HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 8 | JUNE, 1934 | NUMBER 7

CONTENTS

UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOL. 8 | JUNE, 1934 | NO. 7

THE INHERITANCE OF RESISTANCE TO RUST IN THE SNAPDRAGON[1]

S. L. EMSWELLER[2] AND H. A. JONES[3]

INTRODUCTION

THE RUST (*Puccinia antirrhini* D. and H.) of the cultivated snapdragon (*Antirrhinum majus* Linn.), was first observed by Blasdale(2)[4] in 1896. For some time thereafter it was apparently confined to the Pacific Coast, but in 1913 it suddenly appeared in the vicinity of Chicago, Illinois, whence it has spread rapidly to all sections of this country, to Mexico, and to Canada. Within recent months it has appeared in England where it will probably become widespread because of the very favorable climatic conditions.

The work of Mains(4) indicates that the rust is heteroecious and that it probably has pycnia and aecia on an alternate host. All his attempts to infect snapdragon plants with germinating teliospores were unsuccessful. He predicts that the alternate host will probably be found in California on native species of *Antirrhinum* in localities where those plants are naturally infected with rust.

When the disease first appeared in the Middle West, florists were unable to control or check it, so that the growing of snapdragons under glass became exceedingly hazardous. The rapid spread of the rust was probably caused by the method of propagation then in use. Many florists had their own strains, which they increased by cuttings from a desirable plant. The shade and high moisture conditions of the cutting bench afforded ideal conditions for rust, and interstate shipments of rooted cuttings probably caused its wide distribution.

[1] Received for publication September 27, 1933.

[2] Assistant Professor of Truck Crops and Assistant Olericulturist in the Experiment Station.

[3] Professor of Truck Crops and Olericulturist in the Experiment Station.

[4] Superior figures in parentheses refer to Literature Cited, p. 211.

Peltier[6] demonstrated clearly that the disease is not seed-borne. This fact stimulated propagation by seed, which called for varieties more homozygous for type; and in a short time many were developed, while the cutting method of propagation was discontinued. At present, florists can somewhat control the disease under glass by careful regulation of watering, ventilating, and temperatures.

When snapdragons are grown out-of-doors the disease is almost uncontrollable. Since spraying with fungicides has not given satisfactory results, this flower has almost disappeared from the gardens of many sections.

In California, where practically all the American snapdragon seed is produced, the rust presents a grave problem. Frequently the yields amount to only a few pounds per acre, and 75 pounds per acre is very rare. To increase the yields of seed California seedsmen have followed various practices—notably early planting, and the use of land on which snapdragons have not been previously grown.

An early autumn planting usually produces a large, vigorous plant before the rust becomes active in the spring. Such plants flower early and may have some maturing seed by the time the rust appears. Although this practice is probably beneficial in seasons when climatic conditions do not favor the rapid spread of the disease, the writers have seen several such fields very badly infested in early spring.

When snapdragons are planted, according to the second practice, on soil that has not grown a crop previously, they are usually not very heavily infected. If, however, the same land is replanted year after year, the infestation becomes increasingly severe.

The common practice at present is to withhold water from the plants as soon as rust appears. Though undoubtedly unfavorable for plant growth, this precaution is necessary if the spread of the disease is to be retarded.

METHODS AND MATERIALS

In 1929 the writers became interested in trying to control snapdragon rust by means of resistant varieties. They made trips to some of the large flower-seed ranches in California, observing the disease in every field visited. Since diligent search failed to reveal a single plant showing resistance, there are evidently no "escapes" under conditions of severe infestation.

In 1929 several varieties were grown at Davis, California, and individual plants were self-pollinated to determine whether inbred lines vary in their degree of susceptibility. Dr. J. B. Kendrick, of this Station, also supplied some snapdragon seed of resistant selections, obtained from Dr. E. B. Mains of Indiana, whose work has been described from time to time in the annual reports of that Station. In 1930 several hundred seedlings were grown from the Indiana seed and from selfed seed produced at Davis. Seedlings of both lots were planted at Colma in the San Francisco Bay region, and on the Waller-Franklin flower-seed

TABLE 1

RESULTS SECURED BY SELFING RESISTANT PLANTS IN 1931; POPULATIONS GROWN IN 1932

Plant No.	Number resistant	Number susceptible	Deviation	$\frac{D}{P.E.}$
4	41	14	0.25	0.11
10	66	0	....	....
12	52	0	....	....
23	106	34	1.00	0.28
24	73	27	2.00	0.68
26	187	64	1.75	0.37
103	68	0	....	....
107	51	0	....	....

TABLE 2

RESULTS SECURED BY CROSSING RESISTANT PLANTS WITH COMMERCIAL VARIETIES IN 1931; PROGENIES GROWN IN 1932

Resistant parent and susceptible parent	Number of plants	Number resistant	Number susceptible
10 × Apple Blossom	28	28	0
10 × Salmon Pink	31	31	0
10 × Canary Yellow	14	14	0
12 × Apple Blossom	16	16	0
26 × Canary Yellow	26	16	10
24 × Advance	18	7	11

ranch at Guadalupe, California. A number grown from the Indiana seed showed a very high resistance. Although no plants were completely free from rust, several had only a few small sori. These resistant individuals were allowed to open-pollinate, and a large amount of seed was harvested from each. In 1931 their progenies were grown on the University Farm at Davis, on the Ferry-Morse ranch at Salinas, and on the Waller-Franklin ranch at Guadalupe. In these large populations were found several plants that were entirely free from rust. In the fall a few of the most desirable of the resistant individuals were dug and removed to Davis, where they were transplanted into a greenhouse bench. In 1931 most of them were self-pollinated, but a few crosses were made to the commercial varieties Advance, Apple Blossom, Salmon Pink, Canary Yellow, and Beacon.

The selfed and hybrid seed secured in 1931 was grown in 1932, with the results shown in tables 1 and 2. Not all the data are included in these tables—only sufficient to show that the resistant plants were of two types, one homozygous for resistance and the other heterozygous. The results also indicate that resistance is controlled by a dominant gene.

TABLE 3

RESULTS SECURED IN 1933 FROM SELFING AND FROM CROSSING HOMOZYGOUS AND HETEROZYGOUS RESISTANT PLANTS WITH SUSCEPTIBLE VARIETIES

Pedigree	Number resistant	Number susceptible
Line 26 (heterozygous resistant) × susceptible variety	2,664	2,587
Line 26 (homozygous resistant) × susceptible variety	392	0
Line 10 × susceptible variety	562	0
Susceptible hybrids, self-pollinated	0	310
Heterozygous resistant plants, self-pollinated	363	137
Susceptible hybrids back-crossed to susceptible varieties	0	415

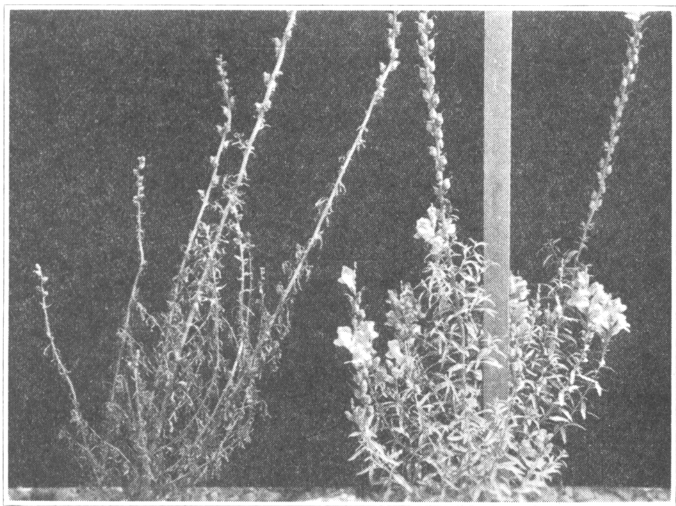

Fig. 1.—A susceptible plant (left) and a resistant plant (right) growing side by side in the field.

In order to check the results further, additional crosses were made by the authors in 1932 between certain resistant plants and some of the more important commercial varieties. Thirty-two resistant plants of line 26 were used as seed parents in crosses with the standard commercial varieties Brilliant Rose, Harmony, Atro-Coccineum, Fascination, Canary Yellow, Snowflake, Cardinal, Apple Blossom, Red Emperor, and Salmon Pink. The resulting progenies were grown in six localities in

California, with the results shown in table 3. The figures given represent the total counts made in the state in 1933.

Of the 32 plants in line 26, 9 proved to be homozygous for resistance. Progeny from all these plants were grown at Davis, Salinas, Guadalupe, Santa Maria, Lompoc, Pasadena, and El Monte. In all locations their reaction toward the rust organism was the same. The results at El Monte were particularly striking; seed was sown in June, 1932, and the plants were wintered-over in the field. In the early spring susceptible plants began to show lesions, and by May they were either dead or badly infected. Figure 1 shows a resistant and a susceptible plant growing side by side in the field.

TABLE 4

BACK-CROSS PROGENIES DESCENDING FROM RESISTANT PLANTS 16 AND 20

	Partially resistant	Susceptible	Resistant
(16 × Salmon Pink) × Salmon Pink	14	29	15
(20 × Beacon) × Beacon	34	61	17

Crosses were also made between plants from the resistant line, No. 10, and the varieties Cheviot Maid Supreme, Apple Blossom, Red Emperor, Beacon, and Advance—all susceptible. All crosses involving plants from line 10 produced only resistant hybrids; all the back-crosses involving a heterozygous plant gave the expected 1:1 ratio; and those back-crosses and self-pollinations involving susceptible plants gave only susceptible progeny.

MODIFYING FACTORS

Besides the resistant plants two slightly susceptible ones were found in 1931, growing in the progenies of the resistant plants that had been open-pollinated in 1930. These two plants, Nos. 16 and 20, were crossed with commercial varieties, the former to Salmon Pink and the latter to Beacon. From these crosses, only 19 hybrid plants were grown; 10 from the first and 9 from the second. All were planted in the greenhouse. In each lot of hybrids 2 were susceptible, the others being recorded at that time as resistant. In each lot a hybrid which was classified as resistant was back-crossed to its commercial parent in 1932. When these back-cross progenies were examined, three types of plants were found in each population—resistant, slightly susceptible, and susceptible. It is improbable that this situation was the result of the appearance of a second strain of rust, for the three types were found in only two populations, both descending from slightly susceptible plants. These populations were completely surrounded by other resistant strains, none of which showed this condition.

For this condition no explanation is offered, other than the probable presence of modifying factors. The numbers, though rather small, indicate that an analysis of the situation should not be difficult. It would be very interesting to know whether the factors responsible are carried in commercial varieties. Whenever a plant from line 10 has been used as the resistant parent, it was found to have complete resistance. This statement, however, does not imply that modifying factors are not present in commercial varieties, since only a few of the latter have been used in the crosses.

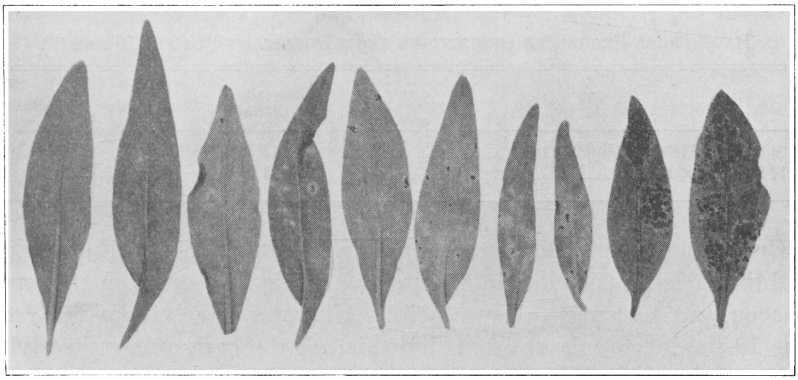

Fig. 2.—Leaves of snapdragons, showing variations from complete resistance to susceptibility.

Until this situation was encountered the origin of the resistant plants found in populations grown from the open-pollinated slightly susceptible plants of 1930 could not be well explained. If modifying factors are present, segregation might be expected eventually to produce plants from which they had been eliminated. The total population of about 5,000 grown in 1930 presented a wide range from complete susceptibility through different degrees of resistance to complete resistance. Only a few plants were of the latter type. Plants 16 and 20 were selected from among the most highly resistant, so the fact that each produced several resistant plants in the back-cross generations is not unusual, if each carried but few of the modifying genes. Since they had susceptible plants, too, in their progeny, they were also probably heterozygous for resistance. Some of the resistant hybrid progeny of plants 16 and 20 must have carried modifying factors even though they showed no rust in the greenhouse, where conditions for rust are not so ideal as in the field, and where very slightly susceptible plants might easily be counted resistant.

Figure 2 shows the various types of resistance found in the two populations derived from plants 16 and 20, together with leaves from completely susceptible specimens. The snapdragon leaves included in this figure, taken from different plants in line 20, represent fairly well the actual range of resistance. Only a few leaves on such plants are attacked, and often a rather thorough examination is necessary to locate any infection whatever. Other resistant plants are rather heavily infected, but never so severely as fully susceptible ones. The leaves depicted display lesions very similar to those on resistant wheat plants shown by Mains and Jackson,[(5)] whose scale for measuring resistance would be a very interesting method of studying the degrees of resistance in snapdragons. Among the large populations grown in 1931 there were undoubtedly plants showing all types of resistance covered in the scale. In the snapdragon, however, completely resistant plants have not even the light flecking on the leaves, that appears on some wheat plants resistant to leaf rust. This situation is somewhat similar to that reported by Briggs,[(3)] who found evidence for factors modifying the resistance of wheat to bunt, and who gives a rather detailed discussion of modifying factors in general.

METHODS OF ISOLATING RESISTANT PLANTS

In 1932 it was found that susceptible plants could be infected and eliminated in the early stages of growth. According to the procedure used, plants of lines known to carry resistance were transplanted to $2\frac{1}{2}$-inch pots. After becoming established, some were placed in coldframes, the remainder on a greenhouse bench. Every fourth row consisted of various known susceptible varieties. Thus a check was made upon the efficiency of inoculation under both environments. All were then covered with cheesecloth. On several successive evenings each lot was thoroughly syringed with water and had heavily rusted branches shaken over it. The cheesecloth covering was kept moist for several days and then removed; thereafter, the plants were watered and tended normally. The first sori appeared in about ten days, and within three weeks all the commercial plants were infected, as well as the susceptible ones in the selfed and back-cross populations.

DESCRIPTION OF RESISTANT LINES AND OF HYBRIDS BETWEEN THEM AND COMMERCIAL VARIETIES

All four homozygous resistant strains are undesirable as commercial types. The plants are bushy, profusely branching, each producing numerous slender-stemmed spikes. The flowers are small, spaced far apart on the spike, and the colors are generally mottled. The blooming period being so late, they must be planted from four to six weeks earlier than standard commercial varieties in order to begin blooming at the same time. Each strain is also somewhat self-sterile and does not set much seed even when open-pollinated, although the pollen and eggs are both func-

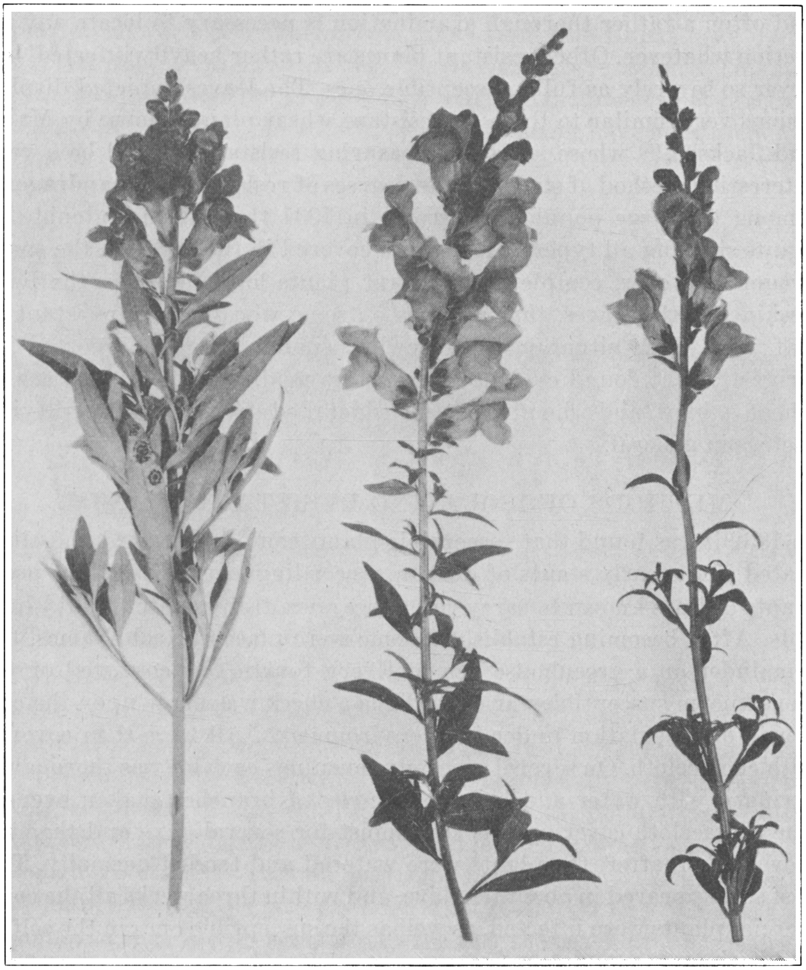

Fig. 3.—Showing inheritance of rust resistance. Left, Red Emperor, susceptible; right, No. 10, resistant; center, F_1, resistant.

tional. These characteristics would practically eliminate these resistant lines from consideration by florists, gardeners, and seedsmen.

Crosses have now been made between resistant types and 15 standard commercial varieties. In all instances the hybrids resemble the commercial parent more closely than the resistant, as shown in figure 3. They exhibit marked vigor, are highly self-fertile, bloom almost as early, and have practically as large flowers as does the commercial parent. When a tall variety of the maximum type has been used in the cross, the hybrids are usually as tall as the taller parent. Low-growing, bushy varieties, such as Red Emperor and the Majestics, when crossed with line 10 produce an F_1 population with a growth habit practically the same as that of the commercial parent.

When an F_1 hybrid plant, free from modifying genes, is self-pollinated, it segregates (for rust) into a ratio of 3 resistant to 1 susceptible. If a number of these resistant segregates were self-pollinated, one-third of them would breed true for resistance, and two-thirds, or those heterozygous for resistance, would again segregate in a 3:1 ratio. This work does not purport to analyze the inheritance of any characters other than resistance. Plants in F_2 populations have exhibited a wide range of colors and types.

METHOD OF COMBINING RESISTANCE WITH DESIRABLE CHARACTERS

In order to secure acceptable commercial types as rapidly as possible, the back-cross method has been used. The variety Red Emperor, a low, bushy type with large, dark-red flowers, was crossed with line 10, a type slightly taller in growth, very much branched, and bearing smaller flowers of a mottled rose-and-white color. The hybrid plants were all taller than either parent; their flower color was a dark cerise; they were all resistant to rust and bloomed about a week later than the variety Red Emperor. Several of these hybrids were then back-crossed to Red Emperor, and a 1:1 ratio for resistance was secured. The susceptible plants were discarded, and only the resistant individuals that most closely resembled Red Emperor were selected for use in a second back-cross. This procedure of back-crossing the resistant plants to the commercial parent should be carried through a number of generations until the back-cross population shows a very high uniformity with Red Emperor. Then the best resistant plants should be self-pollinated. The progeny will segregate in a 3:1 ratio for resistance. A large number of the resistant plants should then be self-pollinated, and those homozygous for resistance will form the basis for a new resistant type, which should very closely resemble Red Emperor.

The number of back-crosses necessary to produce a line homozygous for flower color, habit of growth, and general morphological characters will probably vary with different varieties, according to the genetic relationship of the colors and other characters. The inheritance of color in snapdragons is known to be very complex, as shown by Baur[1] and by

Wheldale,[7] who have demonstrated the presence of at least 18 different genes affecting color. Various combinations produce complex color patterns, such as color of the tube differing from the rest of the corolla, and various degrees of mosaic color patterns. In order that a homozygous combination may be secured as rapidly as possible, the commercial parent used in the first cross and in subsequent back-crosses should be as nearly homozygous as possible for color and type. With such a parent, from three to five back-crosses should suffice to produce a fairly homozygous population.

Fig. 4.—Young bud of snapdragon with perianth and two stamens removed.

The procedure described above has been started with the varieties Cheviot Maid Supreme, Autumn Glow, Ceylon Court Yellow, Canary Yellow, Apple Blossom, Red Emperor, Advance, Majestic Red Chief, Majestic Twilight, and Majestic Orange King. First and second back-cross material has already been sent out to California seedsmen. The results so far have been very promising, many resistant plants in the first back-cross generation appearing identical with the commercial parent.

POLLINATION TECHNIQUE

The snapdragon flower is very easy to manipulate for cross-pollination. Emasculation may be performed at any time before dehiscence of the anthers, which does not occur until the buds are large and the flower is

Fig. 5.—Method of bagging for self and cross-pollination.

within a day or two of opening. A young bud at this stage, with the corolla and two stamens removed, appears in figure 4. At this age, when the flower is not readily injured, the stamens may be removed with ease; they are four in number—two long and two short. In the bud stage the filaments are shorter than the style; but they elongate rapidly until, at dehiscence, the anthers on the longer filaments are in contact with the stigma. The arrangement indicates that self-pollination among snapdragons is common.

When a plant has been selected as a seed parent for a cross, one or more spikes are chosen, and the top of each is pinched out, leaving from 7 to 10 buds. A bag is placed over the spike and fastened to a stake, and a complete record of the cross is placed on a small tag tied below the bag (fig. 5). Emasculation of the buds on each spike may take as long as a week, since the buds progressively mature from the base of the spike to the tip. Pollination is begun as soon as the stigma is receptive—that is, from two to three days after emasculation. Thus both emasculation and pollination may be occurring on a spike at the same time. Pollination is usually accomplished by removing a freshly dehisced anther with a pair of forceps and rubbing the pollen on the stigma. After fertilization, the corolla withers and drops. The seed is harvested as soon as the ovary dehisces, for, if allowed to remain on the plant, it may be partially lost by shattering. The yield will average about 500 seeds per capsule.

RESISTANCE TO RUST IN SOME OF THE OTHER ANTIRRHINUM SPECIES

In 1932 the Division of Foreign Plant Introduction, United States Department of Agriculture, secured seeds of several European species of *Antirrhinum* which were collected by E. Baur (Germany) while on a trip into Spain. In November of 1932, each lot of this seed was planted in the greenhouse at Davis, and in January all were exposed to rust. The seedlings were transplanted to the field in the early spring and were grown in a plot adjacent to susceptible plants of *Antirrhinum majus.* The results of this test appear in table 5.

It is very interesting that resistance to rust should be found in any of the European species. The disease does not occur in Europe, and most likely none of these species have been exposed to this disease at any time during their evolutionary history. Probably, as shown in the table, some were homozygous for resistance, some heterozygous, and others all susceptible. The degree of susceptibility varied considerably, some being attacked very lightly, while others were killed. In all instances the resistance was complete, not a single sorus being found on any of these plants.

Several of the species resembled very closely some of the resistant plants derived from the seed sent by Dr. Mains. The flowers were about the same size, the leaves similar, and the plants also highly self sterile. No attempt has been made by the authors to determine the nature of the resistance in these plants, but most likely the resistant gene secured from the Indiana material had its origin in some of these European species.

The most generally interesting part of this phase of the work is the demonstration of the great potentialities in the field of foreign plant introduction. Very probably, resistance to many diseases of our economic crop plants could be discovered in closely related forms or species growing in other parts of the world. The desired character, even though

TABLE 5

REACTION OF SEVERAL EUROPEAN SPECIES* OF ANTIRRHINUM TO RUST

Number	Species of *Antirrhinum*	Number of resistant plants	Number of susceptible plants
136	*glutinosum* (Capileira)	32	0
137	*glutinosum* (Orgiva)	0	28
138	*hispanicum* (Celorico)	3	12
139	*ibanjezii* (Cartagena)	16	0
140	*molle* (Lerida)	0	21
141	*molle* (Monsech)	18	0
142	*siculum*	24	0
143	*tortuosum*	0	29
144	species ? (Chorro)	3	8
145	species ? (Cintra)	0	16
146	species ? (Lucena)	10	12
147	species ? (Zaragoza)	17	0

* These species were not determined by the authors, but are here published, with locality names, as listed by E. Baur.

found in another species of the genus, may possibly be incorporated with the more desirable characters of our economic plant. The sanctity of species delimitation is slowly fading as reports of synthetic species formation continue to accumulate.

SUMMARY

The rust (*Puccinia antirrhini* D. and H.), of the cultivated snapdragon (*Antirrhinum majus* Linn.), was first observed in California in 1896. In 1913 the disease appeared in the vicinity of Chicago, Illinois; and since then it has spread to practically all parts of the United States.

Methods of control have not proved entirely satisfactory, particularly when snapdragons are grown out-of-doors. Under greenhouse conditions, the disease can be somewhat checked by certain cultural practices.

In 1929 unsuccessful attempts were made to find resistant plants in the seed fields in California. The next year seed was secured from resistant selections made at the Indiana Experiment Station, and large

populations were grown in several localities in California where rust was particularly severe.

Several plants found in the population from the Indiana seed showed a very high resistance to the disease. These were open-pollinated, and a large amount of seed was harvested from each.

In 1931 progenies from these highly resistant plants were grown in various locations in California, and a very few plants from each location were entirely free from rust. A few of these resistant individuals were removed to Davis, where they were self-pollinated and crossed with several known susceptible varieties. The results showed that resistance is controlled by a single dominant gene.

Several highly resistant plants were used in crosses with known susceptible varieties, and the results indicated the presence of modifying genes. This seems to be a logical explanation for the fact that immune plants were secured from highly resistant parents, since segregation would tend to produce some types free from modifying genes.

The original plants are undesirable types, used only because of their resistance. To transfer the resistant gene to good commercial varieties as rapidly as possible, the back-cross method has been utilized. Progress so far has been very encouraging.

ACKNOWLEDGMENTS

The authors are indebted to the following California seedsmen for their help and coöperation in this work, Bodger Seeds, Ltd.; the Ferry-Morse Seed Company; Fraser & Son, Ltd.; F. Lagomarsino and Sons; the Waller-Franklin Seed Company; and the William Macdonald Seed Company. They have generously permitted the use of land and have furnished many valuable suggestions.

LITERATURE CITED

[1] BAUR, E.
1910. Vererbungs und Bastardierungsversuche mit Antirrhinum. Ztschr. Induktive Abstam. u. Vererbungslehre. **3**:34–98.

[2] BLASDALE, W. C.
1903. On a rust of the cultivated snapdragon. Jour. Mycol. **9**:81–82.

[3] BRIGGS, F. N.
1929. Factors which modify the resistance of wheat to bunt, *Tilletia tritici*. Hilgardia **4**:175–184.

[4] MAINS, E. B.
1924. Notes on the life history of the snapdragon rust. Phytopathology **14**:281–287.

[5] MAINS, E. B., AND H. S. JACKSON.
1926. Physiologic specialization in the leaf rust of wheat, *Puccinia triticinia* Erikss. Phytopathology **16**:86–120.

[6] PELTIER, G. L.
1919. Snapdragon rust. Illinois Agr. Exp. Sta. Bul. **221**:535–548.

[7] WHELDALE, M.
1910. Die Vererbung der Blutenfarbe bei *Antirrhinum majus*. Ztschr. Induktive Abstam. u. Vererbungslehre. **3**:321–333.