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INHERITANCE OF RESISTANCE TO THE PEA APHID IN ALFALFA HYBRIDS

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INHERITANCE OF RESISTANCE TO SCALD IN BARLEY

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PHYSIOLOGIC AND GENETIC STUDIES WITH THE STRIPE DISEASE IN BARLEY

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INHERITANCE OF RESISTANCE TO SCALD IN BARLEY[1]

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SCALD, CAUSED BY *Rhynchosporium secalis* (Oud.) Davis, is a leaf disease of barley that is of considerable importance in California. In 1936, when this work was undertaken, none of the varieties grown commercially in this state had a high degree of resistance, and Atlas, the most widely grown variety, was highly susceptible. With the discovery of the resistant varieties reported by Riddle and Suneson (1948),[4] it seemed desirable to study the inheritance of resistance to scald and to inaugurate a breeding program to develop a resistant strain of Atlas.

VARIETIES AND SELECTIONS USED

Four resistant varieties and selections—La Mesita, selection Calif. No. 1311, Trebi, and Turk (C. I. 5611–2)—were used in crosses with susceptible Atlas and with each other. A brief history of each variety is given below.

La Mesita, Calif. No. 1002 originated as a plant selection from California Mariout, which in turn was introduced from Egypt. It was grown commercially for a time in Santa Barbara County, California.

Calif. No. 1311 is a selection from composite cross C. I. 5461, which has been described by Harlan, Martini, and Stevens (1940). It was selected at the Aberdeen Experimental Substation, Aberdeen, Idaho, from the above composite. Calif. No. 1311 was first grown at Davis in 1937 but has not been grown commercially.

Trebi, C. I. 936 originated as a selection from a variety brought to the United States from the south shore of the Black Sea. It was released from the Aberdeen Experimental Substation in 1918 (Harlan and Martini, 1936). This variety is not grown commercially in California.

Turk, C. I. 5611–2, according to Dr. G. A. Wiebe,[5] traces to material collected in 1928 in northeastern Turkey and introduced into the United States in 1930. It is a very late, two-rowed, rough-awned, weak-strawed type, used only experimentally in this country. Because of its high resistance to scald, it was used in the backcross program with Atlas to introduce resistance into that variety.

Atlas, C. I. 4118 (Harlan and Martini, 1936) is the variety of malting barley most widely grown in California. It originated as a pure-line selection made from Coast barley in 1917. Coast was introduced into California by the early Spanish settlers at the time the missions were established in this state. It is very susceptible to scald.

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[4] See "Literature Cited" for citations, referred to in the text by author and date.

[5] Personal correspondence.

RANGE OF INFECTION

Natural Infection in the Field. The reaction of barley varieties and hybrids to scald was studied in the field and to some extent in the greenhouse. Field plantings were made early (late October or early November) contiguous to barley stubble, conditions which generally resulted in adequate natural infection. F_2 and F_3 seeds were spaced 4 inches apart, in rows 1 foot apart and 16 feet long. This spacing generally resulted in more than forty plants that could be examined in place. They were classified when scald development apparently had reached the maximum, usually a few days before heading. Five classes of infection were set up: 0, highly resistant; 1, resistant; 2–3, weak resistance; and 4, susceptible. As with many such arbitrary classifications, the class limits are hard to define, yet they are usable. The presence of other diseases, particularly of net blotch, frequently made field classifications difficult and uncertain.

Artificial Inoculation in the Greenhouse. Classification of greenhouse-grown plants artificially inoculated with scald in the seedling stage was highly satisfactory. Those varieties exhibiting a slight infection of scald at the near-heading stage in the field generally were completely resistant at the time of classification in the greenhouse. Susceptible checks showed a heavy infection.

In the greenhouse, seeds were spaced 1 inch apart, in rows 30 inches long and 3 inches apart. The soil benches were filled to a depth of 6 inches. This gave populations of from 25 to 30 plants per row. About two weeks after emergence, when the third leaf was well started, the plants were sprayed with a spore suspension of the scald fungus. The benches were covered for 48 hours with a cheesecloth tent; the humidity was maintained near 100 per cent and the temperature close to 70° F. Spore suspensions were made from cultures 8 days old. Plants were ready for classification about two weeks after inoculation.

A mixture of six different cultures was used for inoculations in the greenhouse. No attempt was made to determine whether these represented physiological races differing in pathogenicity. Varietal reactions indicated that these cultures represented the same race or mixture of races active in the field at that time.

Hybrid populations involving the varieties mentioned above will be reported in turn.

VARIETAL REACTIONS TO SCALD

The reactions to scald of the several varieties and selections are given in table 1. Turk (C. I. 5611–2) and the lines extracted from Turk × Atlas showed no scald either in the field or in the greenhouse. Calif. No. 1311, Trebi, and La Mesita, all showed some scald in the field under some conditions. They also developed this disease in the greenhouse when allowed to grow beyond the seedling stage. Atlas generally had a type-4 infection.

Atlas × La Mesita. Atlas was highly susceptible when grown either in the field or in the greenhouse. La Mesita was resistant, showing a range of 0–2 type infection in the field but always 0 in the greenhouse at the normal time of classification.

In the field the F_1 reaction was very similar to that of La Mesita. The presence of net blotch as well as of some scald on La Mesita and other resistant plants made the classification of field-grown F_2 plants unsatisfactory. However, an attempted classification of 204 F_3 rows as resistant, segregating, and susceptible was fairly successful. Later, 39 of these rows of about 30 plants each were tested under greenhouse conditions. It was found that most of them had been classified correctly in the field, where the distribution by rows had been 57 resistant: 96 segregating: 51 susceptible (table 3). This led to a

TABLE 1

REACTION OF BARLEY PARENT VARIETIES AND SELECTIONS TO SCALD INFECTION

Grown in the field at Davis, 1937–1943, and in the greenhouse in 1943

Variety or selection	California no.	Infection type on 0–4 scale									
		1937 4/24	1938 3/18	1939 4/1	1940 3/23	1941 3/27	1942		1943 4/10	Greenhouse 1943	
							3/23	4/3		1/29	2/13
Turk, C.I. No. 5611-2	1315	0	0	0	0	0	0	0	0	0	0
P-4229*	1312	..	..	..	..	..	0	0	0	0	0
P-4232*	1313	..	..	..	..	..	0	0	0	0	0
P-4233*	1328	..	..	..	..	..	0	0	0	0	0
P-4236*	1314	..	..	..	..	..	0	0	0	0	0
Calif. No. 1311	1311	..	0	0	0	0	0–2	0–4	1	0	1
Trebi, C.I. No. 936	1004	0	0	0	1	1	0	0–3	2	0	2
La Mesita	1002	0	1	2	1	1	2	tr.	1–2	0	2
Atlas, C.I. No. 4118	....	4	4	4	4	4	4	4	4	3–4	4

* Single-dominant-factor resistant types derived from Turk × Atlas.

tentative conclusion that La Mesita differed from Atlas by a single gene for resistance to scald.

In the greenhouse, no difficulty was experienced in classifying the completely resistant F_2 plants. Out of a total of 815, there were 614, or 75.3 per cent, having the 0 reading like La Mesita (table 2). The other 201 plants had a range of disease intensity from 1 to 4, which was the same as the range of intensities encountered in Atlas (2, 2, 18, 134 plants with reading of 1, 2, 3, and 4 types). Thus, there were similar proportions of the several types in each population.

Thirty-nine F_3 rows from F_2 plants that had not been classified for scald resistance were grown in the greenhouse (table 3). These gave 9 resistant: 24 heterozygous: 6 susceptible, where 9.8 :19.4 :9.8 were expected on the basis of the single factor postulated above. Thus, all the data agree in showing that La Mesita differs from Atlas by a single gene for resistance to scald.

If dominance is based on complete resistance, it would have to be considered somewhat intermediate in the field, although the F_1 plants were as resistant as the resistant parent. In the greenhouse, both the La Mesita and the heterozygous plants were completely resistant at the time readings were made. Later, however, they both developed a little scald.

TABLE 2

DISTRIBUTION OF F_2 PLANTS, FROM CROSSES OF ATLAS WITH RESISTANT VARIETIES AND SELECTIONS

Grown at Davis, 1939–1943

Cross	Classified on 0–4 scale of infection type										
	Number of plants					Total	Per cent of plants				
	0	1	2	3	4		0	1	2	3	4
Atlas × La Mesita*	614	1	2	33	165	815	75.3	0.1	0.2	4.0	20.2
Atlas × Calif. No. 1311*¶	235	6	1	10	70	322	73.0	1.9	0.3	3.1	21.7
Atlas × Calif. No. 1311*¶	137	22	22	22	46	249	55.0	8.8	8.8	8.8	18.5
Atlas × Trebi*¶	311	8	8	18	84	429	72.5	1.9	1.9	4.2	19.6
Atlas × Trebi*¶	172	36	16	13	53	290	59.3	12.4	5.5	4.5	18.3
Turk × Atlas†¶	1479	7	42	10	208	1746	84.7	0.4	2.4	0.6	11.9
Turk × Atlas†¶	821	7	35	18	142	1023	80.3	0.7	3.4	1.8	13.9
Atlas × P-4229†‡	127§	..	..	..	42	169	75.1	....§	....	....	24.9
Atlas × P-4232†	121§	..	..	..	45	166	72.9	....	....	....	27.1
Atlas × P-4233†	145§	..	..	..	55	200	72.5	....	....	....	27.5
Atlas × P-4236†	138§	..	..	..	37	175	78.9	....	....	....	21.1
Atlas × P-42683*	399	..	7	18	114	538	74.2	0.0	1.3	3.3	21.2
Atlas × P-42709*	409	2	5	16	96	528	77.5	0.4	0.9	3.0	18.2

* All data on greenhouse-grown material.
† Data from both field-grown and greenhouse-grown material.
‡ P-4229 to P-42709 are homozygous derivatives from the cross, Turk × Atlas.
§ 1, 2, and 3 classification types not used for these crosses.
¶ Data taken on two dates.

TABLE 3

SUMMARY OF F_2 AND F_3 DATA FROM THE CROSS, ATLAS × LA MESITA

Grown at Davis in 1940 and 1943

	Resistant (type 0)	Segregating	Susceptible (types 1–4)	Chi^2	*P*
Field-grown F_3 (rows)					
Observed	57	96	51	.....	.....
Expected (with single gene difference)	51.0	102.0	51.0	1.0588	0.5–0.7
Greenhouse-grown F_2 (plants)					
Observed	614	..	201	.....	.....
Expected (with single gene difference)	611.3	..	203.7	0.0477	0.8–0.9
Greenhouse-grown F_3 (rows)					
Observed	9	24	6	.....	.....
Expected (with single gene difference)	9.8	19.4	9.8	2.6295	0.2–0.3

Atlas × Calif. No. 1311. Calif. No. 1311 has sometimes shown light infection in the field; the F_2 classification, therefore—as was the case with La Mesita—was unsatisfactory for genetic interpretation.

F_2 populations were grown in the greenhouse and classified on two different dates. The data are reported separately in table 2. The differences in the percentages of plants falling in each infection type are not readily explain-

able. The second set of data reported was obtained under the heaviest infection experienced in the greenhouse. Apparently a greater number of resistant plants showed type 2 and 3 reaction than was the case under lighter infection, although Calif. No. 1311 showed no disease in either case. Both the F_2 population under consideration and the F_3, to be discussed later, trace to the same F_1 plant.

Seventy-two F_3 rows from F_2 plants that had not been classified for scald resistance were grown in the greenhouse, but at a date different from that of either of the F_2 populations. The F_3 data indicate the presence of two

TABLE 4

ANALYSIS OF F_3 DATA FROM THE CROSS, ATLAS × CALIF. NO. 1311, AS RELATED TO F_2 GENOTYPES*

F_2 genotype	Expected F_3 reaction	Number of F_3 rows		Number of F_3 plants					
				Total	Observed distribution in infection types				
		Observed	Expected		0	1	2	3	4
AABB *AABb* *AAbb*	All resistant (0 type)	20	18.0	389	389	0	0	0	0
Aabb	3 (0 type): 1 (†0–4 type)	10	9.0	194	145	22	17	7	3
aabb	Mostly 2 type. Range 0–4	4	4.5	77	1	11	43	17	5
AaBB	3 (0 type): 1 (3–4 type)	7	9.0	128	99	0	0	15	14
AaBb	12 (0 type): 1 (0–4 type): 3 (3–4 type)	21	18.0	406	248	27	26	50	55
aaBb	1 (0–4 type): 3 (3–4 type)	6	9.0	112	0	2	23	52	35
aaBB	All susceptible (3–4 type)	4	4.5	73	0	0	1	25	47
AAbb	(Resistant parent–Calif. No. 1311)	..	....	38	38	0	0	0	0
aaBB	(Susceptible parent–Atlas)	..	....	139	0	0	2	21	116

* It is assumed that the presence of the dominant gene *A* in an F_2 plant results in 0 type reaction and that the recessive *bb* genotype imparts resistance but permits an infection range of 0 to 4 types with most plants in the 1 to 3 groups.

† Actual expected distribution same as for the *aabb* genotype.

independent genes for resistance to scald in Calif. No. 1311, one of which is dominant and the other recessive. If it is assumed that the dominant gene *A* imparts complete resistance and that the recessive gene—when homozygous *bb*—permits the full 0 to 4 range of infection with a mode at 2, some of the F_2 genotypes can be determined quite accurately by the behavior of F_3 rows. In table 4, an attempt is made to group rows of comparable segregation and to assign appropriate genotypes to them. For example, the F_3 rows in which all plants are scald-free are assumed to trace to one of the three genotypes homozygous for *A* (*AABB, AABb,* or *AAbb*). While not all F_3 rows may be assigned with as great certainty as these, a reasonably good case can be made for all. The close agreement of observed with expected numbers of rows demonstrates the probable correctness of the assumption that Calif. No. 1311 differs from Atlas in one dominant and one recessive gene for resistance to scald.

Atlas × Trebi. The field reaction of Trebi has been similar to that of Calif. No. 1311 in showing occasional light infection. As with the two crosses previ-

TABLE 5

ANALYSIS OF F_3 DATA FROM THE CROSS, ATLAS × TREBI, AS RELATED TO F_2 GENOTYPES*

F_2 genotype	Expected F_3 reaction	Number of F_3 rows		Number of F_3 plants					
				Total	Observed distribution in infection types				
		Observed	Expected		0	1	2	3	4
AABB, *AABb*, *AAbb*	All resistant (0 type)	35	33.8	610	610	0	0	0	0
Aabb	3 (0 type): 1 (†0–4 type)	14	16.9	247	198	6	21	15	7
aabb	Mostly 1–3 type. Range 0–4	6	8.4	95	9	25	24	28	9
AaBB, *AaBb*	3 (0 type): 1 (3–4 type); 12 (0 type): 1 (0–4 type): 3 (3–4 type)	52	50.6	894	661	12	22	63	136
aaBb	1 (0–4 type): 3 (3–4 type)	23	16.9	395	27	35	80	117	136
aaBB	All susceptible (3–4 type)	5	8.4	87	0	0	3	13	71
AAbb	(Resistant parent–Trebi)	..	....	40	40	0	0	0	0
aaBB	(Susceptible parent–Atlas)	..	....	78	0	0	0	0	78

* It is assumed that the presence of the dominant gene *A* in an F_3 plant results in 0 type reaction and that the recessive *bb* genotype imparts resistance but permits an infection range of 0 to 4 types with most plants in the 1 to 3 groups.

† Actual expected distribution same as for the *aabb* genotype.

TABLE 6

SUMMARY OF F_2 DATA FROM CROSSES OF ATLAS WITH SIX DERIVATIVES FROM TURK

Grown in the field and in the greenhouse at Davis in 1943

Cross	Observed		Expected (with single gene difference)		Chi^2	*P*
	Resistant (type 0)	Susceptible (types 1–4)	Resistant (type 0)	Susceptible (types 1–4)		
Atlas × P-4229	127	42	126.8	42.2	0.0127	0.9–0.95
Atlas × P-4232	121	45	124.5	41.5	0.3936	0.5–0.7
Atlas × P-4233	145	55	150.0	50.0	0.6667	0.3–0.5
Atlas × P-4236	138	37	131.2	43.8	1.4081	0.2–0.3
Atlas × P-42683	399	139	403.5	134.5	0.2008	0.5–0.7
Atlas × P-42709	409	119	396.0	132.0	1.7071	0.1–0.2
Combined data	1339	437	1332.0	444.0	0.1472	0.7–0.8

ously discussed, field-grown F_2 populations have not yielded data satisfactory for genetic interpretation.

The behavior of greenhouse-tested F_2 populations is very similar to that of Atlas × Calif. No. 1311 (table 2). The second set of data was obtained under the same heavy infection reported for Atlas × Calif. No. 1311.

F_3 data from 135 rows grown in the greenhouse are reported in table 5. An analysis comparable to that used for Calif. No. 1311 indicates that Trebi also differs from Atlas in one dominant and one recessive gene for resistance to this disease.

TABLE 7

DISTRIBUTION OF F_3 ROWS FROM THE CROSS, TURK × ATLAS, IN 5 PER CENT CLASSES OF SCALD INFECTION

Grown in the field and in the greenhouse at Davis, 1940 to 1942

Per cent of plants susceptible to scald (types 3 and 4)	Number of rows	Per cent of rows	Per cent of plants susceptible to scald (types 3 and 4)	Number of rows	Per cent of rows
0	164	30.5	50.0–54.9	1	0.2
0.1– 4.9	26	4.8	55.0–59.9	0	0.0
5.0– 9.9	38	7.1	60.0–64.9	1	0.2
10.0–14.9	48	8.9	65.0–69.9	0	0.0
15.0–19.9	58	10.8	70.0–74.9	0	0.0
20.0–24.9	55	10.2	75.0–79.9	1	0.2
25.0–29.9	35	6.5	80.0–84.9	1	0.2
30.0–34.9	15	2.8	85.0–89.9	0	0.0
35.0–39.9	13	2.4	90.0–94.9	8	1.5
40.0–44.9	6	1.1	95.0–99.9	12	2.2
45.0–49.9	0	0.0	100.0	56	10.4
			Total	538	100.0

Turk (and Its Derivatives) × Atlas. Turk and its single-dominant-gene extractions have shown complete resistance to scald both in the field and in the greenhouse. Because the genetics of resistance to scald in Turk × Atlas has proved to be complex and therefore difficult to analyze, the six extracted resistant lines will be discussed first. Six homozygous plants—P-4229, P-4232, P-4233, P-4236, P-42683, and P-42709—were obtained from three F_3 rows of Turk × Atlas, which were segregating 3 resistant to 1 susceptible plant. Each of these lines gives clear-cut monohybrid ratios in F_2 when crossed with Atlas (table 6). No difficulty was experienced in classifying plants either in the field or in the greenhouse. The crosses necessary to establish the relationship among the genes of these six lines have been studied. All proved to have the same gene (table 8).

The distribution of 538 F_3 rows of the Turk × Atlas cross into 5 per cent classes of scald infection is shown in table 7. These were grown and classified

TABLE 8

THE F_2 OF CROSSES BETWEEN RESISTANT VARIETIES AND SELECTIONS

Grown in the greenhouse at Davis in 1945

Hybrid	Number of plants		Hybrid	Number of plants	
	Total	Susceptible		Total	Susceptible
La Mesita × Calif. No. 1311	499	0	Trebi × Turk	237‡	0
La Mesita × Trebi	302*	0	Trebi × P-4229	194	0
La Mesita × Turk	333†	0	Trebi × P-4232	284	0
La Mesita × P-4229	258	0	P-4232 × P-4233	221	0
La Mesita × P-4232	273	0	P-4232 × P-4236	593	0
Calif. No. 1311 × Trebi	71	0	P-4233 × P-4236	359	0
Calif. No. 1311 × Turk	32	0	P-4236 × P-42683	352	0
Calif. No. 1311 × P-4229	201	0	P-4236 × P-42709	337	0
Calif. No. 1311 × P-4232	267	0	P-42683 × P-42709	269	0

*, †, ‡, further verified by 41, 42, and 42 F_3 rows, respectively, all of which were scald-free.

as follows: (1) In 1940 all plants in 320 field-grown rows were classified on the 0 to 4 scale of infection. All susceptible rows as well as those showing a high percentage of susceptible plants were duplicated and rechecked in 1942. (2) In 1941, all plants in 218 field-grown rows were classified as susceptible, resistant (0 type), or doubtful. All doubtful plants were carried into the F_4 in 1942 and there classified as resistant or susceptible. Of the 218 F_3 rows, 170 were duplicated in the greenhouse in 1942.

When only the 3 and 4 types of infection were considered as susceptible, all distributions were essentially alike and therefore have been combined in table 7. This distribution cannot be explained on the basis of the single gene present in the lines extracted from Turk × Atlas and reported above. There are a few lines with from 50 to 90 per cent susceptible plants, suggesting the presence of a recessive gene. Numerous attempts were made to explain the distribution obtained by the use of additional dominant and recessive genes with and without linkage. In every case, there were serious discrepancies for some parts of the data. It seems best, therefore, to await further data before presenting conclusions as to the genetic constitution of Turk with reference to resistance to scald.

Crosses of Resistant Varieties. Data on the relation of the dominant gene found in La Mesita, Calif. No. 1311, Trebi, and monogenic lines from Turk × Atlas were obtained in the greenhouse and are given in table 8. Not all the crosses between all the resistant varieties were available for study, but a sufficient number was investigated to demonstrate clearly their gene relationship. In no case was a susceptible F_2 plant found. Forty-one, 42, and 42 F_3 rows of La Mesita × Trebi, La Mesita × Turk, and Trebi × Turk, respectively, were grown without a susceptible plant being found. The above varieties and selections appear, therefore, to have a single dominant gene in common.

Level and Transmission of Resistance. The fact that the dominant gene common to all the varieties under consideration does not confer equal resistance on all of them and does not transmit equal resistance to progeny is difficult to interpret. Actually, the varieties appear to fall into two groups as far as level and transmission of resistance are concerned. Turk and its derivatives make up one group, while Calif. No. 1311, Trebi, and La Mesita constitute the other. Three possible explanations are suggested: (1) These two groups of varieties have different modifying gene complexes. In this connection it should be pointed out that this gene from Turk went through seven backcrosses with Atlas in developing the scald resistance of Atlas 46[6] without losing any of its effectiveness in controlling this disease. (2) Two closely linked genes should be considered. Of the 5,082 F_2 plants included in table 8, only 1,748 plus 42 F_3 rows are useful in determining this point. This small number of plants will not eliminate linkage. (3) Different allels of the same gene would account for the differences.

[6] To be reported later.

DISCUSSION

The classification of plants for scald resistance was difficult when other leaf diseases were present, particularly net blotch. When greenhouse-grown plants were artificially inoculated, this trouble disappeared. Therefore, for genetic studies the data collected in the greenhouse were much more useful than field data. However, the study of varietal reaction and the breeding of scald-resistant Atlas 46 were successfully carried out in the field.

La Mesita differs from susceptible Atlas by a single dominant or near-dominant gene for resistance to scald.

The data presented indicate that both Trebi and Calif. No. 1311 have a dominant and a recessive gene for resistance to scald. Since Trebi was one of the parents of a composite cross, from which Calif. No. 1311 was derived, resistance of the latter could trace to Trebi. The dominant gene in both varieties is identical with the one in La Mesita.

Turk has been the source of the highest type of resistance studied thus far. Six single-gene extractions from Turk × Atlas have shown good 3:1 ratios in F_2, with little difficulty in classification either in the field or in the greenhouse. The presence in Turk of one or more additional genes for resistance to this disease has been established from extensive studies involving F_2 to F_4 generations of Turk × Atlas. Thus the number and their mode of inheritance have not been established accurately.

The single gene extracted from Turk appears to be identical with the dominant gene in La Mesita, Calif. No. 1311, and Trebi. Turk and its extractions have been completely resistant in the field, whereas the other three varieties may sometimes show a moderate amount of the disease. These differences may be due to modifying genes, different but closely linked genes, or possibly multiple allels.

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