Breeding for Resistance to Downy Mildew In Sugar Beets

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Introduction

Downy mildew caused by the fungus, *Peronospora schactii* Fuckel, is an important disease of sugar beets in the coastal districts of California. Its seriousness has been demonstrated by Leach (3)[2], who found that infected beets produced 30 to 40 percent less sugar than healthy beets growing in the same field. Losses are particularly severe in seasons characterized by long periods of cool, foggy weather. This may be attributed to the low temperaure and high humidity requirements of the causal organism for germination and infection.

When a severe infection occurs in the seedling stage, young plants may be killed by the disease, thereby causing poor stands. Infection which occurs after thinning ordinarily does not kill the plants, but may cause permanent stunting. Leach (3) has shown that the younger a plant is when infected with mildew the more serious the damage. Losses from mildew are expressed as a reduction in size, in sucrose percentage and in purity of the beet.

The U. S. 15 variety (1) is the most resistant of the commercial varieties, and will withstand moderate attacks of the disease. The U. S. 56 variety (6) has also been shown to be moderately resistant. Leach (3) demonstrated that the mildew resistance of a variety could be improved by selection in the greenhouse, and developed an improved strain of the U. S. 33 variety.

This paper reports progress in breeding sugar beets which are highly resistant to mildew. Emphasis has been placed on the inbreeding method.

Procedure

Selections for resistance to downy mildew were made in the greenhouse at Salinas, California, during the period 1948-1951, using a technique similar to that described by Leach (3). Plantings were made in flats of steam-sterilized soil which were then placed in a warm greenhouse (20° to 24° C.) until the plants had two to four true leaves and were large enough for inoculation.

Following emergence of the seedlings, the flats were uniformly thinned to 150-200 seedlings per flat. Inoculations were made with a spore suspension prepared by washing conidia from young, recently infected beet leaves. The spore suspension was sprayed uniformly over the seedlings, using a pressure sprayer. Following inoculation, the flats were placed in a humid inoculating chamber which was maintained at a temperature of 5° to 10° C. A fresh spore suspension was sprayed over the seedlings at the end of 24 hours. The flats were removed from the chamber 48 hours after the first inoculation, and were placed in a cool, humid section of the greenhouse for disease development.

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[2] Numbers in parentheses refer to literature cited.

As mildew developed, the flats were returned to the inoculating chamber for 48-hour periods at 10-day to two-week intervals. This was continued until 90 percent or more of the plants were infected. Mildew-free plants were transplanted to the field for seed production. When selections were made in easy bolting seed stocks before February 1, it was possible to obtain a seed crop the year the selection was made. Selections made in non-bolting seed stocks and in easy bolting stocks after February 1 were carried over until the following year for seed production.

The progenies of the greenhouse mildew selections were tested for field resistance under conditions favorable for mildew development. In order to obtain a uniformly heavy infection throughout the test plots, two-row strips of a susceptible variety were planted at 20-foot intervals during the fall months. Uniform infection in these strips was obtained by transplanting mildew-infected plants at 15- to 20-foot intervals in the rows. The test plantings were made between the mildewed strips in March at a time when temperature and humidity were expected to be most favorable for infection.

Table 1.—Comparative Downy Mildew Resistance of Varieties and Selections Planted at Salinas, California, March 10, and Counted May 29, 1950.

Strain No.	Description	Percent Mildew
SL 824	Sugar selection U. S. 22/3	50.5
C 973	Greenhouse mildew selection U. S. 22/3	36.2
SL 831	Non-bolting selection U. S. 22/3	41.8
C 975	Non-bolting selection SL 831	31.2
SL 858	Curly-top selection U. S. 56/2	40.0
C 972	Greenhouse mildew selection SL 858	34.5
SL 859	U. S. 56/2	41.4
C 970	Non-bolting selection U. S. 56/2	60.6
SL 715	U. S. 15 (damaged by curly top)	20.8
Difference required for significance (19:1 odds)		5.2

The test material was planted on low beds 20 inches apart in two-row plots, 40 feet long. The beets were thinned to approximately four inches between plants. In order to reduce bias in favor of healthy plants at thinning time, the laborers were provided with 4-inch thinning guides and instructed to thin uniformly without regard to the appearance of the plants. To encourage a heavy infection, the relative humidity was increased by lightly irrigating the plantings every two or three days. Mildew counts were made in May and June.

Results

Field Tests with Varieties and Selections

In 1950, two greenhouse mildew selections and a group of commercial varieties and non-bolting selections from commercial varieties were tested for mildew resistance in a field planting using eight replications. The conditions were favorable for mildew infection at thinning time and for about a month following thinning. As is shown in Table 1, infection ranged from 20.8 to 60.6 percent. The U. S. 15 variety proved to be the most resistant, although the amount of infection may have been influenced by the curly-top disease which damaged this variety. A sugar selection from

U. S. 22/3, designated SL 824, was the most susceptible of the commercial varieties. This selection had previously been shown to be similar in mildew resistance to U. S. 22/3. The greenhouse mildew selection C973 from U. S. 22/3 showed a highly significant superiority in mildew resistance as compared with SL 824. The mildew selection, C972, was significantly more resistant than the parent stock, U. S. 56/3. The non-bolting selections from U. S. 22/3 showed progressively increased improvement in mildew resistance even though they had not been selected for mildew resistance. The most susceptible strain was C970, a non-bolting selection from U. S. 56/2.

A similar group of varieties and selections was tested in 1951 in a field planting consisting of ten replications. A severe infection of mildew occurred while the plants were in the seedling stage, but disease development and further infection were checked by high temperatures shortly after thinning. As is shown in Table 2, the range in infection was less than in 1950.

The U. S. 15 variety was among the more resistant varieties or selections, and the non-bolting selection from U. S. 56/2 was the most susceptible. The two greenhouse mildew selections, C071 and C073, tended to show a lower

Table 2.—Comparative Downy Mildew Resistance of Varieties and Selections Planted at Salinas, California, March 12, 1951, and Counted May 29, 1951.

Strain No.	Description	Mildew	
		Total	Severe
		%	%
SL 824	Sugar selection U. S. 22/3	44.8	9.5
C 071	Greenhouse mildew selection SL 824	42.3	7.7
SL 831	Non-bolting selection U. S. 22/3	42.4	10.7
C 075	Non-bolting selection SL 831	33.6	5.2
SL 859	U. S. 56/2	48.6	13.6
C 073	Greenhouse mildew selection U. S. 56/2	44.6	11.8
C 070	Non-bolting selection U. S. 56/2	63.8	27.0
C 065	Non-bolting selection F_2 (U. S. 56/2 x U. S. 22/3)	33.1	7.7
C 715	U. S. 15	36.0	7.6
Difference required for significance (19:1 odds)		6.4	3.2

incidence of mildew than the parent stocks, but the differences were not significant. The I J. S. 56/2 variety proved to be one of the most susceptible of the commercial varieties, and was more severely damaged than in either the 1950 test or in tests reported by Price, Owen, and Carsner (6) .

The non-bolting selection, C075, which was a direct seed increase of C975 used in the 1950 test, again showed a low incidence of mildew. A new non-bolting selection from the F_2 of a cross between U. S. 56/2 and' U. S. 22/3 showed only 33.1 percent mildew, which was the lowest of any selection or variety in the test.

Field Tests with Inbreds

A preliminary test of inbred lines was made in a non-replicated field planting in 1950 . Infection was heavy and occurred uniformly throughout the planting. Included was a group of inbred sublines which originated from mildew-resistant plants selected in the greenhouse from an S_2 popu-

lation of a cross between the mildew-susceptible SL 453 and the moderately resistant SL 4201.

The results with eight of these sublines and with the SL 4201 and CT9 inbreds are shown in Table 3. All eight of the sublines were more resistant than the moderately resistant female parent, SL 4201. Infection of individual sublines ranged between 2 and 24 percent, thereby making it possible to select highly resistant inbreds for increase and further study. The curly-top-resistant inbred, CT9, proved to be highly susceptible.

In 1951, a group of seven inbreds was tested in a field plot using six replications. Environmental conditions were favorable for infection from the time the seedlings emerged until the beets were thinned. A heavy incidence of mildew occurred on the cotyledons of both the susceptible and resistant inbreds. Many seedlings, particularly in the suceptible inbreds, were killed before true leaves were formed. Mildew counts were made when the plants were six weeks old and the average percent infection occurring in each of the inbreds is shown in Table 4. Infection ranged from 3.4 percent in the P2-20 inbred to 85.0 percent in CT9. Two strains of the non-bolting NB1 inbred showed good resistance, but were inferior to the three inbreds selected for mildew resistance in the greenhouse. The P2-16 and P2-20 inbreds were increases of the two sublines carrying similar numbers in the 1950 test. The original monogerm inbred discovered by Savitsky (7) proved to be intermediate in resistance.

Table 3.—Comparative Downy Mildew Resistance of Inbreds Planted at Salinas, California, March 23, and Counted May 31, 1950.

Strain No.	Description	No. of Plants	Percent Mildew
P2-2	S_3 (SL 453 x SL 4201)	121	10
P2-4	S_3 (SL 453 x SL 4201)	93	3
P2-6	S_3 (SL 453 x SL 4201)	132	14
P2-8	S_3 (SL 453 x SL 4201)	82	24
P2-10	S_3 (SL 453 x SL 4201)	140	6
P2-16	S_3 (SL 453 x SL 4201)	148	3
P2-18	S_3 (SL 453 x SL 4201)	123	15
P2-20	S_3 (SL 453 x SL 4201)	99	2
C 8255	SL 4201 selfed	252	81
SL 69	CT9, Curly-top-resistant inbred	106	92

Infection in the resistant inbreds was limited primarily to localized areas on the leaves. Rarely were plants observed which showed systemic infection of the entire crown. Later in the season, when environmental conditions became unfavorable for mildew, the plants with the localized infection could not be distinguished from non-infected plants.

Discussion

Advantages of the Greenhouse Method

Increased field resistance to mildew can be obtained by selecting in the seedling stage under controlled greenhouse conditions. This method offers some definite advantages over a field selection method, the most

important being dependability. Although environmental conditions favorable for field mildew epidemics may be expected in the spring months along the California coast, the date of their occurrence varies from year to year.

In order to be reasonably sure of obtaining a satisfactory field test, it is necessary to make two or more plantings at progressive dates. Even when this precaution is taken, a heavy infection does not always occur, and a portion of the selected plants merely escape infection. When the greenhouse method is used, temperature and humidity can be controlled, thereby insuring more dependable exposures than are possible in the field.

During a single season, one can test as many plants in a greenhouse with 500 to 1,000 square feet of floor space as can be tested in an acre field plot. This method has the added advantage of utilizing help at a time when the field program is least pressing. Selecting for resistance in the greenhouse is also less costly than in the field.

Table 4.—Comparative Downy Mildew Resistance of Inbreds Planted at Salinas, California, March 23, and Counted June 14, 1951.

Strain No.	Description	Mildew	
		Total	Severe
P2-20	S_4 (SL 453 x SL 4201)	3.4	0.1
P2-16	S* (SL 453 x SL 4201)	5.7	0.9
P3-9	S_3 (U. S. 22/3 x SL 4200-14)	6.1	0.3
C 0502	NB1, Non-bolting inbred	18.3	0.6
C 0504	NB1, Non-bolting inbred	22.3	1.7
SL 101	Monogerm inbred	41.7	1.3
SL 9092	CT9, Curly-top-resistant inbred	85.0	12.6
Difference required for significance (19:1 odds)		7.3	2.5

Advantages of Selecting in Self-fertile Lines

The results of these studies have demonstrated that mildew resistance can be gained more rapidly by selecting in self-fertile lines rather than in cross-pollinated varieties or selections. Even though a group of plants is able to withstand severe exposure to mildew during the selection process, the progenies of the individual plants differ greatly in their resistance.

Unless the selected plants can be selfed and the progenies tested individually, it is difficult to separate the inherently resistant genotypes from those with only moderate resistance. Selections from cross-pollinated varieties cannot ordinarily be selfed, so it is necessary either to make massed seed increases from the group of selected plants or adopt a system of controlled crossing. If the mass increase method is used, the gain in mildew resistance from any given group of plants can be expected to be materially less than when the individual plants are selfed or crossed in pairs.

Although the cultivated sugar beet is normally self-sterile, self-fertile breeding stocks can be readily developed by incorporating the S^f gene described by Owen (4). Through the utilization of cytoplasmic male sterility (Owen, 5), mildew-resistant inbreds can be used in developing hybrid varieties of sugar beets.

Influence of Age of Plants on Resistance

The resistance of any given variety or selection is influenced by the age of the plants and by the growing conditions at the time infection occurs. Mildew is primarily a disease of young, actively growing tissue. Plants which are old and stunted can rarely be infected either in the greenhouse or field. All strains observed in these tests are most susceptible in the cotyledon stage, although strains may vary in their susceptibility at this stage of growth. As true leaves are formed, the difference in resistance between strains become more pronounced.

Summary

The progenies of selections made in the greenhouse under conditions of uniformly heavy mildew infection showed improvements in mildew resistance when tested in the field. The greenhouse method of selection proved more dependable and cheaper than the field method.

The greatest gains in resistance were made by selecting in self-fertile lines rather than in cross-pollinated varieties and selections. The variability in mildew infection among inbred lines ranged from 3 to 85 percent, and demonstrated the heterozygosity of the cultivated sugar beet for mildew resistance. The possibility of developing highly resistant hybrid varieties was suggested.

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