 ± 2.55	44.6 ± 5.1
Red 21	21-22-1-8-S_2	25	**172 ± 11.53	33.6 ± 5.3
Italian Red × Stockton Yellow Globe	13-20-3-45-S_2 × 36-34-45	57	207 ± 12.53	31.9 ± 3.3
Italian Red	13-20-3-45-S_2	81	**177 ± 8.06	41.0 ± 3.7
Stockton Yellow Globe	36-34-45	137	**174 ± 4.36	28.8 ± 1.9
Italian Red × Italian Red	13-20-3-45-S_2 × 13-52-9-6-S_2	16	343 ± 19.18	22.3 ± 4.1
Italian Red	13-52-9-6-S_2	77	**198 ± 6.02	26.6 ± 2.3
Do	13-20-3-45-S_2	120	**202 ± 6.91	20.4 ± 1.4

** Significantly different from hybrid at the 1-percent level.

than those of Stockton Yellow but not much heavier than those of the Red 21 parent (table 22).

TABLE 22.—*Comparison of various selfed lines and their hybrids, Davis, Calif.*

Variety or hybrid	Pedigree	Population	Mean weight per bulb	Coefficient of variation
		Number	*Grams*	*Percent*
Stockton G36 × Yellow Globe Danvers	36-40 × 15-108-1	58	201 ± 8.25	30.8 ± 3.1
Stockton G36	36-40	16	**271 ± 19.49	28.4 ± 5.4
Yellow Globe Danvers	15-108-1	52	**106 ± 4.95	33.6 ± 3.6
Stockton Yellow × Red 21	21-10 × 21-22-1	68	204 ± 9.33	37.7 ± 3.7
Stockton Yellow	21-10	79	*178 ± 8.17	40.8 ± 3.7
Red 21	21-22-1	76	189 ± 6.00	27.1 ± 2.4

* Significantly different from hybrid at the 5-percent level.
** Significantly different from hybrid at the 1-percent level.

CROSSES BETWEEN A MALE-STERILE CLONAL LINE AND MALE-FERTILE VARIETIES

Data presented in the preceding section show that hybrid bulbs of large size can be obtained by making the proper crosses, but when emasculation is necessary to obtain crossed seed, quantity production is impractical because of the labor requirements. This disadvantage, however, is overcome when male-sterile varieties or clones are available for use as female parents. A male-sterile clonal line, Italian Red 13-53, has been available for some time and is being used experimentally for the production of hybrid seed. As described by Jones and Emsweller (*5*), this clonal line is also being used in breeding for resistance to downy mildew. It is the most highly resistant selection found to date; the seed stems are immune, and the foliage is highly resistant. This male-sterile selection is propagated by top sets, or bulbils. Because of its male-sterile character, mother bulbs may be interplanted in the field with male-fertile varieties. Cross-pollinating is done entirely by insects, and good yields of seed are obtained. Varieties or inbred lines, planted in alternate rows with the male-sterile plants to provide pollen, remain uncontaminated.

In 1940, Italian Red 13-53 × Red 21 and Italian Red 13-53 × Lord Howe Island were compared with their pollen parents and with four other varieties at five locations in California. Yields per acre were determined by the weight of the nonbolters per plot. The hybrid Italian Red 13–53 × Red 21 produced exceptionally large yields at Shafter and Milpitas (table 23). Elsewhere there was no significant difference in yields between the two hybrids. At all locations the highest yielding hybrid outyielded by a considerable margin the best producing commercial variety. At Shafter the Italian Red 13–53 × Red 21 hybrid yielded 915 100-pound sacks per acre, while San Joaquin, the highest yielding commercial variety, produced 759. At Milpitas Italian Red 13–53 × Red 21 produced 980 100-pound sacks, while Stockton G36, the highest yielding commercial variety, produced 561. At every location the two hybrids showed a highly significant increase in yield over their respective male parents.

Table 23.—*Yield per acre of onion hybrids and varieties in California, 1940*

Variety or hybrid	Yield in indicated location				
	Milpitas	Davis	Liberty Island	Tracy	Shafter
	100-pound sacks	*100-pound sacks*	*100-pound sacks*	*100-pound sacks*	*100-pound sacks*
Lord Howe Island	77	55	103	158	231
Italian Red 13–53 × Lord Howe Island	731	393	569	556	715
Red 21	350	285	248	328	541
Italian Red 13–53 × Red 21	980	443	454	529	915
San Joaquin	316	297	423	471	759
Crystal Grano	230	211	284	357	618
Stockton G36	561	323	468	441	624
Crystal Wax	82	...	111	97	219
Difference required for significance:					
5-percent level	90	66	126	150	95
1-percent level	122	90	170	209	128

That the nonbolting character of Italian Red 13–53 behaves as an incomplete dominant can be seen by comparing the hybrid Italian Red 13–53 × Lord Howe Island with the highly bolting pollen parent (table 24). At all locations in 1940 the hybrid bolted a great deal less than Lord Howe Island, and in all comparisons the difference was highly significant. The Italian Red 13–53 × Red 21 plants bolted less than the Red 21

Table 24.—*Bolting of onion hybrids and varieties in California, 1940*

Variety or hybrid	Plants bolting at indicated location				
	Milpitas	Davis	Liberty Island	Tracy	Shafter
	Percent	*Percent*	*Percent*	*Percent*	*Percent*
Lord Howe Island	47.6	68.0	61.9	57.9	27.9
Italian Red 13–53 × Lord Howe Island	4.2	15.8	16.3	8.0	.0
Red 21	34.6	13.1	23.0	13.6	.0
Italian Red 13–53 × Red 21	4.1	2.2	34.7	3.4	1.0
San Joaquin	5.9	10.1	4.2	3.7	.2
Crystal Grano	48.8	36.5	26.6	8.3	3.2
Stockton G36[1]	.0	.0	.2	.2	.0
Crystal Wax	11.0	...	13.3	10.5	.0
Difference required for significance:					
5-percent level	13.4	10.4	18.4	10.9	8.1
1-percent level	18.1	14.2	21.9	14.9	11.0

[1] Not included in the analysis.

parent at Milpitas, Davis, and Tracy, but not on Liberty Island. Stockton G36 produced practically no bolters at any of the locations. Because of mild climatic conditions very little bolting occurred at Shafter, except on Lord Howe Island.

In 1941 the hybrids Italian Red 13–53 × Red 21 and Italian Red 13–53 × Lord Howe Island and several varieties adapted to that district were grown at Shafter, Calif., (table 25). Because of the planting arrangement it was not possible to use the data from Crystal Wax and the hybrids in the analysis. Despite this, the differences in yield between the hybrids and the other varieties were so large that there does not seem to be any question as to their significance.

TABLE 25.—*Comparison of onion hybrids and varieties in percentage of bolters, mean weight per bulb, and yield per acre, Shafter, Calif., 1941*

Variety or hybrid	Bolters	Mean weight	Yield
	Percent	*Grams*	*100-pound sacks*
Stockton G36	0.0	189	362
Crystal Grano	.7	173	324
San Joaquin	.0	208	377
Early Grano	.7	166	301
Crystal Wax[1]	7.4	92	147
Italian Red 13–53 × Red 21[1]	.0	254	487
Italian Red 13–53 × Lord Howe Island[1]	.0	352	610
Difference required for significance: 5-percent level	. .	29	50

[1] Not included in the analysis.

In 1942 a sufficient number of plants of Italian Red 13–53 were available to compare with the hybrids and pollen parents (table 26). Bulbs of Italian Red 13–53 × Lord Howe Island and Italian Red 13–53 × Red 21 weighed about the same as Italian Red 13–53. The bulbs of the hybrids and Italian Red 13–53 were much heavier than those of the pollen parents.

TABLE 26.—*Comparison of onion varieties and their hybrids in percentage of bolters, mean weight per bulb, and yield per acre, Davis, Calif., 1942*

Variety or hybrid	Bulbs harvested per replication	Bolters	Mean weight	Yield
	Number	*Percent*	*Grams*	*100-pound sacks*
Red 21	65	0	107	256
Lord Howe Island	54	0	74	97
Italian Red 13–53	72	0	241	411
Italian Red 13–53 × Lord Howe Island	72	0	240	412
Italian Red 13–53 × Red 21[1]	61	0	260	376
Difference required for significance:				
5-percent level	13	. .	36	77.6
1-percent level	18	. .	51	108.7

[1] Not included in the analysis.

The hybrid Italian Red 13–53 × Lord Howe Island has been introduced cooperatively by the California Agricultural Experiment Station and the United States Department of Agriculture as California Hybrid Red No. 1 (fig. 5).

The male-sterile clonal line Italian Red 13–53 has made possible the study of hybrid vigor, but its use does have certain limitations in a general program for the production of hybrid seed, because Italian Red, the variety from which it is derived, is not widely adapted for commercial growing in the United States on account of its late maturity and extremely poor keeping quality. A recent publication by Jones and Clarke (*2*) discusses the mode of inheritance of this male-sterile character and outlines a breeding procedure which makes possible the perpetuation of the male-sterile character through the seed.

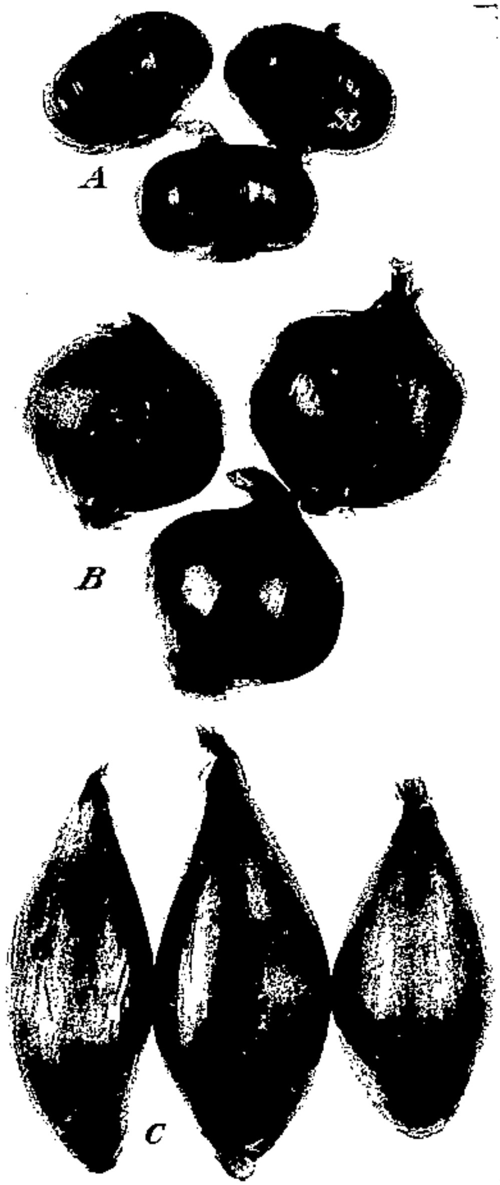

FIGURE 5.—*A*, Lord Howe Island; *B*, F_1 (California Hybrid Red No. 1); *C*, male-sterile Italian Red.

Crosses Between Male-Sterile and Male-Fertile Inbred Lines

GENETIC INTERPRETATION OF MALE-STERILITY

According to Jones and Clarke (*2*), when male-sterile plants of the clonal line Italian Red 13–53 were crossed with various male-fertile plants three types of breeding behavior were observed in the F_1: Some progenies were entirely male-fertile, others were entirely male-sterile; and still others produced both male-sterile and male-fertile plants in a 1 to 1 ratio.

When a self-fertile F_1 plant is selfed the F_2 approximates the ratio 3 normal to 1 male-sterile. When a male-sterile F_1 is backcrossed to the male-fertile parent three types of segregation are obtained as in the F_1. When the Italian Red 13–53 male-sterile parent is backcrossed with an F_1 male-fertile plant a 1 to 1 segregation is obtained. In crosses between certain F_1 male-fertile plants as the female parent and the male-fertile parent line a ratio of 1 male-fertile to 1 male-sterile is obtained, but in the reciprocal backcross when the F_1 male-fertile plant is used as the pollen parent all the progeny are male-fertile.

These results may be accounted for by assuming that the male-sterile condition results from an interaction between a recessive nuclear gene and a nonnuclear, or cytoplasmic, factor. On this hypothesis it is assumed that there are two types of cytoplasm. All plants with normal cytoplasm (*N*) produce viable pollen. All male-sterile plants possess the sterile type of cytoplasm (*S*). The experimental results throw no light on the nature of the nonnuclear, or cytoplasmic, factor which differs in the two types. A gene for male-sterility (*ms*) also influences pollen development when carried by plants with *S* cytoplasm but has no effect when carried by plants with *N* cytoplasm. Consequently, the Italian Red 13–53 male-sterile plants belong to the genotype *S ms ms*. Plants with *N* cytoplasm are male-fertile always and may belong to the genotypes *N Ms Ms*, *N Ms ms*, or *N ms ms*, since the *ms* gene has no effect in the *N* cytoplasm. Plants with the genetic constitution *S Ms Ms* and *S Ms ms* will also be male-fertile in spite of the *S* cytoplasm, because they carry the dominant gene *Ms*.

The nonnuclear, or cytoplasmic, factor is inherited only through the egg (maternal inheritance) and not through the male parent, presumably owing to the very small amount of cytoplasm present in the male gamete. From the cross *S ms ms* × *N Ms Ms* all F_1 plants will be *S Ms ms* and, in spite of the *S* cytoplasm, are male-fertile because they carry the gene *Ms*. *S ms ms* × *N ms ms* gives all male-sterile, and *S ms ms* × *N Ms ms* gives 1 male-sterile to 1 male-fertile. When a male-fertile F_1 plant (*S Ms ms*) is selfed, the expected F_2 ratio is 3 normal to 1 male-sterile.

All male-sterile F_1 plants belong to the genotype *S ms ms* and behave the same as the original male-sterile parent. When the Italian Red 13–53 male-sterile parent is backcrossed with an F_1 male-fertile plant, *S ms ms* × *S Ms ms*, a 1 to 1 segregation is expected.

When an F_1 male-fertile plant, *S Ms ms*, is used as the female parent and backcrossed to *N ms ms* a ratio of 1 male-fertile to 1 male-sterile is obtained. But in the reciprocal backcross *N ms ms* × *S Ms ms* all the progeny are male-fertile, since all carry *N* cytoplasm. The unlike behavior of these reciprocal backcrosses is critical evidence in support of the validity of this hypothesis.

Second backcrosses of the type *S ms ms* × *N Ms ms* gave a 1 to 1 segregation. Second backcrosses of the type *S ms ms* × *N ms ms* gave all male-steriles. This confirms the expectation that 100-percent male-sterile progenies can be obtained in repeated backcrosses to a stock with the genetic constitution *N ms ms*. As shown in the next section, this is of great practical importance in developing a breeding program.

METHOD OF PRODUCING HYBRID SEED COMMERCIALLY

Male-sterile lines have now been developed from Italian Red 13–53 for practically all the important commercial varieties. Fortunately, male-fertile plants with the genotype *N ms ms* have been found in most varieties so far tested, namely, Brigham Yellow Globe, Early Yellow Globe, Sweet Spanish, Southport White Globe, Crystal Wax, Yellow Bermuda, Red Creole, and Stockton G36. The last variety appears to be homozygous for *N ms ms*, as all the plants tested have produced 100-percent male-sterile progenies when crossed with male-sterile plants. The only means of determining whether a fertile line is pure for *N ms ms* is by a breeding test. This method of incorporating the male-sterile character of Italian Red 13–53 into different varieties is illustrated graphically in figure 6, the variety Crystal Wax being used as an example. The rate at which the Crystal Wax genes are incorporated into the male-sterile line is somewhat

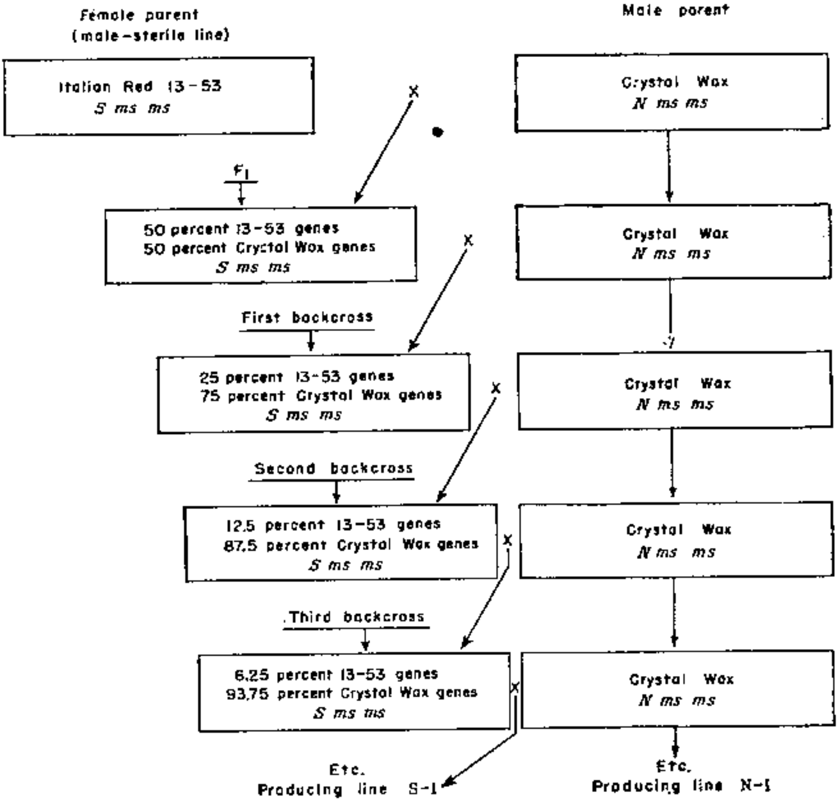

FIGURE 6.—Method of developing male-sterile lines of Crystal Wax from Italian Red 13-53, showing the rate at which Crystal Wax genes are incorporated into the male-sterile line by backcrossing.

faster than indicated in figure 6, because in all the backcross progenies selection is for the Crystal Wax type. The numbers given in the figure show the rate expected for random sampling. After being backcrossed two or three times to the male-fertile parent, the male-sterile and male-fertile lines appear almost identical.

The production of hybrid onion seed of all types and in quantity is now possible. To perpetuate the pure male-sterile line two lines (a male-sterile line of the genotype *S ms ms* and a fertile line of the genotype *N ms ms*) must be carried along. All the progeny of this cross will be male-sterile. Figure 7 illustrates the method of perpetuating the male-sterile line through the seed.

As the male-sterile plants cannot be selfed, seed is obtained by continually backcrossing to the normal, or male-fertile, line. Backcrossing continues as long as the particular male-sterile line is to be perpetuated. After a few backcrossings the male-sterile line should be practically identical with the male-fertile except for the sterility factor of the cytoplasm. This backcross seed makes it possible to perpetuate the male-sterile line, as well as to produce the male-sterile female parents used in the production of hybrid seed.

The next step is to make crosses between the male-sterile line and other selected lines to determine which combination produces the best commercial hybrid (fig. 8). The constitution of the male parent that enters

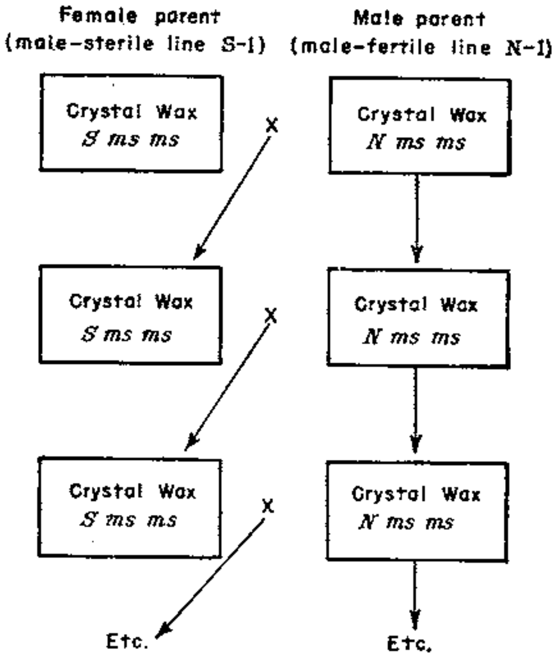

FIGURE 7.—Method of perpetuating a male-sterile line of the variety Crystal Wax.

into the cross for the production of commercial hybrid seed may be *N ms ms*, *N Ms ms*, or *N Ms Ms*, the particular one selected being based on progeny tests. The behavior of the commercial hybrids as to fertility

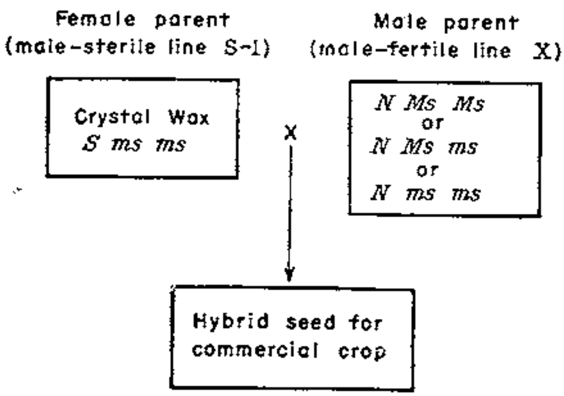

FIGURE 8.—Method of producing hybrid seed for the commercial crop.

is not important, because the commercial crop must be grown from hybrid seed each year. It is important, however, to get a favorable combination of growth factors.

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