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EFFECT OF DOWNY MILDEW ON PRODUCTIVITY OF SUGAR BEETS, AND SELECTION FOR RESISTANCE[1,2]

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INTRODUCTION

FOR MANY YEARS downy mildew has been recognized as a serious disease of sugar beets in the coastal regions of California during seasons when climatic conditions favored the development of the fungus. Farther inland, before 1935, this disease was considered of only minor importance; but in 1935, 1936, and 1937 there were serious epidemics over wide areas in the lower Sacramento Valley.

This disease, caused by *Peronospora schachtii* Fuckel, has been known in Europe since 1852, but was first reported in the United States by R. E. Smith and E. H. Smith (*7*)[4] in 1911. During subsequent seasons downy mildew appeared sporadically in the coastal sugar-beet-producing areas. In 1926 and 1927 Bensel[5] reported severe outbreaks in the Santa Clara Valley. Since 1930 the disease has appeared regularly in the Salinas Valley of Monterey County, the Santa Maria Valley of Santa Barbara County, and in Ventura and Orange counties. There were destructive outbreaks in the Salinas Valley in 1930, 1937, and 1938; moderate epidemics during other seasons. According to a 1937 survey by Mr. Suttie of the Spreckels Sugar Company, covering 3,721 acres, about 22 per cent of the beets were infected by the middle of June. In 1938, up to 80 per cent of the beets were infected in some fields in the Salinas Valley.

The same fungus frequently ruins garden beets grown for the market or for seed, as in 1929, when 40 per cent of the seed crop in the Sacramento Valley

[1] Received for publication September 28, 1943. The field experiments reported in this paper were made possible through financial contributions by the beet-sugar companies operating in California. The project on the selection of sugar beets for resistance to downy mildew was discontinued at the end of the 1940 season; and, with the consent of the sugar companies, all materials that appeared to be of value for further testing or selection were made available to the United States Department of Agriculture, Office of Sugar Plant Investigations, for incorporation in their project on sugar-beet improvement.

[2] The writer wishes to thank M. W. Gardner and J. B. Kendrick for advice during the investigations and the preparation of the manuscript, and to acknowledge assistance in part of this work from B. R. Houston, H. Rex Thomas, Wayne F. Weeks, and David N. Wright.

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[4] Italic numbers in parentheses refer to "Literature Cited," at the end of this paper.

[5] Bensel, G. E., 1927. Mildew of sugar beets (*Peronospora schachtii* Fuckel). Unpublished report. Spreckels Sugar Company, Dept. Agr. Res. Rept. 2:19–21.

was destroyed (*4*). Downy mildew has also been reported on garden beets in Oregon and Washington and observed at times on sugar beets in Colorado.

Though small plants may be killed by a severe infection of downy mildew, this disease is rarely fatal to sugar beets past the thinning stage. Under certain conditions, secondary organisms gain entrance through leaves killed by the mildew, and rot the crown or the entire root. High temperature seems especially favorable for this secondary decay. The direct effects of the fungus on the plant are usually of greater importance. Infected leaves are malformed and smaller, but often more numerous than the leaves on normal plants. Because the infection is systemic in the growing point, there is complete infection of all the new heart leaves formed while conditions favor the fungus. Often new growing points are established on the periphery of the crown; the result is irregularly shaped roots and a divided crown. Some crowns are hollow because of the unequal growth; these, together with the killed leaves, provide openings for secondary organisms. Most of the infected plants recover from the infection with the advent of dry, warm weather and grow almost normally; but a number remain permanently stunted. In the opinion of growers and sugar-company officials, not only is the yield strikingly reduced by the infections, but the sucrose per cent and the apparent purity of beets from mildewed fields is also lower than from disease-free fields, a condition that interferes seriously with sugar extraction.

TABLE 1

EFFECT OF DOWNY MILDEW ON THE PRODUCTIVITY OF SUGAR BEETS, SALINAS, 1930*

	Average root weight, pounds	Sucrose, per cent	Purity, per cent	Relative yield	
				Root weight	Indicated available sugar†
Noninfected beets	3.13	13.5	83.8	100.0	100.0
Infected beets	2.43	11.5	77.3	77.6	61.0
Difference	0.70	2.0	6.5	22.4	39.0
Significant difference, odds 19:1	0.38	1.16	3.07	....	....

* Planted December 1, 1929; harvested July 17, 1930.
† Assuming 100 per cent extraction. Obtained by multiplying yield by sucrose per cent by purity per cent.

Control of downy mildew on sugar beets by fungicidal sprays or dusts does not appear practicable at present. The sporadic appearance of the outbreaks, the partially systemic nature of the infection in the plant, and the long periods during which protection would be necessary contribute to the difficulties of fungicidal control. Apparently, therefore, the use or development of resistant varieties or strains of beets for areas where downy mildew is prevalent would be the most satisfactory solution; this topic is further discussed in a later section of this paper.

EFFECT OF DOWNY MILDEW ON YIELD

Before the present series of experiments was inaugurated, two trials (*5*) had been conducted to determine how downy mildew affects the size and the yield of sugar beets. In each trial—one at Salinas, California, in 1930 and one near Davis in 1935—the sugar beets in nine plots were separated into diseased and healthy groups, and yield determinations were made on each lot. At Salinas each plot consisted of 100 nonbolting beets growing consecutively in a single bed. The segregation into diseased and healthy groups was made entirely on the basis of downy-mildew symptoms at harvest time, July 17.

As table 1 indicates, the average root weight, sucrose per cent, and apparent purity of the beet juices were significantly lower in the diseased than in the healthy beets. According to these data, downy-mildew infection reduced the yield of roots by 22 per cent and the indicated available sugar by 39 per cent in comparison with noninfected plants in the same plots.

Because at harvest it is often difficult to determine whether or not beets had at some time been infected by downy mildew, the record of infected plants in

TABLE 2

EFFECT OF DOWNY MILDEW ON THE PRODUCTIVITY OF SUGAR BEETS, DAVIS, 1935*

	Average root weight, pounds	Sucrose, per cent	Purity, per cent	Relative yield	
				Root weight	Indicated available sugar†
Noninfected beets	2.27	15.7	87.5	100.0	100.0
Infected beets	1.72	14.3	83.7	75.8	66.0
Difference	0.55	1.4	3.8	24.2	34.0
Significant difference, odds 19:1‡	0.48	n.s.	n.s.	....	....

* Planting date not determined; harvested September, 1935.
† Assuming 100 per cent extraction. Obtained by multiplying yield by sucrose per cent by purity per cent.
‡ The abbreviation n.s. indicates that differences are not significant.

the plots at Davis in 1935 was made on May 20. Observations showed that in this locality there was no spread of downy mildew in the plots after this date. At harvest time (September) the plants previously recorded as infected in each of the nine test rows were segregated from the disease-free plants. As yield data (table 2) reveal, plants not affected developed significantly larger roots than infected plants. The average sucrose per cent and the purity of the healthy plants appeared greater than those of the diseased; but, in this test, the differences were not statistically significant.

Trials at Santa Maria in 1937.—During the spring of 1937, sugar beets were planted at Santa Maria, in coöperation with the Union Sugar Company in order to determine further the effect of downy mildew on the yield of sugar beets and to observe the relative susceptibility of some commercial varieties. Nine varieties were planted in 4-row plots, 100 feet long, and were replicated five times in randomized blocks. Observations were made at intervals of 2 weeks from the time mildew was first observed until near the date of harvest. At each observation the newly infected plants were marked with a stake painted a distinctive color. At the end of the season, therefore, it was possible to segregate the infected beets in each plot according to the period during which mildew symptoms first appeared. Figure 1 shows the increase in per cent of plants infected during the growing season. The planting was made on March 5, and most of the infections were first evident during June. From 2 to 3 weeks is usually required from the time infection actually occurs until the systemic invasion of newly formed leaves can be observed. The period of most abundant infection, therefore, was about May 10 to June 15, when the beets were 65 to 100 days of age. This period coincided with a series of mornings characterized by high humidity, heavy dews, but no actual rainfall.

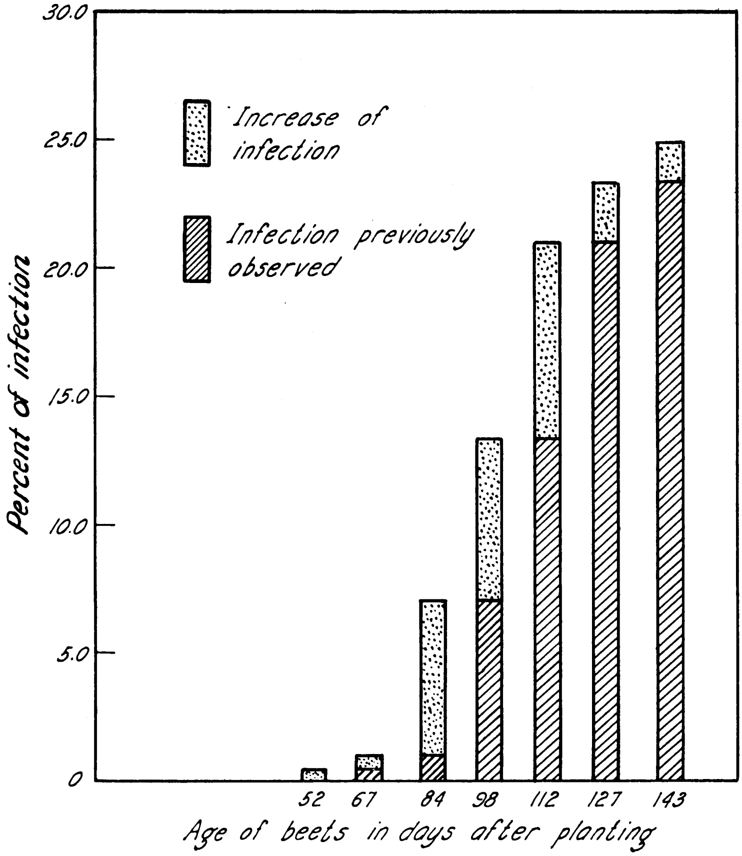

Fig. 1.—The increase of downy-mildew infection on sugar beets planted March 5, 1937, at Santa Maria. The greatest increases of infection were observed between May 28 and June 25, or 84 to 112 days after planting.

On August 17 to 19, when the plots were harvested, the beets first observed to be infected on each of the several dates of observation (fig. 2) were grouped, and their average root weight was determined. In general the results here indicate that the earlier the date of infection, the smaller the beet root at harvest time. An exception is noted in that the beets observed to be infected 52 days after planting show an average root weight about 0.3 pound heavier than the group observed to be infected 2 weeks later; but this difference may be due to experimental error, since the first group contained only a small number of infected roots. The other unusual feature is the fact that the groups of beets first observed to be infected as late as 127 and 143 days after planting showed a higher average root weight than the nonmildewed beets. Actively growing beets are known to be more susceptible to downy mildew than slow-growing ones. In addition, since infection could first be detected only on systemically infected new growth, only the actively growing plants exhibited symptoms of infection. When the observations were made on July 10 and 26, symptoms of recent mildew infection were occurring almost exclusively on large, actively growing beets. Apparently, therefore—because of greater susceptibility or more active growth—there was a tendency for larger-than-average beets to be included in the infection groups during July.

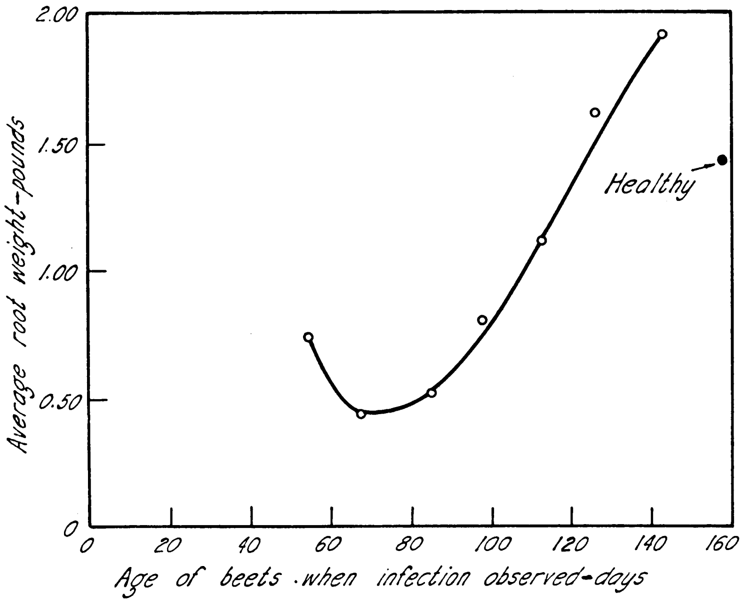

Fig. 2.—The relation between time of downy-mildew infection on sugar beets and the average root weight at harvest. Plants infected within 100 days of planting showed average root weights of less than 1 pound, whereas beets infected later exceeded this amount. Santa Maria, 1937.

To determine further the importance of earliness of infection, the beets were collected into three groups: early-infected plants upon which downy mildew was observed within 100 days after planting, late-infected plants which showed infection between 100 and 150 days after planting, and healthy or noninfected plants. Five samples were selected from each of the three groups in each of the nine varieties and were analyzed for sucrose and apparent purity. Each figure in table 3 represents, therefore, an average of 27 determinations.

As the table reveals, early-infected beets were less than half as large as healthy ones, whereas late-infected beets were nearly normal in size. The sucrose of both early- and late-infected beets was lower by 2 per cent than that of the noninfected. In the same way the average purity of both groups of infected beets was lower by 5 per cent than that of the noninfected beets in the same plots. The group infected between 100 and 150 days of age included beets that were stunted by mildew infection and others that, because of vegetative vigor, weighed more than the average of noninfected beets. Both of these factors may have contributed to the lowered sucrose and purity. Perhaps the beets showing infection after 120 days of age were not adversely affected as to either yield or sugar production.

On the average, to judge from the relative yields shown in the last two columns of the table, the infected beets produced 72.6 per cent as much weight and 58.2 per cent as much sugar per plant as the noninfected. Whereas the late-infected group produced a nearly normal weight and 80 per cent as much sugar per plant as the healthy group, the yield of the early-infected was less than half that of the noninfected.

According to these results, downy mildew interfered with normal production by reducing the average root weight and the sucrose per cent. The death

TABLE 3

EFFECT OF EARLY AND OF LATE DOWNY-MILDEW INFECTION ON THE PRODUCTIVITY OF SUGAR BEETS, SANTA MARIA, 1937

	Average root weight, pounds	Sucrose, per cent	Purity, per cent	Relative yield	
				Root weight	Indicated available sugar*
Noninfected beets	1.35	17.77	81.92	100.0	100.0
Infected beets	0.98	15.42	76.10	72.6	58.2
Early-infected beets (prior to 100 days of age)	0.65	15.12	75.65	48.0	37.6
Late-infected beets (between 100 and 150 days of age)	1.32	15.58	76.29	97.6	79.4

* Assuming 100 per cent extraction. Obtained by multiplying yield by sucrose per cent by purity per cent.

of a considerable number of infected beets is still another factor that reduces productivity; and extraction of sugar is interfered with because of the reduced purity. Infections early in the life of the beet appear considerably more serious in relation to all these factors than are late infections.

Trials at Salinas in 1938.—During the season of 1938, a somewhat similar trial was conducted at Salinas in coöperation with the Spreckels Sugar Company. Ten varieties, some the same as in the previous trial, were planted in 4-row strips, 100 feet long, and replicated six times in randomized blocks.

The seed was planted on January 14; but because of cold, wet weather the plants grew very slowly and were not thinned until early in April. The first mildew count was made shortly after thinning, with later counts following at 2- or 3-week intervals until July 15. Detailed observations were made on only four of the ten varieties to secure additional information on the effect of the mildew and to permit comparison with the 1937 trials at Santa Maria. These four varieties were U.S. 14, U.S. 33, Hartmann, and R. & G. Old Type. At each interval the newly infected plants were distinguished with a colored stake, a different color being used at each interval. Thus at the end of the season the plants in each plot of these four varieties could be segregated into groups according to the period during which mildew symptoms were first observed. Figure 3 shows the increase in per cent of infection during the growing season. The highest rate of increase in infection was observed between May 5 and June 3. Since 2 to 3 weeks usually elapses between infection and the expression of visible symptoms, apparently the most abundant infection occurred between April 15 and May 15, when the beets were 90 to 120 days of age.

The plots were harvested October 10 to 13; the infected beets in each of the four varieties were grouped according to their stake color, representing the date of infection; and the average root weight was determined for each group. As the results show (fig. 4), the earlier the date of infection, the lower the average root weight. In the groups that showed infection between 90 and 160

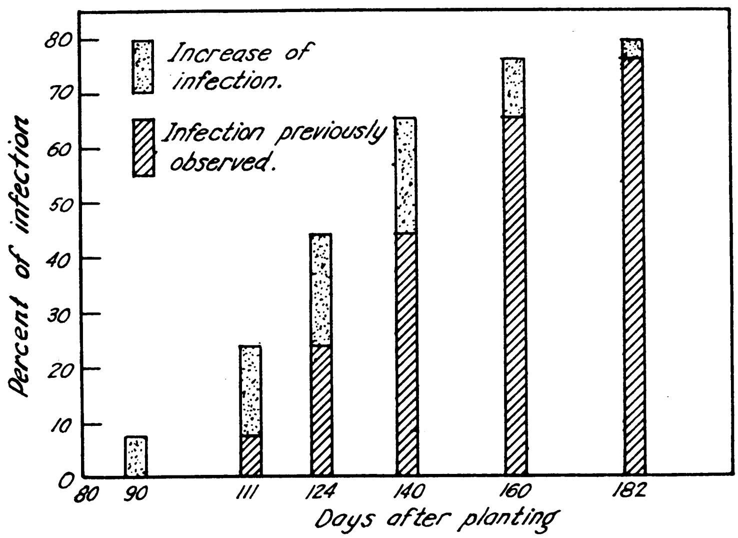

Fig. 3.—The increase of downy-mildew infection on sugar beets planted on January 14, 1938, near Salinas. The greatest increase of infection was observed between May 5 and June 3, or 111 to 140 days after planting.

days after planting, the average root weight for each successive infection group was 0.10 to 0.15 pound more than in the preceding group. The healthy beets show an average root weight 0.13 pound heavier than the beets observed to be infected at the 160- or 182-day interval, and approximately double the average root weight of those infected at the first observation.

To determine how infection at various stages of growth affected the sucrose per cent, the purity, and the yield, six composite samples were collected in each of the four varieties from beets infected prior to 125 days after planting, from beets infected after the 125-day interval, and from noninfected beets. These represented, respectively, early- and late-infected, and healthy groups.

Table 4 shows that early-infected beets were less than two thirds, late-infected beets over four fifths, as large as healthy beets. There was no appreciable difference between the sucrose per cent of the early- and the late-infected groups, and the healthy beets showed an improvement of only about 0.5 per cent over the infected. The coefficient of apparent purity differed very slightly between the infected and the noninfected groups.

On the average, according to the relative yields shown in table 4, the infected beets produced 73.64 per cent as much weight and 71.22 per cent as much sugar per plant as the noninfected.

In this trial, the main effect of downy-mildew infection was to reduce the average root weight of the infected beets and thus also to decrease the tonnage

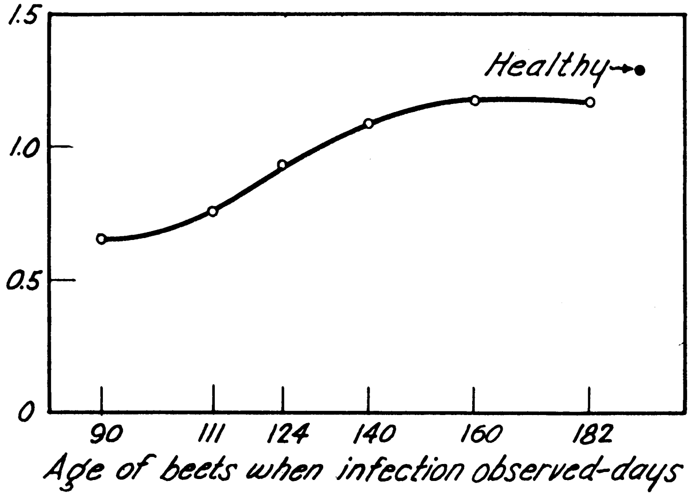

Fig. 4.—The relation between the age of beets when infection was first observed and the average root weight at harvest time. Beets showing infection within 125 days after planting gave average root weights of less than 1 pound, whereas beets infected later exceeded this amount. Salinas, 1938.

TABLE 4

EFFECT OF EARLY AND OF LATE DOWNY-MILDEW INFECTION ON THE PRODUCTIVITY OF SUGAR BEETS, SALINAS, 1938

	Average root weight, pounds	Sucrose, per cent	Purity, per cent	Relative yield	
				Root weight	Indicated available sugar*
Noninfected beets	1.29	18.27	87.74	100.00	100.00
Infected beets	0.95	17.72	87.49	73.64	71.22
Early-infected beets (prior to 100 days of age)	0.82	17.68	87.37	63.57	61.26
Late-infected beets (between 100 and 150 days of age)	1.11	17.76	87.61	86.05	83.52

* Based on 100 per cent extraction. Obtained by multiplying yield by sucrose per cent by purity per cent.

and the sugar production. Differences in purity and sucrose had very little influence in lowering of the total sugar production.

At Salinas the sucrose content and the purity were less affected by mildew than in the Santa Maria trials of the previous year. A possible reason is the difference in the harvesting dates of the two trials. As mentioned above, the greatest wave of mildew infection occurred at about the same dates in each trial, with infection falling off rapidly about the middle of July. Although the

Salinas plot was planted much earlier than the other, the thinning dates of the two were within a few days of each other. Since, however, the harvesting date at Santa Maria was 2 months earlier than at Salinas, the infected beets in the latter trial had 3 months after the mildew epidemic in which partially to recover and build up size, sucrose per cent, and purity, whereas those at Santa Maria were harvested before recovery could take place.

As indicated by the relative yields in tables 3 and 4, the weight of infected beets was about 27 per cent lower than that of noninfected beets at both Santa Maria and Salinas. The effect of downy mildew upon the indicated available sugar was, however, more pronounced in the Santa Maria trial because there the mildew caused a greater reduction in purity and in sucrose.

RELATIVE SUSCEPTIBILITY OF SUGAR-BEET VARIETIES TO DOWNY MILDEW

The planting of available commercial varieties that are resistant would seem to offer the simplest method of decreasing losses from downy mildew, but information on the relative susceptibility of varieties is extremely limited.

In France, Singalovsky (*6*) tested numerous beet varieties and reported that only two cultivated varieties remained free of downy-mildew infection and that the native species of wild beet, *Beta maritima* L., showed great susceptibility.

As previously stated, the 1937 trials at Santa Maria provided an opportunity to compare the susceptibility of nine sugar-beet varieties under a moderately severe natural epidemic of downy mildew. In this experiment (according to the per cent of infection shown in table 5), Hartmann and Eagle Hill were significantly less susceptible than the other varieties tested. Several, such as R. & G. Normal, R. & G. Old Type, U.S. 33, and U.S. 12, apparently fell into an intermediate group, whereas U.S. 14 proved to be the most susceptible of those tested.

As table 5 shows, the yield in tons per acre was in general greater for the varieties with a low or moderate per cent of infection. An exception is U.S. 14, which outyielded U.S. 12 and A-600 despite considerably higher infection. In sucrose per cent there were no significant differences except that Hilleshög, which produced a relatively low average root weight and tonnage, was exceptionally high in sucrose. The six varieties with the lowest per cent of infection showed, almost equally, the highest yield of gross sugar per acre, followed in order by U.S. 14, A-600, and U.S. 12. Since the differences in purity coefficients of the varieties were not significant, the yield of gross sugar per acre was a better measure of performance than the indicated available sugar.

From the weights, sucrose per cent, and purity of the healthy beets in each plot could be calculated the theoretical yield that would have been obtained from each variety in the total absence of downy mildew. Judging from these results, if the influence of mildew were eliminated there would be little difference between the sugar yields of the varieties except U.S. 12 and A-600, which appeared less productive under the conditions of these trials.

When the theoretical yields in the absence of mildew were compared with the actual yields, it was found that the 15 per cent mildew infestation on the

Hartmann variety reduced the yield by 0.7 ton of beets and 300 pounds of sugar per acre, whereas the 36 per cent infestation on U.S. 14 reduced the yield by 1.4 tons of beets and 730 pounds of sugar per acre. Other varieties showed losses intermediate between these figures, but in proportion to the percentage of infection.

The 1938 trials at Salinas provided an opportunity to compare the susceptibility of ten sugar-beet varieties under a very severe natural epidemic of downy mildew. According to the per cent of infection shown in table 6, the variety R. & G. AA, related to R. & G. Old Type, was significantly less susceptible than any of the others. It showed, however, a lower yield than several other varieties because it lacked uniformity in size and showed a relatively low sucrose per cent. Several commercial varieties such as Hartmann, Braune, U.S. 33, and R. & G. Old Type fell into an intermediate group, A-600 and U.S. 12 being somewhat more susceptible, and U.S. 14 the most susceptible of the varieties tested.

TABLE 5

SUSCEPTIBILITY TO DOWNY MILDEW, AND YIELD OF NINE SUGAR-BEET VARIETIES; SANTA MARIA, 1937*

Variety	Infected beets	Sucrose	Acre yield: Gross sugar†	Acre yield: Beets
	per cent	*per cent*	*pounds*	*tons*
Hartmann	15.1	17.26	5,930	17.19
Eagle Hill	16.9	17.38	5,640	16.21
Hilleshög	21.5	19.04	5,800	15.22
U.S. 33	22.5	17.19	5,460	15.87
R. & G. Normal	25.6	16.83	5,570	16.54
R. & G. Old Type	26.3	17.68	5,680	16.06
U.S. 12	26.4	17.06	4,340	12.70
A-600	30.6	17.18	4,810	14.00
U.S. 14	36.3	16.65	5,130	15.39
Significant differences:				
Odds 19:1	3.68	0.94	850	2.35
Odds 99:1	4.96	1.27	n.s.‡	n.s.

* Planted March 5, 1937; harvested August 17 to 19, 1937.
† Obtained by multiplying yield by sucrose per cent.
‡ The abbreviation n.s. indicates that the differences are not significant at the odds given.

The yield in tons per acre (table 6) indicates that the per cent of mildew infection was not the major factor involved in determining the tonnage produced. Two of the more susceptible varieties, U.S. 12 and A-600, showed the lowest yield; but U.S. 33, only moderately susceptible, yielded significantly lower than all others except the varieties mentioned above, whereas the yield of U.S. 14, the most susceptible variety, was significantly exceeded only by the highest-yielding variety. On July 15 the bolting per cent was highest in three of the domestic varieties, a fact that explains the lower yields of these varieties. Furthermore, the bolting in R. & G. Old Type, Hartmann, and U.S. 14 developed relatively late in the season and probably had little effect on the yield. U.S. 33, A-600, and U.S. 12 showed both the highest bolting and the lowest average root weights of the ten varieties. It should be noted that this plot was planted on January 14 and was, therefore, particularly unfavorable for varieties with a high bolting tendency.

From the weights, sucrose per cent, and purity of the noninfected beets it was possible to calculate the theoretical yield that should have been obtained in the total absence of downy mildew from the four staked varieties. Judging from these results, downy mildew infestations of 62 to 80 per cent reduced the yield of sugar beets by 3.56 to 5.84 tons per acre, an average reduction of 20.3 per cent of the tonnage.

TABLE 6

SUSCEPTIBILITY TO DOWNY MILDEW, AND YIELD OF TEN SUGAR-BEET VARIETIES; SALINAS, 1938*

Variety	Mildew†	Bolting‡	Sucrose	Acre yield	
				Beets	Indicated available sugar
	per cent	*per cent*	*per cent*	*tons*	*pounds*
R. & G. AA	43.3	1.5	16.8	21.53	6,240
Hartmann	57.5	16.0	18.3	19.70	6,380
Braune	59.0	7.4	18.4	24.30	7,950
Braune (new type)	59.8	8.8	18.3	22.37	7,230
U.S. 33	62.0	41.4	17.2	14.76	4,450
R. & G. Old Type	62.2	15.6	18.3	19.60	6,340
Pioneer	63.0	6.4	18.7	19.39	6,410
A-600	66.9	40.8	16.4	12.69	3,590
U.S. 12	70.1	48.7	17.4	12.12	3,710
U.S. 14	79.9	13.6	17.7	21.22	6,510
Significant differences:					
Odds 19:1	4.37	2.38	1.07	1.63	505
Odds 99:1	5.84	3.18	1.43	2.17	675

* Planted January 14, 1938; harvested October 10 to 13, 1938.
† Percentage infection on June 3, 1938.
‡ Percentage on July 15, 1938.

A similar planting was made near Salinas in 1939. Nine varieties believed to be somewhat resistant to downy mildew or found relatively resistant in previous trials were replicated six times along with U.S. 14, known to be very susceptible. As table 7 shows, the lowest per cent of infection occurred upon U.S. 15, R. & G. AA, and R. & G. Old Type, although the infection on four other varieties was not significantly higher. Two varieties, R. & G. Old Type and U.S. 15, with low mildew infection and bolting, produced the highest yields by a wide margin. R. & G. AA, with similarly low mildew infection and bolting, was intermediate in yield. The varieties U.S. 14, which showed the highest mildew infection, and Braune and U.S. 23, with intermediate mildew infection and moderately high seedstalk formation, were the lowest in productivity. Data on the effect of time of infection on productivity were not collected from the 1939 trials.

Comparing the three variety plantings conducted in different years, one notes significant differences in the relative susceptibility of varieties. Evidently, however, certain named varieties do not show the same relative susceptibility or yielding capacity in the different trials. R. & G. Old Type, for example, showed intermediate susceptibility and yield in 1937 and 1938, and intermediate bolting tendency in 1938. In 1939, however, the same variety was low in mildew infection and bolting, but very high in productivity. The same seed lot of R. & G. Old Type used in the 1939 trials had been planted along with four other varieties by the Spreckels Sugar Company in 1938 in a field adjacent to the 1938 mildew plots. Although the other four varieties (U.S. 12, U.S. 14, U.S. 33, and A-600) showed yields of only about 3 tons per acre more in the Spreckels plots, R. & G. Old Type yielded 12.75 tons per

TABLE 7

RESULTS OF THE SUGAR-BEET VARIETY TRIALS; SALINAS, 1939*

Variety	Mildew infection, June 23	Bolting, August 10	Sucrose	Yield per acre	
				Beets	Indicated available sugar
	per cent	*per cent*	*per cent*	*tons*	*pounds*
U.S. 15†	13.3	0.3	15.22	51.46	13,010
R. & G. AA	13.6	1.4	14.86	42.37	10,400
R. & G. (Old Type)	14.0	4.1	14.83	52.92	13,030
Eagle Hill 472	15.8	7.1	14.40	45.24	10,480
Glostrup	16.2	12.0	14.60	45.92	10,900
U.S. 23†	17.1	23.0	14.13	39.20	8,880
Eagle Hill 651	17.2	7.1	13.68	46.20	10,120
Hartmann	18.6	11.4	13.85	48.21	10,570
Braune	24.2	15.2	14.48	40.36	9,480
U.S. 14	35.0	11.1	13.12	42.92	8,960
Significant differences:					
Odds 19:1	3.64‡	2.52‡	1.00	2.25	970
Odds 99:1	4.86	3.37	1.34	3.00	1,300

* Planted January 24, 1939; harvested October 11 and 12, 1939.
† Seed furnished by Division of Sugar Plant Investigation, United States Department of Agriculture.
‡ These data have also been converted to degrees and analyzed on the basis of the transformation, $p = \sin^2 \theta$. The conclusions are unchanged except for the bolting tendency of varieties U.S. 15 and R. & G. AA. The transformed data indicate a significant difference between these varieties.

acre more than the same variety in the mildew test plots. In the same way the variety Hartmann showed low mildew infection and high productivity in the 1937 trials, but was intermediate in both categories in the 1938 and 1939 trials; and Braune, the highest yielder in 1938, fell below the average of all varieties in 1939. These apparent inconsistencies may be due to interaction of seasonal factors upon disease reaction and varietal productivity, or perhaps may result from variations in the performance of different strains or seed lots distributed under the same variety name. Judging from these results, there are significant differences in the susceptibility of commercial sugar-beet varieties to downy mildew, but similar relative differences occurred when different seed lots of the same variety were planted in different seasons.

In the single trial in which it was included, variety U.S. 15 showed low susceptibility to downy mildew, low bolting tendency, and high productivity. Variety R. & G. AA appeared to equal it in resistance to downy mildew and showed a low bolting tendency, but exhibited extreme variability in growth habit and was only moderately productive in comparison with other varieties.

U.S. 14 was the most susceptible variety in each of the three trials, while other varieties tested appeared moderately susceptible.

Evidently no commercial variety now available can be considered highly resistant to downy mildew; there is a real need for one combining downy-mildew resistance with favorable agronomic characteristics for planting in the coastal areas of California.

SELECTION FOR RESISTANCE TO DOWNY MILDEW

One can improve the resistance of established varieties by plant selection or by hybridization. Since no highly resistant strain of beets was located, since the commercial strains are highly heterozygous, and since even the strains selected for other characters show considerable differences in susceptibility to downy mildew, it appeared that selections made within acceptable commercial varieties would be most likely to attain the desired objective.

Seedling-Inoculation Method.—At the start of these trials it was not known whether seedling resistance was correlated with field resistance. Since, however, the fungus usually infects only young seedlings or young leaves of older plants, the seedling-inoculation method of selection was chosen.

Large numbers of sugar-beet seed balls of several commercial varieties were planted in chemically or steam-sterilized soils in a greenhouse. After producing their first pair of true leaves, the seedlings were sprayed at intervals of 2 to 5 days with a spore suspension.

The inoculum was prepared according to a method first suggested to the writer by Makato Hiura. Young infected leaves were collected during the afternoon, and the entire coating of conidia and conidiophores was washed off under a spray of water. Then the leaves, having been shaken to remove films or drops of water, were placed in a glass moisture chamber and incubated for 24 hours at 12° or 15° C, temperatures favorable for sporulation of this fungus. By the following afternoon the incubated leaves had usually produced an abundance of conidiophores bearing young viable conidia. Their viability was readily determined by germination trials in water drops on clean slides. Sporulating leaves were placed in a dish containing tapwater; and with a soft brush the conidia were washed and removed from the leaf surface into the water. The concentration of the spore suspension could be judged by its opacity and confirmed by microscopic examination.

Before inoculation the seedlings were moistened with a mist to provide small droplets of water on the leaves. Then the spore suspension was sprayed uniformly over the seedlings with an atomizer or—in larger quantities—with a 1-quart pressure sprayer. After inoculation the beds containing the seedlings were enclosed with muslin-covered frames moistened with a water spray. Plantings were so arranged that inoculations could be made during the season when night temperatures in the greenhouse ranged between 5° and 12° C, temperatures previously found favorable for conidial germination of *Peronospora schachtii* (*4*). For several weeks, similar inoculations were repeated at intervals of 2 to 5 days.

Infection upon seedlings was observed 5 to 10 days after inoculation, depending upon the mean day and night temperatures. As soon as the fungus had evidently entered the growing point and all newly formed leaves were systemically invaded, the infected seedlings were removed from the beds to provide inoculum for additional inoculations on the surviving seedlings. When 90 to 95 per cent of the seedlings had been eliminated because of infection, the inoculations were discontinued, and the survivors of each variety were transplanted into separate isolation plots. Plantings were usually made in the greenhouse between October 1 and December 1, and the seedlings were transplanted to isolation plots between January 1 and March 1.

Isolation and Seed Production of Selected Plants.—Selections from nonbolting varieties usually produced no seedstalks the first season and were therefore maintained in place until the second summer, when seed was harvested from the selected plants. Among varieties noted for bolting tendencies, from 20 to as high as 70 per cent of the selections produced seedstalks the first season. To avoid, however, additional selection toward a bolting tendency (*1*), the seed from the first-year bolters was discarded except for the small amount that was used for comparative downy-mildew inoculations to test the effect of a single selection on susceptibility in comparison with the parent material. Seed produced the second summer from the remaining plants was used for reselection by the seedling-inoculation method and also for field comparisons under conditions favorable to downy mildew.

Although the plants in a given isolation plot were permitted to cross-pollinate without restriction, conceivably the progeny of certain individual mother plants might differ in resistance from others in the same selection group. The seed from each plant was therefore harvested separately, and then a composite sample from all plants was prepared for large-scale trials while the individual plant progenies were tested separately under downy-mildew exposures. The first selections by the seedling-inoculation method were made in the winter of 1935–36, when 8,650 seedlings were inoculated with spore suspensions of downy mildew nine times within 60 days. A total of 777 seedlings or 8.9 per cent remained uninfected. In the following year 21,472 seedlings were inoculated, and only 313 or 1.45 per cent remained free of infection. The next two seasons, 1937–38 and 1938–39, about 9,000 were inoculated, whereas during the winter of 1939–40 about 25,900 were inoculated, including 15,000 progeny of primary selections made in previous years. In each case a few plants remained free from infection and were saved for increase and reselection. Usually, under natural conditions, field selections of sugar beets for resistance to downy mildew have one disadvantage: the percentages of infection are not high enough to permit rigid selection; and the possibility of selecting susceptible but disease-escaping plants is therefore as great as the chance of picking out truly resistant individuals.

In the 1938 trials near Salinas, however, the field infection was unusually severe; several varieties showed infections of 60 to 80 per cent. Under these conditions a number of mildew-free plants with desirable agronomic characters were selected from each of four commercial varieties. The roots were transplanted into an isolation plot in such a manner that two plants from the same variety grew about 6 inches apart, while adjacent pairs of plants were separated by about 6 feet. When seedstalks were formed, the entire inflorescences of the pair of plants were enclosed in a wooden frame supporting an insectproof muslin cover. This plan had two advantages: first, it provided sufficient cross-pollination to insure seed production from most pairs of plants, whereas self-sterility often prevents a single-bagged plant from producing seed (*2, 3*); and, second, out of twenty pairs selected at random from a given variety, there is a strong possibility of associating two highly resistant individuals in one or more pairs, although other pairs might be composed of one resistant and one susceptible or of two susceptible plants. Inoculation tests upon the progeny are, of course, necessary to distinguish the favorable from the unfavorable combinations.

COMPARISON OF SELECTED STRAINS AND PARENTAL MATERIAL

Greenhouse Evaluation.—The first opportunity to compare the susceptibility of a selected strain with the parent material occurred in the winter of 1937–38. The material originated from the 1936 commercial increase of variety U.S. 33, and the seedlings were heavily inoculated and rigidly selected in the winter of 1936–37. The next summer the seed produced on the first-year bolters was saved, and during the fall of 1937 it was planted in the greenhouse in rows alternating with seed of the parent material. After the first true leaves had been formed on the seedlings, they were sprayed with a spore suspension at intervals of 2 to 5 days. Seventy-five days after planting, 64 per cent of the unselected seedlings were infected, as compared with 37 per cent of seedlings of the primary selection. At the end of 115 days the infection on the unselected and selected strains was 81.4 per cent and 58.8 per cent respectively. Although such trials are less reliable than field comparisons under natural epidemics, the results do indicate that a single selection by the seedling-inoculation method produced a significant difference in susceptibility.

Test at Salinas in 1939.—After elimination of the plants that formed seed stalks during the first year, seed was harvested the following summer (1938) from the remaining plants of the selection mentioned in the paragraph above. This selected seed was planted near Salinas, California, in 4-row strips for observation of its susceptibility and its growth habit. Since not enough seed of the parent strain of U.S. 33 was available for a field planting, comparisons were made with similar plantings of two commercial strains of this variety, one of which was believed to be from the same source as the parent material for this selection.

This trial showed (table 8) that the downy-mildew infection was only one third as severe on the selected material as on the commercial strains closely related to the parental variety. Equally striking was the difference in seedstalk formation between the selection and commercial strains. On May 24, when the commercial strains showed 10.9 and 19.8 per cent bolters, the selection showed only 0.6 per cent seedstalks; and on June 23, when the commercial strains showed 24.4 and 42.6 per cent, the selection showed only 2.3 per cent seedstalks.

In producing seed of this selection, over 40 per cent of the selected plants had been eliminated because they produced seed the first summer; but this elimination could hardly account for the striking effect on the degree and lateness of seedstalk formation. One possible explanation is that in some varieties susceptibility to downy mildew in the seedling stage may be correlated with early bolting, and thus the elimination of over 98 per cent of the most susceptible seedlings may have also eliminated a high percentage of early-bolting individuals. Although definite proof of this possibility is not available, reference to the variety comparisons reported in this paper (table 7) will show that most varieties with low bolting tendencies also show low percentages of downy-mildew infection. Variety U.S. 14, with a moderate bolting tendency and extreme susceptibility to downy mildew, is an exception. The two commercial varieties with the lowest infection, U.S. 15 and R. & G. AA, had been selected not for downy-mildew resistance but for agronomic characters, including a nonbolting tendency; their low susceptibility to downy mildew was discovered after they were released for field trials.

As is shown by the comparative yields of the commercial and selected strains (table 8), early bolting and downy-mildew infection strikingly reduced the

TABLE 8

COMPARATIVE SUSCEPTIBILITY OF U.S. 33 AND A SELECTION FROM THIS VARIETY, TO INFECTION BY DOWNY MILDEW; SALINAS, 1939*

Variety	Mildew, June 23	Bolting, August 10	Sucrose	Yield per acre	
				Beets	Indicated available sugar
	per cent	*per cent*	*per cent*	*tons*	*pounds*
U.S. 33†	27.9	53.2	9.72	17.09	2,490
U.S. 33‡	27.3	39.3	13.92	21.89	4,830
Selection from U. S. 33†	9.8	16.0	15.08	37.15	9,400

* Planted January 24, 1939; harvested October 11 and 12, 1939.
† From 1936 seed increase.
‡ From 1937 seed increase.

productivity of the commercial strains of variety U.S. 33 when planted as early as January 24, but the selected strain[6] was much less affected by these factors.

Field Plantings in 1940.—In the winter of 1939–40 the progeny of sixteen different selections among five varieties were compared with the parent material by means of greenhouse seedling inoculations. Twelve of the selections appeared to be less susceptible than the parents, while four showed no difference in susceptibility from the source material. Seedlings not infected by the greenhouse inoculations were transplanted to a field near Salinas, to be observed under outdoor conditions. In adjacent rows similar selections were planted from seed along with parental varieties. The most striking evidences of resistance were observed in the progeny from certain individual plant selections, although the progeny of some sister plants from the same selection group appeared to be as susceptible as the parent variety. The individual plant selections also showed striking differences in agronomic characters.

The selections included in these trials originated from five different commercial varieties—three of European origin and two developed in this country by the United States Department of Agriculture.

[6] During the preparation of the manuscript the writer was advised (letter from Dr. Eubanks Carsner, April 24, 1943) that the Division of Sugar Plant Investigations, after extensive evaluation of this selection, has arranged for its multiplication for commercial use.

The European varieties are all susceptible to curly top. Even, therefore, if strains highly resistant to downy mildew could be produced from them, such strains would be useful only for early planting or for planting in areas not seriously affected by curly top.

The highest degree of resistance to downy mildew among the selections, as judged by both greenhouse inoculations and field observations, occurred in a field selection from R. & G. AA increased by the paired-root method previously described. This selection, besides being resistant to downy mildew, showed a strong nonbolting tendency. Being very susceptible to curly top, however, and variable in top and root development, it would be valuable only for reselection or for hybridizing with varieties that possess more favorable agronomic characteristics.

According to observations on the selections from R. & G. Old Type, although some progress has been made in improving resistance to downy mildew, no selection from this source showed sufficient promise to warrant further testing.

Some selections from the variety Hartmann appeared highly resistant to downy mildew. The progenies of two individual plant selections showed only 8.2 and 18.4 per cent infection respectively, as compared with 44.3 per cent infection on commercial Hartmann plants in adjacent rows. These selections, because of their origin, are susceptible to curly top; but in all other respects they offer possibilities.

Selections by the seedling-inoculation method from variety U.S. 14 proved, for the most part, to be nearly as susceptible to downy mildew as the parent variety; there was no evidence that satisfactory strains could be developed in this manner.

The most promising material available at the end of the 1940 season consisted of selections from the curly-top-resistant variety U.S. 33. In table 8 appear the results of a comparison between a mass selection from this source and commercial U.S. 33. According to observations on individual plant selections from U.S. 33, several are much less susceptible to downy mildew than the parent variety, and are also lower in bolting tendency. Additional trials would be necessary to determine whether any of these selections or reselections from them might combine sufficient resistance to downy mildew and other favorable characteristics to be of commercial value.

SUMMARY

Downy mildew reduces the yield of sugar beets by retarding the growth of the root, by interfering with normal sugar production, and by lowering the purity of the beet. Plants showing infection of the growing point before they were 100 days old produced roots about half as large as disease-free plants. Infection on plants over 150 days old, however, resulted in only slight reduction in size.

The sucrose content and the purity of infected beets harvested within 2 months after the termination of a severe mildew outbreak were considerably lower than those of healthy beets. When harvest was delayed for 3 or 4 months after the termination of the epidemic, the sucrose content and the purity were nearly normal. The results of trials during two years indicate that infected beets produce from 30 to 40 per cent less sugar than healthy beets growing in the same field.

Several commercial varieties of sugar beets grown on the Pacific Coast were compared for susceptibility to downy mildew during three years. The most resistant varieties in these tests were U.S. 15, R. & G. AA, and one strain of R. & G. Old Type. Among European varieties some strains or seed lots appeared to be more susceptible than other strains of the same variety.

No varieties were found with enough resistance to provide a satisfactory control for downy mildew.

Selections by the seedling-inoculation method have been made in five commercial varieties. Seedlings growing in a greenhouse during the fall and winter were sprayed repeatedly with spore suspensions of downy mildew. After 95 to 98 per cent of the seedlings were infected, the remainder were transferred to isolation plots for seed production.

Comparison of the progeny of selected seedlings with parental material shows that, in some lines, resistance has been considerably improved.

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