

Inheritance of Reaction to *Puccinia hordei* in Barley.

III. Genes in the Cultivars Cebada Capa and Franger

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ABSTRACT

Genes conditioning reaction to *Puccinia hordei* in the barley cultivars Cebada Capa (C.I. 6193) and Franger (C.I. 8811) are at the Pa_5 and Pa_4 loci, respectively. Pa_4 is linked with Ml_a on chromosome 5. Linkage was detected between Pa_3 in cv. Estate

(C.I. 3410) and Pa_5 in Cebada Capa, with recombination estimated at $33.8 \pm 3.4\%$. The second gene in cv. Bolivia, previously designated Pa_x , is now relabeled Pa_6 . *Phytopathology* 60:788-790.

The barley cultivars Cebada Capa (C.I. 6193) and Franger (C.I. 8811) have been widely used in breeding programs as sources of resistance to leaf rust (*Puccinia hordei* Oth.) and powdery mildew (*Erysiphe graminis* DC. f. sp. *hordei* Marchal). Both Cebada Capa and Franger have a gene for mildew resistance at the Ml_a locus on chromosome 5 (3, 6, 8). Since the mildew resistance gene in Franger is linked with the rust resistance gene (3), the identification of this rust resistance gene with a previously recognized gene (5) would permit assigning a labeled rust-conditioning gene to a linkage group. The allelic relationships between the leaf-rust-conditioning genes of Cebada Capa and Franger and the labeled genes of other varieties are reported herein.

The methods used have been described previously (4), except that in the present study a mist was applied to the test plants for 30 min prior to inoculation, and no wetting agent was used. An isolate of race 4, culture 57-19 of *P. hordei* was used throughout the study. The Cebada Capa and Franger lines were single plant selections from seed stocks of the World Barley Collection maintained by the USDA, Beltsville, Maryland.

RESULTS.—The F_2 progenies from Cebada Capa, crossed with susceptible cultivars Moore and Egypt 4, segregated on the basis of a single gene pair for resistance, but the F_3 from the cross with Moore had a deficiency of homozygous susceptible lines (Table 1). Cebada Capa segregated in crosses with all other resistant cultivars except Quinn, which possesses Pa_2 and Pa_5 (5). Since it segregated with cultivars Reka 1 and Weider, each having a gene at the Pa_2 locus, it was concluded that the gene in Cebada Capa is at the Pa_5 locus.

Quinn and Cebada Capa are similar in appearance and reaction to *P. hordei*. To assure that the Cebada Capa \times Quinn progenies actually resulted from crossing, F_3 lines derived from one F_1 plant were inoculated with a culture of *E. graminis* f. sp. *hordei*, race 9, to which Quinn is very susceptible and Cebada Capa is resistant (7). Of 116 F_3 lines which were homozygous-resistant to the leaf rust fungus, 41 were homozygous-resistant to mildew, 57 segregated, and 18 were homozygous-susceptible. This verified that we were working with a cross between Cebada Capa and Quinn,

and that both cultivars have a pair of genes at the Pa_5 locus.

Acceptable fits to expected ratios were obtained in all crosses except that of Cebada Capa \times Estate, where there was a deficiency of susceptible types (Table 1). Since both Cebada Capa and Estate segregated on the basis of a single gene for resistance here and in previous studies (5, 7), the F_2 data indicate that Pa_3 and Pa_5 are linked with $33.8 \pm 3.4\%$ recombination, as estimated by Allard's method of maximum likelihood (1).

The two genes in the cultivar Bolivia were designated previously as Pa_2 and Pa_x (5). The Pa_x designation was given because the locus could not be distinguished from that of Pa_5 in Quinn, both Bolivia and Quinn having the Pa_2 gene in common. At that time, Pa_5 had not been found in any variety except Quinn. Since Cebada Capa was shown in this study to have a gene at the Pa_5 locus, an opportunity was presented for determining the relationship between Pa_x and Pa_5 . In the cross between Cebada Capa and Bolivia, an acceptable fit to a three-gene ratio was obtained, indicating that Pa_x and Pa_5 are different (Table 1). Therefore, Pa_x is redesignated Pa_6 .

Franger, when crossed with susceptible Moore, segregated on the basis of one gene pair for resistance (Table 2). Franger segregated in crosses with cultivars having Pa , Pa_2 , and Pa_3 , but did not segregate when crossed with those having Pa_4 . Franger was not crossed with cultivars having Pa_5 and Pa_6 . Genes at Pa , Pa_2 , and Pa_3 were independent of Pa_4 .

The cultivars bearing Pa_4 were Gold and Lechtaler, each with two-rowed spikes. When the six-rowed Franger was crossed with these, there was no problem in identifying crosses among them. Segregation of two-rowed and six-rowed plants was observed among the F_2 plants of Franger \times Gold, confirming that the 123 F_3 lines indicating allelism between the Franger gene and the Pa_4 locus of Gold are from a cross between these two varieties.

DISCUSSION.—The foregoing results indicate that Cebada Capa has a gene at or closely linked to the Pa_5 locus found previously in Quinn (5). Since Quinn has two genes for resistance, Pa_2 and Pa_5 , extremely large populations would have to be studied to distinguish allelism from close linkage. We are currently trying to establish lines from crosses of Quinn \times Moore

TABLE 1. Results from crosses of Cebada Capa with barley cultivars having various *Pa* genes conditioning reaction to *Puccinia hordei*

Cultivar crossed with Cebada Capa and gene designation	Generation studied	Observed ratio ^a	Expected ratio	P from chi square for expected ratio
Moore (Susceptible)	F ₂	177:62	3:1	> 0.7
	F ₃	132:239:96	1:2:1	> 0.05
Egypt 4 (Susceptible)	F ₂	263:90	3:1	> 0.9
Oderbrucker (<i>Pa</i>)	F ₂	394:36	15:1	> 0.05
Speciale (<i>Pa</i>)	F ₂	544:33	15:1	> 0.5
	F ₃	89:84:9	7:8:1	> 0.3
Sudan (<i>Pa</i>)	F ₂	269:13	15:1	> 0.2
	F ₃	52:58:11	7:8:1	> 0.3
Reka 1 (<i>Pa</i> ₂)	F ₂	431:26	15:1	> 0.5
	F ₃	63:60:9	7:8:1	> 0.5
Weider (<i>Pa</i> ₂)	F ₂	358:20	15:1	> 0.3
	F ₃	27:35:5	7:8:1	> 0.7
Estate (<i>Pa</i> ₃)	F ₂	813:24	15:1	< 0.01
	F ₃	242:183:15	7:8:1	< 0.01
Gold (<i>Pa</i> ₄)	F ₂	716:38	15:1	> 0.1
	F ₃	43:45:5	7:8:1	> 0.8
Lechtaler (<i>Pa</i> ₄)	F ₂	444:19	15:1	> 0.05
	F ₃	121:106:11	7:8:1	> 0.05
Quinn (<i>Pa</i> ₂ + <i>Pa</i> ₅)	F ₂	362:0	63:1	
	F ₃	405:0:0	37:26:1	
Bolivia (<i>Pa</i> ₂ + <i>Pa</i> _x)	F ₂	293:2	63:1	> 0.2
	F ₃	84:44:1	37:26:1	> 0.2

^a In F₂, the observed ratio is the number of plants with nontype 4:number with type 4 pustules. In F₃, the observed ratio is the number of lines homozygous for nontype 4 pustules:number segregating:number homozygous type 4.

that separate *Pa*₂ and *Pa*₅. These lines will be useful in further verifying allelism at the *Pa*₅ locus in Quinn and Cebada Capa.

In the cross between Cebada Capa and Estate, *Pa*₅ appeared to be linked with *Pa*₃. Although linkage be-

tween duplicate genes is difficult to estimate accurately, our data indicate linkage with $33.8 \pm 3.4\%$ recombination (1). Although linkage between *Pa*₃ and *Pa*₅ is suggested, neither gene has been identified with a linkage group.

TABLE 2. Results from crosses of Franger with barley cultivars having various *Pa* genes conditioning reaction to *Puccinia hordei*

Cultivar crossed with Franger and gene designation	Generation studied	Observed ratio ^a	Expected ratio	P from chi square for expected ratio
Moore (Susceptible)	F ₂	213:79	3:1	> 0.8
	F ₃	37:51:31	1:2:1	> 0.2
Speciale (<i>Pa</i>)	F ₂	251:18	15:1	> 0.7
	F ₃	50:50:8	7:8:1	> 0.7
Reka 1 (<i>Pa</i> ₂)	F ₂	248:15	15:1	> 0.7
	F ₃	18:29:7	7:8:1	> 0.05
Weider (<i>Pa</i> ₂)	F ₂	362:19	15:1	> 0.3
	F ₃	45:66:6	7:8:1	> 0.3
Estate (<i>Pa</i> ₃)	F ₂	245:16	15:1	> 0.8
	F ₃	22:19:2	7:8:1	> 0.5
Gold (<i>Pa</i> ₄)	F ₂	262:0		
	F ₃	123:0:0		
Lechtaler (<i>Pa</i> ₄)	F ₂	128:0		

^a In F₂, the observed ratio is the number of plants with nontype 4:number with type 4 pustules. In F₃, the observed ratio is the number of lines homozygous for nontype 4 pustules:number segregating:number homozygous type 4.

A consistent deficiency of susceptible plants was characteristic of most Cebada Capa crosses, even though the ratios obtained fitted acceptably those expected. This consistent deficiency suggests that Cebada Capa may have two closely linked genes conditioning resistance to account for this small deficiency of susceptible plants. However, the reaction types found among the F_2 and F_3 progenies do not clearly indicate segregation of more than one gene pair. Further study is needed to clarify the reason for this deficiency of susceptible segregates from crosses involving Cebada Capa.

The Franger gene was found to be at the Pa_4 locus of Gold and Lechtaler. Moseman & Greeley (2) earlier reported the similarity of reaction of Franger to that of these two cultivars, and suggested that all three may have the same gene-conditioning reaction to *P. hordei*.

Moseman & Reid (3) found the leaf rust resistance gene in Franger, now assumed to be Pa_4 , to be linked with the powdery mildew resistance gene MI_a . Since MI_a is on chromosome 5 (6), it follows that the Pa_4 genes in Gold and Lechtaler are also on chromosome 5. Pa_4 is the only one of six *Pa* loci (5) which has been associated with a specific chromosome.

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