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LINKAGE RELATIONS OF THE GOLDFOIL FACTOR FOR RESISTANCE TO MILDEW IN BARLEY [1]

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INTRODUCTION

Seven different genetic factors for resistance to race 3 of mildew (*Erysiphe graminis hordei*) in barley (*Hordeum vulgare*) have been discovered in the writers' work with this disease (*7*).[2] Six of these factors have either occurred singly in varieties or have been set up in hybrid lines. Two, the Algerian factor Ml_a and the Kwan factor Ml_k, are linked (*2*). The others appear to be independent. Since all seven linkage groups have been established in barley (*6*), the linkage groups to which these seven mildew-resistant factors belong may be ascertained. Linkage relations of the Goldfoil factor are now available.

Incidental to this study, data were accumulated on a factor pair for red vs. green stem color that has not heretofore been reported. Linkage relationships were established for this factor also.

MATERIALS AND METHODS

Briggs and Barry (*1*) reported that the resistance of Goldfoil was due to a single dominant factor, Ml_g, and pointed out that this factor was independent of six-row vs. two-row and long vs. short-haired rachilla, characters available in the cross between Goldfoil and Atlas, and known to belong to linkage groups I and V, respectively. Since these findings were reported Goldfoil has been crossed with susceptible varieties carrying markers for four of the remaining groups. The cross with Nepal 595 was investigated first because it was segregating for two factor pairs each in groups III and IV. Group 3 was marked by hulled vs. naked, *Nn*, and by one of a complementary factor pair for blue vs. white aleurone, Bl_1bl_1, recently reported by Myler and Stanford (*4*). Group IV was marked by hooded vs. awned, *Kk*, and by the other complementary factor pair for blue vs. white, *Blbl*.

Goldfoil is resistant to mildew, is hulled, awned, and white, but carries the *Bl* factor for blue aleurone. Under favorable light conditions it develops red pigment in the stems. Nepal 595 is susceptible to mildew, is naked, hooded, and white, but has the Bl_1 factor for blue. In contrast to Goldfoil it has green stems.

As in previous experiments, the mildew tests were made in the greenhouse with race 3 of the fungus. Mildew classifications were based on the reaction of F_3 progeny, which were grown in greenhouse benches and which in most cases were represented by 25 to 30 plants. Every tenth row was seeded to Atlas as a check. The plants were inoculated in the three-leaf stage by dusting with spores from diseased plants grown for that purpose. The F_3 rows were classified as resistant,

[1] Received for publication March 27, 1942.

[2] Italic numbers in parentheses refer to Literature Cited, p. 5.

segregating, or susceptible. Since this factor for mildew resistant is dominant, a segregating row indicated a resistant F_2 plant and is so considered in the calculations.

When light intensity was sufficient to cause the red stem color to develop, the F_3 rows were also classified for this character. Homozygous red and segregating rows were listed as red.

The cross-over values and their probable errors were all taken from Immer's tables (*3*).

EXPERIMENTAL RESULTS

A total of 795 F_2 plants of Goldfoil×Nepal 595 were grown in the field in 1939–40 and classified at harvest time for hooded vs. awned, hulled vs. naked, and blue vs. white aleurone. Of these, 770 were tested for mildew reaction in F_3 in the greenhouse during 1940 and 1941, while 25 lines were discarded either because of insufficient seed or because the population was too much reduced by damping-off. It soon became apparent that the Goldfoil factor for mildew resistance was linked with hooded vs. awned and consequently with the blue vs. white factor pair belonging to group IV. Resistance, accordingly, was independent of the factors represented by group III. Only the data involving factors in group IV will be presented in connection with mildew resistance.

The single contrasting characters all conform to expectations on the basis of factors previously assigned to them. There were 562 hooded: 208 awned, where 577.5:192.5 were expected on the basis of a single factor (*6*). This gives a P value greater than 0.2. As pointed out above, Myler and Stanford (*4*) found the blue aleurone color to be due to complementary factors. There were 412 blue:358 white, where 433.1:336.8 were expected on the basis of the 9:7 ratio, giving a P value between 0.1 and 0.2. Finally, there were 588 mildew resistant: 183 mildew susceptible, where 578.25:192.75 were expected on the basis of a single factor, which gives a P value greater than 0.3.

Table 1 shows the data involving hooded vs. awned and resistance vs. susceptibility.

TABLE 1.—*The F_2 segregation of the characters listed from a cross of Goldfoil ($kk\ Ml_gMl_g$)×Nepal 595 ($KK\ ml_gml_g$) with expected numbers based on independence and on a cross-over value of 18.77 percent*

Characters	Observed number	Expected number on the basis of a 9:3:3:1 ratio	χ^2 on the basis of a 9:3:3:1 ratio	Expected number on the basis of a cross-over of 18.77 percent	χ^2 on the basis of a cross-over of 18.77 percent
Hooded resistant	387	433.1	4.907	391.8	0.059
Hooded susceptible	175	144.4	6.484	185.7	.616
Awned resistant	201	144.4	22.185	185.7	1.261
Awned susceptible	7	48.1	35.119	6.8	.006
Total	770	770.0	68.695	770.0	1.942
P value			Very low		>0.3

In table 1 the observed numbers for the character combinations deviate significantly from the numbers expected on the basis of the 9:3:3:1 ratio. A cross-over value of 18.77±2.33 percent was indicated by the data. The numbers expected on the basis of this value agree satisfactorily with those obtained, giving a $P>0.3$.

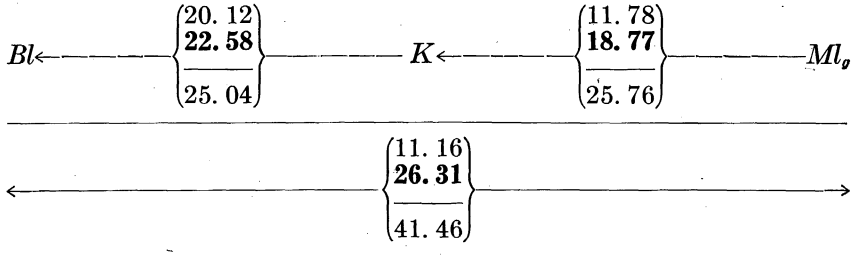
Table 2 shows the data regarding blue vs. white aleurone and resistance vs. susceptibility to mildew.

TABLE 2.—*The F_2 segregation of the characters listed from a cross of Goldfoil (Bl_1Bl_1 $blbl$ Ml_gMl_g) × Nepal 595 (bl_1bl_1 Bl Bl ml_gml_g) with expected numbers based on independence and on 26.31 percent crossing over*

Characters	Observed number	Expected number on the basis of a 27:9:21:7 ratio	χ^2 on the basis of a 27:9:21:7 ratio	Expected number on the basis of a cross-over of 26.31 percent	χ^2 on the basis of a cross-over of 26.31 percent
Blue resistant	289	324.8	3.946	298.7	0.315
Blue susceptible	123	108.3	1.995	134.4	.967
White resistant	299	252.7	8.483	278.8	1.464
White susceptible	59	84.2	7.542	58.1	.014
Total	770	770.0	21.966	770.0	2.757
P value			Small		>.2

Robertson et al. (*5*) have shown that the *Bl* factor for blue aleurone is linked with hooded with a cross-over value of 22.58 ± 0.82. Since Myler and Stanford (*4*) have shown that this gene is present in Goldfoil, it follows that mildew resistance should show linkage with blue aleurone. Obviously the data in table 2 do not conform to independent segregation. The numbers observed agree satisfactorily, however, with those expected on the basis of 26.31 ± 5.05 percent. recombination.

The data clearly show that the Goldfoil factor pair for resistance vs. susceptibility to mildew is linked with the hooded vs. awned and the blue vs. white aleurone factor pairs, known to belong to group IV. The data are not sufficient to establish the order of these three gene pairs. The linkages reported in this paper have high probable errors because the genes entered the hybrid in the repulsion phase. The most probable cross-over values, with the maximum and minimum that might be expected based on ± 3 probable error, with the suggested order, follows:



As will be seen, the most probable value of the cross-over percentages for *Bl*—*K* and *K*—Ml_g together equals 41.35, which is just within the maximum range expected for *Bl*—Ml_g. In no other case will the sum of any two most probable values fall within the expected range of the third. The most likely order therefore seems to be *Bl*, *K*, Ml_g.

Incidental to the mildew studies, data were accumulated on red vs. green stem color, the genetics of which has not previously been reported. Goldfoil shows considerable red pigment in the stems when grown under favorable light conditions, whereas Nepal 595 produces

no red. Of the 607 plants classified for stem color, 442 were either homozygous red or segregating, while 165 were green. The numbers expected on the basis of the 3:1 ratio are 455.25:151.75, giving a probability greater than 0.2. Red stem will hereafter be designated by the symbol *Rs*.

Hulled vs. naked segregated on the basis of 3:1, which is in agreement with the results of numerous other workers (*6*). There were 448 hulled: 159 naked, where 455.25:151.75 were expected, giving a $P>0.3$. As pointed out above, blue vs. white aleurone segregated in this cross on the basis of complementary factors. The segregation of the 607 plants under consideration here agreed satisfactorily with that hypothesis, having a *P* value greater than 0.2.

It soon became apparent that red vs. green stem color was associated with hulled vs. naked. Table 3 gives the data involving these characters.

TABLE 3.—*The F_2 segregation of the characters listed from a cross of Goldfoil (NN RsRs)×Nepal 595 (nn rsrs), with expected numbers based on independent segregation and on a cross-over value of 14.5 percent*

Characters	Observed number	Expected number on the basis of a 9:3:3:1 ratio	χ^2 on the basis of a 9:3:3:1 ratio	Expected number based on a cross-over of 14.50 percent	χ^2 based on a cross-over of 14.50 percent
Hulled red	403	341.5	11.075	414.4	0.314
Hulled green	45	113.8	41.594	40.8	.432
Naked red	39	113.8	49.166	40.8	.079
Naked white	120	37.9	177.847	111.0	.730
Total	607	607.0	279.682	607.0	1.555
P value			Very small		>0.3

Obviously the observed numbers do not conform to those expected on the basis of independent segregation, but agree satisfactorily with those expected on the basis of 14.50 ± 1.06 percent crossing over. Thus the factor for red stem color belongs to linkage group III.

As Myler and Stanford (*4*) have shown, the complementary factor for blue aleurone (Bl_1) discovered by them belongs to group III and showed a cross-over percent of 9.88 ± 0.44, with naked. This gene is carried by Goldfoil. Red stem color should be linked, accordingly, with blue aleurone. That this is so may be seen from table 4.

TABLE 4.—*The F_2 segregation of the characters listed from a cross of Goldfoil (Bl_1Bl_1 RsRs blbl)×Nepal 595 (bl_1bl_1 rsrs BlBl), with expected numbers based on independent segregation and on a cross-over of 9.07 percent*

Characters	Observed number	Expected number on the basis of a 27:21:9:7 ratio	χ^2 on the basis of a 27:21:9:7 ratio	Expected number based on a cross-over of 9.07 percent	χ^2 based on a cross-over of 9.07 percent
Red blue	305	256.0	9.379	321.7	0.867
Red white	137	199.2	19.422	133.5	.092
Green blue	20	85.4	50.084	19.7	.005
Green white	145	66.4	93.042	132.1	1.260
Total	607	607.0	171.927	607.0	2.224
P value			Very small		>0.3

The expected numbers based on independent segregation deviate markedly from those observed. Those observed conform, however, to the numbers expected on the basis of 9.07 ± 1.24 percent crossing over.

Although the data are too few to indicate the order of the three gene pairs, they suggest that these genes are in the order of *N*, Bl_1, *Rs*.

SUMMARY

In a cross between Goldfoil, which carried the Goldfoil factor (Ml_g) for resistance to mildew, and which is awned and hulled, with Nepal 595, which carries the contrasting characters, it was found that mildew resistance was linked with hooded (*K*) 18.77 ± 2.33 percent, and with the *Bl* factor for blue aleurone with a cross-over of 26.31 ± 5.05 percent. As Robertson et al. (*5*) had previously shown, *K* and *Bl* are linked with a value of 22.58 ± 0.82 percent. These factors have been assigned to linkage group IV (*6*). Because the factors in this cross enter it in the repulsion phase, the probable errors are relatively high, and the order of the three genes under consideration is not clearly indicated. The order suggested is *Bl*, *K*, Ml_g.

Red stem color in this cross was found to be due to a single factor which was designated as *Rs*. This factor was found to be linked with hulled (*N*), 14.50 ± 1.06 percent, and with a second factor for blue aleurone color (Bl_1) with a cross-over value of 9.07 ± 1.24 percent. These genes have been assigned to linkage group III (*4*, *6*). Here, again, the order of the genes under consideration is not definitely indicated, but the suggested order is *N*, Bl_1, *Rs*.

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