

# Genetic Basis of Resistance to Fall Armyworm (Lepidoptera: Noctuidae) and Southwestern Corn Borer (Lepidoptera: Crambidae) Leaf-Feeding Damage in Maize

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**ABSTRACT** Leaf-feeding damage by first generation larvae of fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), and southwestern corn borer, *Diatraea grandiosella* Dyar (Lepidoptera: Crambidae), cause major economic losses each year in maize, *Zea mays* L. A previous study identified quantitative trait loci (QTL) contributing to reduced leaf-feeding damage by these insects in the maize line Mp704. This study was initiated to identify QTL and their interactions associated with first generation leaf-feeding damage by fall armyworm and southwestern corn borer. QTL associated with fall armyworm and southwestern corn borer resistance in resistant line Mp708 were identified and compared with Mp704. Multiple trait analysis (MTA) of both data sets was then used to identify the most important genetic regions affecting resistance to fall armyworm and southwestern corn borer leaf-feeding damage. Genetic models containing four and seven QTL explained southwestern corn borer and fall armyworm resistance, respectively, in Mp708. Key genomic regions on chromosomes 1, 5, 7, and 9 were identified by MTA in Mp704 and Mp708 that confer resistance to both fall armyworm and southwestern corn borer. QTL regions on chromosomes 1, 5, 7, and 9 contained resistance to both insects and were present in both resistant lines. These regions correspond with previously identified QTL related to resistance to other lepidopteran insects, suggesting that broad-spectrum resistance to leaf feeding is primarily controlled by only a few genetic regions in this germplasm.

**KEY WORDS** fall armyworm, insect resistance, maize, QTL, southwestern corn borer

Resistant maize, *Zea mays* L., germplasm has been developed through selection for reduced leaf-feeding damage after infestation with neonate southwestern corn borer, *Diatraea grandiosella* Dyar (Lepidoptera: Crambidae), and fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) (Scott and Davis 1976, Williams and Davis 1982, Williams et al. 1990). Plant characteristics such as density of leaf hairs, density of cuticular wax layer, and juvenile-adult phase transition have been correlated with larval nonpreference and reduced weight gain, resulting in less foliar damage (Williams et al. 2000). Biochemical analysis also has implicated various molecules such as maysin in the silks, chlorogenic acid, cell wall/cellulose buildup, and unique proteins in reducing feeding damage by these pests (Snook et al. 1993). Laboratory feeding trials have demonstrated the effect of these

characteristics on larval feeding, preference, and weight gain (Davis et al. 1998). Evidence also suggests a relationship between genes for resistance to fall armyworm and southwestern corn borer and resistance to other insect pests of corn, such as European corn borer, *Ostrinia nubilalis* (Hübner), and corn earworm, *Helicoverpa zea* (Boddie) (Thome et al. 1992, Bohn et al. 2001, Cardinal et al. 2001).

During the process of applying selective pressure with fall armyworm and southwestern corn borer on breeding lines, Williams et al. (1989) observed that lines resistant to one insect tended to be resistant to the other, suggesting a broad-based resistance mechanism. General combining ability also was correlated between the two insects for several traits used to measure resistance levels, including leaf-feeding damage ratings.

The first germplasm line released by USDA-ARS at Mississippi State, MS, as a source of resistance to these insects was Mp496, which was released in 1981. Mp496 was derived by direct selection from Antigua Gp02, a population obtained from International Maize and Wheat Improvement Center (CIMMYT, El Batán, Mexico), while being exposed to southwestern corn borer feeding injury (Scott and Davis 1981). Many of the subsequent germplasm releases with resistance to

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southwestern corn borer and fall armyworm trace their ancestry back to the Antigua Gpo2 population, suggesting that genes conferring resistance may be similar among these lines. Both Mp704 and Mp708 have Mp496 in their backgrounds (Williams and Davis 1982, Williams et al. 1990).

Broad-based resistance is also in evidence with other leaf-feeding pests. Bushman et al. (2002) identified higher levels of chlorogenic acid in silks of resistant line Mp708 than in susceptible lines. Chlorogenic acid has been implicated in resistance to leafhopper *Dalbulus maidis* DeLong & Wolcott, cabbage looper, *Trichoplusia ni* (Hübner), and corn earworm (Dowd and Vega 1996, Duffey and Stout 1996, Beninger et al. 2004). Mp708 was developed under selection for fall armyworm and southwestern corn borer resistance, suggesting that chlorogenic acid may play a role in resistance to these insects as well. Bohn et al. (1997) and Groh et al. (1998) found that quantitative trait loci (QTL) conferring resistance to southwestern corn borer also imparted resistance to sugarcane borer, *Diatraea saccharalis* (F.). This further strengthens the importance and magnitude of impact of this resistance and justifies more in-depth study.

In a previous study, QTL associated with fall armyworm and southwestern corn borer leaf-feeding damage were identified in Mp704 (Brooks et al. 2005). Regions on chromosomes 6, 9, and 10 influenced resistance to both insects. Mp704 is a parent of Mp708, a line that has been assessed for QTL related to traits associated with corn earworm and sugarcane borer resistance. Bushman et al. (2002) identified candidate loci controlling chlorogenic acid production in a population derived from the lines A619 and Mp708. This same population was used in this study in an effort to identify key genetic causes of resistance to fall armyworm southwestern corn borer in lines released by the Corn Host Plant Resistance Research Unit in Mississippi State. The objectives of this study were to (a) estimate and characterize a genetic model for resistance to first generation fall armyworm and southwestern corn borer leaf feeding damage conferred from the resistant line Mp708, (b) compare the model to one for the parental line Mp704, (c) find genomic regions that confer resistance to both insects, and (d) suggest candidate genes associated with these regions.

### Materials and Methods

The A619 × Mp708 population was created at the University of Missouri Agronomy Research Center, Columbia, MO, and consisted of 427 F<sub>2</sub> individuals. Plants were grown at the University of Missouri Agronomy Research Center, Columbia, MO, in summer 1998 (Bushman et al. 2002). DNA was extracted from lyophilized leaf tissue and genotyped using simple sequence repeat (SSR) markers. A linkage map consisting of 91 SSR markers was generated that represented a total genetic distance of 1353 cM.

A subset of this population was self-pollinated to create 213 F<sub>2,3</sub> families that were evaluated in 2002 at Mississippi State, MS, for resistance to first generation

leaf-feeding damage by southwestern corn borer and fall armyworm. Evaluations consisted of two replications for each insect planted in tandem. Plots were grown in 5.1-m-long rows in a randomized complete block design. Thirty fall armyworm or southwestern corn borer larvae were placed on V7 stage plants (Richie et al. 1986). Neonate larvae mixed with corn cob grits were placed in the plant whorl with a mechanical dispenser, and plants were rated for leaf-feeding damage 14 d after infestation (Wiseman et al. 1980). Slightly different rating criteria were used to accommodate differences in damage patterns. Visual ratings for fall armyworm feeding damage ranged from 0, no damage, to 9, many leaves destroyed; and for southwestern corn borer, they ranged from 0, no visible leaf damage, to 9, long lesions on most leaves (Williams et al. 1989). Individual plant ratings were used to calculate plot means. An analysis of variance (ANOVA) was performed using the general linear model procedure in SAS (PROC GLM, SAS Institute 1990). Least-squares means of fall armyworm and southwestern corn borer damage ratings were computed for each family and generation (A619, Mp708, F<sub>1</sub>, and F<sub>2</sub>).

In a previous study, a Mp704 × Mo17 population consisting of 230 F<sub>2,3</sub> families were tested in the 2000 through 2002 growing seasons at Mississippi State, MS, for first generation leaf-feeding damage by southwestern corn borer and fall armyworm, as described by Brooks et al. (2005). Replicated trials were planted in three different years. Infestation techniques and rating criteria were identical to those described above for the A619 × Mp708 population. Both populations were evaluated in the same research fields under similar agricultural practices.

Marker groups and ordering were determined using Carthage mapping software (Schiex and Gaspin 1997). Minimum logarithm of the odds (LOD) scores of 3.0 and a maximum recombination fraction of 0.5 were the designated criteria for rendering linkage groups. Initial estimates for QTL were determined using composite interval mapping in QTL Cartographer 2.5 (Zeng 1993, 1994). QTL estimates were used as a basis for initiating multiple interval mapping (MIM) (Kao and Zeng 1997, Kao et al. 1999). MIM analysis proceeded along the following steps: 1) search for additional QTL to add to the model, 2) reestimate QTL positions, 3) test for interactions, 4) retest components of model for significance, and 5) return to step 1 and repeat steps 1–5 until no additional QTL/interactions can be added to the model. The optimal model includes estimates for QTL positions, genetic effects, LOD scores, proportion phenotypic variation explained, and interaction effects for each component. Models were considered superior if they had a lower Bayesian information content (BIC), explained a larger portion of the phenotypic variance, and did not overestimate explained phenotypic variance. Model development was intentionally conservative to reduce chance of false positives, thereby excluding an additional QTL candidate on chromosome 5. Table 1 lists genetic information for loci that were kept in the

**Table 1. Quantitative trait loci contributing resistance to leaf damage ratings by southwestern corn borer(SWCB) and fall armyworm(FAW) in the population A619 × Mp708**

QTL	Trait	Chromosome/ bin <sup>a</sup>	Marker/position <sup>b</sup>	LOD( <i>a/d</i> ) <sup>c</sup>	Effect( <i>a</i> ) <sup>d</sup>	Effect( <i>d</i> ) <sup>e</sup>	%Var <sup>f</sup>	Genetic variance
1	SWCB	3.08	phi046/146.5	0.5/0.9	0.95	2.20	2.6/7.6	
2	SWCB	5.04	umc1192/113.9	1.3/0.2	1.45	-0.88	6.4/1.4	
3	SWCB	6.05	umc1187/115.6	1.7/-	1.55	-0.25	6.1/0.0	
4	SWCB	9.05	umc1357/105.0	1.2/0.3	1.26	-1.07	4.9/2.5	
1 × 4	SWCB	D × D		0.7		4.15	7.6	0.39
1	FAW	1.03	umc1021/75.4	2.6/0.1	2.40	0.48	9.3/0.4	
2	FAW	2.02	bnlg1017/3.3	1.6/0.7	1.82	-1.61	3.7/0.9	
3	FAW	5.07	bnlg1346/155.1	1.7/0.3	2.15	1.26	6.1/0.2	
4	FAW	6.05	umc1187/104.7	1.1/1.0	1.67	-2.04	3.6/2.1	
5	FAW	7.03	bnlg339/87.0	2.6/0.1	2.27	-0.57	5.3/0.4	
6	FAW	9.03	phi065/51.7	2.0/-	2.29	0.36	7.8/0.1	
7	FAW	9.07	bnlg1588/110.5	2.3/-	2.32	-0.14	6.8/0.1	
4 × 7	FAW	A × A		0.8	1.87		1.5	0.48

<sup>a</sup> Chromosome number and bin location.

<sup>b</sup> SSR name of left most adjacent marker to QTL and its map position in centiMorgans.

<sup>c</sup> Log10-likelihood ratio.

<sup>d</sup> Additive effect associated with the locus.

<sup>e</sup> Dominance effect associated with the locus.

<sup>f</sup> Percentage of genotypic variance of trait associated with the QTL (additive/dominant).

model. Included are estimates of additive [Effect(*a*)] and dominant [Effect(*d*)] effects that describe the magnitude and type of inheritance for the locus. Estimates for the reduction in leaf feeding damage attributed to a locus and overall are described as percentage of variation explained (%Var). Multiple trait analysis (MTA) (Jiang and Zeng 1995) was performed on A619 × Mp708 and Mp704 × Mo17 data sets, based on the observed correlation of fall armyworm resistance and southwestern corn borer resistance. Chromosomal regions that repeatedly contained resistance-related QTL and linked candidate genes from the literature are discussed.

## Results

**A619 × Mp708 QTL Analysis.** *Southwestern Corn Borer.* Damage ratings for southwestern corn borer and fall armyworm were similar to those obtained in previous experiments (Williams et al. 1989). Mean southwestern corn borer damage ratings were significantly different between parental lines ( $P = 0.0087$ ) with Mp708 = 6.575 and A619 = 8.72. Mp708 sustained significantly lower levels of feeding damage for southwestern corn borer than A619 (Fig. 1).

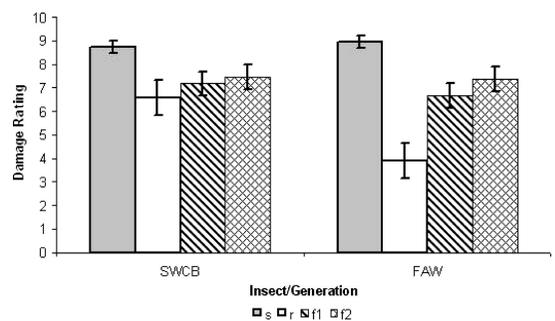
Multiple interval mapping produced a final model containing four QTL and one interaction that explained 39% of the total phenotypic variation for southwestern corn borer damage. QTL included both significant dominant and additive effects (Table 1). A dominant × dominant epistatic interaction between QTL on chromosome 3 and 9 accounted for nearly 8% of phenotypic variance. The other identified QTL were located on chromosomes 5 and 6 and were primarily additive in nature. In each case, the QTL imparting resistance was contributed by Mp708.

*Fall Armyworm.* Differences in damage between Mp708 and A619 were greater for fall armyworm than southwestern corn borer (Fig. 1). This likely resulted

in better genetic resolution for fall armyworm resistance. Fall armyworm damage ratings were significantly lower in the resistant parent ( $P = 0.0019$ ) with Mp708 = 3.9 and A619 = 8.95.

The genetic model best fitting the data for fall armyworm resistance contained seven QTL and one interaction that explained 48% of phenotypic variance (Table 1). QTL were primarily additive, and they ranged from 3.6 to 9.3% of explained variation. As with southwestern corn borer, Mp708 contributed the resistance allele that reduced feeding damage.

*Comparison with Mp704 × Mo17.* A619 × Mp708 exhibited a greater degree of variance than the Mp704 × Mo17 mapping study where high levels of feeding damage, especially fall armyworm feeding, tended to reduce the variance within the test (Brooks et al. 2005). Damage ratings of the F<sub>1</sub> and F<sub>2</sub> generations fell between the resistant and susceptible parents for both traits. The correlation of damage ratings for F<sub>2,3</sub> families between southwestern corn borer and fall armyworm was  $r = 0.4$  ( $P < 0.0001$ ), slightly higher than in the Mp704 × Mo17 study ( $r = 0.3$ ,  $P < 0.0001$ ).



**Fig. 1.** Mean leaf damage ratings and confidence intervals from each generation of the A619 × Mp708 mapping population. s, A619; r, Mp708; fl, A619 × Mp708 hybrid; and f<sub>2</sub>, mean of 230 F<sub>2,3</sub> families.

**Table 2. Summary of multiple trait analysis for fall armyworm and southwestern corn borer resistance QTL from two mapping studies**

Mp704 × Mo17			A619 × Mo708		
Marker <sup>a</sup>	Location <sup>b</sup>	LR <sup>c</sup>	Marker	Location	LR
umc1515	1.05	19.7	blg1953	1.02	25
umc1630	1.11	16.11	-	-	-
-	-	-	bnlg1017	2.02	13.8
bnlg105	5.02	21.7	bnlg1287	5.04	16.2
-	-	-	bnlg1346	5.07	16.2
-	-	-	umc1187	6.05	22.8
bnlg1094	7.02	27	bnlg155	7.03	15.8
umc1782	7.04	17.2	-	-	-
phi115	8.03	23	-	-	-
bnlg127	9.03	53	phi065	9.03	20
-	-	-	umc1357	9.05	27.5
umc1246	10.04	29	-	-	-

<sup>a</sup> Markers on the same row represent similar QTL locations in both populations.  
<sup>b</sup> Chromosome and bin location of marker.  
<sup>c</sup> Likelihood ratio test statistic.

Interactions between loci tended to be on a per environment basis, nor were any interactions consistent from one population to the other. In addition, only one interaction contributed significantly to resistance (7.6% variance explained) (Fig. 1). Chromosomes 5 and 10 had regions with multiple interactions, but their effects were only minor (<6% variance explained).

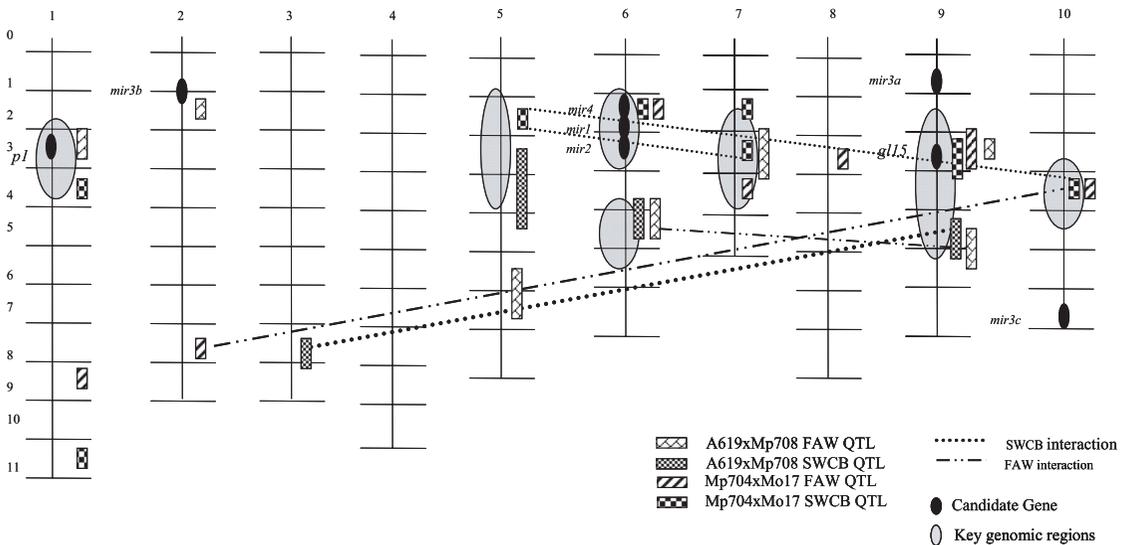
**Multiple Trait Analysis.** MTA was performed for southwestern corn borer and fall armyworm resistance in the A619 × Mp708 and Mp704 × Mo17 populations for comparison (Table 2). MTA produces a genetic picture of the relationship between traits that is useful for improving the detection power and precision in locating QTL (Jiang and Zeng 1995). QTL

affecting resistance to both traits were generally centered around similar regions identified by MIM. In the A619 × Mp708 study, regions with high LOD scores in MTA were similar to MIM loci (1.03, 6.5, 9.03, and 9.05). These regions encompass QTL for both traits and further substantiate dual resistance effects. When MTA of A619 × Mp708 is compared with MTA for Mp704 × Mo17, similarities are more apparent than when comparing individual MIM analysis. Significant QTL identified by MTA on chromosome 1, 5, 7, and 9 occur in both populations (Fig. 2). Unlike in the A619 × Mp708 MTA, chromosome 6 did not have a locus that significantly influenced resistance to both insects in Mp704 × Mo17.

**Discussion**

**Characteristics of Resistance.** In this study, between 40 and 50% of the variation in leaf-feeding damage by southwestern corn borer and fall armyworm was attributed to Mp708. Loci tended to be simply inherited in an additive or dominant manner with only one epistatic interaction having substantial impact on resistance expression. These results are similar to those found previously for Mp704 (Brooks et al. 2005).

Similarities in genetic loci for resistance are expected between Mp704 and Mp708, because Mp704 is a parent of Mp708 and likely the donor of most of its resistance genes (Williams and Davis 1982). Differences among QTL found between the two lines, such as the apparent shift of major loci on chromosomes 6 and 9 (Fig. 2), could be the result of environmental error, or background genetic effects of the different susceptible parents, in addition to unique resistance genes. Many of these differences may be a byproduct of limited resolution caused by environmental vari-



**Fig. 2.** Summary of QTL influencing feeding damage by in two QTL mapping studies. AMPFAW and AMPSWCB represent fall armyworm and southwestern corn borer QTL, respectively, in the A619 × Mp708 mapping study; MpMoFAW and MpMoSWCB represent fall armyworm and southwestern corn borer QTL, respectively, in the Mp704 × Mo17 study. Lines connecting QTL represent epistatic interactions.

ability and the confines of analysis and not actual differences in the genes involved (Kearsey and Farquhar 1998).

Loci exhibiting resistance to both insects were present in each population. Mp704, although being selected for southwestern corn borer resistance, also exhibited resistance to fall armyworm and demonstrated the broad-spectrum character of this resistance in early generations. Selection in the Mp708 line involved evaluating both southwestern corn borer and fall armyworm damage, which led to greater levels of resistance to each insect. Therefore, selecting for resistance to southwestern corn borer has proven to be adequate for improving resistance to both insects, although exposing plants to both insects should further enhance gains (Williams et al. 1989). Evaluating for damage to both insects is a means of improving selection efficiency by accounting for more of the genotype  $\times$  environment interactions. This resistance can potentially be extended further to include other related leaf-feeding insects, such as corn earworm, European corn borer, and sugarcane borer.

**Candidate Genes.** Several genes shown to play a role in resistance to leaf feeding in maize fall within the significance ranges of QTL identified in this study. Candidate genes, such as *glossy15*, and *p1*, and their related pathways have been well characterized and provide a starting point for further study. A QTL on chromosome 9, a region encompassing the *gl15* locus that conferred resistance to both insects in multiple environments and genetic backgrounds, was identified in this study. *Glossy15* regulates the transition of young plant leaves from juvenile to adult stages in maize (Moose and Sisco 2003). Early transition from juvenile to adult stage reduces survival and growth rates of fall armyworm and southwestern corn borer larvae (Williams et al. 1998). This QTL contributed 5–36% of measured resistance in a given environment to leaf-feeding damage of both insects in the two studies and was a key genomic region. Willcox et al. (2002) documented a significant effect on resistance to southwestern corn borer when this same region on chromosome nine was moved, via marker-assisted selection, into improved lines. This trait is heritable and has been successfully bred into lines Mp704 and Mp708 (Williams and Davis 2002).

Chalcone synthase and its antibiosis-related product chlorogenic acid have previously been shown to have higher expression in Mp708 than in alternative lines susceptible to corn earworm (Szalma et al. 2002). Although the study involved a different insect and a later plant stage (2 d postsilk emergence versus V7 stage of growth), QTL overlapping regions containing these genes significantly influenced resistance to fall armyworm and southwestern corn borer. Most notable was a QTL on chromosome 1 that contains the *p1* locus (Fig. 2). This QTL region was significant for one insect in each population, and it was significantly correlated in the multiple trait analysis (LR = 19 and 25) (Table 2). The *p1* locus also regulates the maysin pathway (Lee et al. 1998). Maysin is a flavone that affects corn earworm resistance. Evidence that chlo-

rogenic acid, chalcone synthase, and maysin confer resistance to late-stage ear feeding of corn earworm suggests that some or all of them also may contribute to resistance to leaf feeding by southwestern corn borer and fall armyworm (Wiseman et al. 1992). The *p1* locus also could regulate additional unknown pathways affecting resistance to leaf-feeding damage.

The *mir* gene family has previously been identified by proteomic analysis as being associated with resistance. This family consists of at least five homologs, three of which are clustered on chromosome 6 in a resistance-conferring region for both insects (Jiang et al. 1995). Characterized as cysteine proteinases, these genes were differentially expressed in leaf tissue exposed to insect feeding where greater expression was associated with higher levels of resistance. Mp708 was demonstrated to express cysteine proteinase more rapidly and at higher levels than susceptible lines when exposed to larval feeding (Pechan et al. 2000). This region contained resistance QTL to both insects in Mp708 (Fig. 2). Unlike in the Mp708 MTA, however, this region of chromosome six did not have a locus that significantly influenced resistance to both insects in Mp704.

The analogous nature of QTL associated with resistance to early generation leaf feeding damage by fall armyworm and southwestern corn borer in the two populations suggests that resistance is consistently inherited. Because each population consisted of different susceptible lines (Mo17 and A619), resistance seems to be uniformly expressed in multiple genetic backgrounds. Analysis also identified regions that affect both insect pests implying that resistance mechanisms are broad-spectrum in nature. Therefore, it is expected that selection efforts should be effective in transferring resistance with little concern for genetic background. Results should influence feeding damage to both southwestern corn borer and fall armyworm so that selection efforts necessary to maintain resistance may be simplified in a resistance breeding program.

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