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W. C. SNYDER AND H. REX THOMAS

UNIVERSITY OF CALIFORNIA • BERKELEY, CALIFORNIA

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BJARNE DUNDAS

INHERITANCE OF RESISTANCE TO POWDERY MILDEW IN BEANS^{1,2}

BJARNE DUNDAS³

POWDERY MILDEW (*Erysiphe polygoni* D.C.), frequently causes considerable loss in beans (*Phaseolus vulgaris* L.) grown in the coastal districts of California. Among the numerous bean varieties grown in test plots at Berkeley each season by W. W. Mackie, of the Division of Agronomy, differences in varietal susceptibility have been apparent.

In the summer of 1932 the mildew was very abundant at Berkeley, but the Pinto and some other varieties were not infected. The following winter crosses were made in the greenhouse between these and certain other varieties with the idea of studying the inheritance of resistance and introducing resistance into commercial varieties which lack it.

METHODS EMPLOYED IN INOCULATION TESTS

The reaction of the bean plants to mildew was determined by inoculating detached leaflets floated on a sugar solution in petri dishes, a method used by Yarwood^{ω} ⁴ in his work with the powdery mildew of red clover. This method has numerous advantages. Plants may be grown in the greenhouse and tested at any time of the year, and uniformity of inoculum and environmental conditions during inoculation tests are insured. The same single-spore culture of the mildew was propagated in petri dishes free from contamination by other strains of mildew and was used in all of the inoculation tests, which extended over a period of more than three years.

Length of Life of the Detached Leaflets.—Tests made to determine what substrate was most favorable to prolonged life of the detached bean leaflets showed that a 10 per cent solution of sucrose was superior to several higher and lower concentrations tested and to pure water or Hoagland culture solution. In petri dishes leaves floated on a 10 per cent sucrose solution or lying on cotton saturated with this solution remained alive (turgid and normal green in color) two to three weeks at room temperature and over a month at 8° C with a maximum of 55 days at 8°, 12 days at 25°, and 7 days at 31°. Time of day of collection of the

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³ Graduate student in the Division of Plant Pathology.

⁴ Superscript numbers in parentheses refer to Literature Cited at end of this paper.

leaflets seemed to be unimportant. Leaves lived about two days longer in light than in the dark. The third youngest unfolded leaf was found to be similar to older leaves in its reaction to mildew and was generally used. In their mildew reaction, leaves from greenhouse plants were similar to those from field plants. Infection with the mildew was found to shorten the life of the detached leaflets by 2 to 8 days.

Optimum Conditions for Production of Inoculum and for Infection. Spores of powdery mildew produced in the light germinated somewhat better than those produced in the dark, and young spores from colonies 3 to 6 days old germinated much better than those from colonies over 19 days old. Spores produced under relative humidities^(2, 3) of 8 per cent (over KOH), 33 per cent (over MgCl₂·6H₂O) and 79 per cent (over NH₄Cl) germinated about equally well and somewhat better than those produced at 0 (over P₂O₅) or 100 per cent relative humidity.

It was found that spores would germinate on dry slides as well as on water. Germination of dry spores (25–77 per cent) on dry slides occurred promptly at temperatures between 8° and 25° C, at ordinary room humidities as well as in saturated air and in darkness or in light. In fact, a low percentage of spores germinated at temperatures as high as 28° and 31° C and at room temperature in a relative humidity of 8 per cent. No spores germinated at approximately zero relative humidity.

The time of day when spores were applied to the leaflets made no difference in the resultant growth of mildew. On leaflets on 10 per cent sugar solution the mildew developed equally well in the dark and in the light, but on weaker or stronger sugar solutions it developed better in the light. It developed well at 15° C and at room temperature (about 21°) but less abundantly at 25° and not at all at 31° . At 8° , 22 days were required for it to reach a stage of development such as that arrived at in 8 or 9 days at room temperature. It was found to develop well over a wide range of relative humidity.

Inoculation of Leaves.—Inoculum was produced on leaflets on 10 per cent sugar solution in petri dishes stored in the light at room temperatures, and the spores were used when the colonies were 6 to 10 days old.

In order to determine the relative susceptibility of individual plants, the third youngest unfolded leaf was placed in a petri dish on cotton soaked with a 10 per cent sucrose solution with the upper epidermis uppermost. To obtain spores for inoculation, heavily mildewed portions of a leaflet were cut out and held with a forceps over the leaflet to be inoculated, and by tapping the forceps the spores were dislodged. Or the spores were deposited by gently touching the leaflet with the mildewed leaf fragment. The dishes containing the inoculated leaflets were then stored in the light at room temperatures, and readings of mildew severity were made after 7 to 9 days, and again on resistant leaflets two weeks after inoculation. Very little difficulty was caused by contamination with molds. To supplement such tests, potted plants in the greenhouse were also occasionally inoculated.

Scale of Severity of Infection.—The severity of the mildew was estimated on a scale of 0 to 4 as follows:

0: No mycelium; spores germinate and may cause small necrotic spots by killing a few epidermal cells.

t (trace) : Scant mycelium present; no spores; colonies few; necrotic spots present.

1: Mycelium scant; a few spores formed; colonies few; necrotic spots present.

2: Mycelium more abundant; spores formed rather generally on the mycelium; necrotic spots present.

3: Mycelium and spores fairly abundant; very few necrotic spots.

4: Mycelium and spores very abundant, covering the leaflet; spores formed within 4 days.

Readings between 0 and 2 designate resistance; 3 and 4, susceptibility.

RELATIVE SUSCEPTIBILITY OF BEAN VARIETIES TO MILDEW

The relative severity of mildew on certain varieties of beans in the field as a result of natural infection and in the greenhouse as a result of inoculation of potted plants is compared in table 1 with the severity of mildew on inoculated detached leaflets of the same varieties. Inoculation of the detached leaflets is shown to be a more severe test than is afforded by field or greenhouse infection. In no instance did field or greenhouse infection occur on varieties showing less than a 2 reaction in the dish test. Numerous inoculation tests were made and the results in table 1 are typical.

The varieties Hungarian, Lady Washington, Pinto, Yellow, and Pink, were resistant; Frijole negros, Long Roman, and *Phaseolus vulgaris* 5003, intermediate; and Robust and Red Kidney susceptible. The Pink variety was slightly less resistant than the other four in that group, and in the seedling stage was much more susceptible than in later stages. Three other resistant varieties also showed a trace of infection in the seedling stage.

Reaction of Parental Material—the Pinto, Long Roman, and Robust Varieties.—As parental material for a study of the inheritance of mil-

dew resistance, the varieties Pinto, Long Roman, and Robust were selected. Pinto (4369) has always given a negative reaction in dish tests. In 1932, 1933, and 1935 no mildew developed on it in the field, but in 1934 a small amount developed owing to the presence of a new physiologic form of the mildew that year. Long Roman (4521) has been susceptible in dish tests, usually giving a reading of 3. In the field in 1932 no infection appeared before late in the fall when most varieties

	1	Mildew readings*								
			Grown i house 19	n green- 932–1933	Gı					
	Variety‡	Field 1932	Plant† inocula- tion	Dish test, old	Field†	Dish test		Field notes 1935†		
						Seedling	Old			
	(Hungarian (4404)	0	0	0	0	0	0	0		
	Lady Washington [84(213)32]	0	0	0	0	t	0	0		
Resist-	{ Pinto (4369)	0	0	0	0	0-t	0	0		
ant	Yellow (4429)	0	0	0	0	t	0	0		
	(Pink (4436)	0	0	0–1	0	34	0–1	0		
Semi-	(Frijole negros (5033)	0	m	2	0	3	2-3	m		
resist-	{ Long Roman (4521)		m	3	m	3-4	3	m		
ant	Phaseolus vulgaris (5003)	t	m	3	m	3	3	m		
Suscep-	∫Robust (4458)	3	m	4	 m	4	3-4	 m		
tible	Red Kidney (4764)	4	m	4	m	4	4	m		

TABLE 1	
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MILDEW SUSCEPTIBILITY OF CERTAIN VARIETIES AS INDICATED BY THE DISH TEST, BY NATURAL INFECTION IN THE FIELD, AND BY INOCULATION OF PLANTS IN THE GREENHOUSE 1932-1933

* Field notes for 1934 are not included because a different strain of mildew was present which attacked the resistant varieties.

† It is merely indicated whether mildew developed (m) or not (0). ‡ Numbers given in this column are accession numbers of the California Experiment Station.

were harvested. In 1933 and 1935 a very small amount of infection was present, but in 1934 it was more severely infected. Robust (4458) from 1932 to 1935 showed a light to medium-heavy field infection. It is highly susceptible in the dishes, usually with a reading of 4.

MILDEW REACTION OF THE F_1 , F_2 , AND F_3 PROGENIES OF ROBUST \times PINTO

Crosses between resistant and susceptible varieties were made in the greenhouse in the winter of 1932-33. The F_1 generation was grown in the field the following summer. F_2 generations have been grown both in the greenhouse and in the field. Only in the field has enough seed for conclusive F_3 tests been obtained. F_3 generations have been grown in the

greenhouse. For routine work the F₂ and F₃ were mostly planted in sterile soil in 6-inch pots, 6 seeds in each. Less damping-off was experienced in sterile soil than in nonsterile soil. To insure prompt germination, the seed was scarified. The temperature in the greenhouse has been about 60° to 70° F.

The F_1 plants of the Robust \times Pinto cross and their parents were grown in the field. The mildew reaction was determined by the dish tests both in the seedling and in older stages. The F_1 hybrids and their resistant Pinto parent were about equally resistant, as shown in table 2. Some additional F₁ plants grown in the greenhouse were tested approxi-

Parent or cross	Nun	nber of inf	Total	D				
	0	t	1	2	3	4		Ē
Robust	0	0	0	0	3	15	18	
Pinto	18	0	0	0	0	· 0	18	
F1	5	1	0	0	0	0	6	
F2	121	9	0	0	9	34	173	0.07

TABLE 2 MILDEW INFECTION ON ROBUST AND PINTO BEANS AND THEIR F_1 and F_2 Progenies

* D Deviation from expected ratio number

 \overline{E} Probable error of the number of the population

mately every week during the first two months, and it was found that the mildew reaction of young plants was 0-1 and of older plants, almost always 0, like that of the resistant parent. The younger stages of Pinto showed somewhat more resistance than the younger stages of F_1 hybrids, a fact which indicates that the complete pair of factors for resistance is more potent than a single one.

For the F_2 generation, the progenies from two F_1 plants were observed separately, but since the two sets presented no genetic differences they are treated together. One primary leaf from each F₂ plant was tested for mildew susceptibility 7 to 10 days after the seedlings emerged and one leaf from each plant was tested when the plants were mature. The two tests were found to agree, so that in this cross the early test was reliable and susceptibility did not decrease with age. Furthermore the ratios of resistant to susceptible were the same in the plants tested twice as in those that had died before the second test was made. The results are included in table 2.

 \mathbf{F}_1 plants of Robust \times Pinto may give a reading of t at the age of two months. This approximates the age of the F_2 plants at the second reading. For the resistant parent, Pinto, a reading of t was not obtained later

TABLE 3

F2 plant		Number	of F ₃ pla	ants with	Ratio resistant	D	Families in		
Ño.	0	t	1	2	3	4	susceptible	\overline{E}	F2 group
4	24	9					33:0)
6	27	7	1				35:0	••••	
10	21	9	3				33:0		
13	31	3			· · · ·		34:0		
16	28	7					35:0		12
18	26	8					34:0		homozygou
21	21	5					36:0		resistant
25	25	8			1		33:0		
30	27	7					34:0		
36	30	5				1	35:0		
38	24	2					26:0		
41	29	4					33:0		IJ
1					17	15	0:32		1
8					10	24	0:34		
14		••	•••	1	4	18	0:22		
19	••				1	17	0:17	••••	10
27	••				5	26	0:31	••••	homozygous
33	••				3	14	0:17	••••	susceptible
35	••	••			17	14	0:35	• • • •	susceptible
42	••				7	25	0:32		
42	••	••			8	23	0:32		
45 45	••	••		· · ·	4	22	0:30		
2	17	7	1		3	3	05.0	1.07	
3	.17	18	1		4	3	25:6 28:7		
а 5	9 11	18	3		3	4	28:7	1.01	
7	9	13	3		7	4	24:11	0.88 1.30	
9	9 16	12 9	3		4	4	24:11 26:8	0.29	
	16	3			4 5				
11 12	10 5	3 10	· · ·	· · ·	5		29:5	2.06	
		-	5				22:5	1.15	
15 17	13 2	13 14			6 2	4	26:10	0.57	
20	2 13	14	11 2	1	2 5	4	28:8 27:7	0.57	11
20 22	13 20	10			3	4	27:7	0.88	23
22	20 17	10		•••	3 9		27:7	0.88	
23 24	23	10			9	2	27:9 25:6	0.00 1.07	<pre>heterozygou heterozygou</pre>
24 26	23 14	2		••	4 5	5	25:10	0.72	resistant
20 28	14	9 8			3	5	25:10	0.72	
28 29	17	8 6			9		25:8 25:9	0.15	11
29 31	19	10	· · 2		1	 6	25:9 25:7	0.29	
31 32						1	1		11
	14	7	•••		4	4	21:8	0.48	
34	15	5			6	1	20:7	0.16	11
37	9	10	4	1	5	7	24:12	1.71	
39	20	8			5	3	28:8	0.57	
40	14	6			6	3	20:9	1.11	
44	18	7	2		3	3	27:6	1.34	11

Mildew Reading of \mathbf{F}_3 Plants of a Robust $\times\,\mathbf{Pinto}\,\,\mathbf{Cross}$

than 16 days after planting; later readings were all 0. The F_2 hybrids which in the second test showed a reading of t may thus be heterozygous rather than homozygous for resistance, while those that gave a reading of 0 may be either homozygous or heterozygous. Although a definite distinction between plants homozygous and heterozygous for resistance was not established, they are both in the resistant group, which by lack of plants in the intermediate classes 1 and 2 is distinctly separated from the susceptible group. The ratio 130:43 fits almost perfectly a 3:1 ratio and indicates that resistance to mildew in Pinto is due to a single dominant Mendelian factor.⁽³⁾

From each of 45 F_2 plants (the progeny of one F_1 plant) grown in the field in 1934, 36 seeds were planted in the greenhouse the following winter. The mildew reaction of the F_2 parents was unknown. The mildew reaction of each plant of the 45 F_3 progenies was determined by dish tests in the young stage. The results, including the ratio of resistant to susceptible plants in each family, are given in table 3. The F_3 families are grouped on the basis of the readings, and it may be seen that the 45 parental F_2 plants may be classified as follows: homozygous resistant, 12; heterozygous resistant, 23; homozygous susceptible, 10. This is a ratio of 35 resistant to 10 susceptible. The $\frac{D}{E}$ is 0.64. This approximates a 1:2:1 ratio or a ratio of 3 resistant : 1 susceptible, as was found in the tests with the F_2 generation, and establishes that the resistance in Pinto is due to a main single Mendelian factor pair.

There is a rather wide variation in the readings of the 23 heterozygous F_3 families. For instance family 17 has the average of its 28 resistant readings between t and 1 with two plants in the 0 class and one in the 2 class, while family 22 has 20 readings of 0 and 7 of t, with none in classes 1 and 2. This indicates that there are factors or combinations of factors present which modify the resistance. Although some of the heterozygous F_3 families have more plants with intermediate readings than did the F_2 generation as shown in table 2, there is nevertheless a distinct difference between the resistant and susceptible plants.

MILDEW REACTION OF THE F_1 , F_2 , AND F_3 PROGENIES OF LONG ROMAN \times PINTO

It will be recalled that Pinto is resistant and Long Roman is somewhat resistant in the field but shows susceptibility in the dish tests. The seven F_1 plants were grown in the field, and when tested in the dishes all were resistant to the mildew and gave a reading of 0, like the resistant parent Pinto (table 4).

An F_2 generation was grown in the greenhouse. Tests made when the plants were young showed more variation in mildew resistance than did tests made when the plants were older, and a few plants changed from susceptible when young to resistant when older. The readings given in table 4 represent the average of 7 to 10 individual leaves taken from each plant at different times and tested by the dish method. The constancy of the later readings and the rather distinct separation of resistant and

	F ₁	AND F:	PROGE	NIES				-
Parent or cross	Num	Total	<u>D</u> *					
	0	t	1	2	3	4		E
Grown in greenhouse								
Long Roman	0	0	₹0	0	9	0	9	
Pinto.	9	0	0	0	0	0	9	
F ₂	45	29	9	0	8	10	101	2.47
Grown in field								
Long Roman	0	0	0	0	13	0	13	
Pinto	13	0	0	0	0	0	13	
F1	7	0	0	0	0	0	7	
\mathbf{F}_2	53	15	13	4	12	9	106	1.83

TABLE 4
MILDEW INFECTION ON LONG ROMAN AND PINTO BEANS AND THEIR
F_1 and F_2 Progenies

* D Deviation from expected ratio number

E Probable error of the number of the population

susceptible groups by the absence of class 2 as shown in table 4 indicate that the F_2 generation should give a reliable picture of the inheritance of resistance. Although there are a larger number of readings of t and 1 than in the Robust × Pinto F_2 hybrids, the results, like those of the previous cross, indicate the presence of a main factor pair for resistance in the Pinto variety.

 F_2 plants from seed from the same F_1 plant used for those grown in the greenhouse were also grown in the field in 1934. Seedlings were tested in the dishes for mildew resistance within 4 days after emergence and a second test was made when the plants began to bloom. The readings on the older plants are given in table 4. They give about the same fit to a 3:1 ratio of susceptible to resistant as the greenhouse series. A few plants changed from susceptible in the seedling stage to resistant when older. There are 4 plants with a reading of 2, and class 3 is relatively larger than in the greenhouse series. A similar difference between field and greenhouse-grown plants has been observed in other trials.

The F_3 generation was grown from seed from 47 resistant and 10 susceptible F_2 plants grown in the field in 1934, including the 4 plants with

TABLE 5

	F2					F3			
Mil- dew	Plant		Number o	of plants w	ith mildew	readings		Ratio resistant	D*
read- ing	No.	0	t	1	2	3	4	susceptible	E
0	$\left(\begin{array}{c}1\\2\\3\\4\\5\\6\\7\\8\\9\\10\\11\\12\\13\\14\\15\\16\\17\\.18\\19\\20\\21\\22$	28 24 25 19 34 21 13 33 27 31 14 26 22 40 19 28 26 23 24 20 17 19	6 8 3 8 1 7 4 1 2 2 1 0 6 2 1 2 1 6 1 0 2 6	0 2 0 2 3 0 0 0 0 0 0 0 0 0 0 0 0 0	1 0 1 3 7 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	$\begin{array}{c} 35:0\\ 34:0\\ 28:0\\ 30:0\\ 35:0\\ 33:0\\ 27:0\\ 34:0\\ 29:0\\ 15:4\\ 29:0\\ 15:4\\ 29:5\\ 42:13\\ 22:6\\ 30:6\\ 27:8\\ 29:5\\ 42:13\\ 22:6\\ 30:6\\ 27:8\\ 29:7\\ 26:7\\ 20:5\\ 19:9\\ 25:10\\ \end{array}$	 0.59 0.74 2.06 0.35 0.65 1.71 0.43 1.14 0.74 0.86 1.29 0.72
t	23 24 25 26 27 28 29 30 31 32 33 34 34	39 39 19 25 27 24 18 32 30 22 19 30	0 0 6 10 8 3 5 0 1 1 8 8 8	0 3 0 1 0 1 0 0 0 0 0	0 0 1 0 2 0 0 0 0 0 0 0 0	0 0 0 1 7 7 5 7 8 9	0 0 0 0 2 0 4 1 1 1	39:0 39:0 36:0 29:1 24:9 32:7 31:9 23:8 27:9 40:10	0.45 0.45 1.51 0.54 0.15 0.00 1.21
1	$\left(\begin{array}{c} 35\\ 36\\ 37\\ 38\\ 39\\ 40\\ 41\\ 42\\ 43\end{array}\right)$	25 22 19 18 20 20 36 28 19	1 3 1 2 10 3 1 4 2	0 0 1 1 0 0 0 2 0	0 0 1 1 0 1 1 0	7 5 2 4 4 4 4 7 14 6	0 1 8 10 1 1 1 0 5	$\begin{array}{c} 26:7\\ 25:6\\ 21:10\\ 22:14\\ 23:5\\ 38:9\\ 35:14\\ 21:11 \end{array}$	$\begin{array}{c} 0.74\\ 1.07\\ 1.38\\ 2.86\\ 1.54\\ 1.29\\ 1.38\\ 0.86\\ 1.82 \end{array}$
2	44 45 46 47	16 16 14 14	9 7 8 5	$\begin{array}{c}1\\0\\0\\2\end{array}$	3 0 0 0	7 4 0 5	12 4 6 4	39:19 23:8 22:6 21:11	$\begin{array}{c} 2.03 \\ 0.15 \\ 0.65 \\ 1.82 \end{array}$
3	\ 48 49 50 51	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	$\begin{array}{r} 5\\10\\4\\15\end{array}$	10 12 18 8	0:15 0:22 0:22 0:23	· · · · · · · · ·
4	(52 53 54 55 56 57	0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0	$ \begin{array}{r} 11 \\ 10 \\ 12 \\ 12 \\ 2 \\ 7 \\ 7 \end{array} $	$5 \\ 15 \\ 12 \\ 23 \\ 16 \\ 15$	0:16 0:25 0:24 0:35 0:18 0:22	···· ····

Mildew Readings of \mathbf{F}_2 Plants and Their \mathbf{F}_3 Progeny from a Long Roman \times Pinto Cross

* D Deviation from expected ratio number

 \overline{E} Probable error of the number of the population

† Thought to be the result of a mixture.

a mildew reading of 2 (table 4). The F_2 plants were the progenies of one F_1 plant. The populations of the 47 F_3 families from resistant F_2 plants range from 19 to 58 with only 9 below 30. The susceptible F_2 plants (mildew reading of 3 or 4) yielded a comparatively small amount of seed owing to the injury from mildew, and the population of their F_3 families ranges from 15 to 36.

Of the 47 resistant F_2 plants (readings 0, t, 1, and 2) tested, 16 proved to be homozygous and 31 heterozygous for resistance, a result which is very close to the 1:2 ratio expected from a random sample. The 31 heterozygous F_2 plants segregated in the F_3 in accordance with the singlefactor hypothesis. The susceptible F_2 plants (readings 3 and 4) gave only susceptible progeny. The resistance observed in Long Roman has not interfered with the expression of the Pinto resistance in this test.

The F_2 readings give an indication as to the homozygosity or heterozygosity of the plants in that F_2 mildew readings of 1 and 2 all represented heterozygous plants, while readings of 0 and t represented both homozygous and heterozygous plants in about equal numbers.

SUMMARY

For use in determining the susceptibility of beans (*Phaseolus vulgaris* L.) to powdery mildew (*Erysiphe polygoni* D.C.), the mildew was grown in petri dishes on detached bean leaflets supported on cotton soaked in a 10 per cent sucrose solution. Use of the dish-culture method permitted the continuous use of one physiological race of the mildew and offered numerous other advantages.

The susceptibility of different varieties and individual plants was determined by inoculating detached leaves. The results were in most cases found to be in close agreement with field and greenhouse infection. In no case was infection less severe in the dishes. Mildew readings were made on a scale of 0 to 4.

The varieties Hungarian, Lady Washington, Pinto, and Pink were found to be resistant, and Robust and Red Kidney were susceptible, as tested in the dishes and in field and greenhouse. Frijole negros was resistant in the field and greenhouse, but semiresistant in the dishes. Long Roman was semiresistant in the field and greenhouse and susceptible in the dishes.

The F_1 , F_2 , and F_3 progenies of a cross between the susceptible Robust and the resistant Pinto were tested by the dish method. Of the 45 F_2 plants tested, 12 proved to be homozygous resistant, 23 heterozygous resistant, and 10 homozygous susceptible.

The F_1 , F_2 , and F_3 progenies of a cross between the semiresistant

Long Roman and the resistant Pinto were similarly tested and of the 47 resistant F_2 plants tested, 16 proved to be homozygous and 31 heterozygous. Readings of 0 and t in the F_2 plants indicated homozygosity or heterozygosity for resistance; 1 and 2, heterozygosity only; and 3 and 4, homozygosity for susceptibility.

In the crosses with Robust and Long Roman, the Pinto is seen to have a single Mendelian factor pair for resistance to the strain of powdery mildew used.

Plants were often somewhat more susceptible in the seedling stage than later.

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