INHERITANCE OF RESISTANCE TO BUNT, TILLETIA TRITICI, IN SHERMAN AND ORO WHEAT HYBRIDS

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INTRODUCTION

In previous publications, the inheritance of resistance to bunt, *Tilletia tritici* (Bjerk) Wint., in hybrids with eight resistant varieties of wheat, has been reported. The resistance of Martin (BRIGGS 1926), White Odessa (BRIGGS 1930b), Banner Berkeley (BRIGGS 1931), and Odessa (BRIGGS 1932b) wheat varieties has been shown to result from the same dominant factor in each case. This factor has been designated as the Martin factor (*M*). Hussar wheat (BRIGGS 1926, 1930a) depends on two factors for its resistance, the Martin and Hussar (*H*) factors. This second factor is not completely dominant, as bunt occurs on a part of the heterozygous plants. Selections 1418 and 1403 each have only the Hussar factor. Turkey 1558 and Turkey 3055 (BRIGGS 1932a) each have a single factor for resistance to this disease which has been designated as the Turkey factor (*T*). This factor is similar to the Hussar factor in effect.

Data are presented here to show the number of factors for resistance to bunt in Sherman and Oro wheats. The crosses necessary for identifying these factors are available.

METHODS AND MATERIALS

The parental varieties and hybrid populations were grown in the field at the University Farm, Davis, California. The method of handling and the source of inoculum have been described in a number of the publications referred to above. A single collection of bunt has been propagated and used continuously since 1917.

TABLE 1

Annual percentages of bunt infection at Davis, California in the parent wheat varieties during the years indicated.

VARIETY	PERCENTAGE OF BUNTED PLANTS				
	1929	1930	1931	1932	AVERAGE
Oro	0	0	0	0.1	.03
Sherman	0	0	0	0.1	.03
Martin	0	0	0	0	0
Turkey 3055	0.1	2.0	1.2	1.8	1.3
Baart			47.2	85.5	66.3
White Federation	78.6	59.3	43.0	73.2	63.5

Seed of Sherman and Oro were supplied in 1928 by Dr. K. S. QUISENBERRY, Division of Cereal Crops and Diseases, UNITED STATES DEPARTMENT OF AGRICULTURE. These varieties were known by Dr. QUISENBERRY to be resistant to bunt. The record of these varieties at Davis may be seen in table 1.

Duplicate rod rows of Sherman and Oro were grown in 1929 and 1930. Four rod rows of each were grown in 1931 and 20 rod rows in 1932. One plant of Sherman and two of Oro became infected in 1932. Compared with these resistant varieties, Baart and White Federation may be considered completely susceptible.

Sherman and Oro each were crossed with Baart to determine the number of bunt-resistant factors in each of these two resistant varieties. Crosses also were made with Martin and Turkey 3055 to test for the presence of the Martin and Turkey factor respectively. The cross with Selection 1403, which is the tester for the Hussar factor, was not obtained because of the difference in heading dates. As will be seen later, this cross was not necessary for identifying the resistant factors in Oro and Sherman wheats.

TABLE 2

Percentage of bunted plants in the parents and F_2 of the crosses named. Grown at Davis, California.

PARENT OR CROSS	YEAR GROWN	PLANTS GROWN NUMBER	PLANTS BUNTED	
			NUMBER	PERCENT
Sherman	1931	185	0	0.0
	1932	1265	1	0.1
Oro	1931	176	0	0.0
	1932	1305	2	0.2
Turkey 3055	1931	145	0	0.0
	1932	622	9	1.5
Martin	1931	86	0	0.0
	1932	434	0	0.0
Baart	1931	362	170	47.0
	1932	2370	2061	87.0
Sherman×Baart	1931	641	92	14.4
	1932	623	168	27.0
Sherman×Turkey 3055	1931	483	14	3.2
	1932	684	48	7.0
Martin×Sherman	1931	478	0	0.0
	1932	871	0	0.0
Oro×Baart	1931	585	103	17.6
	1932	1264	412	32.3
Oro×Turkey 3055	1931	499	3	0.6
	1932	679	7	1.0
Martin×Oro	1931	427	8	1.9
	1932	894	24	2.7

EXPERIMENTAL RESULTS

F_1 seeds were not inoculated because of the small number available. Where F_2 plants were being grown as a source of seed to be inoculated in F_3, they were kept free from bunt. By doing this, there was no elimination of susceptible progeny by bunt in F_2.

F_2 data do not permit a satisfactory Mendelian analysis because some susceptible plants usually escape infection, and resistant and heterozygous plants may be infected occasionally. An F_2 population was inoculated the year previous to growing the F_3 and another population the same year as the F_3. These data are of value because they give some indication of the number of factors by which the resistant and susceptible varieties differ. Also they indicate the percentage of bunt to expect in F_3 rows of the same genotype. Therefore, the F_2 data are given in table 2.

In 1931, the percentages of bunt in the parent varieties, as well as in the F_2 populations were only about half those secured in 1932. In fact, the infection in 1931 was the lowest obtained during the 13 years that records have been available here. That a number of susceptible F_2 plants escaped infection in 1931 may be seen from the fact that the F_2 of Sherman × Baart had 14.4 percent of bunted plants that year and 27.0 percent in 1932. Similar results were secured with the other crosses. The classification of F_2 plants on the basis of bunt obtained in F_3 rows is much more satisfactory. F_3 rows contained from 30 to 70 plants, usually about 50. These data may be seen in table 3.

The rows in the 0–5 percent class for bunt infection were subdivided into those without bunt and those with 1–5 percent because the former group always is of interest.

The hybrids with Sherman may be considered first. The distribution of rows in the Sherman × Baart cross is shown in figure 1. This curve resembles the Martin curves previously published (BRIGGS 1926, 1930b, 1931, 1932b). The number of rows under the three modes agrees satisfactorily with the 1:2:1 ratio. Accepting 7.5 and 52.5 as minima, there are 54.5 resistant, 146.5 heterozygous and 70 susceptible rows where 67.75, 135.5, and 67.75 were the numbers expected. This gives a value of P greater than 0.1. The heterozygous F_3 rows, which are of the same genotype as the F_2 population, averaged 24.2 percent of bunt compared with 27.0 percent for the F_2 grown in the same nursery. The susceptible rows had 82.2 percent of diseased plants under the same conditions that Baart produced 87.0 percent. The data then indicate that Sherman differs from Baart in one major factor for resistance to bunt. This factor is similar to the Martin factor in effect.

The identity of the factor in Sherman is established by the cross with

TABLE 3

Distribution of parent and F_3 rows of the crosses named into 5 percent classes for bunt infection, when grown at Davis, California, 1932.

PARENT OR CROSS	DISTRIBUTION OF ROWS HAVING A BUNT INFECTION (PERCENT) OF																				TOTAL NUMBER ROWS
	0–5		5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55–60	60–65	65–70	70–75	75–80	80–85	85–90	90–95	95–100	
	0:	1–5																				
Sherman	17	1																				18
Oro	16	2																				18
Turkey 3055	4	3	1																			8
Martin	6																					6
Baart																	3	9	13	9	1	35
Sherman×Baart	28	26	1	4	27	64	28	17	4	0	2	0	1	2	3	7	12	17	15	10	3	271
Sherman×Turkey 3055	65	24	20	6	7	8	3	2	1	0	0	1	1	0	1	1						140
Martin×Sherman	140																					140
Oro×Baart	18	45	18	7	17	20	30	27	19	21	8	5	9	9	7	13	11	7	3	2	1	297
Oro×Turkey 3055	71	57	9																			137
Martin×Oro	50	23	11	7	3	2	3	0	0	2	0	1	1	0	1							104

Martin. The fact that these hybrids did not segregate for bunt resistance shows that Sherman is identical with Martin in its resistance to this fungus.

The cross of Sherman with Turkey 3055 may be considered briefly even though it did not happen to be necessary for establishing the identity of the resistant factor in Sherman. It was made for that purpose at the same time the other crosses were made. As would be expected in the light of the above data, this cross gave a segregation typical of those obtained previously with two factors (BRIGGS 1926, 1930a). In such a cross, the susceptible rows are the only ones that can be recognized readily. There were 4

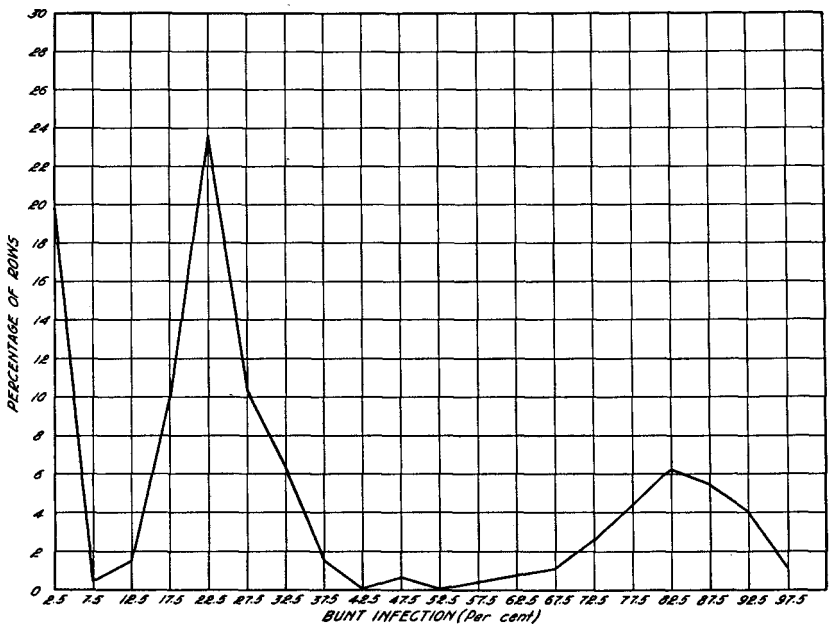

FIGURE 1.—Distribution of F_3 rows of Sherman×Baart into 5 percent classes for bunt infection.

susceptible rows where 8.8 were expected, thus giving the value for P between 0.1 and 0.2.

Considering now the crosses with Oro it is interesting to compare these with the Sherman crosses. As will be seen presently, these two varieties depend on different genetic factors for their resistance to bunt. The Oro× Baart hybrids gave a monohybrid ratio as shown by figure 2. There were 84.5 resistant, 148 heterozygous, and 64 susceptible F_3 rows where 74.25, 148.5 and 74.25 respectively were the numbers expected, giving P a value greater than 0.2. The F_2 of Oro×Baart had an average of 32.3 percent of bunt compared with 31.4 percent for the heterozygous F_3 rows. This is 7.2 percent more than found on the heterozygous rows of Sherman× Baart, indicating that some heterozygous plants become infected.

The susceptible rows of Oro×Baart had an average of 71.4 percent of bunt which is lower than produced by Baart. This does not appear to be

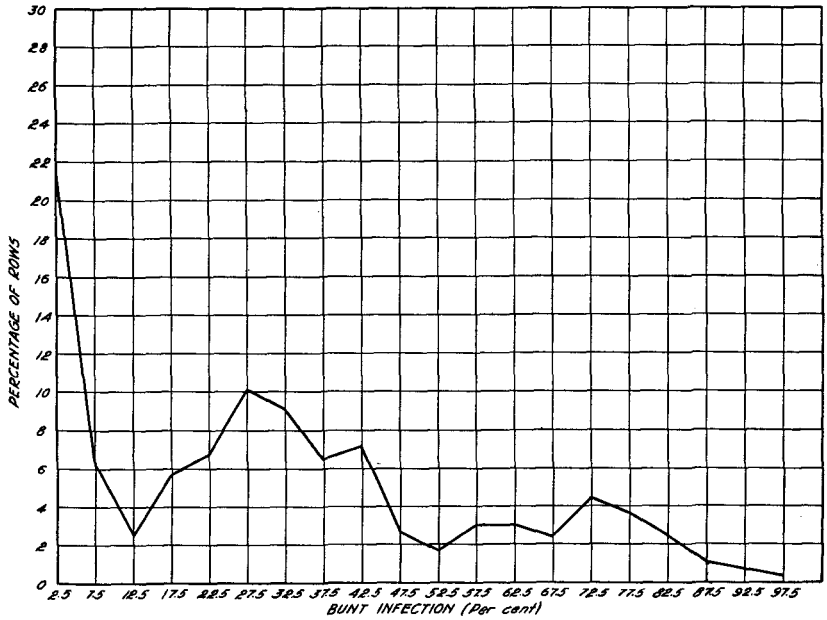

FIGURE 2.—Distribution of F_3 rows of Oro×Baart into 5 percent classes for bunt infection.

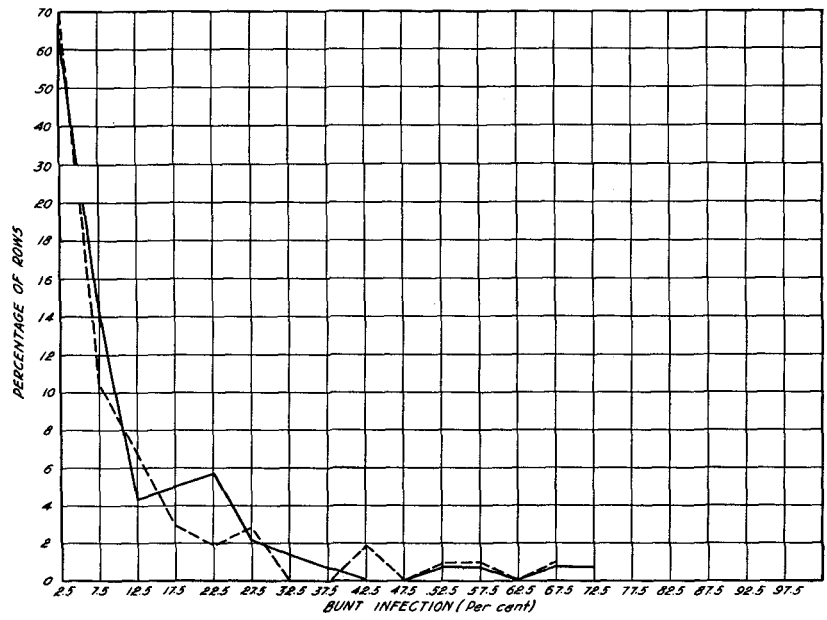

FIGURE 3.—Distribution of F_3 rows of Martin×Oro (broken line) and Sherman×Turkey 3055 (solid line) into 5 percent classes for bunt infection.

due to place effect in the nursery because the rows of Baart grown within the same area had percentages of bunt about average for that variety. The reasons for the lower percentage of bunt for the F_3 rows are not known. It may be due in part at least to modifying factors.

The Oro×Baart curve is distinctly different from the Sherman×Baart curve which is typical for the Martin factor. It is similar, however, to the curve resulting from the Hussar factor (BRIGGS 1930a) and the Turkey factor (BRIGGS 1932a). That the Turkey factor, but not the Hussar factor, is responsible for the resistance of Oro is shown by the Turkey 3055×Oro cross. No susceptible rows were found in a population of 137 rows. This cross averaged 1.3 percent of bunt which is slightly more than the average of the parents.

Oro was crossed with Martin at the time the other crosses were made. This was not a critical cross for identifying the bunt resistant factor in Oro. However, it is interesting to compare it with the Sherman×Turkey 3055 cross because the same two bunt resistant factors are involved in each cross but contributed in each case by different varieties. This comparison may best be made by referring to figure 3. These curves are very similar considering the relatively small number of rows grown from each cross.

DISCUSSION AND SUMMARY

Data were presented to show that Sherman and Oro differ from the susceptible variety, Baart, in one major factor for resistance to bunt. The factor in Sherman was identified as the Martin factor and the one in Oro as the Turkey factor. This makes ten varieties that have been studied. The genetic constitution of these as regards bunt resistance may be seen in table 4.

TABLE 4

The genetic constitution of ten bunt resistant varieties of wheat as determined by the author.

VARIETY	BUNT RESISTANT FACTORS		
Martin	*MM*	*hh*	*tt*
White Odessa	"	"	"
Banner Berkeley	"	"	"
Odessa	"	"	"
Sherman	"	"	"
Hussar	*MM*	*HH*	*tt*
Selection 1418 and 1403	*mm*	*HH*	*tt*
Turkey 1558	*mm*	*hh*	*TT*
Turkey 3055	"	"	"
Oro	"	"	"

The first five varieties depend on the Martin factor, *M*, for their resistance to bunt. Hussar has the Hussar factor, *H*, in addition to the *M* factor. Selections 1418 and 1403 which are from Hussar×Hard Federation only

have the *H* factor. The last three varieties, Turkey 1558, Turkey 3055, and Oro each have the Turkey factor, *T*, only.

It is entirely possible that in some of these varieties there are other factors for resistance to bunt which are not apparent in the presence of the collection of bunt used in these experiments. If the *M* factor discovered in Martin, White Odessa, Banner Berkeley, Odessa, and Sherman is the only factor for resistance to bunt in these varieties, they should react the same to each collection of bunt. If some other resistant factor is present in one or more, but not in all five varieties, a differential reaction should be obtained with some collections. Furthermore, Hussar should be resistant to all collections to which Martin is resistant but in addition should be resistant to some which attack Martin, because of the presence of *H*. Finally, if the above analysis is correct, only three differential hosts are available in the above list of varieties. Other resistant factors undoubtedly exist in other varieties. Recently, CHURCHWARD (1931, 1932) has published data to show that Florence differs from susceptible varieties in a single recessive factor. This factor must be different then from any of the three listed above.

The predictions made above may be tested out in so far as data are available. REED (1928), GAINES (1928), and BRESSMAN (1931) have studied the reaction of some of the above varieties to a number of collections of bunt. In general, their results agree with the genetic interpretation given in table 4. Considering REED'S results first, comparisons are available for Martin, Odessa, and Hussar. He used two strains of Turkey which were different from each other. Since their relation to the above strains of Turkey is not known, they will not be considered. There is one outstanding difference in the infection of Martin and Odessa by one collection of bunt. The collection of *Tilletia tritici* from West Seneca, New York, produced 54 percent of bunt on Odessa but only an average of 7 percent on Martin. This same collection produced 8 percent on Hussar 527, and 23 percent on Hussar 814. This suggests the presence of a factor for resistance to bunt in Martin which is not present in Odessa or perhaps Hussar wheats. In no other case is Martin resistant to a collection which readily infects Odessa or Hussar. As might be expected, he found a case in which Hussar was resistant but Martin and Odessa susceptible. Hussar's resistance here may be attributed to the *H* factor.

GAINES (1928) reported one case where 32 percent of White Odessa plants were infected but only 1 percent of Martin and 1 percent of Hussar plants showed the disease. Otherwise his data conform to those of REED.

BRESSMAN (1931) inoculated a number of resistant varieties with various collections of bunt. He states: "White Odessa, Martin, Banner Berkeley, and Regal gave results similar to those obtained with Albit."

Regal and Albit have not been studied by the author. However, Albit may be assumed to have only the *M* factor for resistance because it is a selection from Hybrid 128 × White Odessa made by GAINES at WASHINGTON STATE COLLEGE (CLARK, PARKER and WALDRON 1927). Hybrid 128 is very susceptible and probably contributed nothing to the resistance of Albit. A few cases were found where some one of these varieties appeared to be susceptible while the others were resistant. For example, collection 7c produced 26 percent of bunt on White Odessa in 1928 and only 3 percent on Martin and 1 percent on Banner Berkeley. The following year at Corvallis these varieties had 0, 3, and 6 percent respectively, indicating that White Odessa probably is resistant to this collection. Other similar cases were encountered.

Results at Corvallis in 1929 made possible a comparison of Albit and Hussar in their reaction to all 94 collections of bunt. In a number of cases, Hussar is resistant to collections but Albit is susceptible. Hussar's resistance again may be attributed to the *H* factor. In every instance, with the possible exception of collection 4, if Hussar is susceptible Albit also is susceptible. BRESSMAN uses the results with collection 4 at Corvallis 1929 as a type for his physiologic form II, presumably because Hussar produced 20 percent of bunt, while Albit had 6 percent, Ridit 4 percent, and Oro 3 percent. However, the year before, Albit had 12.5 percent of bunt and Hussar had 1.5 percent.

If the assumption that Albit has only the Martin factor for resistance is correct, then three of the four varieties finally chosen by BRESSMAN as differential hosts each have a different genetic constitution as seen in table 4. Albit, Hussar, Oro, and Ridit were the varieties used by him.

Ridit is different from the other three varieties in its reaction to these collections of bunt. The genetic constitution of Ridit is not known at present, but something is known about the genetics of its parents. This variety was selected by GAINES at WASHINGTON STATE COLLEGE from a cross of Turkey with Florence (CLARK, LOVE and PARKER, 1926). As pointed out earlier, CHURCHWARD (1931, 1932) believes that the resistance of Florence is due to a single recessive factor. The writer has shown that the resistance of Turkey depends on the *T* factor. Ridit then may be assumed to have either one or both of these factors. In this connection, a comparison of the reaction of Ridit to the various collections of bunt with that of Oro is of interest. Oro is known to have only the *T* factor. Forty-three comparisons are available from BRESSMAN'S data. Oro is resistant to 42 of these collections, and Ridit is also resistant to these same collections. This may be attributed to the *T* factor. However, Oro is susceptible to collection 28, but Ridit is resistant to it. Ridit's resistance to this collection may be

attributed, for the purpose of this discussion, to the factor inherited from Florence.

Recently, SMITH (1932) has differentiated three physiologic races of bunt by the reaction of Martin. Martin was resistant to T1, gave 19 percent of bunted heads with T2, and 71 percent with T3. Furthermore, bunted heads resulting from T2 had very small smut balls. BRESSMAN (1931) reported a few abnormalities with some of his collections. The reaction of Martin to the above three forms of bunt is not readily explained on the basis of a single factor. It is entirely possible that the difference in reaction to T1 and T2 may be due to a modifying factor.

From the above discussion, it is apparent that a genetic analysis of other resistant varieties is desirable. Also more data are needed on the physiologic races of this disease. Pure lines of the fungus are highly desirable in this connection. BRESSMAN (1931) found that some of the collections of bunt received by him were a mixture of the two species of Tilletia. It seems equally certain that some of the collections may have been mixtures of physiologic forms. Improvements in the purity of the inoculum are being made.

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