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C. O. BLODGETT[2] AND G. A. L. MEHLQUIST[3]

INTRODUCTION

THROUGH THE EFFORTS of a number of workers, especially of Mains[4] and Emsweller and Jones,[5] it appeared in 1934 and 1935 as though the serious problem of rust on snapdragons would soon be solved. Some valuable commercial strains[6] had been released to the seed trade in 1931 and 1932, and development of others was proceeding at a rapid pace. Mains had warned of the possibility of the occurrence of physiologic forms[7] in the *Antirrhinum rust* (*Puccinia antirrhini* D. and H.), but when in 1936 the so-called "resistant" snapdragons began to show severe symptoms of rust, especially in the Salinas Valley, the question was raised by commercial seed growers as to whether this was due to a "breakdown" in the resistance resulting from breeding and cultural practices. Yarwood,[8] however, clearly demonstrated that the susceptibility of the resistant strains was due to the presence of one or more different forms of the rust, which evidently had not been prevalent before that time in the district where the earlier work had been done.

The purpose of this paper is to place on record the results of trials conducted during the seasons of 1937 and 1938, in an attempt to locate species, varieties, or strains of *Antirrhinum* immune, or at least highly resistant, to new as well as old forms of rust. It was hoped that, if such an *Antirrhinum* strain could be found, it might be used in the breeding of resistant or immune types suitable for floriculture and ornamental gardening.

This work is in part a continuation of that started by Emsweller and Jones. During the first season, 1936–37, the work was conducted through

[1] Received for publication June 30, 1939.

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[4] Mains, E. B. Rust resistance in *Antirrhinum*. Phytopathology 25(11):977–91. 1935.

[5] Emsweller, S. L., and H. A. Jones. The inheritance of resistance to rust in the snapdragon. Hilgardia 8(7):197–211. 1934.

[6] Throughout this paper the word "strains" is used in the sense that it includes a smaller category of snapdragons than either "species" or "varieties"—that is, there were in certain cases in our trials, several strains of certain varieties of commercial snapdragon.

[7] In speaking of rusts, "forms" will be used to designate the different "races" or "physiologic forms."

[8] Yarwood, Cecil E. Physiologic races of snapdragon rust. Phytopathology 27(1): 113–15. 1937.

the Division of Truck Crops at the University Farm at Davis. In 1937, the work was transferred to the Division of Genetics at Berkeley, and it has been continued with Berkeley as headquarters.

MATERIALS AND METHODS

For these trials, seeds of about one hundred and forty samples of different species and strains of *Antirrhinum* were collected. Some of the commercial strains were obtained from wholesale seed companies located in California. Others were specially developed strains from four experiment stations in this country.

Practically all of the species, as distinguished from the commercials, were originally introduced by the United States Department of Agriculture, although some were purchased from seed houses, or obtained from private collectors. The sources of the various strains are indicated by the following abbreviations, used in tables 2 and 4:

Brus.: Botanic Gardens, Brussels, Belgium
Buch.: Botanic Gardens, Bucharest, Rumania
Germ.: Kaiser Wilhelm Institute, Berlin-Dahlem, Germany, via United States Department of Agriculture Division of Foreign Plant Introduction
Göt.: Göteborg, Sweden, via United States Department of Agriculture Division of Foreign Plant Introduction
Lom.: Collected by T. Little at Lompoc, California
Palm.: Palmero, Italy, via United States Department of Agriculture Division of Foreign Plant Introduction
Paris.: Museum of Natural History, Paris, France
Stock.: Botanic Garden, Stockholm, Sweden, via United States Department of Agriculture Division of Foreign Plant Introduction
T. & M.: Thompson and Morgan, Seedsmen, Ipswich, England
Turk.: Collected by the Westover-Wellman expedition in Turkey, received via United States Department of Agriculture Division of Foreign Plant Introduction
Vent.: Ventimiglia, Italy, via United States Department of Agriculture Division of Foreign Plant Introduction

Elaborate, detailed attempts to identify or verify the species in our trials has not been undertaken, although some self-evident examples of misnamed species have been corrected. For the most part, the species have been grown under the name under which they were received.

Of the commercial strains used, some were selected from the older standard rust-susceptible varieties (designated by "S" in the tables), in order to provide adequate checks for the resistant (designated by "R") strains and new species. A plus or minus sign following the "S" or "R" indicates "highly resistant" or "fairly resistant" as the case may be, as reported by the donor.

The seed for the strains tested in 1937 was sown in the greenhouse at

Davis in the winter of 1936–37 and carefully guarded from possible rust infection until the plants were large enough for transplanting; the young plants were then shipped to various localities in the state. Strains were tested at twelve localities, in 1937, but all strains were not grown at each locality. Eleven of these localities are listed in table 1. Unfortunately the trials at Eureka in the northern part of the state were a complete failure owing to lack of care, but the other trials were well cared for and gave very definite results.

The strains tested in 1938 were started under glass in Berkeley, where the same precautions were taken to prevent rust infection before transplanting, as were taken at Davis.

In 1937, twenty-five plants of each strain were used in the trials, except at Berkeley, Davis, and San Jose, where smaller numbers of certain strains were sometimes used because of insufficient plants, due to poor germination or other causes. The greatest number of accessions, however, were grown at the three localities just mentioned. These three places fairly well covered the range in climate from the relatively hot interior Sacramento Valley at Davis to the cool coastal situation at Berkeley, with an intermediate climate at San Jose.

Because the rust reaction of the various snapdragon strains had been similar in Berkeley and San Jose to what it was in the coastal and inland areas, respectively, in 1937, the trials were restricted to these two localities in 1938. Further reason for thus restricting the trials was that as much information regarding rust reaction could be obtained from smaller numbers of plants.

The plantings at Berkeley were thoroughly inoculated with a mixture of the rusts growing in the Salinas Valley and at Berkeley; in 1937 the inoculations were made twice, first after the plants were about half grown and again just before blooming; and in 1938 once only, just before blooming. No inoculations were made at any of the other localities; the plants were grown normally in the garden or field and were given no special treatment.

All trials were examined at least three times during the season. The ratings with respect to variability and rust reaction are generally those last observed. Whenever the variability was great—that is, 3—the *amount* of rust given represents the approximate average of all plants in that row at the time the observation was recorded.

RESULTS OF TRIALS

A comprehensive summary of the results of these trials is given in tables 1 and 2, for the 1937 trials, and in tables 3 and 4 for the 1938 trials.

With the exception of Berkeley mentioned above, these tables give the

TABLE 1

RUST REACTION OF DIFFERENT STRAINS OF ANTIRRHINUM MAJUS IN ELEVEN LOCALITIES, 1937

Source of seed and strain no.	1937 Culture no.	Berkeley		Davis		San Jose		Santa Maria		Guadalupe		San Diego		El Monte		Lompoc		Salinas		Sacramento		Chico	
		Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†
California Agr. Exp. Sta.:																							
1S	1	3	1	—‡	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2R	2	1	1	0	1	4	2	0	1	10	1	5	1	5	1	3	2	10	2	0	1	0	1
4R	3	0	1	0	1	10	1	—	—	10	1	—	—	5	1	2	2	10	1	0	1	—	—
Univ. of Michigan:																							
1R	4	6	2	0	1	8	1	9	2	10	1	3	2	6	2	0	1	9	1	0	1	0	1
2R	5	—	—	0	1	2	1	—	—	10	1	—	—	—	—	—	—	9	1	—	—	—	—
3R§	6	3	2	0	1	—	—	—	—	—	—	—	—	—	—	6	1	—	—	—	—	—	—
4R	7	5	2	0	1	2	3	6	2	10	2	2	1	10	1	1	1	7	2	0	1	0	1
Michigan Agr. Exp. Sta.:																							
1R'35	8	3	2	0	1	0	1	—	—	—	—	—	—	2	1	—	—	—	—	2	1	—	—
1S'36																							
2R	9	1	1	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3R	10	2	1	0	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4R	11	1	1	0	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Massachusetts Agr. Exp. Sta.:																							
1R—	12	3	2	0	1	5	1	—	—	10	1	—	—	—	—	—	—	—	—	—	—	—	—
2R—	13	1	1	0	1	2	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3R—	14	3	2	0	1	2	2	3	1	10	2	2	1	5	2	0	1	7	1	0	1	0	1
Ferry-Morse Seed Co.:																							
1S	15	9	2	0	1	9	3	—	—	—	—	—	—	10	1	1	2	—	—	—	—	—	—
2R	16	4	1	0	1	3	2	6	1	10	1	1	1	8	2	3	3	8	2	0	1	0	1
3R	17	4	1	0	1	0	1	2	2	10	1	2	1	3	2	1	1	—	—	0	1	0	1
4R	18	7	1	0	1	4	1	9	2	10	1	2	1	2	1	2	1	9	2	0	1	0	1

Waller-Franklin Seed Co.:																							
1R	19	6	2	0	1	4	1	8	1	10	1	8	2	2	1	3	2	9	2	0	1	0	1
2S	20	8	1	0	1	9	2	1	2	—	—	—	—	5	1	—	—	—	—	—	—	—	—
3R¶	21	2	2	0	1	1	1	2	2	10	2	2	1	4	2	1	1	4	1	0	1	0	1
4R	22	2	1	0	1	1	1	1	1	—	—	1	1	1	2	0	1	1	1	0	1	0	1
Macdonald Seed Co.:																							
1S	23	9	1	0	1	10	3	—	—	—	—	4	2	—	—	—	—	10	1	—	—	0	1
2R	24	5	2	0	1	2	2	2	2	10	1	10	1	7	3	2	3	6	2	0	1	0	1
3R	25	4	2	0	1	3	2	—	—	10	1	2	1	5	1	1	1	7	2	0	1	0	1
4R	26	4	1	0	1	2	1	1	2	10	1	2	1	4	2	1	1	8	2	0	1	0	1
Bodger Seeds Ltd.:																							
1R+	27	8	1	0	1	5	1	4	1	10	1	2	1	8	1	1	2	10	2	0	1	0	1
2R−	28	8	1	0	1	4	3	8	1	10	1	6	2	—	—	4	2	9	2	0	1	0	1
3R−	29	5	2	0	1	4	1	2	1	10	1	4	2	—	—	1	1	6	2	0	1	0	1
4S	30	9	1	0	1	10	2	9	1	—	—	6	2	—	—	—	—	—	—	3	1	0	1
Burpee Seed Co.:																							
1R	31	9	1	0	1	9	3	8	2	10	1	4	2	7	2	9	1	9	1	4	2	0	1
2S	32	9	1	0	1	10	1	—	—	—	—	1	1	—	—	—	—	8	1	2	2	0	1
3R	33	5	1	0	1	3	3	3	2	10	1	4	2	7	2	3	2	8	1	0	1	0	1
4S	34	9	1	0	1	9	2	9	3	10	1	—	—	10	1	—	—	—	—	—	—	—	—
5R	35	9	2	0	1	3	1	7	2	10	1	4	2	2	2	8	2	10	2	0	1	0	1
6R	36	8	2	4	2	9	2	7	1	10	1	7	2	4	2	—	—	8	2	1	2	0	1
7R§	37	6	2	0	1	6	1	2	1	10	1	2	1	4	2	1	2	8	2	2	2	0	1

* Amount of rust reaction ranges from 0, no rust, to 10, the plants either covered with rust or killed by it.
† Variability ranges from 1, uniform reaction of all plants within the strain, to 3, almost clean and heavily rusted plants in the same strain.
‡ Dashes indicate that the strain or species was not on trial in that locality.
§ Withstood the heat well at Davis and Sacramento.
¶ This line showed good resistance to "wilt" (pathogen not determined) at Davis and Sacramento.

TABLE 2

RUST REACTION OF DIFFERENT SPECIES OF ANTIRRHINUM IN ELEVEN LOCALITIES, 1937 ·

Species, culture no., and source of seed*	Berkeley		Davis		San Jose		Santa Maria		Guadalupe		San Diego		El Monte		Lompoc		Salinas		Sacramento	
	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†	Amount*	Variability†
Antirrhinum Asarina L.																				
No. 38, Buch	F§	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
No. 39, Göt	F	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
No. 40, Paris	F	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
No. 41, T. & M	0	1	—¶	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. Coulterianum Benth.																				
No. 42. Brus.‖	—	—	0	1	D**	D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 43, T. & M	F	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. chrysothales																				
No. 44, Paris	0	1	0	1	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. glandulosum Lindl.																				
No. 45, T. & M	—	—	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. glutinosum Boiss.																				
No. 46, Buch	9	1	0	1	10	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 47, T. & M	F	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
A. hispanicum Chav.																				
No. 48, Buch	8	1	0	1	9	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 49, Paris††	4	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. latifolium D. C.																				
No. 50, Paris‡‡	—	—	—	—	10	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 51, Vent	9	1	0	1	10	2	—	—	9	2	2	1	5	1	3	2	10	1	5	1
A. maurandioides Gray																				
No. 52, Brus	—	—	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 53, Buch.§§	1	1	0	1	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 54, Paris	2	1	0	1	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—

A. molle L.																				
No. 55, Buch	F	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
No. 56, T. & M	2	2	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. meonanthum Hffgg.																				
No. 57, Paris	—	—	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. Orontium L.																				
No. 58, Brus.¶¶	—	—	0	1	D	D	0	1	1	1	D	D	D	D	0	1	0	1	D	D
No. 59, Göt	—	—	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 60, Palm	—	—	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 61, Paris	—	—	0	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 62, Vent	1	1	0	1	0	1	0	1	1	1	1	1	0	1	0	1	1	1	0	1
A. sempervirens Lapeyr.																				
No. 63, T. & M.|||	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. siculum Ucr.																				
No. 64, Buch	1	1	—	—	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 65, Palm	F	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
No. 66, Paris	2	1	0	1	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. tortuosum Bosc.																				
No. 67, Palm	2	1	0	1	8	4	3	1	6	3	1	1	3	2	1	1	5	1	0	1
No. 68, Turk	9	2	0	1	10	1	10	3	10	2	4	1	8	3	7	3	10	1	5	1

* See text, p. 570 for explanation of abbreviations of sources.
† Amount of rust reaction ranges from 0, no rust, to 10, the plants either covered with rust or killed by it.
‡ Variability ranges from 1, uniform reaction of all plants within the strain, to 3, almost clean and heavily rusted plants in the same strain.
§ F indicates failure of the seed to germinate or failure of seedlings before transplanting.
¶ Dashes indicate that the strain or species was not on trial in that locality.
‖ Typical *A. Orontium;* not *A. Coulterianum.*
** D indicates plants died in the field before observations could be made.
†† Typical *A. majus;* not *A. hispanicum.*
‡‡ Probably *A. majus;* not *A. latifolium.*
§§ Not *A. maurandioides* Gray.
¶¶ Different form of *A. Orontium* from others in trial.
‖‖‖ Only one plant reached maturity; it showed medium infection at Berkeley.

reactions of the various strains under natural conditions at the localities where they were tested.

Although certain reservations and qualifications should be made in some cases, because all strains were not tried in all localities, and because of the necessary condensation of the information in the tables, yet, in

TABLE 3

RUST REACTION OF DIFFERENT COMMERCIAL STRAINS OF ANTIRRHINUM MAJUS IN BERKELEY AND SAN JOSE, 1938

Sources of seed and strain no.	Culture no.		Berkeley		San Jose	
	1937	1938	Amount *	Variability†	Amount *	Variability†
California Agr. Exp. Sta.:						
2R	2	74	10	2	8	2
4R	3	79	10	1	5	2
1S	1	70	10	1	—‡	—
36-5-2-21 R	—	80	10	1	10	1
36-5-8-4 R	—	81	10	1	10	1
43-14-1-22 R	—	82	10	1	2	1
47-15-9-2 R	—	83	10	1	9	1
64-15-10-16 R	—	84	10	1	10	1
64-29-4-5 R	—	85	10	1	—	—
Univ. of Michigan:						
3R	6	72	10	1	8	1
4R	7	77	10	1	6	1
Michigan Agr. Exp. Sta.:						
2R	9	71	10	1	6	1
3R	10	78	4	1	3§	1
4R	11	73	3	1	3	1
Massachusetts Agr. Exp. Sta.:						
1R	12	76	10	1	4	1

* Amount of rust reaction ranges from 0, no rust, to 10, the plants either covered with rust or killed by it.

† Variability ranges from 1, uniform reaction of all plants within the strain, to 3, almost clean and heavily rusted plants in the same strain.

‡ Dashes indicate that the strain or species was not on trial in that locality.

§ Rust pustules mostly on seed pods.

summarizing the two years' trials as a whole and speaking in general terms, the following statements seem justified.

Susceptibility of Strains Tested.—No commercial strain tested where conditions for infection were severe, was found to be immune to rust. Some strains of certain species appeared to be immune during the limited trials to which they were subjected, but it is by no means certain that these same strains would not have become infected had it been possible to subject them to more extensive trials, or to the more severe conditions encountered at Guadalupe.

Several strains, however, both of commercial selections and of distinct

TABLE 4

RUST REACTION OF DIFFERENT SPECIES OF ANTIRRHINUM IN BERKELEY AND SAN JOSE, 1938

Species, culture no., and source of seed*	Berkeley		San Jose		Species, culture no., and source of seed*	Berkeley		San Jose	
	Amount†	Variability‡	Amount†	Variability‡		Amount†	Variability‡	Amount†	Variability‡
Antirrhinum Barrelieri Bor.					*A. latifolium* D. C.				
No. 87, Germ.§	9	1	—¶	—	No. 104, Germ.	10	1	—	—
No. 88, Germ.§	10	1	—	—	No. 105, Germ.	10	1	—	—
A. calycinum Lam.					*A. Linkianum*				
No. 89, Germ.	D‖	D	—	—	No. 106, Germ.	10	1	D	D
A. Charidemi Lge.					*A. litigiosum*				
No. 90, Germ.	2	1	—	—	No. 107, Germ.	6	1	—	—
A. chrysothales					*A. majus L.*				—
No. 91, Germ.	F**	..	..	..	No. 108, Germ.	3	1	—	—
A. glandulosum Lindl.					No. 109, Germ.	9	1	—	—
No. 86, Lom.††	0	1	0	1	No. 110, Germ.	10	1	—	—
A. glutinosum Boiss.					No. 111, Germ.	10	1	—	—
No. 92, Germ.	10	1	—	—	No. 112, Germ.	10	1	—	—
No. 93, Germ.‡‡	2	1	—	—	No. 113, Germ.	10	1	10	1
No. 94, Germ.	8	1	—	—	No. 114, Germ.	6	1	—	—
No. 95, Germ.‡‡	2	1	—	—	No. 115, Germ.	6	1	—	—
No. 96, Germ.	5	1	—	—	No. 116, Germ.	10	1	10	1
No. 97, Germ.	10	1	—	—	No. 117, Germ.	8	1	—	—
No. 98, Germ.	9	1	—	—	No. 118, Germ.	10	1	—	—
No. 99, Germ.	5	1	—	—	No. 119, Germ.	10	1	—	—
No. 100, Germ.	4	1	—	—	No. 120, Germ.	8	1	—	—
No. 101, Germ.	9	1	—	—	*A. meonanthum* Hffgg.				
A. hispanicum Chav.					No. 121, Germ.	10	1	—	—
No. 102, Germ.§§	10	1	—	—	*A. molle* L.				
No. 103, Germ.	F	..	..	..	No. 122, Germ.	F	..	..	..
A. Ibanjezii Pau.					No. 124, Germ.	F	..	..	..
No. 131, Germ.	2	1	—	—	*A. Orontium* L.				
No. 132, Germ.	8	1	10	1	No. 126, Germ.	0	1	—	—
No. 133, Germ.	2	1	—	—	*A. sempervirens* Lapeyr.				
No. 134, Turk.	F	..	..	..	No. 127, Germ.	F	..	..	..
No. 135, Turk.	10	1	—	—	*A. siculum* Ucr.				
No. 136, Turk.¶¶	10	1	10	1	No. 128, Germ.	2	1	3	1
No. 137, Turk.	8	1	10	1	No. 140, Stock.	4	1	1	1
No. 138, Turk.	8	1	10	1	*A. tortuosum* Bosc.				
No. 139, Turk.	5	1	3	1	No. 129, Germ.	F	..	..	..
					No. 75, no. 67 in 1937 trials	10	1	4	1
					A. valentinum F. Qu.				
					No. 130, Germ.	5	1	—	—

* See text, p. 570, for explanation of abbreviations of sources.
† Amount of rust reaction ranges from 0, no rust, to 10, the plants either covered with rust or killed by it.
‡ Variability ranges from 1, uniform reaction of all plants within the strain, to 3, almost clean and heavily rusted plants in the same strain.
§ These two strains are quite different things.
¶ Dashes indicate that the strain or species was not on trial in that locality.
‖ D indicates plants died in the field before observations could be made.
** F indicates failure of the seed to germinate or failure of seedlings before transplanting.
†† Collected in its native habitat.
‡‡ Not *A. glutinosum*.
§§ Doubtful identity.
¶¶ Looks like *A. majus*, *nanum grandiflorum* type.

species, were found to exhibit considerable resistance; so much so, in fact, that apparently little injury was sustained with respect to the seed set, although the plants themselves in some cases were noticeably infected. By comparing results for the different localities and, where possible, for the two years, it may be observed from the tables that the most outstanding lines in this respect are, among the commercials, Michigan Agricultural Experiment Station's nos. 3 and 4, and Waller-Franklin's nos. 3 and 4. Among the species, the most outstanding in resistance and seed set proved to be:

Antirrhinum Asarina L., culture no. 41
A. chrysothales, culture no. 44
A. glandulosum Lindl., culture no. 86
A. maurandioides Gray, culture nos. 53 and 54
A. Orontium L., culture nos. 58 and 62
A. Ibanjezii Pau., culture no. 133
A. siculum Ucr., culture no. 128

These species, however, are so far removed taxonomically from *Antirrhinum majus* that it is doubtful whether they will be of much value in a breeding program.

It is interesting to compare this list of resistant species with those enumerated by Mains.[9] He also found *Antirrhinum Ibanjezii, A. Asarina,* and *A. maurandioides* highly resistant; but *A. Orontium,* which he found "moderately resistant," was found to be uniformly highly resistant in these trials. His strain of *A. Barrelieri* was susceptible, as were both our strains, but he reports *A. glandulosum* as being susceptible, whereas we found the native *A. glandulosum* completely immune in 1938. Also the differences in rust reaction between the various strains of the different species, noted by Mains, showed up prominently in our trials. This was especially noticeable with *A. siculum* in 1937 and 1938 and with *A. Ibanjezii* and *A. glutinosum* in 1938. Also the differences in rust reaction between the various strains of the different species, noted by Mains, showed up prominently in our trials. This was especially noticeable with *A. siculum* in 1937 and 1938 and with *A. Ibanjezii* and *A. glutinosum* in 1938.

Effect of Climate on Rust Reaction.—Until fairly late in the season of 1937—after the middle of September—practically no rust was found on *any* of the strains in trials at Davis and Chico, and only a little on some strains at Sacramento. Apparently the low humidity and high temperature, such as were encountered there that season, were not conducive to rust development. After cool weather set in, however, there appeared an almost perfect differentiation in the three Sacramento Valley localities: strains which had been sent to us as "resistant" were *immune,* while

[9] Mains, E. B. Rust resistance in *Antirrhinum.* Phytopathology 25(11):977–91. 1935.

"susceptible" strains were all rusted. None of the wild species sent us were designated "susceptible" or "resistant," but the rust reaction discussed here was consistent with that in other localities for the wild species that were tried. Although infection was much less serious at Chico and at Davis than at Sacramento, comparable rust reactions of the various strains were plainly consistent. From this it seemed clear that there was only one rust strain present in these three localities during the 1937 trials.

The relation between temperature and humidity and extent of rust infection and damage was also noticeable in the 1938 trials at Berkeley and San Jose. In only two cases, those of *Antirrhinum Ibanjezii* and *A. siculum,* were there heavier infections at San Jose than there were at Berkeley, in all others, infections were the same or lighter at San Jose, where temperatures are higher and humidity lower.

Severity of Test at Guadalupe.—The heaviest infection in 1937 was at Guadalupe. Most of the strains were killed in this trial, and those that did survive until late in the season were badly injured. From the standpoint of testing rust resistance, this locality also proved to furnish the most severe test of any of the eleven localities where trials were grown. Mains (see footnote 9) also mentions that Guadalupe provided a very severe test for rust reaction in 1929.

But right here an interesting yet unsolved problem arises. In 1936, surveys made during field trips by the authors showed that rust infection at Guadalupe was very light while at Lompoc, some 30 miles south, the rust infection was so heavy that *Antirrhinum* seed crops were seriously damaged.

Yet, in 1937, the year these trials were grown in the two localities, conditions of rust infection were completely reversed: Lompoc showed an extremely light infection, while the crops at Guadalupe were damaged severely. Why the rust epidemic should vary so from year to year and be opposite in extent in two localities so close to each other and with such similar climates, is not known.

Evidently other forces than those exerted by hereditary factors play a rôle in determining the relative severity of rust infection.

Consistency of Rust Reaction.—The behavior relative to rust reaction of any given strain, as compared with others used in these trials, was fairly consistent in the different localities, with the exceptions noted above in the trials at the three Sacramento Valley localities. That is, a strain which was highly resistant at Berkeley or Guadalupe gave a very similar reaction in all other places, while the very susceptible strains showed approximately the same degree of susceptibility wherever they were grown except at Davis, Sacramento, and Chico, where only the

"susceptible" commercials showed any rust and they only late in the season. The fact that only the "susceptible" strains became infected late in the season at Davis, Sacramento, and Chico, but that this infection was heavy indicates that only the earlier known form or the more virulent form of rust was present in the Sacramento Valley, and that it did little damage until the weather became cool enough for it to become established.

Comparison of Rust Reaction with Seed Yields.—Fairly heavy seed yields were obtained in some strains in spite of rather severe rust infection, while very poor yields were obtained in other cases with a fairly high degree of resistance. Poor seed yield associated with a high degree of resistance was especially noticeable in several strains obtained from experiment stations. Apparently those strains had been selected for resistance to the rust with little regard to the factors concerned with seed yield.

Wind as a Factor in Spread of Rust.—Results of the trials indicate that wind aids rust dissemination to a very great extent. This is shown by the fact that in all trials the rust infection was greater on the leeward side, away from the wind, and noticeably less on the windward side, towards the wind; and this statement seems to hold, whether for single plants, single rows, or for a series of rows.

DISCUSSION

The occurrence of two or more forms of *Antirrhinum* rust is what one might readily suspect in the light of the difficulties encountered by the cereal breeders in producing rust-resistant small grains. But why the additional form of rust did not appear until approximately three years after several so-called "resistant" strains of snapdragon had been developed and introduced, and why it then became noticeable only in certain localities along the coast—that is, at Salinas, Guadalupe, and Lompoc—is a perplexing problem. This phenomenon might be accounted for on the basis of mutation or by hybridization among the rust fungi, and this explanation seems reasonable since the "newer" forms of rust were first observed at Salinas, then at Guadalupe, and later at Lompoc.

While discussing this problem early in 1937, Walter Lammerts of Ontario, California, presented what seems to be a plausible explanation. He was of the opinion that possibly the "newer" forms of rust had been present in these localities for some time, but had been unnoticed until the so-called "resistant" strains of snapdragon were introduced, because these rust forms were slower in action than those which so severely attacked the older-type, susceptible snapdragons. Yet if the various forms of rust had been prevalent in California for some time, there should not

have occurred the extremely noticeable differentiation among the *Antirrhinum* strains which was observed at Sacramento, that is, the "newer" forms of rust should have been present there also. On the other hand, the explanation suggested by Lammerts seems more likely because, in the most resistant strains of *Antirrhinum,* the rust apparently does not cause severe damage until late in the season, so late in fact, that it only slightly interferes with seed production.

Whatever the origin or mode of action of the different rust forms, the fact remains that from now on the development of rust-resistant commercial snapdragons does not present a simple problem in plant breeding.

SUMMARY

No commercial variety tested in two or more localities was found to be immune to rust (*Puccinia antirrhini* D. and H.), but several proved to be highly resistant.

The species *Antirrhinum Asarina, A. chrysothales, A. glandulosum, A. maurandioides, A. Orontium, A. Ibanjezii,* and *A. siculum* were found to be highly resistant. These species, however, are so far removed taxonomically from *A. majus* that it is doubtful whether they will be of much value in a breeding program.

The results indicate that the second form of rust has not yet appeared in the Sacramento Valley; possibly it is confined to the coast areas.

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