# HILGARDIA

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# BREEDING FOR RESISTANCE TO ONION DOWNY MILDEW CAUSED BY PERONOSPORA DESTRUCTOR[1]

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(Results of a coöperative investigation conducted by the United States Department of Agriculture Bureau of Plant Industry and the California Agricultural Experiment Station.)

## INTRODUCTION

THE ONION DOWNY-MILDEW FUNGUS, *Peronospora destructor* (Berk.) Casp., is practically world-wide in distribution (*2, 5*).[5] It was first described in 1841 by Berkeley (*1*) in England, and reported by Trelease (*12*) from Wisconsin in 1884. Subsequently it has been found in a number of other states and has frequently assumed epidemic proportions.

Because adequate control measures have not been developed, the disease continues to cause losses of varying magnitude. Such losses are usually most severe under conditions of moderate temperature and high humidity.

Even though recent work by Yarwood (*14, 15*) and by McWhorter and Pryor (*7*) indicates the fungicidal efficacy of certain chemical mixtures, the more satisfactory means of prevention involves the development of disease-resistant varieties. In this paper are presented data relative to varietal reaction to mildew, discussion of resistant types that have been found, and the present status of the breeding work designed to transmit resistance to varieties of commercial importance. The studies were made at Davis, California, and at other experimental tracts, as mentioned in the text.

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

## PREVALENCE AND DESTRUCTIVENESS IN THE UNITED STATES

Downy mildew, though sporadic in occurrence, is probably the most destructive disease of onions in the United States. It has been abundant at times in each of the principal bulb-producing states, with the exception of Texas, and in each of the seed-producing states with the exception of Idaho. The disease demanded attention in Massachusetts, New York, Michigan, Oregon, and California during the eleven years from 1928 to 1938. The work in the states has been generally focused on host-parasite relations, on factors contributing to or aiding infection, and on fungicidal control. The disease frequently spreads rapidly and ruins large acreages, becoming most prevalent under conditions of high humidity.

On the crops grown for green bunching or for bulbs, downy-mildew infection may significantly reduce the quality and yield of the crop but rarely, if ever, causes complete loss. In New York, Cook (*2*) reported that bulb enlargement is significantly reduced if the plants become infected when small. In early 1938, at Davis, Sacramento, and Milpitas, in California, many plants of the extremely susceptible varieties Yellow Bermuda and Crystal White Wax were killed by mildew before the bulbs were one-fourth grown. Obviously the injury to the bulb crop is due primarily to killing of the foliage and consequent reduction in the size of the mature bulbs. Although bulbs are occasionally invaded by the mycelium, direct injury from bulb infection does not appear to be serious in America. In crops grown for bulbs or bunching, infected plants may survive and produce a fair crop even after a severe attack on the foliage.

In California the disease is particularly serious in the crop grown for seed. Total loss of seed fields has been observed. Frequently, satisfactory yields are obtained even though the leaves are killed by mildew, but if the seedstalks are severely infected the seed yield is reduced. Mother bulbs are planted from September to January, according to the variety; and, since the seed does not mature until July or August, the foliage is frequently exposed to infection for a period of six months. Normally considerable rainfall, fog, and dew occur from December to April; these conditions combined with favorable temperatures provide ideal conditions for infection, sporulation, and spread of the fungus. As a rule, in the interior valleys conditions become unfavorable for mildew after this time because the humidity decreases and the temperature increases. Along the coast, however, conditions may remain favorable for spread of mildew considerably longer. Seedstalks usually appear after February 15, the time varying with the variety and date of planting. Obviously, decreases in seed yield are determined by the time and resulting severity of infection. The disease in California, during the last nineteen years, has caused losses as high as 60 to 80 per cent (table 1). In some

TABLE 1

ESTIMATED LOSSES DUE TO DOWNY MILDEW INFECTION OF THE ONION SEED CROP IN CALIFORNIA FROM 1920 TO 1938, INCLUSIVE

| Year | Severity | Average loss in seed crop, per cent |
|---|---|---|
| 1920 | Moderately severe, localized; maximum loss 30 per cent | 2 |
| 1921 | Similar to 1920 | 2 |
| 1922 | No reports available | .. |
| 1923 | No reports available | .. |
| 1924 | No reports available | .. |
| 1925 | Extremely severe on both seed and bulb crop | 60–80 |
| 1926 | Severe; losses exceeding 50 per cent common in central California and coastal region | 40 |
| 1927 | Moderately severe on seed crop in localized areas | 3 |
| 1928 | Widely distributed on seed crop | 5 |
| 1929 | Little or none in Sacramento Valley; trace in coastal region | 0 |
| 1930 | Severe in localized areas; maximum loss in any area, 75 per cent | 25 |
| 1931 | Severe and general during March; little spread during April and May but moderately severe in local areas during June | 10 |
| 1932 | Little infection on seed onions, slight on bulb crop | 1 |
| 1933 | Practically none on seed onions | 0 |
| 1934 | Severe and generally distributed on seed onions | 50 |
| 1935 | Similar to 1934 | 50 |
| 1936 | Less than in 1934 and 1935 | 5 |
| 1937 | Of little consequence in seed-producing districts | 2 |
| 1938 | Severe in localized districts | 8 |

Source of data:
Observations reported in the *Plant Disease Reporter* for certain years with corresponding volume and page citations as follows: 1920, **16**:237; 1921, **22**:354; 1925, **45**:68–69 (supplement); 1926, **54**:279; 1927, **61**:261; and 1928, **68**:59. All other observations are by the authors.

seasons, the disease became epidemic by March but subsequent environmental conditions were such that only relatively slight infection was evident on seedstalks.

## SOURCES OF INOCULUM

*Mycelium in Bulbs.*—There is abundant evidence that infected onion bulbs harbor the mycelium of the organism, as was first demonstrated by Murphy and McKay (*8*). Plants systemically infected with mildew have been found in seed fields in California, and these are probably the initial sources of inoculum. Additional importance has been given to this method of hibernation by Newhall's observation (*10*) that infected Egyptian or topset onions and potato or multiplier onions serve as important sources of primary downy-mildew inoculum in the important onion-bulb sections of New York state.

*Oöspores in Leaves and Seedstalks.*—Oöspores are formed in the tissues of infected plants, but reports in the literature differ as to their abundance. Murphy and McKay in an early paper (*8*) reported that oöspores rarely occurred in fields under their observation but in a later paper (*9*) stated that oöspores are sometimes present in abundance. In central California, large numbers have been found in both infected leaves and seedstalks during several seasons. McKay (*5*) reported germination of oöspores five years old and later (*6*) observed stimulation of germination in 0.01 and 0.02 per cent potassium permanganate.

*Infected or Contaminated Seed.*—Several investigators have reported infection of flower parts of onion by downy mildew, and Cook (*2*) has demonstrated the presence of mycelium within the ovule. He also found a few oöspores in water used to wash a quantity of commercial seed. Stuart and Newhall (*11*) later reported circumstantial evidence of seed transmission, but no conclusive evidence of the commercial importance of seed transmission has yet been presented.

## PRACTICAL DIFFICULTIES IN RELATION TO FUNGICIDAL CONTROL

The fungicidal efficiency of certain chemicals and their toxicity to conidia of many species of the Phycomycetes have been well demonstrated. The literature need not be reviewed here. The problem in connection with onion downy mildew has been to discover chemical mixtures which will adhere to the waxy surfaces of the leaves and seedstalks, particularly during rainy weather. Definite progress has been made in securing such mixtures.

Several factors contribute to the actual inefficiency of these fungicidal materials when applied to the bulb crop of the so-called "intermediate" group of onions. It is the intermediate bulb crop that is most frequently attacked by mildew. On the peat lands, especially, the foliage growth is very rank and does not dry off readily following fog and dew, which provides ideal conditions for infection and sporulation. In California, this crop is usually seeded in the nursery in late August or early September, and the seedlings are transplanted to the field in December and January. On the sedimentary soils, plants are usually set on raised beds spaced about 3 feet from center to center, with seedlings 3 inches apart in the row and two rows to the bed. On peat soils the plants are set on level ground and the rows are spaced about 9 to 10 inches apart. Development aboveground is relatively slow during January and February but increases thereafter with the rise in temperature. Since growth occurs mainly at the center and base of the plant, new portions of the younger growing leaves are continually becoming exposed to infection. Thus, it is necessary to make frequent applications in order to protect this new growth. This practice, in itself, is almost impossible of execution because the soil is frequently too wet to permit machine applications. Furthermore, while the disease is not epidemic every year, it sometimes appears suddenly and spreads rapidly during favorable weather.

Difficulties are also encountered in spraying the seed crop; frequent spraying is necessary to keep the developing seedstalks covered with fungicide because these, too, grow at the base and continually expose new areas of the stem to infection. Seedstalks, being long and slender, can be completely covered with fungicides only with great difficulty.

The late bulb crop which is usually seeded in the field in January is seldom injured by mildew because the plants make most of their development during the time of year when the air is relatively dry.

## LEAF PRUNING AS A CHECK TO SPREAD OF MILDEW

In 1934, mildew appeared very early in some of the small onion-breeding increase plots at Davis. In a plot of the variety strain Stockton G36 (fig. 1, *A*) practically all of the leaves were infected by March 21. A few of the seedstalks had emerged through the surrounding sheaths. It had been observed that where leaf growth was extremely luxuriant, especially following warm, wet winters, mildew was usually much more severe than on sparse foliage; probably this is because the foliage did not dry so quickly after a fog, dew, or rain, or because such leaves may be more susceptible to injury.

In an effort to protect the above-mentioned plot as much as possible against seedstalk infection, all the leaves were trimmed off and the seedstalks left exposed as shown in figure 1, *B*. The seedstalks continued to grow, very little infection occurred, and a good crop of seed was harvested (fig. 1, *C*). While no unpruned plants were left for comparison, the removal of the leaves seemed to have very little deleterious effect on the normal development of the seed crop.

## RELATIVE SUSCEPTIBILITY OF VARIETIES

Comparisons of susceptibility were made in 1934 on a number of commercial varieties and foreign introductions planted under overhead irrigation. From one to eight small plots of each lot of the garlic or onion types listed in table 2 were planted in a compact block. On March

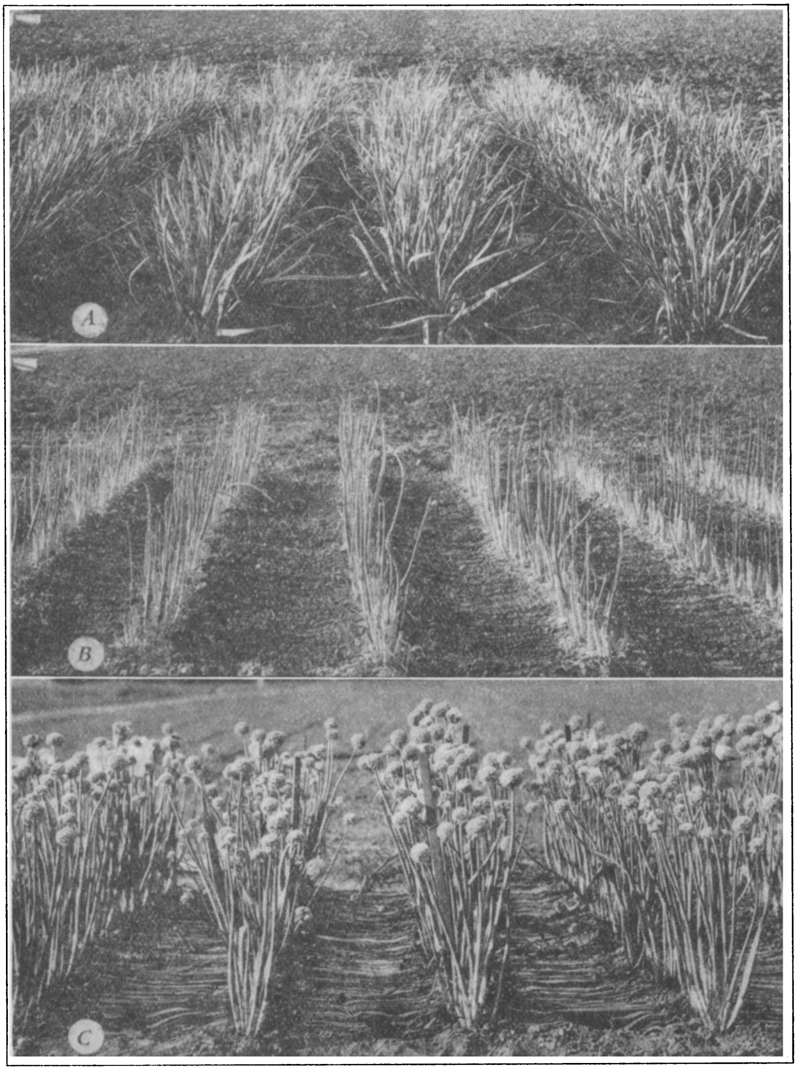

Fig. 1.—*A,* Increase plot of Stockton G36 with luxuriant growth of foliage heavily infected with mildew; photographed March 21, 1934. *B,* The same plot with the mildewed leaves removed to expose the young seed stems; photographed March 22, 1934. *C,* The same plot in full bloom. A normal crop of seed was harvested, indicating that leaf pruning probably did not reduce vigor.

9, and at intervals of a few days thereafter, all plants were sprayed with a suspension of downy-mildew conidia. Humid conditions were maintained by overhead sprinkling. The first sporulation was observed on March 15, and by March 22 infection was abundant and severe on most of the plants. Since in this case the interval (6 days) between inoculation and sporulation was considerably less than that reported by other workers (*2, 13*) under controlled conditions, it appears likely that part of the infection originated from diseased plants previously transplanted into the plot or from wind-borne conidia.

Ratings of the severity of infection on leaves and on seedstalks were made on April 10. The degree of infection was rated from 0 (no infection) to 10 (severe infection), and the results are summarized in table 2. The leaves of all onion varieties showed infection and only commercial Italian Red, Italian Red 13–20–3, and F.P.I. no. 101113 could be considered even moderately resistant. A satisfactory rating of infection on seedstalks could be obtained on only those varieties that produced well-developed seedstalks by April 15, since conditions became unfavorable for uniform infection after that time. Among the varieties forming seed stems early, Italian Red 13–20–3, Early Grano, White Sweet Spanish, and Yellow Strassburg showed the least seedstalk infection; among the most susceptible were Crystal White Wax, Yellow Bermuda, Creole, White Persian, and all of the foreign plant introductions except numbers 101112 and 101113. No infection was observed on garlic.

In the same year an epidemic occurred early in the season on the foliage of the bulb crop of the intermediate varieties such as California Early Red. The leaves of these were badly infected with the exception of Italian Red 13–53, a selection that had been carried along in the breeding plots because of its male sterility. Also the $F_1$ seedstalks of a cross between Red 21 and 50–6–1, a strain of Stockton Yellow Flat, showed immunity. The foliage and seed stems of all hybrids between *Allium fistulosum* and *Allium cepa* were extremely susceptible (fig. 2).

Another severe downy-mildew epidemic occurred in the breeding plot at Davis in the early months of 1935. Bulbs of certain varieties of the 1934 crop, harvested in July, had been planted in September. The foliage of most plants was badly infected, resulting in premature death of the leaves soon after seedstalk emergence; but the foliage of Italian Red 13–53 again manifested marked resistance. Complete infection was evident on the seedstalks of all varieties and strains except the two Italian Red selections, 13–53 and 13–20–3. Even under the most extreme conditions of infection the seedstalks appeared immune—no lesions were found on them. Many inbred lines and hybrids of susceptible varieties were killed. In other progenies the primary seedstalks were killed and the secondary stalks were so severely injured that relatively low yields of seed were secured.

TABLE 2

RELATIVE SEVERITY OF DOWNY MILDEW ON THE FOLIAGE AND SEEDSTALKS OF ONION VARIETIES AND GARLIC AT DAVIS IN 1934

| Variety or type | Degree of infection* | |
|---|---|---|
| | Leaves | Seedstalks |
| Late garlic | 0.0 | .... |
| Italian Red 13-20-3 | 6.3 | 2.5† |
| Italian Red (commercial) | 5.0 | .... |
| Yellow Strassburg | 8.3 | 2.5 |
| Early Grano | 10.0 | 2.5 |
| White Sweet Spanish | 8.3 | 3.0 |
| F. P. I. 101113 | 5.0 | .... |
| F. P. I. 101112 | 8.3 | 5.0 |
| Mountain Danvers | 10.0 | 5.0‡ |
| Southport Yellow Globe | 7.5 | 5.0 |
| White Portugal | 8.3 | 5.0 |
| Ohio Yellow Globe | 8.3 | 7.0 |
| Extra Early Red Flat | 8.3 | 6.2 |
| Ebenezer | 8.3 | 6.2 |
| Australian Brown 5-24 | 10.0 | 6.2 |
| Yellow Globe Danvers | 8.3 | 7.5 |
| Southport Red Globe | 8.3 | 7.5 |
| Southport White Globe | 8.3 | 7.5 |
| Red Wethersfield | 8.3 | 7.5 |
| Prizetaker | 10.0 | 7.5 |
| Early White Barletta | 10.0 | 7.5 |
| White Persian | 7.5 | 8.3 |
| Creole | 10.0 | 8.3 |
| Yellow Bermuda | 10.0 | 9.2 |
| Crystal White Wax | 10.0 | 10.0 |
| F. P. I. 101171 | 10.0 | 10.0 |
| F. P. I. 101224 | 10.0 | 10.0 |
| F. P. I. 101460 | 10.0 | 10.0 |
| F. P. I. 101461 | 10.0 | 10.0 |
| F. P. I. 101499 | 10.0 | 10.0 |
| F. P. I. 101515 | 10.0 | 10.0 |

* In the original field data, five degrees of infection were distinguished ranging from 0 (no infection) to 4 (very severe) with plus or minus ratings to identify intermediate groups. To conform to the system of rating used to measure mean injury (table 4) the original ratings were converted to a scale ranging from 0 to 10.

† Although these seedstalks were not examined microscopically, later examination of other seedstalks of this strain showed that similar mildewlike lesions were free from mildew mycelium.

‡ Rating unreliable owing to late formation of seedstalks.

In 1936 several domestic varieties and foreign introductions of *Allium cepa* were grown at Berkeley. White Persian, a thrips-resistant variety recently described by Jones, *et al.* (*3*), was found to be particularly susceptible, many plants being killed by downy mildew before emergence of the seedstalks. Relatively severe infection occurred in leaves and seedstalks of Yellow Bermuda, Nebuka, Red Creole, Lord Howe Island, Earliest Express, Giant White Italian Tripoli, Yellow Strassburg, and Southport White Globe. Leaf infection was not noted on Italian Red 13–53. Small mildewlike spots appeared on seedstalks of Italian Red 13–20–3 and were at first thought to indicate downy-mildew infection.

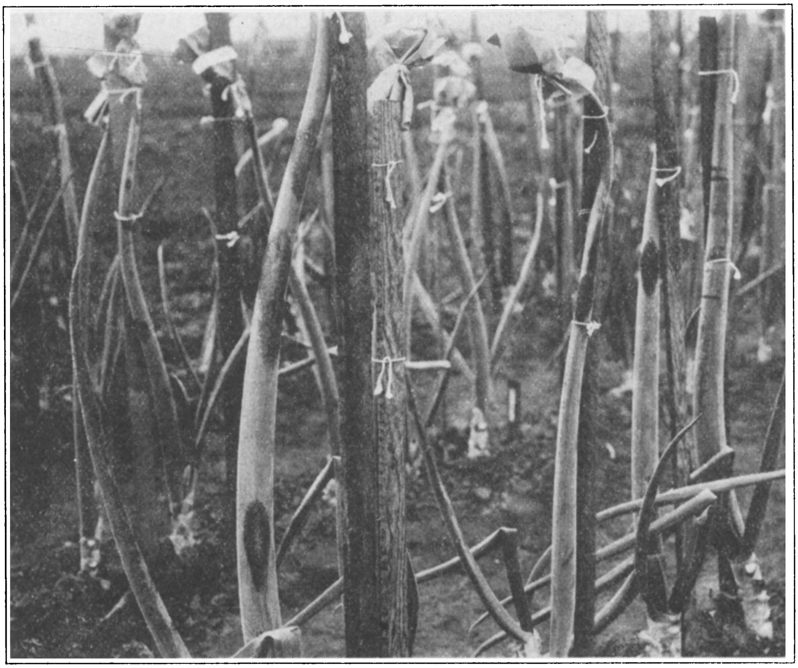

Fig. 2.—Severely infected seedstalks on $F_1$ plants of Nebuka (*Allium fistulosum* × Australian Brown) in the breeding plot at Davis, California, in March, 1934.

As indicated later, however, the seedstalks of 13–20–3 were immune from infection at Milpitas in 1937 and 1938[6] when 100 per cent infection was noted on many commercial varieties. This apparent discrepancy needs explanation. Small mildewlike lesions frequently occur on seedstalks of 13–53 and 13–20–3 but sporulation has never been observed and microscopic examination of cross sections of such material has never revealed either mycelium or haustoria of the mildew fungus. It is possible that the seedstalk infection charged to 13–20–3 at Berkeley was not actually downy mildew.

[6] Dr. C. E. Yarwood was responsible for the readings made in Berkeley in 1936. He also gave valuable assistance in making the readings at Milpitas in 1937 and 1938.

## BREEDING FOR DOWNY-MILDEW RESISTANCE

Three onion strains resistant to downy mildew have been isolated to date. In 1934 the $F_1$ population (M18) of Red 21 × 50–6–1 produced mildew-free seedstalks. Since Red 21 is susceptible, the resistance of M18 was probably inherited from 50–6–1. The latter strain was an inbred line of Stockton Yellow Flat; and, because seed is no longer available, data on its response to mildew cannot be secured.

The two other resistant strains, numbers 13–53 and 13–20–3, are selections from the variety Italian Red. This variety is of minor importance in California and is seldom grown in other states. Seed is planted in late August, seedlings are transplanted in late November or December, and the plants mature in July in central California. The bulbs are torpedo-shaped, large, red, and mild-flavored. High yields are the rule. The bulbs are poor keepers and for this reason mother bulbs are usually planted in the field in September. Seedstalks of this variety are usually tall and vigorous, producing relatively heavy yields of seed.

*Italian Red 13–53.*—The Italian Red population from which strain 13–53 was selected was grown at Davis in 1924. In August, a considerable number of desirable bulbs were selected and planted for self-pollination. In April, 1925, the umbels were covered with manila-paper bags when the first flowers opened. The bags were tapped frequently to facilitate self-pollination. These bagged heads were harvested on August 8, and the seed threshed, washed, and dried. From the 5 seed heads of plant 53, 136 bulbils were secured, but no seed. This discovery appeared to have no immediate practical importance, but certainly was of value in a study of sterility. Accordingly, the bulbils were planted and large bulbs were harvested in the summer of 1926. The latter were planted in August, 1926, and another crop of bulbils harvested in July, 1927. In this manner, 13–53 has been asexually propagated since 1925. Bulbil development and type are shown in figures 3 and 4. Interest soon developed in hybrid onions, and 13–53 served as the female parent in a number of crosses (*4*).

Monosmith[7] found that failure of 13–53 to set seed was due to impotent pollen. She found meiosis in the pollen mother cells to be regular but later certain of the tapetal cells degenerated abnormally, with subsequent death of many or all of the microspores. At dehiscence, the pollen-sac contents were cemented together, remaining within the anther.

[7] Monosmith, Helen Ruth. Male sterility in *Allium cepa* L. Unpublished thesis on file at the University of California Library, Berkeley. 1928.

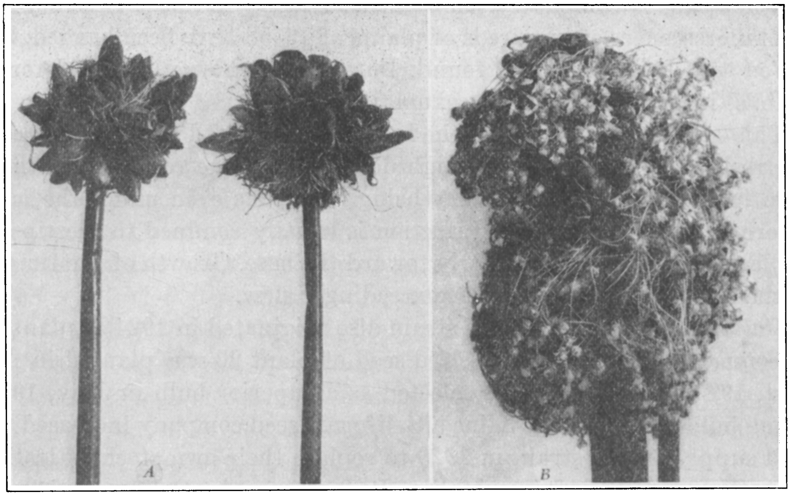

Fig. 3.—*A,* Mature seed heads of Italian Red 13–53 with flower parts removed to show development of bulbils. Although this strain is male-sterile, hybrid seed is readily produced, by using pollen from plants of other varieties. The umbels shown in *B* were bagged with an umbel of an $F_1$ plant of 13–53 × Red 21. Note the excellent set of seed in the dehisced capsules; also the bulbils in the same head.

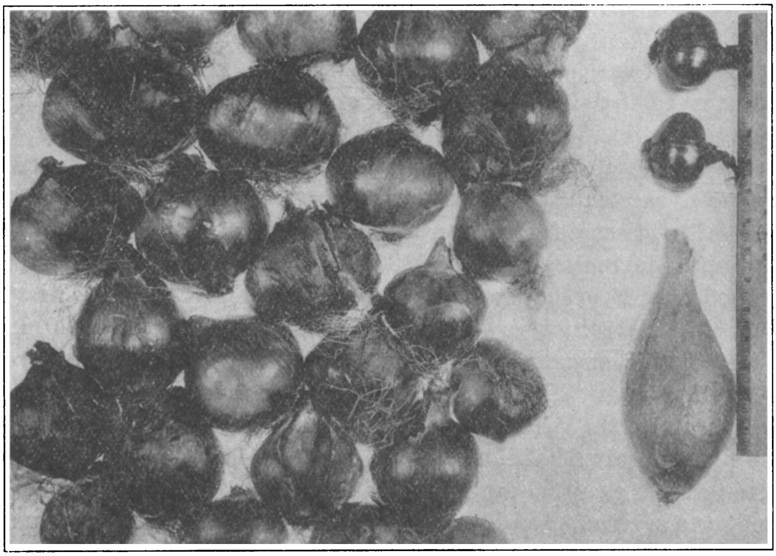

Fig. 4.—At the lower right is a bulb of Italian Red 13–53; at the upper right are bulbs of Lord Howe Island, and at the left is a group of $F_1$ bulbs involving these two varieties. Note the apparent hybrid vigor of the $F_1$ hybrid.

The strain is completely male-sterile. During the past twelve years the inflorescences of hundreds of plants of 13–53 have been bagged, but selfed seed has never been found. Fortunately, however, 13–53 forms bulbils, insuring continued asexual propagation.

This selection appears to be the best parent isolated to date for breeding resistant onions. It has a high degree of foliage resistance in field plantings, the amount of injury being negligible even under the most severe epidemic conditions. Infection is usually confined to the tips of the leaves and then grows slowly toward the base. Growth of the fungus in the leaf tissues appears to be exceedingly slow.

*Italian Red 13–20–3.*—This strain also originated in 1924 as plant 20 of commercial Italian Red. Selfed seed of plant 20 was planted in August, 1925, and plant 3 was selected as a superior bulb in July, 1926. Using bulbs of the 13–20–3 line a California seed company increased the seed supply of this strain in 1929 to replace their own stock of Italian Red. Some of the present Italian Red acreage in California is now 13–20–3. It is similar in type to 13–53 but not male-sterile. This line is well colored and of excellent shape but lacks somewhat in vigor because of inbreeding, and the foliage is not as resistant as that of 13–53.

Since 13–53 and 13–20–3 represent bulbs from the same population of Italian Red, it is evident that there existed in this lot of seed the gene or genes for resistance to downy mildew.

*Resistance Tests at Milpitas in 1937.*—Because downy-mildew infection at Davis varied significantly from year to year, and because the mildew when it did occur existed in epidemic form only early in the season, it was decided to expose the breeding stocks to infection at Milpitas in the Bay Region, where the disease had been epidemic for several successive years and where conditions most years are favorable for the spread of the disease for a longer time than at Davis. Bulbs were planted at Milpitas during September, 1936, and leaf and seedstalk infection recorded from February to July, 1937. To hasten infection, the first five plants of each strain were artificially inoculated on November 20, 1936, with a conidial suspension from heavily mildewed greenhouse-grown plants. On January 7, 1937, only the inoculated plants showed infection, and, therefore, the remaining population was inoculated at this time. Possibly these artificial inoculations were unnecessary, but because a severe test was essential for evaluating resistance an attempt was made to induce a severe and uniform epidemic. Mildew defoliation of known susceptible types was complete by May 18.

On March 25, when the mean number of leaves to the plant was approximately 35, the total number of leaves and of infected leaves was determined for each lot. The mean percentage of infected leaves is presented in table 3. Between 74 and 84 per cent of the leaves of Red 21, Stockton G36, Lord Howe Island, and Red Rocco were infected, as compared with only 2 per cent of those of 13–53. As in preceding observations, infection of 13–53 was confined to the tips of the leaves, with no serious interference of the normal leaf functions. Although 30 per cent of all the leaves of 13–20–3 were infected, the injury was not particularly severe. Considerable variation was evident in the amount of leaf infection of the various $F_1$ hybrids involving 13–53. M23, an $F_1$ of 13–53 $\times$ 13–52–9–6–$S_4$, manifested only 16 per cent infection, whereas approximately 75 per cent was observed on two $F_1$ populations of 13–53 $\times$ Crystal White Wax. Percentage of infected leaves, however, is not a particularly good measure of resistance, for it does not give a true picture of amount of injury. Most of the leaves might be infected and still the amount of injury be negligible.

The seedstalks of each plant were carefully examined on June 18 and indexed according to an arbitrary rating from 0 to 10 (table 3). The rating of 0 indicated no mildew lesions visible. Microscopic examination of many small mildewlike lesions on strain 13–53 failed to detect the organism. A rating of 10 indicated the most severe degree of infection, usually so weakening the seedstalk that only a very small quantity of seed was matured. Damage was of strictly minor importance until the stage represented by a rating of 4 was reached. From a breeding standpoint, plants rating 1 or 2 are almost as valuable as those which merit rating of 0, and only those plants manifesting stage 4 or higher are considered as suffering from mildew injury.

The seedstalks of 13–53, 13–20–3, M22, M23, and M24 were immune. Actually, mildew did not cause serious damage to any plants of M16, M4, M5, or M17. The nonuniformity of infection of the $F_1$ hybrids involving 13–53 may be attributed to the fact that neither 13–53 nor several of the commercial varieties had been inbred before making the respective crosses. The reaction of the various $F_1$ hybrids seems to indicate that resistance is inherited as a dominant character and that the resistant parent is heterozygous for resistance.

The varieties, Stockton G36, Red 21, Red Rocco, and Lord Howe Island were all badly infected. Among 23 plants of Lord Howe Island, two remained free of seedstalk infection; but it is thought that these are escapes rather than an expression of resistance. In most cases the populations were too small to get a good frequency distribution of the different classes of infection.

TABLE 3

RELATIVE RESISTANCE OF ONION VARIETIES, STRAINS, AND HYBRIDS AT MILPITAS, IN 1937

| Pedigree | Variety or parents | Generations inbred, or hybrid generations | Leaves infected on March 25, per cent | Number of plants | Distribution of plants among the following eleven classes of seedstalk infection on June 18: | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Mean |
| 13-53 | Italian Red (male-sterile) | .. | 2 | 26 | 26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| 13-20-3 | Italian Red | 7 | 30 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| M22 | 13-53×Red Rocco | $F_1$ | 47 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| M23 | 13-53×13-52-9-6-S | $F_1$ | 16 | 15 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| M24 | 13-53×13-20-3 | $F_1$ | 25 | 32 | 32 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| M16 | 13-53×Lord Howe Island | $F_1$ | 52 | 24 | 18 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 |
| M5 | 13-53×Stockton G36 | $F_1$ | 76 | 8 | 5 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.9 |
| M4 | 13-53×Crystal White Wax | $F_1$ | 74 | 21 | 9 | 5 | 6 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.0 |
| M4 | 13-53×Crystal White Wax | $F_1$ | 76 | 18 | 9 | 2 | 2 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1.4 |
| 13-52-9-6-S2 | Italian Red | 5 | 54 | 7 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2.9 |
| M17 | 13-53×Red 21 | $F_1$ | 53 | 85 | 16 | 20 | 20 | 27 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1.8 |
| M18 | 50-6-1×Red 21 | $F_2$ | 58 | 36 | 16 | 4 | 5 | 5 | 3 | 1 | 1 | 0 | 1 | 0 | 0 | 1.7 |
| MB10 | (50-6-1×Red 21)×Red 21 | $F_1$ | 72 | 44 | 4 | 4 | 4 | 6 | 4 | 7 | 9 | 2 | 2 | 1 | 1 | 4.2 |
| MB11 | (50-6-1×Red 21)×50-6-1 | $F_1$ | 51 | 187 | 1 | 6 | 8 | 32 | 36 | 33 | 24 | 23 | 14 | 9 | 1 | 5.0 |
| 36-40 | Stockton G36 | 1 | 83 | 9 | 0 | 0 | 1 | 0 | 3 | 0 | 2 | 0 | 1 | 2 | 0 | 5.8 |
| 21-22-1 | Red 21 | 2 | 84 | 40 | 0 | 0 | 1 | 0 | 7 | 11 | 3 | 4 | 9 | 5 | 0 | 6.2 |
| 10 | Lord Howe Island | .. | 75 | 23 | 2 | 0 | 1 | 2 | 0 | 0 | 2 | 4 | 3 | 4 | 5 | 6.9 |
| 70 | Red Rocco | .. | 74 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 9.5 |

Figure 5 shows the high degree of resistance of both seed stems and foliage of 13–53. Figure 6 shows Crystal White Wax with all leaves killed and all seedstalks very severely injured. These two figures show better than any system of noting the high degree of resistance of 13–53 and the extreme susceptibility of Crystal White Wax.

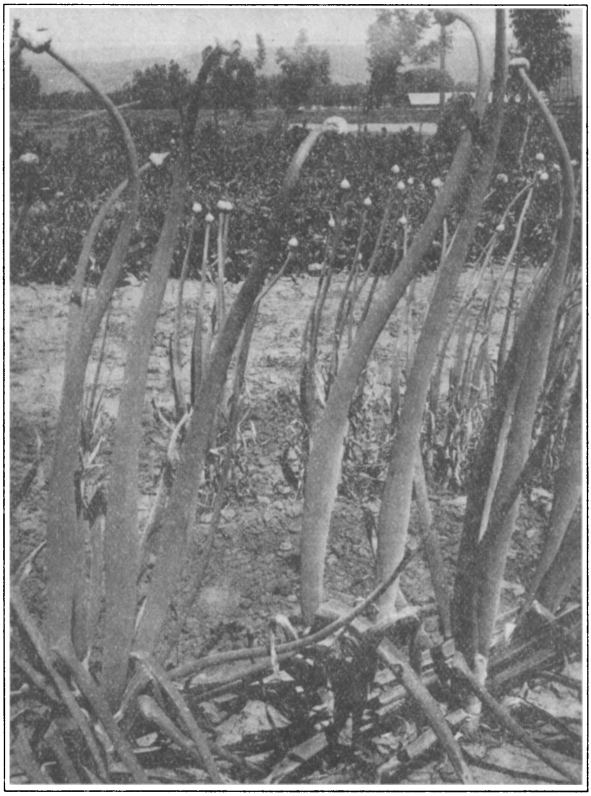

Fig. 5.—Indicating the immunity to downy mildew of seedstalks of Italian Red 13–53 at Milpitas, California, in May, 1937. Note also that the leaves are not severely injured.

*Resistance Tests at Milpitas in 1938.*—Bulbs for seed production were planted at Milpitas in September, 1937, in the same field where mildew had been so severe that same spring. Many bulbs used had been produced at Milpitas and Sacramento in 1937 and possibly some of these may have also served as sources of infection from perennial mycelium. Weather conditions from December to May were ideal for sporulation and infection. Accordingly, artificial inoculation was unnecessary.

Symptoms were first observed in late December of 1937 and by January 12, 1938, diseased plants were well distributed throughout the plot.

Development of conidia was noted on the foliage on April 6, and these entries appear in table 4 with ratings from 0 to 10, inclusive, as used in other tables. Very striking is the difference in sporulation between Crystal White Wax and the 13–20–3 series as well as that of MB16.

Fig. 6.—Showing extreme susceptibility to mildew of Crystal White Wax at Milpitas, California, in May, 1937. Note the dead leaves and the badly infected seedstalks.

Mother bulbs of 13–53 were not available for inclusion in the seed plot, but seedlings of 13–53 produced by August-planted bulbils were included in the bulb plot at Milpitas. Mildew appeared in this bulb plot in early February. On May 10 and again on June 4 the various populations were rated according to foliage injury. Based on comparative ratings from 0 to 10 on 13–53, foliage injury was only 1 and 2 on the two dates. Lord Howe Island gave readings of 9 to 10 and Crystal White Wax 10 and 10. Strain 13–20–3, however, was only moderately resistant, manifesting stages 4 and 5 injury. Many $F_1$ populations between susceptible varieties and 13–53 appeared to be about equally resistant, being intermediate between the two parents.

The final readings on injury to the seedstalks, made on July 5, together with the other data are presented in table 4. The sixteen varieties and inbred lines tested may be arranged as follows in the order of decreasing amount of injury: Crystal White Wax, Yellow Bermuda, Yellow Globe Danvers, Early Yellow Globe, Lord Howe Island, Southport

TABLE 4

RELATIVE RESISTANCE OF ONION VARIETIES, STRAINS, AND HYBRIDS AT MILPITAS, IN 1938

| Pedigree | Parents or variety | Average degree of sporulation on leaves April 6 | Number of plants | Distribution of plants among the following eleven classes of seedstalk infection on July 5: | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Mean |
| 13–20–3 | Inbred Italian Red | 1.5 | 28 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| ........ | Crystal White Wax | 8.6 | 70 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 70 | 10.0 |
| ........ | Yellow Bermuda | 7.6 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 10.0 |
| ........ | Yellow Globe Danvers | .... | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 6 | 9.2 |
| ........ | Southport Yellow Globe | 6.2 | 10 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 6 | 8.3 |
| ........ | Early Yellow Globe | 6.6 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 5 | 9.0 |
| ........ | Lord Howe Island | 7.8 | 49 | 2 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 40 | 8.9 |
| ........ | Southport White Globe | 6.7 | 10 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 6 | 8.6 |
| ........ | White Portugal | 7.8 | 38 | 0 | 0 | 1 | 0 | 5 | 2 | 2 | 1 | 3 | 3 | 21 | 8.1 |
| ........ | Red Rocco | 7.9 | 22 | 1 | 0 | 1 | 0 | 3 | 1 | 0 | 0 | 1 | 0 | 15 | 8.0 |
| ........ | Red 21 | 2.8 | 36 | 0 | 1 | 1 | 1 | 1 | 4 | 5 | 3 | 5 | 8 | 7 | 7.3 |
| ........ | Early Grano | 4.5 | 29 | 2 | 0 | 2 | 0 | 4 | 1 | 2 | 0 | 1 | 0 | 17 | 7.4 |
| ........ | Ebenezer | 5.6 | 33 | 4 | 0 | 5 | 4 | 8 | 2 | 2 | 1 | 1 | 3 | 3 | 4.5 |
| ........ | Australian Brown | 7.1 | 35 | 1 | 0 | 9 | 3 | 3 | 0 | 3 | 0 | 2 | 0 | 14 | 6.1 |
| ........ | Sweet Spanish | 4.4 | 37 | 4 | 2 | 6 | 3 | 2 | 2 | 3 | 4 | 1 | 2 | 8 | 5.2 |
| ........ | Stockton G36 | 6.7 | 27 | 10 | 0 | 3 | 1 | 1 | 0 | 2 | 0 | 3 | 0 | 7 | 4.4 |
| M4–1–1 | 13–53×Crystal White Wax $F_3$ | 6.4 | 43 | 3 | 2 | 2 | 2 | 3 | 1 | 2 | 1 | 3 | 1 | 23 | 7.2 |
| M4–1–2 | 13–53×Crystal White Wax $F_3$ | 7.1 | 36 | 3 | 1 | 0 | 1 | 2 | 2 | 2 | 5 | 3 | 0 | 17 | 7.3 |
| M4–1–3 | 13–53×Crystal White Wax $F_3$ | 7.2 | 37 | 4 | 0 | 3 | 0 | 2 | 2 | 1 | 1 | 2 | 1 | 21 | 7.4 |
| M4–1–4 | 13–53×Crystal White Wax $F_3$ | 7.1 | 39 | 2 | 0 | 1 | 2 | 5 | 1 | 2 | 0 | 3 | 1 | 22 | 7.6 |
| M4–1–5 | 13–53×Crystal White Wax $F_3$ | 6.8 | 27 | 3 | 0 | 3 | 0 | 1 | 3 | 1 | 1 | 5 | 0 | 10 | 6.6 |
| M4–1–6 | 13–53×Crystal White Wax $F_3$ | 7.3 | 44 | 4 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 2 | 5 | 28 | 8.2 |
| M4–1–7 | 13–53×Crystal White Wax $F_3$ | 6.2 | 49 | 2 | 2 | 2 | 5 | 2 | 5 | 2 | 1 | 3 | 1 | 24 | 7.1 |
| M16–2–1 | 13–53×Lord Howe Island $F_3$ | 3.7 | 90 | 52 | 10 | 16 | 5 | 4 | 2 | 1 | 0 | 0 | 0 | 0 | 1.0 |
| M16–2–2 | 13–53×Lord Howe Island $F_3$ | 3.8 | 74 | 41 | 14 | 10 | 3 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0.9 |
| M16–2–3 | 13–53×Lord Howe Island $F_3$ | 3.7 | 78 | 37 | 7 | 4 | 7 | 3 | 8 | 8 | 3 | 1 | 0 | 0 | 2.1 |
| M16–2–4 | 13–53×Lord Howe Island $F_3$ | 2.7 | 10 | 3 | 0 | 2 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2.5 |
| M16–2–5 | 13–53×Lord Howe Island $F_3$ | 4.7 | 17 | 10 | 0 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 1.8 |
| M28–1–1 | 13–53×Red Wethersfield $F_3$ | 6.0 | 6 | 4 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1.6 |
| M28–1–2 | 13–53×Red Wethersfield $F_3$ | 6.7 | 26 | 24 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 |
| M28–1–3 | 13–53×Red Wethersfield $F_3$ | 5.4 | 15 | 11 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1.1 |
| M28–1–4 | 13–53×Red Wethersfield $F_3$ | 6.8 | 20 | 12 | 4 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1.0 |
| M28–1–5 | 13–53×Red Wethersfield $F_3$ | 4.0 | 90 | 59 | 6 | 10 | 6 | 1 | 1 | 3 | 1 | 2 | 1 | 0 | 1.1 |
| M28–1–6 | 13–53×Red Wethersfield $F_3$ | 4.7 | 46 | 28 | 3 | 3 | 4 | 3 | 5 | 0 | 0 | 0 | 0 | 0 | 1.3 |
| MB2 | (13–53×Crystal White Wax)×Crystal White Wax | 7.1 | 30 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 27 | 9.7 |
| MB12 | (13–53×Early Grano)×Early Grano | 3.4 | 83 | 31 | 5 | 12 | 10 | 2 | 4 | 6 | 2 | 4 | 2 | 5 | 2.8 |
| MB13 | (13–53×Red Wethersfield)×Red Wethersfield | 5.8 | 16 | 10 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2.5 |
| MB15 | (13–53×Lord Howe Island)×Lord Howe Island | 4.5 | 59 | 22 | 4 | 8 | 5 | 8 | 2 | 3 | 1 | 3 | 1 | 2 | 2.6 |
| MB16 | (13–53×13–20–3)×13–20–3 | 0.4 | 17 | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |

White Globe, Southport Yellow Globe, White Portugal, Red Rocco, Early Grano, Red 21, Australian Brown, Sweet Spanish, Ebenezer, Stockton G36, and Italian Red 13–20–3. Again the 13–20–3 family produced mildew-immune seedstalks, and microscopic examination failed to detect mildew mycelium in the yellowed areas of the seedstalks. Although seedstalks of a few plants of Stockton G36 and other varieties were apparently immune, it is more likely that they escaped infection. The seedstalks of Australian Brown, Ebenezer, and Sweet Spanish emerged much later than those of early and intermediate varieties; this may account for the small amount of damage, since even at Milpitas the conditions become increasingly unfavorable for mildew as the season advances.

All bulbs in the various families of the M4 series were white segregates from the $F_2$ populations. If there is linkage between color and resistance, then it is possible that all the bulbs selected were susceptible, and that the individuals given a rating of 0—and perhaps those of 1 and 2—were escapes.

Bulbs in families M16–2–1 to M16–2–3 were selected at random from the $F_2$ population. In families M16–2–4 and M16–2–5, flat bulbs were selected. It is almost impossible to classify the present data into well-defined resistant and susceptible classes, since it is not known if the spots found in the seedstalks of plants in classes 1, 2, and possibly 3, are similar to those found on 13–53 which proved to be free from the mildew fungus. Before the definite mode of inheritance can be determined, the seedstalks of borderline plants will probably need to be examined microscopically to determine definitely in what classes they belong. Also, some means must be established to determine the number of escapes in the apparently immune class. The plants in all of the M16 families were extremely prolific, producing many seedstalks per plant and seed heads of large size. The high degree of immunity and vigor exhibited in these $F_3$ families indicates the early production of an intermediate variety with resistant foliage and immune seedstalks.

The resistance of the six $F_3$ families of 13–53 $\times$ Red Wethersfield (M28 series) was even more striking than the $F_3$ of the M16 series; but here again the precautions mentioned above will need to be taken in order to determine definitely the mode of inheritance. It is possible that family M28–1–2 is homozygous-resistant since the two plants in class 2 may actually belong to the immunes. The plants were vigorous and produced a high seed yield.

The data for several backcross progenies, indicated as MB strains, are included in table 4. These backcrosses were made in order to develop mildew-resistant strains typical of the various varieties. These populations, backcrossed to the susceptible parents, had many plants in the immune and highly resistant classes with the exception of MB2, the backcross to Crystal White Wax.

The Italian Red backcross (13–53 × 13–20–3) × 13–20–3 produced mildew-immune seedstalks. This was to be expected, since those of both parents were immune. Although the foliage of 13–20–3 is usually severely damaged under epidemic conditions, relatively little injury is found on the leaves of 13–53. The degree of sporulation recorded in table 4 is 0.4 which suggests that this population when isolated would be subject to rather light spore inoculation. Probably greater foliage resistance can be incorporated by backcrossing to the 13–53 parent, but by doing this pollen sterility will also be increased. Some one of the progenies from this cross may be the foundation stock for a highly resistant variety which should be adapted to about the same range of conditions as the present Italian Red variety—chiefly those of central California.

## SUMMARY

Adequate control measures are still lacking for onion downy mildew, and because the disease frequently appears suddenly in epidemic proportions, heavy losses are often incurred by the bulb and seed grower.

Actual losses incurred by seed growers in California, vary from 0 to 80 per cent, with weather conditions the main conditioning factor. During the past nineteen years, the annual reduction in seed yield has been 10 per cent or higher during six seasons, with a maximum between 60 and 80 per cent in 1925, and several annual losses exceeding 40 per cent.

Certain practical difficulties exist in fungicidal control, making especially desirable the development of resistant varieties.

Three sources of resistance have been found. The most promising is strain 13–53, a male-sterile selection from the Italian Red variety. The seedstalks of this strain are immune and the foliage is highly resistant.

Another strain of Italian Red, designated as 13–20–3, likewise manifests seedstalk immunity but the foliage is only slightly resistant. This latter strain, however, is superior to 13–53 in type.

Seedstalk immunity was also found in the year 1934 in an $F_1$ hybrid between Red 21 and two inbred lines of Stockton Yellow Flat, namely, 50–6 and 50–6–1.

Measured evidence of varietal and hybrid resistance is indicated in the tables and discussed in the text. Certain $F_3$ and backcross populations involving 13–53 as the resistant parent are particularly promising.

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