VOL. 4 APRIL, 1930 NO. 14

HILGARDIA

A Journal of Agricultural Science

PUBLISHED BY THE

California Agricultural Experiment Station

CONTENTS

UNIVERSITY OF CALIFORNIA PRINTING OFFICE
BERKELEY, CALIFORNIA

HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE

PUBLISHED BY THE

CALIFORNIA AGRICULTURAL EXPERIMENT STATION

VOL. 4 APRIL, 1930 No. 14

STUDIES OF THE BREEDING OF SUGAR BEETS FOR RESISTANCE TO CURLY TOP

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INTRODUCTION

The nature of the injury caused by curly top and the importance of this disease to the sugar-beet industry in certain western states have been recognized for many years and have been discussed by Ball,[2] Carsner and Stahl,[5] and Severin.[9, 10]

Studies of the behavior of beets affected with curly top have shown that individual beets vary as to their susceptibility to this disease. Reference is made here not only to observations of the writer but to those of Carsner and Stahl[5] and Carsner.[3] These observations have suggested the possibility of developing curly-top-resistant strains by selecting the least affected individuals among infected beets in commercial fields.

Carsner[3] has shown that resistance to curly top is an inherent characteristic in individual beets. Several of the strains which he selected for resistance to curly top were definitely more resistant than the commercial beets with which they were compared. Furthermore, he found that some other morphologically uniform strains which were developed without reference to curly top showed constant differences in susceptibility to this disease.

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Some conclusive results with regard to resistance of sugar beets to curly top have also been obtained by the writer. The work upon which these results are based was started by the Spreckels Sugar Company in the Salinas Valley, and was later transferred to the Branch of the College of Agriculture, Davis, California. Several strains resistant to the disease have been developed and their characteristics studied during three years at King City, California, and during two more years at Davis. This work is reported in this paper.

METHOD OF BREEDING FOR RESISTANCE

Curly-top-resistant strains were developed by selection. Plants which showed resistance in commercial fields, in which the beets were severely affected by curly top, served as the initial selections. The appearance of the leaves was employed as the basis of the first selection, which was usually undertaken several weeks before harvest. However, the plants which were seemingly less affected by the disease showed in every case symptoms of curly top; that is, immunity was not observed. At harvest time the previously marked beets were selected for size and shape of root.

The progenies of these mother beets were tested under exposure to infection, and selections were made again within those progenies that showed the highest degree of resistance. In addition to a selection for size and shape, the percentage of sugar of individual roots was determined, and those of low quality were eliminated.

The seed from each mother beet was kept separate and was planted in individual rows. A commercial strain of sugar beet served as a check. The commercial variety known as 'Old Type,' which is produced by the German firm, Rabbethge and Giesecke, was used for this purpose in every case, with the exception of the King City planting of 1925, when a commercial strain produced by the French firm, Vilmorin and Company, was used as a check.

Seed-bed conditions made necessary the sowing of seed at a heavy rate and by machine. Consequently, the amount of seed from individual mother beets was not sufficient to make more than two or three replications of each progeny. The commercial seed which served as a check was planted in many replications. The usual practice was to sow four progenies in four individual rows 50 or 100 feet long, and the fifth row with commercial seed for a check. Whenever possible the sets of five rows were repeated two or three times. This method was somewhat modified in 1929 when each progeny was sown in four rows 25 feet long, and the fifth and sixth rows were employed as a check.

The preparation of the seed bed was similar to that of a commercial beet field. Manure and commercial fertilizers were not applied in the King City experiments. The Davis tests were conducted upon a field which had been manured repeatedly in the past. The irrigation water was applied at two-week intervals, and the cultivation was done with wheel hoes.

The harvesting was done by hand. The total weights were determined in the field. Since some of the beets had to be saved for propagation, the topping was not done in the usual manner, but the leaves were cut off about one inch above the crown. With the exception of the 1929 test, this procedure was followed throughout. In 1929 the beets were topped in a manner followed in commercial practice.

The methods of propagating the seed will be discussed in connection with the description of the resistant strains.

METHODS AND CONDITIONS OF TESTING FOR RESISTANCE

Resistance Tests in the Salinas Valley.—According to Severin and Henderson,[11] the interior regions of the Salinas Valley are within the boundary of the natural breeding areas of the beet leafhopper (*Eutettix tenellus* Baker). They have been subject to epidemics of curly top almost every year since the beginning of beet culture in these regions, and the disease appeared consistently in a form which Carsner[4] designated as severe. For this reason the King City and the Greenfield districts, which are located in the interior of the Salinas Valley, were selected for the resistance trials. In order to assure a severe natural infection it was only necessary to plant the seed late in the spring, so as to have the beets at a very young stage at the time of appearance of the beet leafhopper. Carsner and Stahl[5] have shown that beets are most susceptible to curly top in their early stages.

During the three seasons when extensive trials were conducted in the Salinas Valley, the conditions for infection with curly top were favorable. In 1925 the beets at Greenfield were sown on March 13, eleven days before the influx of leafhoppers, and at King City on March 24, after leafhoppers had appeared in the beet fields. As a rule, the conditions with regard to curly top at Greenfield are very similar to those at King City, but in 1925 the plot at Greenfield was exposed to a more severe infection than the other. The beets at Greenfield were up when the leafhoppers appeared. Before they reached the thinning stage the commercial beets adjoining the trial field were plowed under, and the leafhoppers accumulated upon the experimental plot. At King City, on the other hand, no exceptionally large accumulations of insects were observed upon the test plot; the beets came up after the first appearance of the leafhoppers, and the adjoining beet fields were not plowed under. Also, with regard to cultural and soil conditions, the King City plot was far better placed. Consequently, although at the beginning of June every plant in the check rows in both plots was showing unmistakable symptoms of curly top, the effect of the disease upon the King City beets was not so detrimental as upon those in the plot at Greenfield. The beets on both plots were harvested in the middle of November.

In 1926 the beets were planted on March 29 and 30 at King City. The first influex of leafhoppers occurred on April 19, when the beets were still too small for thinning. As the trial plot was the only planting of beets in that section of the farm (the nearest commercial beet field was about six miles away), the insects during the spring flights apparently congregated upon this plot. A count of the number of leafhoppers taken at this time showed a population of 20 to 30 insects to 100 feet of row. Because of warm weather at the time of influx, symptoms of the curly-top disease developed very rapidly, and on May 15 all of the beets in the check rows were diseased. The beets were harvested in the latter part of October.

In 1927 the plantings were made at King City at two different dates—one on April 4, before the influx of leafhoppers, the other on May 5, after the influx. During the entire season the two plantings showed a considerable difference in the general development of the beets. The earlier planting was exposed not only to a very severe infection with curly top, but also to other unfavorable growth conditions. In the first stages of germination the young seedlings were weakened through the formation of a crust on the surface of soil after a rain, and they developed only slowly on account of the cold weather, which persisted until the latter part of April. About April 21 a sudden rise of temperature occurred, and great numbers of aphids and leafhoppers appeared in the beet plots. The number of leafhoppers was found to be 30 per 100 feet of row. In the latter part of May all of the commercial beets showed symptoms of the disease. As to the beets that were planted later, the weather was moderately warm during germination of the seed, and the seedlings were not weakened by crust formation or by aphis injury. Throughout the season the May-planted beets had a healthier appearance than those planted in April, although by the middle of June the percentage of diseased beets was the same in both plots. Thus, as in 1925, the beets that were up at the time of influx were injured far more than those that were sown after the leafhoppers had appeared. The April planting was harvested on October 17 and 18, and the May planting on October 27.

Resistance Tests at Davis.—In the fall of 1927 the work on resistance was transferred to the Branch of the College of Agriculture, Davis, California. The conditions here were very different so far as concerns natural infestation by the leafhopper.

According to Severin and Henderson(11) the Davis district is located in a migratory area of the leafhopper. Observations of the past have shown that the outbreak of the disease can be expected here with less certainty than in the Salinas Valley, especially in years of decreased population of *Eutettix tenellus.* In fact, no influx of leafhoppers was observed in 1928 and 1929, and the insects had to be introduced artificially. A stock of viruliferous leafhoppers was reared in a greenhouse upon potted sugar beet plants in insect cages of the type shown by Severin.(9) In the spring the insects were released upon the young beets in the trial field.

During the winter of 1927–28 about 6000 leafhoppers were reared, and the beets were inoculated by dropping three to four viruliferous nymphs between the heart leaves of each plant. The beets were sown on March 17 and were up on March 24; and the nymphs were added on May 15. Exceptionally favorable weather conditions were responsible for quick germination of the seed and for the rapid growth of plants. Consequently, when the leafhoppers were released (May 15) the beets were far advanced in their development and were only slightly injured by the disease. On June 10, the check rows showed 100 per cent infection, and on June 26 they could readily be distinguished from the rows of resistant beets by the yellow color of the older leaves and by the severe symptoms, such as distorted veins and warty protuberances, upon the younger. The reduction in yield, however, was very much less than in other years. The beets were harvested by the middle of October.

In 1929 the conditions for testing for resistance were far more favorable than in 1928. It was possible to rear a larger population of insects and have them available at an earlier date than in the previous season. The beets were planted on March 15 and 21; they were up on March 25 and 31, and the insects were released on April 23 and 27, respectively. Approximately 15,000 adult leafhoppers were released upon an area of 20,000 square feet. This time the insects were not placed upon individual beets, but were distributed over the whole area as uniformly as possible by being shaken out of the cages along the rows of beets.

The beets, which were thinned a week before the date when the insects were released, had four foliage leaves on the day of inoculation. The warm, dry weather of the following week was very favorable for the development of curly top. The first symptoms appeared on May 1. A few days after the first irrigation, given on May 14, all the beets in the check rows showed symptoms of the disease with the exception of a few individuals which evidently escaped the inoculation at the beginning. On May 21 the first nymphs of the new brood were observed. The disease continued to spread, and on July 17 all the beets in the check rows were infected. The beets were harvested during the first part of October.

DEVELOPMENT AND TESTS OF THE P19 STRAIN

The breeding experiments with sugar beets with regard to resistance to curly top were started by the Spreckels Sugar Company in 1919,[2] during a year of a disastrous outbreak of the disease. The extent of injury caused by curly top in 1919 may be well demonstrated by the low yield of sugar beets at King City, which amounted to only 1.4 tons per acre as an average from 2600 acres. Carsner and Stahl[(5)] also showed that the yield of sugar beets in several districts of California reached one of its lowest limits in 1919, owing to losses caused by curly top. The severely infected fields offered excellent opportunities for the initial selection of beets for resistance to the disease.

Origin of the P19 Strain.—Five thousand apparently resistant beets were selected in the fall of 1919 in diseased commercial fields at King City. The following season these roots were transplanted for seed production. During the period of blooming the seed beets were covered with hoods of unbleached muslin. Although beet pollen can pass through this type of cloth, it offered considerable protection against cross-pollination, since all the beets that went to seed were covered.

In 1920, 183 of the five thousand beets developed seed stalks. The progenies of these mothers were tested for resistance in 1921. Only one of these progenies was found to exhibit marked resistance to curly top. This one also showed considerable uniformity of morphological characters.

[2] The data covering the work before 1924 were obtained from the unpublished reports of the Spreckels Sugar Company's Experiment Station at Spreckels, California. Messrs. W. J. Hartung, E. A. Schwing, G. T. Scott, A. A. Tavernetti, and W. W. Thomas of that Station made the first selections for resistance. From 1924 the writer was in charge of the work.

The beets of this resistant progeny were planted for seed production as a group at Spreckels, California. They were not covered during bloom but were sufficiently removed from seed beets of other origin to prevent contamination from foreign pollen. Five mother beets of this group yielded seed in 1922.

All five progenies from these mothers showed resistance to curly top in 1923; one progeny, consisting of seven beets, was conspicuously less affected than others, and it was saved for further propagation. This one progeny yielded in later years a comparatively uniform and markedly resistant strain which has been designated as the 'P19,' the 'P' standing for the parental generation and the '19' for the year of selection of the parent root.

Propagation of the P19 Strain.—From 1925 to 1929 the P19 strain was subjected to five successive trials for resistance. Seed for the third filial generation was obtained from the seven mother beets of 1923. These mother beets were not hooded during blooming but were isolated by distance in groups and individually. Mothers 1, 4, and 7 were left as a group at King City; 2 and 3 were planted together at Spreckels; 5 and 6 were isolated individually at other points in the Salinas Valley. The respective distances between the groups were as follows: between group 2–3 and mother 5, 14 miles; between mothers 5 and 6, 30 miles; between mother 6 and group 1–4–7, about five miles. The seed of these mother beets was tested in 1925. Mothers 1, 2, 3, 4, and 7 gave progenies that were very similar morphologically and markedly resistant to curly top; 5 failed to set seed; and 6 gave a progeny which was far less resistant than the other P19 progenies, and which also deviated from the latter in its morphological characters. No further selections were made from progeny 6.

For the purpose of gaining time in the development of the P19 strain some seed from five (mothers 1, 2, 3, 4, and 7) of the 1923 mother beets was planted in August, 1924, immediately after harvest. No selection was made either for resistance or sugar content. The roots were transplanted in February, 1925, and were exposed to cross-pollination within the group. Twenty-three progenies of the fourth generation were obtained for the trial of 1926.

The test for resistance of 1927 included 100 progenies of the fourth generation from beets selected from progenies 1, 2, 3, 4, and 7 in 1925. For seed production these mother beets were segregated into three groups, according to their size and sugar percentage. There was free cross-pollination within the groups, but the distances between the groups were 10 and 15 miles. Beets which were isolated individually failed to set seed. The three groups of progenies which were derived from the three groups of mother beets did not show any significant differences from one another.

The beets selected from the P19 strain in 1926 and 1927 gave the progenies of the fifth generation, some of which were still kept separate and were tested for resistance in 1928 and 1929. A few progenies of the fourth generation were tested again in 1929.

TABLE 1

RESULTS OF THE RESISTANCE TESTS OF THE P19 STRAIN (1925 TO 1929)

Location of test plots	Date of seeding	Strain	Generation of P19	Number of P19 progenies	Number of beets per 100 feet of row		Percentage of beets that survived	Roots per 100 ft. of row, kgm.	Average weight per beet, grams
					Early in season	At harvest			
Greenfield	March 13, 1925	P19	Third	5		39		11.25	289
		Check				81		7.94	98
King City	March 24, 1925	P19	Third	5		52		30.76	592
		Check				86		21.45	249
King City	March 29, 1926	P19	Fourth	19		49		22.73	464
		Check				17		1.97	116
King City	April 4, 1927	P19	Fourth	100	28	25	89	8.57	342
		Check			74	37	49	3.78	102
King City	April 4, 1927	P19	Fourth	44	29	26	90	8.90	342
		Check			71	35	49	3.57	102
King City	May 5, 1927	P19	Fourth	44	55	54	99	24.41	452
		Check			130	80	62	13.55	169
Davis	March 17, 1928	P19	Fifth	6	102	99	97	67.98	687
		Check			107	101	94	66.92	663
Davis	March 15, 1929	P19	Fifth	9	76	69	91	24.25	351
		Check			138	49	36	6.47	132
Davis	March 15, 1929	P19	Fourth	3	119	112	94	26.87	240
		Check			143	67	47	10.09	151

Resistance Tests of the P19 Strain.—Table 1 presents the results obtained with the P19 strain during five successive seasons. The pairs of data represent the averages of the P19 progenies and of their corresponding check rows. The P19 progenies were grouped according to generations and to dates of seeding. Of the two pairs of data which are given for the April planting of 1927, one presents the average of all the hundred progenies of the fourth generation, and the other the average of those forty-four progenies of the fourth generation which were also planted in May of the same year.

In 1925 and 1926 the number of beets was determined only at harvest time; in 1927, 1928, and 1929 the beets were also counted at the beginning of the season, and the percentage of beets which survived during the test was calculated from these data. It is necessary to point out here that the P19 strain usually gave inferior seed germination, so that the rows of P19 required very little thinning. The small number of beets harvested per row in the P19 resulted, as a rule, from the low viability of the seed. A better stand was obtained with P19 in the Davis plantings, owing to the heavier rate of seeding and better condition of the seed bed; in addition, the seasonal conditions in 1928 were exceptionally favorable for germination. In the

Fig. 1. The effect of curly top upon the foliage of the P19 resistant strain (right) and of a commercial susceptible strain (left). King City, June 18, 1925.

commercial seed the germination was generally satisfactory every season, and the low numbers of harvested beets were due to losses from disease.

It will be noted from table 1 that regardless of the unsatisfactory stand, the P19 strain gave a very much higher yield than the commercial check in every trial except in 1928, when the beets were less affected by curly top.

In figures 1 and 2, two progenies of the P19 strain are shown in comparison with their corresponding checks. Figure 1 shows the effect of curly top upon the foliage of resistant and susceptible beets, and figure 2 upon the yield of roots. In both cases the stand of beets in the P19 row was comparable at the beginning of the season with that in the check row.

Characteristics of the P19 Strain.—The tests over a series of years have shown that the P19 strain is decidedly resistant to curly top and gives a considerably higher yield than a commercial strain when both strains are exposed to a severe infection of the disease. The percentage of beets which survived the infection was consistently very much higher in the P19 strain, and this strain yielded roots of larger average size than the commercial seed.

Immunity, however, was never observed in this strain; all P19 beets were infected at the end of the season, although as a rule they

Fig. 2. The effect of curly top upon the yield of roots of the P19 resistant strain (left) and of a commercial susceptible strain (right). The respective yields per 100 feet of row were 41.73 kgm, and 7.40 kgm. King City, October 17, 1927.

developed only the transparent venation, and this symptom was discernible only with some difficulty. The average size of roots was smaller and the percentage of surviving beets was lower when the tests were more severe, a fact which also indicates that the resistance of the P19 strain does not constitute immunity.

The P19 progenies of the third, the fourth, and the fifth generations showed marked uniformity with regard to the tendency to develop only faintly discernible transparent venation and to yield a high percentage of surviving beets. The repeated selections for resistance within the strain, followed by a grouping of the closely related mother beets for seed production, did not increase the resistance of the strain.

There was also a comparatively small range of variation in the type of top and root. In general the P19 strain shows low vigor. The foliage appears light green in comparison with that of other beets. The tops are sparse, and the leaves form a flat, spreading rosette. The roots are, on the average, short and broad, often semi-globular (fig. 3). They show a greater tendency to develop a split crown than other beets grown under similar conditions. As this splitting frequently occurs at an early stage, multiple crowns are a common characteristic of larger P19 beets. There is usually a tinge of pink on the epicotyl, which frequently spreads upon the hypocotyl and the petioles of the leaves.

The greatest differences between the individual progenies of the P19 strain were found in the viability of the seed. A significant variation was also observed in the average size of the plants, which was correlated not with the differences in the stands of beets but with variation in vigor and degree of resistance in the individual progenies.

Sugar Analyses of the P19 Strain.—Determinations of the sugar content were made in 1925, 1926, and 1927, for the purpose of selection of mother beets for further propagation. Only roots of the best shape and size were chosen for the sugar test, and each root was analyzed individually. In 1927, 1928, and 1929, samples of beets of some of the P19 progenies and of their corresponding check rows were also tested as composite samples like ordinary field samples.

The sugar percentage was determined by a method of simple polarization, the Herzfeld modification of the Sachs–Le-Docte process being employed. At Spreckels the process was carried out by hot-water digestion, and at Davis by cold-water digestion. One-fourth of the 'normal weight' of pulp (the universally adopted 'normal weight' of sugar-containing substance for the polarimetric method of analysis is 26 grams) was digested with one-fourth of the 'constant volume' of lead subacetate solution (the 'constant volume' in the Sachs–Le-Docte process is 177 cc), which was prepared according to the directions given in handbooks of sugar analysis. Pulp samples were obtained with the Keil boring rasp.

Table 2 shows the averages of the results of the sugar analyses of individual beets of 1925, 1926, and 1927. It gives a comparison, with regard to sugar content, of P19 and commercial beets of approximately the same size. The number of analyzed beets was very small in the commercial checks because a high percentage of the plants in the check rows had died or were severely stunted at the end of the season. Rarely a plant had grown to a fair size either because of some accidental combination of favorable factors, or because it possessed a certain degree of resistance. These occasional individuals were selected and tested for sugar, with the object of using them as new initial selections for resistance.

The unsatisfactory seed germination caused a wide spacing of the beets in most P19 rows. When the area that is available to a beet plant is greater than is necessary for its normal nutrition, vegetative growth is favored and the sugar percentage is reduced. Unsatisfactory stands may have caused a reduction of sugar percentage in the P19 beets. However, since early in the season the check rows also

TABLE 2

AVERAGES OF THE RESULTS OF SUGAR ANALYSES OF INDIVIDUAL BEETS OF THE P19 STRAIN AND OF THE CORRESPONDING COMMERCIAL CHECKS, 1925, 1926, 1927

Location of test plots	Date of seeding	Strain	Number of beets tested	Average weight per beet, grams	Sugar: Average per cent	Sugar: Grams per beet	Sugar: Range of variation, per cent: Lowest	Sugar: Range of variation, per cent: Highest
Greenfield	Mar. 13, 1925	P19	53	608	15.3	93	9.0	19.2
		Check	10	603	18.5	112	15.6	20.0
King City	Mar. 24, 1925	P19	191	910	14.7	134	8.0	19.0
		Check	37	859	17.8	153	13.8	20.8
King City	Mar. 29, 1926	P19	306	773	13.0	100	8.8	17.6
		Check	21	752	13.8	104	10.4	19.4
King City	April 4, 1927	P19	363	865	12.6	109	9.4	16.5
		Check	20	1064	13.2	140	10.4	19.4
King City	May 5, 1927	P19	465	984	13.1	129	8.2	19.2
		Check	69	1030	16.1	166	12.6	21.6

showed deficient stands under the influence of the disease, the values obtained for the sugar percentage of the P19 and the commercial beets can justly be regarded as comparable.

Table 3 presents the results of sugar analyses of composite samples. In addition to the late spring plantings, some seed was sown in 1927 on January 27, i.e., three months before the appearance of the leafhoppers. These beets were comparatively old when the inoculation first took place (April 21) and the effect of the disease was not sufficiently strong to reduce the yield of the commercial seed below that of the P19. The test plot of 1928 was also subjected to a mild infection. The April planting of 1927 and the planting of 1929 were very severely affected by curly top. Thus, the data given in table 3 may be grouped in two distinct sets: one comparing the P19 beets and the commercial seed under conditions of mild infection, the other under those of a severe infection.

When the pulp samples were made up the two sets of beet samples had to be treated somewhat differently. In the lots grown under more favorable conditions none of the beets were stunted by the disease, and all could be sampled with the sampling machine. The two other lots, on the other hand, contained some roots which were too small for sampling (below 45 grams in weight). These were eliminated. In calculating the sugar per 100 feet of row, the discarded beets were assumed to have the same sugar percentage as the beets that were tested. When severely affected by curly top, the P19 lots contained on the average 80 per cent of beets suitable for sampling, and the commercial checks 40 per cent.

TABLE 3

SUGAR ANALYSES OF COMPOSITE SAMPLES OF THE P19 AND THE CORRESPONDING CHECK ROWS, 1927, 1928, 1929

Location of test plots	Date of seeding	Strain	Average weight per beet, grams	Sugar		
				Per cent	Grams per beet	Kilograms per 100 feet of row
King City	Jan. 27, 1927	P19	643	15.6	100	9.20
		Check	794	17.9	142	13.06
King City	April 4, 1927	P19	425	13.3	56	2.74
		Check	225	14.9	34	0.51
Davis	March 17, 1928	P19	725	15.0	109	10.20
		Check	718	18.0	129	12.05
Davis	March 15, 1929	P19	492	14.1	69	3.42
		Check	264	16.1	43	1.04

The sugar analyses, as given in tables 2 and 3, show that the P19 beets tested consistently lower than the commercial. The sugar percentage varied in both the P19 strain and in the commercial seed. In general, the more severe the test, the lower was the sugar percentage in both strains. Thus, in 1926, 1927, and 1929 the beets tested lower than in 1925 and 1928, and in 1927 the April-planted beets had a lower sugar percentage than the January beets. The difference between the P19 and the commercial seed decreased somewhat with increase of the severity of the test.

It has not been determined whether the increase in the degree of infection alone was responsible for a decrease in sugar percentage. In all probability, in the cases described, this decrease resulted from a combination of several unfavorable factors of growth, one of these being the severe infection with curly top.

Under more favorable conditions the total yield of sugar per 100 feet of row was higher in the commercial beets than in the P19. However, under conditions of severe infection the P19 gave a higher yield in total sugar than the commercial seed.

Conclusions Concerning the P19 Strain.—The P19 strain was found to possess a decided resistance to curly top. Evidently, however, this strain has no commercial value, owing to the following characteristics: (1) the low viability of seed; (2) the reduced vigor; (3) the comparatively low sugar percentage; and (4) the undesirable shape of root.

This strain may, however, be profitably employed in hybridization work. This would involve hybridization of the P19 strain with those of greater vigor, of higher sugar percentage, and with better shape of root. Improvement of the viability of the seed is also expected from such hybridization.

HYBRIDIZATION EXPERIMENTS WITH THE P19 STRAIN

Method of Hybridization.—The hybridization experiments were only of a preliminary nature. Hand-pollination methods were not used. The two beets to be crossed were merely set out together and were allowed to cross-pollinate freely. If one of the two beets sent up seed stalks earlier than the other, these were cut back, and in this manner both beets were forced to bloom simultaneously. The distance between the two plants was only two feet, so that during blooming the branches of the plants were partly intertwined. Furthermore, the seed stalks were frequently shaken during anthesis.

Usually a high percentage of hybrids can be expected in the progenies of beets planted under such conditions. Archimovitch[1] found, in progenies of 17 sugar beets which were distributed among table beets, an average of 90.75 per cent hybrid plants. The lowest percentage of hybrids observed was 70.20. In all probability these values would have been still higher if it were possible to recognize not only the hybrids between the table and the sugar beets, but also those between the sugar beets themselves. Hallquist[7] analyzed 131 progenies of sugar beets which were exposed to cross-pollination with table beets. They were planted in a field of table beets in such a manner that the distance between the sugar beets themselves was 25 meters, but they were surrounded by table beets. He found cross-fertilization in 98.4 per cent of the cases. The lowest percentage of identified hybrids was 75.6, and the highest, 100.

Individual beets exhibit considerable variation with regard to self-fertility, as has been shown by Grinko.[6] On the average, however, cross-fertilization is the rule, especially in strains which show high sterility under conditions of self and close-pollination. Sterility was strongly pronounced in the P19 beets which were isolated individually or in groups of closely related plants.

Results of Hybridization.—In the discussion of the results obtained with P19 beets which were exposed to cross-pollination with beets of other origin, no attempt will be made to analyze the inheritance of resistance or any other character. The data at hand are not sufficient for such an analysis. It is possible to show, however, that some definite changes of the characteristics of the P19 strain have been secured.

With regard to improvement of vigor and shape of root, the most successful results were obtained by exposing a P19 beet to cross-pollination with a beet of the California resistant strain developed by Dr. Eubanks Carsner of the United States Department of Agriculture. The two strains show marked morphological differences. The P19 beet roots are short and broad; those of the California, long and tapering. The tops of the P19 are sparse, form a flat rosette, and have a pale green color; those of the California are more dense and erect, and the leaves are of a darker color. Both strains are markedly resistant to curly top, and are low in sugar.

The seed from the two mother plants which were crossed was kept separate. Some of the seed from each mother was planted immediately after harvest, and the stecklings were transplanted in groups and individually in the spring of 1928. Two progenies of the F1 generation (reciprocal crosses) were available for the test of 1928, and several lots of F2 progenies for the test of 1929.

Both plants of the parental generation yielded abundant seed of high viability. The resulting progenies showed a markedly increased vigor. This character was observed during the second as well as during the first year of growth, for the transplanted roots developed unusually vigorous seed stalks, and seed was set abundantly.

With regard to resistance, sugar percentage and morphologic characteristics, the two progenies (i.e., reciprocal crosses) of the F1 generation were similar. The characteristics of the top of the California beet, such as length of petioles, erectness, and darker color, appeared to be dominant. The roots were long, resembling those of the California strain. The sugar percentage was comparable with that of the parent strains.

As the conditions of curly-top inoculation were not favorable in 1928, the reduction in yield in the commercial beets was slight in comparison with the P19 strain (see tables 1 and 5). The hybrid progenies, however, gave a very much higher yield than either the commercial or the P19 seed, owing to their higher vigor.

Table 4 gives the weight and sugar percentage of the mother plants, and table 5 presents the results obtained with the F1 generation.

The progenies of the F2 generation of the P19 × California hybrid, which were tested under conditions of severe infection in 1929, showed a remarkably high degree of resistance. They gave a yield not only

TABLE 4

CHARACTERISTICS OF P19 AND CALIFORNIA MOTHER BEETS WHICH WERE USED FOR HYBRIDIZATION

Pedigree No.	Weight of root, grams	Sugar	
		Per cent	Grams per beet
628/26—P19	577	16.4	95
814/26—Calif	1,615	14.6	236

TABLE 5

RESISTANCE TEST OF THE F1 GENERATION OF THE P19 × CALIFORNIA HYBRID, 1928

Strain	Roots per 100 feet of row, Kgm.	Average weight per beet, grams	Sugar	
			Per cent	Kilograms per 100 feet of row
P19 ♀ ×Calif. ♂ F1	157.69	1,460	14.2	22.39
Calif. ♀ ×P19 ♂ F1	140.71	1,393	14.2	19.98
P19 fifth generation	67.98	687	15.0	10.20
Checks	62.03	634	17.9	11.10

very much higher than the commercial checks, but also higher than any other resistant strain. Furthermore, while every beet in the commercial checks and in all other strains, including the P19, showed symptoms of curly top, the hybrid progenies had a high percentage of beets which failed to develop the symptoms. A possible explanation of this condition is that the curly-top virus might have been extremely attenuated in the symptom-free beets. Cases of such extreme attenuation of the virus in resistant beets have been reported by Lackey.[8]

Table 6 presents the results obtained with the F2 generation. Plate 1 shows the behavior of the F2 progenies under the severe infection of 1929. Figures 3, 4, 5, and 6 show the effect of hybridization upon the shape of the P19 root.

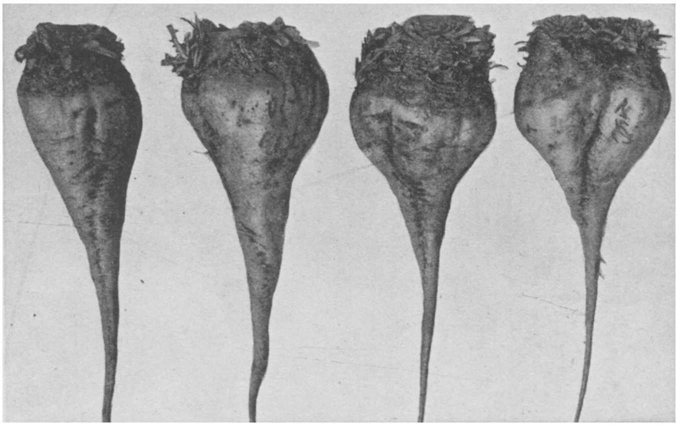

Fig. 3. Types of roots of the P19 strain. The three types represented on the right-hand side occur more commonly than the one on the extreme left.

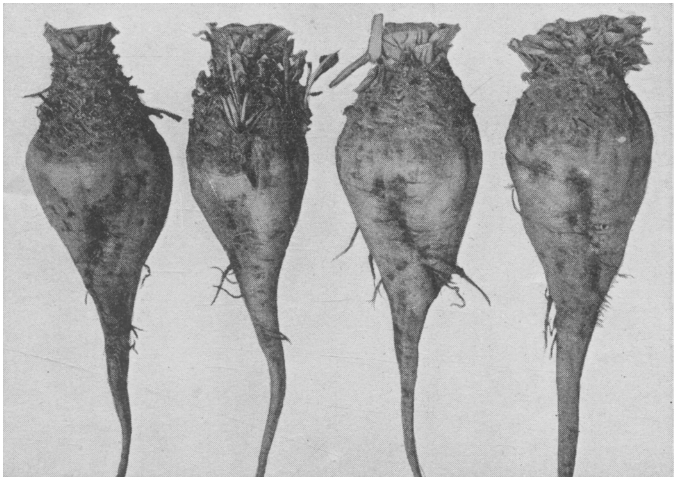

Fig. 4. Types of roots of the California strain.

Tables 5 and 6, figures 3 to 6, and plate 1 show that the progenies obtained through hybridization of the P19 with the California strain are far superior to the P19 strain with regard to vigor and to shape of root.

With the object in view of increasing the percentage of sugar in the P19 strain, a P19 beet was exposed to cross-pollination with a beet of the strain 651–3 produced by Dr. Dean A. Pack of the United States Department of Agriculture. This strain was developed for high yield and high sugar percentage and without reference to curly top. Incidentally it was found to be somewhat resistant to curly top.

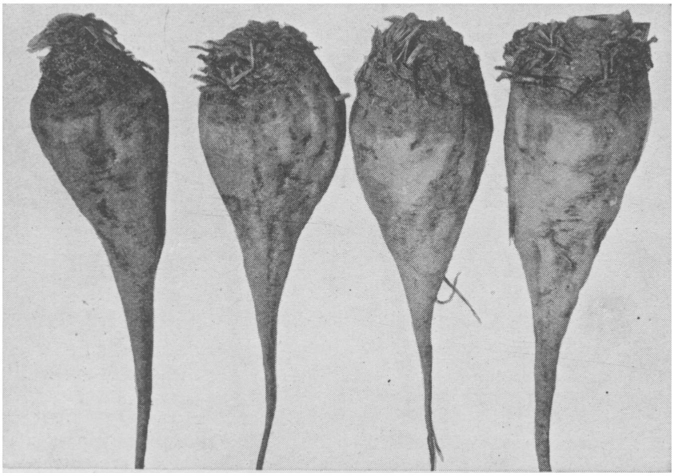

Fig. 5. Types of roots of a P19 ♀ × California ♂ progeny.

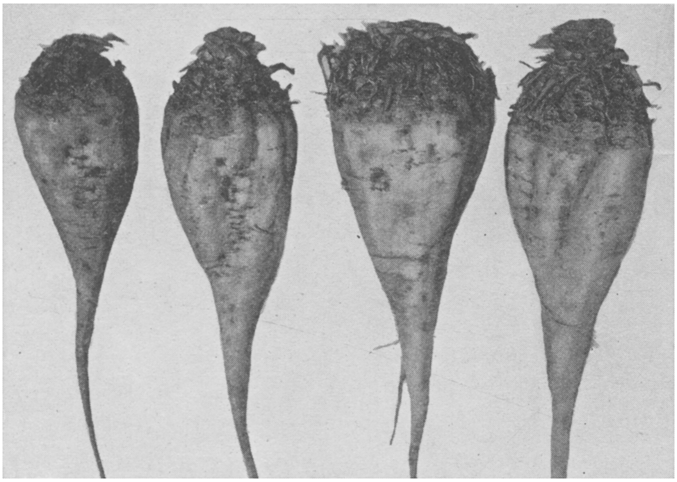

Fig. 6. Types of roots of a California ♀ × P19 ♂ progeny.

Table 7 shows the characteristics of the mother plants, and table 8 presents in a preliminary way the results of the resistance test of the F1 generation.

Table 8 shows that the P19 × 651–3 hybrid progenies of the two reciprocal crosses have a marked degree of resistance and a high sugar percentage. A comparison of this table with tables 2 and 3 shows that these hybrid progenies are far superior to the P19 with regard to sugar percentage.

TABLE 6

RESISTANCE TEST OF THE F2 GENERATION OF THE P19 × CALIFORNIA HYBRID, 1929

Strain	Number of beets per 100 feet of row		Percentage of beets that survived	Percentage of beets that remained free from symptoms	Beets per 100 feet of row, Kgm.		Average weight per beet, grams		Sugar	
	On May 8	At harvest			Tops	Roots	Tops	Roots	Per cent	Kilograms per 100 feet of row
P19 ♀ ×Calif.♂ F2	140	134	96	67	31.98	136.40	239	1018	13.7	18.69
Calif. ♀ ×P19♂ F2	140	129	92	53	32.34	112.95	251	876	12.7	14.34
P19 ♀ ×Calif.♂ F1	128	124	97	54	43.95	151.55	355	1222	12.8	19.14
Average of checks	139	55	40	0	0.87	7.32	16	133	16.2	1.19
P19 fifth generation	76	69	91	0	7.59	24.25	110	351	14.1	3.42
Average of checks	138	49	36	0	1.67	6.47	34	132	16.1	1.04

TABLE 7

CHARACTERISTICS OF P19 AND 651–3 MOTHER BEETS WHICH WERE USED FOR HYBRIDIZATION

Pedigree No.	Weight of roots grams	Sugar	
		Per cent	Grams per beet
1973/27—P19	1,928	11.0	212
1975/27-651-3	1,162	17.0	198

TABLE 8

RESISTANCE TEST OF THE F1 GENERATION OF THE P19 × 651–3 HYBRID

Strain	Number of beets per 100 feet of row		Percentage of beets that survived	Beets per 100 feet of row, kgm.		Average weight per beet, grams		Sugar	
	On May 8	At harvest		Tops	Roots	Tops	Roots	Per cent	Kilograms per 100 feet of row
1973/27-P19 ♀ / 1975/27-651-3♂ F1	133	130	98	8.75	33.16	67	255	17.2	5.70
1975/27-651-3 ♀ / 1973/27-P19♂ F1	144	130	90	8.07	43.09	62	332	17.3	7.46
Average of checks	145	65	45	1.99	8.53	31	131	15.8	1.35

MASS SELECTIONS FOR RESISTANCE

Seed Production.—Additional selections for resistance in commercial fields and in commercial check rows in the trial plots were carried out each season. The mother beets of the later selections were treated *en masse,* because suitable locations for the isolation of seed beets were scarce, and most of them were reserved for the P19 strain. The initially selected beets were planted together and were allowed to cross-pollinate freely within the group. However, the seed from individual mother beets was kept separate. In the succeeding generations the mother beets were grouped according to size and sugar percentage, but were not hooded.

It was found that most of the beets of initial selections did not produce any seed; and those that did go to seed yielded, with a few exceptions, progenies which showed at least some degree of resistance when compared with an ordinary commercial strain. Carsner and Stahl[5] call attention to the fact that curly top materially affects the production of beet seed. Curly-top-diseased beets either fail to go to seed in the second year or produce only dwarfed, diseased stalks. The probability is that in the case of the initial selections from severely diseased beets in commercial fields, the majority of beets which did not possess an inherent resistance failed to go to seed. Accidental factors may have influenced the growth of such individuals during the first year, making them appear resistant regardless of the presence of symptoms upon the foliage. In the second year, after transplanting, however, such beets in most cases would show the effect of the disease by developing severe symptoms and by failing to go to seed normally. A practice was adopted to aid this second natural selection for resistance by eliminating before anthesis those individuals which produced only dwarfed or small seed stalks.

Table 9 shows the behavior of the different selections for resistance during the second year of growth. Apparently the development of seed stalks in the second year in curly-top-infected beets is correlated with resistance.

It will be noted that the percentage of seed stalks was higher in the initial selections from check rows than in the initial selections from commercial fields. The reason is that a more severe selection for resistance was made among the beets of the check rows because they were planted under conditions most favorable for the development of curly top.

Test for Resistance of Mass-selected Progenies.—The progenies of the later selections were tested for resistance together with the P19 strain and under similar conditions. With the exception of 1928, the

TABLE 9

PERCENTAGE OF SEED STALKS DEVELOPED NORMALLY DURING THE SECOND YEAR OF GROWTH IN VARIOUS STRAINS SELECTED FOR RESISTANCE

Kind of selection	Year of selection	Number of beets selected	Beets which produced normal seed stalks	
			Number	Per cent
Initial selections from commercial fields	1919	5,000	183	3.7
	1923	3,000	24	0.8
	1924	1,176	101	8.6
	1925	472	25	5.3
Initial selections from check rows	1925	38	13	34.2
	1926	12	3	25.0
Second selections	1925 (P23)	50	31	62.0
	1926 (P24)	143	82	57.3
Third selections	1925 (P19)	219	185	84.5
	1926 (P19)	76	64	84.2

TABLE 10

RESULTS OF THE RESISTANCE TEST OF MASS-SELECTED PROGENIES (1925 TO 1929)

Location of test plots	Date of seeding	Strain	Generation	Number of progenies	Number of beets per 100 feet of row		Percentage of beets that survived	Roots per 100 feet of row, kgm.	Average weight per beet, grams
					Early in season	At harvest			
Greenfield	Mar. 13, 1925	P23	First	8		93		13.17	142
		Check				74		5.75	78
King City	Mar. 24, 1926	P24	First	101		41		9.79	239
		Check				10		0.76	76
King City	April 4, 1927	P24	First	16	63	50	79	16.07	321
		Check			66	33	50	2.65	80
King City	April 4, 1927	P25	First	24	81	61	75	16.64	273
		Check			71	26	37	1.83	70
Davis	Mar. 17, 1928	P24	Second	36	111	108	97	115.76	1,072
		Check			113	111	98	128.30	1,156
Davis	Mar. 21, 1929	P25	Second	18	130	110	85	33.26	302
		P19 check			95	86	91	21.51	250
		Commercial check			141	48	34	7.05	147

conditions for curly-top infection were favorable every year. In 1928 leafhoppers were not disseminated upon the mass-selected progenies, and as they were removed some distance from the plots where nymphs were distributed, they became infected very late and to no appreciable

Fig. 7. Resistance test of mass-selected progenies. Row 1, resistant mass-selected progeny. Row 2, commercial check. Row 3, resistant mass-selected progeny. King City, September 26, 1927.

Fig. 8. The same progenies as in figure 7 shown at harvest time. The respective yields per 100 feet of row were: (1) 21.55 kgms; (2) 0.91 kgms; (3) 22.23 kgms. King City, October 18, 1927.

extent. Table 10 presents the results obtained with the mass-selected progenies, and figures 7 and 8 show the effect of curly top upon two of the progenies and the corresponding check row.

Sugar Analyses of the Mass-selected Progenies.—The beets of the initial selections were not analyzed for sugar. Their size and shape were the two principal characteristics upon which the selection was based. In the first filial generation, however, the future mother beets were also tested for sugar. The analyses were conducted according to the same methods as were followed in the case of P19 beets. Tables 11 and 12 below give the results of the analyses.

TABLE 11

AVERAGES OF THE RESULTS OF SUGAR ANALYSES OF INDIVIDUAL BEETS OF THE FIRST FILIAL GENERATION OF MASS-SELECTED BEETS AND OF THE CORRESPONDING COMMERCIAL CHECKS

Year	Strain	Number of beets tested	Average weight per beet, grams	Sugar	
				Per cent	Grams per beet
1925	P23	61	628	18.1	114
	Check	10	603	18.5	112
1926	P24	409	706	14.4	102
	Check	10	690	15.6	108
1927	P24	85	1,003	14.1	141
	P25	131	934	15.4	144
	Check	19	1,053	14.3	151

TABLE 12

SUGAR ANALYSES OF COMPOSITE SAMPLES OF THE MASS-SELECTED PROGENIES AND OF THE CORRESPONDING COMMERCIAL CHECKS

Location of test plots	Date of seeding	Strain	Generation	Average weight per beet, grams	Sugar	
					Per cent	Kilograms per 100 feet of row
King City	April 4, 1924	P24	First	421	14.6	2.81
		P25	First	376	15.0	1.90
		Check		190	14.8	0.31
Davis	Mar. 17, 1928	P24	Second	1,056	16.6	19.22
		Check		1,163	16.5	21.17
Davis	Mar. 21, 1929	P25	Second	463	16.5	5.49
		P19 check		334	13.8	2.97
		Commercial check		318	16.0	1.13

Results Obtained with the Mass-selected Progenies.—Some of the progenies of mass-selected beets showed a considerable degree of resistance in the first and in the second generations. Owing to better germination and better stands, they gave in most cases a higher yield than the average of the P19 progenies. The percentage of surviving beets was higher and the average size of roots larger than in the commercial checks.

Unlike the P19 strain, the mass-selected progenies showed little uniformity with regard to the degree of resistance and to morphological characteristics. The plants, even within the individual progenies, showed variation in the severity of symptoms developed, and in many cases the most advanced symptoms could be observed in some beets of the most resistant progenies. When exposed to infection the mass-selected progenies showed a lower percentage of surviving beets and usually a smaller average size of roots than the P19.

The sugar percentage was found to be as high in these strains as in the commercial checks. The total sugar content was considerably higher than in the commercial beets, when the trial was conducted under exposure to infection.

SUMMARY

1. The breeding of sugar beets for resistance to the curly-top disease was conducted for five years.

2. Plants that were apparently less injured by the disease in severely infected commercial sugar beet fields served as initial selections for the development of resistant strains.

3. The seed obtained from such beets was tested for resistance, together with ordinary commercial seed under exposure to a severe infection with curly top.

4. Resistance to curly top was found to be an inherent characteristic of many individual beets selected in commercial fields.

5. In the case of one of the most resistant strains, designated as P19, a consistent transmission of this characteristic through five successive generations was observed.

6. When grown under exposure to infection, the P19 strain gave a higher yield, a higher percentage of surviving beets, and a higher average size of roots than the commercial strain (R. & G. Old Type), with which it was compared.

7. Immunity was not observed in the P19, or in any other resistant strain; the P19 beets, however, developed as a rule only the transparent venation, which was discernible only with some difficulty.

8. The resistance of the P19 strain was found to be relative; under exposure to more severe conditions of testing for resistance the percentage of surviving beets decreased somewhat and the yield became lower, although it was always much higher than in the corresponding check rows.

9. With regard to sugar analyses, the P19 strain tested usually 2 to 3 per cent lower than the commercial beets which were grown under similar conditions. When not exposed to a severe infection with curly top, the total sugar per unit area was higher in the commercial beets; when subjected to a severe infection the P19 strain gave a much higher yield of total sugar per unit area than the commercial.

10. The P19 strain was found to be of no value for commercial purposes owing to (1) the low viability of seed, (2) the low sugar content, (3) the reduced vigor, and (4) the undesirable shape of the root.

11. With the object in view of improving the undesirable characteristics of the P19 strain, some hybridization experiments have been started. Cross-pollination between P19 and another resistant strain, of greater vigor and with a better shape of root, gave very resistant progenies, which also showed marked increase in vigor and a better shape of root. This hybrid, however, was low in sugar. Cross-pollination between the P19 and a strain less resistant but high in sugar, gave resistant progenies which showed an increase in sugar percentage in comparison with the P19.

12. In addition to the work with the P19 strain, selections of resistant mother beets in the commercial plantings were carried out repeatedly for several years and were propagated *en masse*. The progenies of these mother beets were compared with ordinary commercial seed and with the P19 under exposure to infection with curly top.

13. The mass-selected progenies were markedly resistant to curly top, although less uniform with regard to this characteristic than the P19 strain.

14. The mass-selected progenies were as high in sugar percentage as the commercial checks with which they were compared.

ACKNOWLEDGMENTS

The writer wishes to acknowledge the cooperation of the Spreckels Sugar Company, which organization initiated these investigations, and provided facilities for conducting a major part of them; also the advice of the late Mr. G. E. Bensel, who was in charge of the experiment station of that company; the valuable suggestions of Dr. E. Carsner of the United States Department of Agriculture; and the criticism of the manuscript by several members of the College of Agriculture of the University of California.

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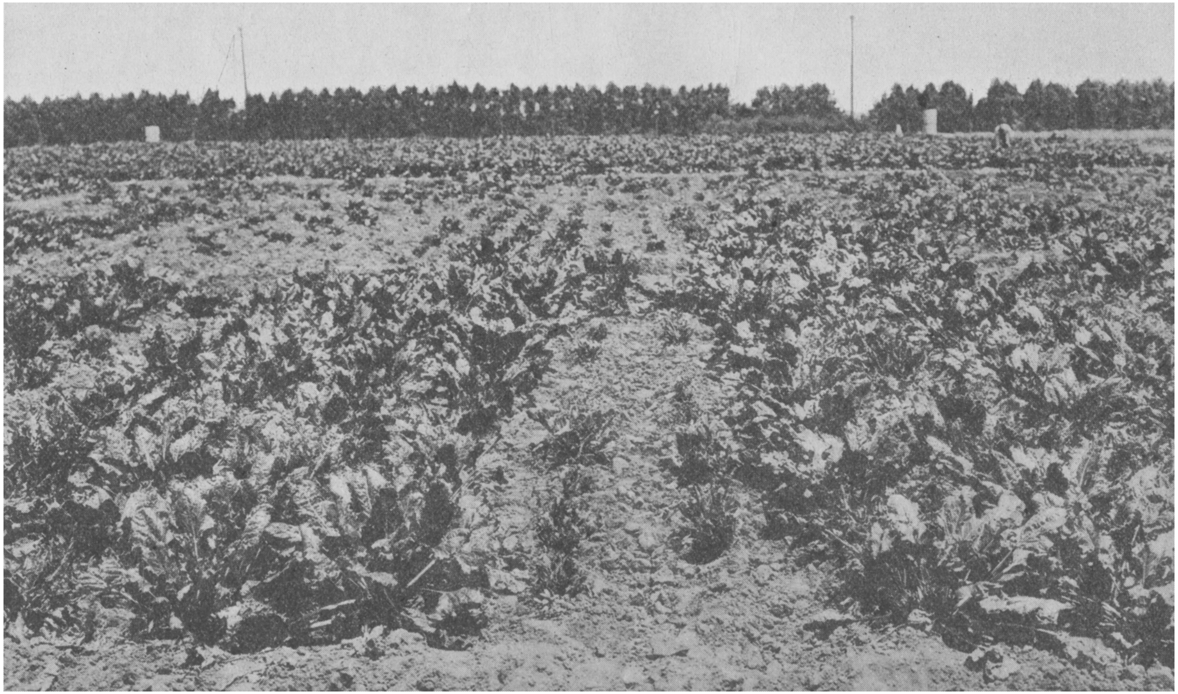

The P19 ♀ × California ♂ hybrid progenies (4 rows left and right) and commercial beets (2 rows in the center) under exposure to a severe infection with curly top. Davis, California, July 8, 1929.

The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
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