A Major Gene for Powdery Mildew Resistance Transferred to Common Wheat from Wild Einkorn Wheat

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ABSTRACT

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A major gene for resistance to wheat powdery mildew (*Blumeria graminis* f. sp. *tritici* = *Erysiphe graminis* f. sp. *tritici*) has been successfully transferred into hexaploid common wheat (*Triticum aestivum*, 2*n* = 6*x* = 42, AABBDD) from wild einkorn wheat (*Triticum monococcum* subsp. *aegilopoides*, 2*n* = 2*x* = 14, AA). NC96BGTA5 is a germ plasm line with the pedigree Saluda × 3/PI427662. The response patterns for powdery mildew resistance in NC96BGTA5 were tested with 30 differential isolates of *B. graminis* f. sp. *tritici*, and the line was resistant to all tested isolates. The analyses of P_1, P_2, F_1, F_2, and BC_1F_1 populations derived from NC96BGTA5 revealed two genes for wheat powdery mildew resistance in the NC96BGTA5 line. One gene, *Pm3a*, was from its recurrent parent Saluda, and the second was a new gene introgressed from wild einkorn wheat. The gene was determined to be different from *Pm1* to *Pm21* by gene-for-gene and pedigree analyses. The new gene was identified as linked to the *Pm3a* gene based on the F_2 and BC_1F_1 populations derived from a cross between NC96BGTA5 and a susceptible cultivar NK-Coker 68-15, and the data indicated that the gene was located on chromosome 1A. It is proposed that this new gene be designated *Pm25* for wheat powdery mildew resistance in NC96BGTA5. Three random amplified polymorphic DNA markers, $OPX06_{1050}$, $OPAG04_{950}$, and $OPAI14_{600}$, were found to be linked to this new gene.

Twenty-seven major alleles have been reported at 21 loci for resistance to wheat powdery mildew (*Blumeria graminis* (DC.) E.O. Speer f. sp. *tritici* Em. Marchal = *Erysiphe graminis* DC. ex Merat f. sp. *tritici* Em. Marchal), and most of them were derived from the wild relatives of wheat (15). Because the presence and frequency of virulence genes continuously change in the *B. graminis* f. sp. *tritici* pathogen population, genes for resistance are frequently overcome by new isolates of *B. graminis* f. sp. *tritici* (7,12,14). Therefore, it will be useful to identify new resistance genes and to transfer these genes into common wheat if they are present in alien sources.

Molecular markers have been widely used to tag genes for disease resistance in plants (16). Among 21 major gene loci for powdery mildew resistance in wheat, restriction fragment length polymorphism (RFLP) markers linked to *Pm1*, *Pm2*, *Pm3*, *Pm4*, *Pm12*, *Pm13*, and *Pm18*, and random amplified polymorphic DNA (RAPD) markers linked to *Pm18* and *Pm21* have been reported (3,5,6,8,13,19).

Wild einkorn (*Triticum monococcum* L. subsp. *aegilopoides* (Link) Thell = *T. boeoticum*) (2*n* = 2*x* = 14, AA) should be a valuable source of genes for diversifying fungal disease resistance in wheat. Valkoun et al. (22) reported on reaction to leaf rust in four accessions of *T. monococcum* subsp. *aegilopoides*, and three of them were resistant. A gene, *Sr22*, for resistance to wheat stem rust has been successfully transferred into common wheat from *T. monococcum* subsp. *aegilopoides* (18). However, genes for wheat powdery mildew resistance have not been identified from this wild wheat relative. We recently released the common wheat germ plasm NC96BGTA5 with powdery mildew resistance transferred from the wild einkorn accession PI427662 (17). The objective of this research was to evaluate the inheritance of the resistance and to identify RAPD markers linked to the resistance gene. A preliminary report has been published (20).

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MATERIALS AND METHODS

Plant materials. NC96BGTA5 is a new common wheat germ plasm with the pedigree Saluda × 3/PI427662 (17). PI427662 is a wild einkorn accession collected in Iraq. Saluda (PI480474) is a soft red winter wheat cultivar released in Virginia (21) that contains the *Pm3a* gene for resistance to wheat powdery mildew (11). Twenty differential lines (listed in Table 1) with known genes (*Pm1* to *Pm21*, except *Pm10*, *Pm11*, *Pm14*, *Pm15*, and *Pm18*), the recurrent parent Saluda, and two susceptible cultivars, Chancellor and NK-Coker 68-15, were used to check response patterns in comparison with NC96BGTA5. Genes *Pm10*, *Pm11*, *Pm14*, and *Pm15* are not effective against *B. graminis* f. sp. *tritici* (15) and were not considered here; *Pm18* was unavailable.

Inheritance and allelism tests. F_1 hybrid seed was obtained from crosses between NC96BGTA5 and NK-Coker 68-15, NK-Coker 9803, and Saluda (Table 2), and F_2 and BC_1F_1 populations were developed during the 1994 to 1995 and 1995 to 1996 greenhouse seasons.

Powdery mildew evaluation. Powdery mildew evaluations were performed using a detached leaf technique (11). Assessment of reaction was based on a descriptive scale of reaction types (11), in which 0 to 3 = resistant, 4 to 6 = intermediate, and 7 to 9 = susceptible. Thirty differential isolates of *B. graminis* f. sp. *tritici* were used to test response patterns of resistance to powdery mildew in NC96BGTA5. A series of lines with known powdery mildew resistance genes were also included in each test. Five *B.*

graminis f. sp. *tritici* isolates, well characterized for virulence, were used to test the segregating populations.

DNA extraction and RAPD analysis. The genomic DNA was extracted from fresh leaves of wheat plants (4). Random 10-base primers (kits OP-A through OP-AN) were obtained from Operon Technologies Inc. (Alameda, CA). The polymerase chain reaction (PCR) procedure described by Williams et al. (23) was followed with minor modifications. Each reaction consisted of 2.4 µl of reaction buffer mix, 1.2 µl of dNTPs (2.5 mM), 5 µl of primer (4 or 5 ng/µl), 0.2 µl of *Taq* polymerase (5 Ug/µl), 1.2 µl of unacetylated bovine serum albumen, and 5.0 µl of genomic DNA (4 or 5 ng/µl). A total of 41 cycles of PCR amplification were performed using a standard RAPD program, in which each cycle consisted of denaturation at 92°C for 1 min, annealing at 35°C for 1 min, and extension at 72°C for 2 min. The reaction products were then visualized by electrophoresis on 1.2 to 1.5% agarose gels in 1× Tris-borate-EDTA.

Bulked segregant analysis. A total of 71 DNA samples extracted from the BC_1F_1 individuals derived from the cross of NK-Coker 9803 × 2/NC96BGTA5 population were pooled into two separate groups, labeled "R" and "S," for bulked segregant analysis. The R group consisted of 30 DNA samples from 30 BC_1F_1 individuals that were highly resistant to isolate 209a2 of *B. graminis* f. sp. *tritici*, and the S group was composed of 30 DNA samples from 30 BC_1F_1 individuals that were susceptible to isolate 209a2 of *B. graminis* f. sp. *tritici*. The other 11 DNA samples from the same BC_1F_1 population were not pooled into the R or S groups, because the plants were intermediate or variable for resistance to isolate W72-27. A total of 156 10-base random primers were used to screen for RAPD markers in Saluda, NC96BGTA5, the R and the S groups.

TABLE 3. Segregation of resistance to *Blumeria graminis* f. sp. *tritici* in three F_2 populations

Cross	Isolate	No. of individuals		Expected ratio	χ^2 value
		Resistant	Susceptible		
Saluda/NC96BGTA5	209a2	189	77	3:1	2.21
	W72-27	189	77	3:1	2.21
	#8	266	0	1:0	0.00
	E_325	266	0	1:0	0.00
NK-Coker 9803/NC96BGTA5	209a2	147	42	3:1	0.78
	W72-27	102	22	3:1	3.48
NK-Coker 68-15/NC96BGTA5	209a2	129	35	3:1	1.17
	W72-27	129	35	3:1	1.17
	#8	138	26	3:1	7.32**[a,b]
				15:1	25.80**
	E_325	138	26	3:1	7.32**
				15:1	25.82**

[a] ** is significant at $P = 0.01$.
[b] The frequency of recombination between *Pm3a* and *Pm25*, $r = 0.204$, in which r was calculated based on the formula $([1 - r]/2)^2 = 26/(138 + 26)$.

TABLE 1. Reactions of 25 wheat lines for powdery mildew resistance after inoculation with 10 isolates of *Blumeria graminis* f. sp. *tritici*

Line	Gene	Chromosome	Isolates of *B. graminis* f. sp. *tritici*									
			E_314	E_325	Wkin91	209a2	W72-27	127	144	85063	137a1	#8
NK-Coker 68-15	None		S[a]	S	S	S	S	S	S	S	S	S
Chancellor (Cc)	None		S	S	S	S	S	S	S	S	S	S
Axminster/8 × Cc	*Pm1*	7AL	R	S	S	R	S	R	R	S	R	S
Ulka/8 × Cc	*Pm2*	5DS	R	R	S	R	R, I	S	R	R	S	R
Asosan/8 × Cc	*Pm3a*	1AS	R	R	S	S	S	R	S, I	R	S	R
Chul/8 × Cc	*Pm3b*	1AS	R	R	R	R	R	S, I	S	R	I	R
Sonora/8 × Cc	*Pm3c*	1AS	R	S	S	R	I	S	S	R	S	S
Michigan Amber/8 × Cc	*Pm3f*	1AS	I	S	S	…	S	S	S	R	S	S
Khapli/8 × Cc	*Pm4a*	2AL	S	S	R	S	S	R	S	R	S	S
Ronos	*Pm4b*	2AL	S	S	R	R	R	R	R	R, I	R	S
Kormoran	*Pm5*	7BL	S	S	S	S	S	S	S	I	S	S
C747	*Pm6*	2BL	R	I	S	S	S	I	S	I	S	S, I
Transec	*Pm7*	4B/5R	S	S	S	S	S	S	S	S	S	S
Kavkaz	*Pm8*	1BL-1RS	S	S	R	R	R	R	R	S	R	S
Normandie	*Pm9 + 1 + 2*	7AL+5DS	R	R, I	I	R	R, I	S	R	R	R	R
Line #31	*Pm12*	6BS-6SS.6SL	R	R	R	R	R	R	R	R	R	R
Chinese Spring	*Pm13*	3B+3D	R	R, I	R	R	R	R	R	R	R	R, I
BRG 3N/76	*Pm16*	4A	R	R	S, I	R	R	R	R	R	R	R, I
Amigo	*Pm17*	1AL-1RS	S	I	R	R	I	R	R	S, I	I	S
D85350	*Pm19*	7D	R, I	I	S, I	I	S	I	S, I	R	S, I	S, I
TAM 104/Thatcher	*Pm20*	6BS-6RL	R	R	R	R, I	R, I	R	R	R	R, I	R
PM941181	*Pm21*	6AL-6VS	R	R	R	R	R	R	R	R	R	R
NK-Coker 9803	?	R	S	S	S	S	R	S	R	S	S	
Saluda	*Pm3a*	1AS	R	R	S	S	S	R	S, I	R	S	R
NC96BGTA5	*Pm25 + 3a*	1A	R	R	R, I	R, I	R	R, I	R	R	R	R

[a] R = resistant, I = intermediate, and S = susceptible.

TABLE 2. Reactions to five isolates of *Blumeria graminis* f. sp. *tritici* in four F_1 progenies and their parents

Line or F_1	n[a]	209a2 $\overline{X} \pm S_n$	W72-27 $\overline{X} \pm S_n$	#8 $\overline{X} \pm S_n$	E_325 $\overline{X} \pm S_n$	Wkin91 $\overline{X} \pm S_n$
NC96BGTA5	10	0.3[b] ± 0.46	0.6 ± 0.66	0.2 ± 0.40	0.8 ± 1.17	0.9 ± 1.22
NK-Coker 68-15	10	8.9 ± 0.30	8.9 ± 0.30	8.4 ± 0.80	8.6 ± 0.66	8.7 ± 0.64
NK-Coker 9803	10	8.5 ± 0.67	8.0 ± 0.89	8.6 ± 0.66	8.5 ± 0.67	8.8 ± 0.40
Saluda	10	8.4 ± 0.80	8.9 ± 0.30	0.6 ± 0.49	0.4 ± 0.66	9.0 ± 0.00
NK-Coker 68-15/NC96BGTA5	30	0.4 ± 0.80	0.8 ± 1.07	4.0 ± 0.93	3.7 ± 1.39	4.0 ± 0.85
NC96BGTA5/NK-Coker 68-15	13	0.4 ± 0.49	1.2 ± 1.31	2.5 ± 1.74	3.0 ± 1.52	3.8 ± 1.31
Saluda/NC96BGTA5	8	0.1 ± 0.33	1.4 ± 1.87	0.4 ± 0.48	0.0 ± 0.00	3.0 ± 1.32
NK-Coker 9803/NC96BGTA5	16	0.6 ± 0.93	0.7 ± 0.75	1.9 ± 1.78	1.8 ± 1.95	3.3 ± 1.30

[a] n = the number of samples, $\overline{X}$ = mean, and S_n = standard deviation.
[b] Scale of resistant type in which 0 to 3 = resistant, 4 to 6 = intermediate, and 7 to 9 = susceptible.

Linkage analysis. The 71 DNA samples extracted from the BC_1F_1 individuals derived from the cross of NK-Coker 9803 × 2/NC96BGTA5 population were also used to identify RAPD markers linked to the powdery mildew resistance gene in NC96BGTA5. Linkage of loci segregating in the BC_1F_1 was analyzed based on the maximum likelihood method (1). The genetic map was constructed by using MapMaker V2.0 for Macintosh (10). The recombination frequency was transformed into centimorgans (cM) according to the Kosambi function (9).

TABLE 4. Segregation of resistance to *Blumeria graminis* f. sp. *tritici* in four BC_1F_1 populations

Cross	Isolate	No. of individuals: Resistant	Susceptible	Expected ratio	χ^2 value
Saluda × 2/NC96BGTA5	209a2	35	31	1:1	0.24
	W72-27	35	31	1:1	0.24
	#8	66	0	1:0	0.00
	E_325	66	0	1:0	0.00
NK-Coker 9803 × 2/NC96BGTA5	209a2	39	36	1:1	0.12
	W72-27	44	31	1:1	2.25
NK-Coker 9803/NC96BGTA5 × 2	209a2	46	0	1:0	0.00
	W72-27	46	0	1:0	0.00
NK-Coker 68-15 × 2/NC96BGTA5	209a2	55	52	1:1	0.08
	W72-27	60	47	1:1	1.58
	#8	65	42	1:1	4.94*[a,b]
				3:1	11.59**
	E_325	65	42	1:1	4.94*
				3:1	11.59**

[a] * and ** are significant at $P = 0.05$ and 0.01, respectively.
[b] The frequency of recombination between *Pm3a* and *Pm25*, $r = 0.215$, in which r was calculated based on the formula $(1 - r)/2 = 42/(65 + 42)$.

RESULTS AND DISCUSSION

Reaction of resistance. The reactions of 25 wheat lines for powdery mildew resistance after inoculation with 10 isolates of *B. graminis* f. sp. *tritici* are listed in Table 1. NC96BGTA5 and the lines carrying *Pm12*, *Pm13*, *Pm20*, and *Pm2l* were resistant to all tested isolates. It is unlikely that the present gene in NC96BGTA5 is identical to any of these four genes *Pm12*, *Pm13*, *Pm20*, or *Pm2l*, because they were not derived from the A genome. The resistance in NC96BGTA5 is also unlikely to be controlled by *Pm18*, because this gene was identified in a common wheat cultivar, Weihenstephan M1N, and contained no A genome diploid parent in its pedigree.

Segregation and inheritance. All four F_1 progenies, NK-Coker 68-15/NC96BGTA5, NC96BGTA5/NK-Coker 68-15, Saluda/NC96BGTA5, and NK-Coker 9803/NC96BGTA5, were rated as resistant or moderately resistant to isolates 209a2, W72-27, #8, E_325, and Wkin91, which indicated either complete or partial dominance of resistance (Table 2).

The F_2 segregation ratios for resistance in three populations to *B. graminis* f. sp. *tritici* isolates 209a2 and W72-27 were in accordance with a 3R:1S ratio expected for segregation of a single dominant gene (Table 3). The BC_1F_1 segregation ratios conformed to a 1R:1S ratio to isolates 209a2 and W72-27 when the susceptible cultivars were used as recurrent parents (Table 4). The dominant action of the resistance gene was further observed where all

TABLE 5. Cosegregation of resistance gene *Pm25* and random amplified polymorphic DNA (RAPD) markers in the NK-Coker 9803 × 2/NC96BGTA5 BC_1F_1 population

Locus A	Locus B	Phenotype[a]: RM	Rm	SM	Sm	χ^2_A (1:1)	χ^2_B (1:1)	χ^2_{AB} (1:1:1:1)	Recombination (%)
Pm25	$OPAG04_{950}$	32	6	2	31	0.352	0.127	43.085**[b]	11.3 ± 3.76
Pm25	$OPX06_{1050}$	31	7	4	29	0.352	0.014	34.183**	15.5 ± 4.29
Pm25	$OPAI14_{600}$	28	10	4	29	0.352	0.690	27.084**	19.7 ± 4.72
		Genotype[c]: M_aM_b	M_am_b	m_aM_b	m_am_b				
$OPAG04_{950}$	$OPX06_{1050}$	33	1	2	35	0.127	0.014	59.648**	4.2 ± 2.38
$OPAG04_{950}$	$OPAI14_{600}$	30	4	2	35	0.127	0.690	49.845**	8.5 ± 3.31
$OPX06_{1050}$	$OPAI14_{600}$	32	3	0	36	0.014	0.690	60.211**	4.2 ± 2.38

[a] R = resistant, S = susceptible, M = the marker present, and m = the marker absent. Phenotype RM = resistant with the RAPD marker, Rm = resistant without the marker, SM = susceptible with the marker, and Sm = susceptible without the marker.
[b] ** is significant at $P = 0.01$.
[c] Genotype M_aM_b = the RAPD markers are present, M_am_b = the marker A is present but the marker B is absent, m_aM_b = the marker A is absent but the marker B is present, and m_am_b = the two markers are absent.

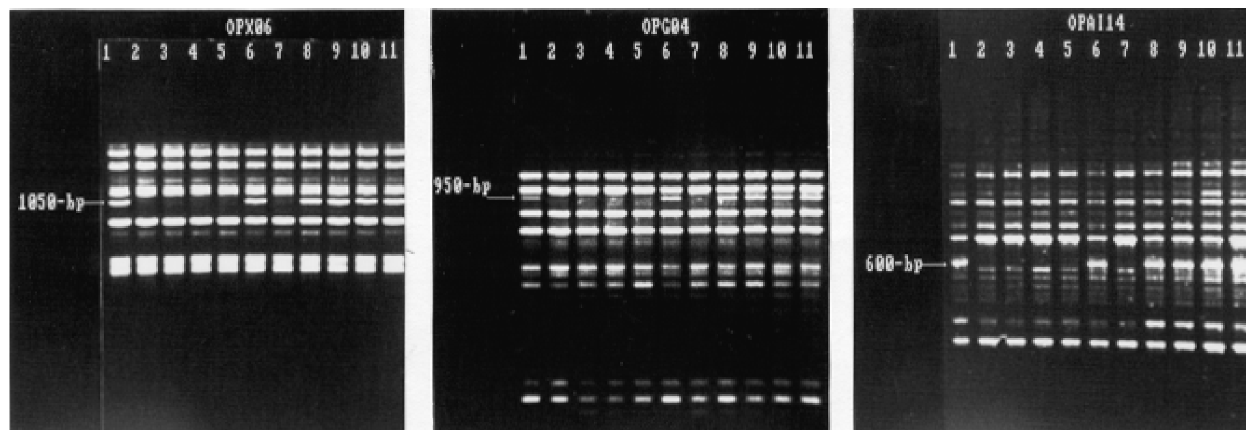

Fig. 1. Amplification pattern of DNA detecting $OPX06_{1050}$, $OPAG04_{950}$, and $OPAI14_{600}$ random amplified polymorphic DNA fragments in the NK-Coker 9803 × 2/NC96BGTA5 BC_1F_1 population. Lanes 1 to 5 are from susceptible plants and lanes 6 to 11 are from resistant plants, with lanes 1 and 7 indicating recombinants.

BC_1F_1 plants were resistant to isolates 209a2 and W72-27, when NC96BGTA5 was used as the recurrent parent (Table 4).

Allelism tests revealed the presence of *Pm3a* in NC96BGTA5. All individuals were resistant to isolates #8 and $E_3$25 in the Saluda/NC96BGTA5 F_2 population and the Saluda × 2/NC96BGTA5 population (Tables 3 and 4). These results indicated one common allele for resistance to powdery mildew in Saluda and NC96BGTA5. Because Saluda contained *Pm3a*, which confers resistance to isolates #8 and $E_3$25, NC96BGTA5 should also carry the resistance allele *Pm3a*. Therefore, resistance to powdery mildew in NC96BGTA5 is controlled by two dominant genes. One gene, *Pm3a*, was from its recurrent parent Saluda, and the second was a new gene from wild einkorn wheat. It is proposed that this new gene for wheat powdery mildew resistance in NC96BGTA5 be designated *Pm25*.

The resistance gene in NC96BGTA5 was found to be linked to *Pm3a*, based on the F_2 and BC_1F_1 populations derived from the crosses between NC96BGTA5 and a susceptible cultivar NK-Coker 68-15. The cosegregations of *Pm3a* and *Pm25* for resistance to #8 and $E_3$25 did not fit the 15R:1S or 3R:1S ratios expected for independent segregation of two dominant genes in F_2 and BC_1F_1 populations, respectively (Tables 3 and 4). The recombination frequency between the two genes was approximately 0.21, based on the pooled F_2 and BC_1F_1 data and calculated from the formula $([1 - r]/2)^2 + (1 - r)/2 = 42/(65 + 42) + 26/(138 + 26)$ (Tables 3 and 4). *Pm3a* is located on chromosome 1A (2), while *Pm18*, the only A genome differential we were unable to evaluate, is located on chromosome 7A (6).

Marker analysis. Three RAPD markers, $OPX06_{1050}$, $OPAG04_{950}$, and $OPAI14_{600}$, revealed clear polymorphisms (Fig. 1) and were found to be linked to gene *Pm25*. The frequencies of recombination between the gene *Pm25* and the three markers were 11.3 ± 3.76%, 15.5 ± 4.29%, and 19.7 ± 4.72%, respectively (Table 5); i.e., the linkage distance between them was 12.8 ± 3.96 cM, 17.2 ± 4.48 cM, and 21.6 ± 4.88 cM, respectively. The frequencies of recombination between the RAPD markers were 4.2 ± 2.38%, 8.5 ± 3.31%, and 4.2 ± 2.38%, respectively (Table 5); i.e., the linkage distance between them was 4.4 ± 2.43 cM, 12.8 ± 3.36 cM, and 4.4 ± 2.43 cM, respectively. A genetic map of the new gene *Pm25* region was constructed based on the data from the NK-Coker 9803 × 2/NC96BGTA5 BC_1F_1 population (Fig. 2). The three markers were not detected in 25 wheat lines that contained other *Pm* genes. They may be useful for distinguishing *Pm25* from other *Pm* genes and for genetic mapping of chromosome 1A. However, marker-assisted selection for *Pm25* by use of the three markers will be difficult because of the distance between the markers and *Pm25*.

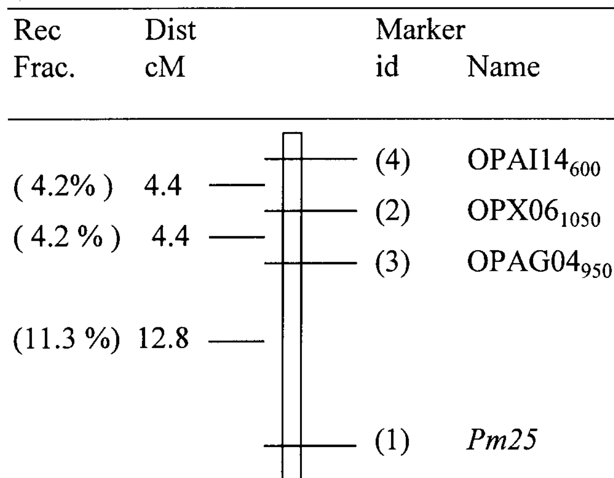

Fig. 2. A genetic map of the region carrying *Pm25* constructed from the NK-Coker 9803 × 2/ NC96BGTA5 BC_1F_1 population.

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