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RESEARCH ARTICLE

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Comparative QTL mapping of resistance to sugarcane mosaic virus in maize based on bioinformatics

Abstract The development of genomics and bioinformatics offers new tools for comparative gene mapping. In this paper, an integrated QTL map for sugarcane mosaic virus (SCMV) resistance in maize was constructed by compiling a total of 81 QTL loci available, using the Genetic Map IBM2 2005 Neighbors as reference. These 81 QTL loci were scattered on 7 chromosomes of maize, and most of them were clustered on chromosomes 3 and 6. By using the method of meta-analysis, we identified one "consensus QTL" on chromosome 3 covering a genetic distance of 6.44 cM, and two on chromosome 6 covering genetic distances of 16 cM and 27.48 cM, respectively. Four positional candidate resistant genes were identified within the "consensus QTL" on chromosome 3 via the strategy of comparative genomics. These results suggest that application of a combination of meta-analysis within a species with sequence homology comparison in a related model plant is an efficient approach to identify the major QTL and its candidate gene(s) for the target traits. The results of this study provide useful information for identifying and cloning the major gene(s) conferring resistance to SCMV in maize.

Keywords maize, sugarcane mosaic virus, quantitative trait loci, comparative gene mapping

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1 Introduction

American and German scholars studied the genetics of resistance to maize dwarf mosaic disease (MDMD) originating from maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus (SCMV), respectively (Werham and Scheifele, 1968; Dollinger et al., 1970; Johnson, 1971; Naidu and Josephson, 1976; Mikel et al., 1984; Rosenkranz and Scott, 1984), and they mapped the resistant genes and analyzed the gene effects (McMullen and Louie, 1989; Simcox et al., 1995; Melchinger et al., 1998; Xia et al., 1999; Xu et al., 1999; Duβle et al., 2000; Duβle et al., 2003; Yuan et al., 2003). Gao et al. (2000) and Cheng et al. (2001) indicated that MDMD in major maize growing areas in China is caused by SCMV. Based on the identification of the resistant germplasm (Chen et al., 1996; Wang et al., 2003b), scholars in China started resistant genetics analysis and gene mapping (Cao et al., 1987; Wang et al., 2003a; Chen et al., 2005; Zhang et al., 2003b; Wu et al., 2002a, 2002b). A large number of QTLs have been detected in different populations and environments, however, the mapping results are far from similar due to the differences in molecular markers, populations, experimental design and statistical methods adopted.

Recently, bioinformatics and genomics were successfully utilized for the comparative analysis of genes/QTLs for important traits. Fulton et al. (1997) discovered collinear QTLs among tomato-cultivated species and two wild species. Li et al. (2005) found 15 drought-tolerant "general QTLs" by synthesizing a total of 181 QTLs related to the drought tolerance trait. However, relying only on synthesized QTL positional information may lead to deviations (Thomson et al., 2003). Meta-analysis can analyze and evaluate data from diverse sources in a single study (Rudner et al., 2002). Meta-analysis, which combines integrated QTL information, in this study, established the most likely number of 'real' QTLs underlying a pool of QTLs from independent experiments, which led to a two-fold increase in the precision in QTL position estimation. The length of the confidence interval of the consensus position could be reduced if it is compared with

the smallest confidence interval of the initial QTL (Goffinet and Gerber, 2000). Chardon et al. (2004) integrated 313 QTLs related to maize flowering time, and obtained 62 consensus QTLs by adopting meta-analysis. Comparative mapping of genes/QTLs for important traits can not only help to decrease the number of matching genes, but also facilitate the identification of relevant positional candidate genes. Evaluating resistant QTLs from different populations and environments and digging major resistant genes and related linked markers are the preconditions for carrying out maize MAS of SCMV resistance. In this study, the authors will construct the integrated map of maize SCMV-resistant genes by compiling available QTLs resistant to SCMV in maize, project them on the reference high density map IBM2 2005 Neighbors, and identify consensus QTLs and linked markers.

2 Methods

2.1 Compiling QTL information for SCMV resistance

By reviewing the website (http://www.maizegdb.org/) and publications, QTL information for SCMV resistance was compiled. The information included QTL name, chromosome position, adjacent marker, mapping population, etc.

2.2 Integrating QTL information for SCMV resistance

The position and confidence interval of each QTL are important parameters of information integration. Confidence intervals were estimated with the formula $C.I. = 530/(N \times R^2)$, where N is the size of the population and R^2 is the proportion of phenotypic variance explained. This expression is appropriate for both backcross and F_2 populations.

Using the high-density genetic linkage map IBM2 2005 Neighbors as reference map and comparing the initial map with the reference map, the comparative marker and the coordinate of the resistant QTL were identified. The adjacent marker to the resistant QTL can be directly used as comparative marker if it emerges in both two maps, and its location in the reference map should be recorded correctly. If the adjacent marker can not be found in the reference map, the comparative marker needs to be identified by comparing the two maps for the nearest marker to the resistant QTL. QTLs in the initial map were projected onto the reference map, using markers shared by both maps, by means of a homothetic function. Therefore, QTL mapping in different populations was integrated.

The calculation method of the homothetic function was described by Chardon et al. (2004). The QTL should not be adopted if its marker orders are different between the initial and reference maps.

2.3 Constructing integrated QTL map for SCMV resistance

Based on the compiled QTL information and selecting its marker and coordinate from the reference map, the referred chromosome regions were decided upon. Then, an integrated map was constructed by projecting all initial maps that contained resistant QTLs to the reference map with BioMercator2-1 software.

BioMercator2-1 is supported by Generation Challenge Program (GCP). It provides users with a tool for map display, QTL project and QTL meta-analysis. By using it, all the information from different genetic maps can be pooled into a unique map to determine the consensus QTL number and position estimate.

2.4 Analyzing consensus QTL for SCMV resistance

Meta-analysis was adopted for estimating the position and confidence interval of the consensus QTL in this study. The algorithm devised by Goffinet and Gerber (2000) can help to determine if N-QTL detected from independent experiments in the same region of a chromosome is consistent with the 1-, 2-, 3-, 4- or N-QTL models (the N-QTL models being those where there are as many 'real' QTLs as input QTLs). For each of these five models, the most likely QTL distribution was determined by means of the maximum likelihood method. Then an Akaike-type criteria value (AIC value) indicates the best model among the five, which is the model with the least AIC value. Meta-analytic computations are based on the position of the QTL and on the variance of this position. The formula is as follows:

$$\mathrm{var}(QTL) = \frac{1}{\sum \frac{1}{\delta_i^2}},$$

where δ_i^2 stands for the position variance of each QTL distributed on the chromosome; the 95% confidence interval of consensus QTL is: $C.I. = 3.92 \times \sqrt{\mathrm{var}(QTL)}$.

In this paper, BioMercator2-1 was used in the meta-analysis to estimate the consensus-resistant QTL, as well as its position and confidence interval chromosome, for each linkage group involving more than 5 mapped QTLs.

2.5 Identification of positional candidate genes for SCMV resistance

By selecting all the markers on the IBM2 2005 Neighbors within the consensus QTL and by downloading the related EST and gene or DNA sequences from the website MaizeGDB, identification of the high homology sequences with resistance-related genes of the Gramineae crop was done, based on the gene sequence homology comparison in the genome data base, with the help of the internet software

BLAST from NCBI and the Gramene website. Conditions for comparison were nucleotide sequence exceeding 150 bp and E-value less than $1.0e^{-6}$. Defining homologous sequence-coded amino acids and Open Reading Frames (ORF) was done by using gene finding software from www.softberry.com or DNAMAN, then protein functional analysis was carried out by searching the conserved domain of this amino acid sequence with the help of BLAST software from NCBI website. Finally, we determined if it can be used as a positional resistant candidate gene.

3 Results

3.1 QTL information compilation

Information was compiled on maize SCMV-resistant QTLs from published papers from 1998–2005. The information involved 8 mapping populations and a total of 81 QTL loci, which were scattered on chromosomes 1, 2, 3, 5, 6, 9 and 10. QTL loci 46 and 35 were found, respectively, from 4 exotic and domestic mapping populations.

Melchinger et al. (1998) reported the genetic basis of European maize inbreeding lines D21, D32 and FAP1360A with RFLP and SSR markers. These findings uncovered the *Scmvl* (chromosome 6) and *Scmv2* (on chromosome 3) resistance genes. Xu et al. (1999) precisely mapped the two genes with AFLP, RFLP, SSR markers and FAP1360A × F7 (BC5 population). Xia et al. (1999) constructed the linkage map, which involved a population of 219 F_2 derived from the cross between D32 × D145 and 94 markers, and analyzed QTLs based on two years' SCMV resistance assessment. Five QTLs were detected on chromosomes 1, 3, 5, 6 and 10, among them, the QTLs on chromosomes 3 and 6 displayed the major effect. Furthermore, Duβle et al. (2000; 2003) and Yuan et al. (2003) constructed a more precise linkage map in the two chromosome regions and identified resistant genes on chromosomes 3 and 6.

SCMV-resistant QTLs were detected on chromosomes 3, 6 and 10 by utilizing the Huang Zaosi and YE107 populations. Among them, the QTLs on chromosomes 3 and 6 displayed the major effect (Wang et al., 2003a). Zhang et al. (2003b) indicated the QTLs distributed on chromosomes 1, 3, 5, 6 and 10. SCMV-resistant QTLs were detected on chromosomes 2, 3, 5, 6 and 9 by using the X178 and B73 ($F_{2:3}$) populations (Chen et al., 2005). Wu et al. (2002a; 2002b) found the recessive resistant gene on chromosome 6 by utilizing Huang Zaosi and Mo17 populations, and two complementary dominant resistance genes on chromosomes 3 and 6 by using Siyi and Mo17.

3.2 QTL information integration

According to the compiled maize SCMV-resistant QTL information, we selected the segments on chromosomes 1, 2, 3, 5, 6, 9 and 10 of genetic map IBM2 2005 Neighbors to draw the IBM segment linkage map. Based on the integrated resistant QTLs detected from several independent tests made by using BioMercator2-1 software, the integrated map of maize SCMV resistant QTLs was constructed. During the integration of resistant QTLs, Wu et al. (2002a; 2002b) found the recessive resistant gene on chromosome 6 by utilizing the Huang Zaosi and Mo17 populations, but the marker order was different from that of the reference map as a lesser marker on the initial map; two complementary dominant resistance genes were found on chromosomes 3 and 6 by utilizing Siyi and Mo17, and resistant genes found by Melchinger et al. (1998) and Duβle et al. (2000) with no genetic map, were consequently adopted as directly comparative markers for resistant QTL integration. The other resistant QTLs were integrated with the project function of BioMercator2-1. It was found after information integration that the resistant QTL was detected on chromosome 6 in all mapping populations, and the resistant QTL was also detected on chromosome 3 in all the populations except for the $F_{2:3}$ population from Huang Zaosi and Mo17 (Wu et al., 2002b) (Fig. 1).

3.3 Consensus QTL analysis

We optimized the SCMV-resistant QTLs on chromosomes 3 and 6 based on the integration of resistant QTL through meta-analysis for an optimized model. Three consensus-resistant QTLs were found on chromosomes 3 and 6 (Fig. 1, Table 1). For one consensus QTL on chromosome 3, the map coordinate on IBM2 2005 Neighbors was 305.6 cM and the genetic distance was 6.44 cM. For the second consensus QTL on chromosome 6, the map coordinates were 56.18 and 110.84 cM, respectively. The genetic distances were 6.16 and 27.48 cM, respectively. These indicate that there are possibly two resistant genes on chromosome 6. The interval span of consensus QTL on 110.84 cM of chromosome 6 was comparatively large, and needed to be diminished with much mapping information.

3.4 Identification of positional candidate genes based on consensus resistant QTL

The number of genes and markers within the consensus-resistant QTL from the integrated map of chromosomes 3 and 6 are listed in Table 2. There are 7 sequenced genes, 4 SSR markers, 13 RRLP markers and 38 BAC clones within the map coordinates 302.38–308.82 cM of chromosome 3; 1 SSR marker, 10 RFLP markers, and 4 BAC clones within 53.10–59.26 cM of chromosome 6 (hereinafter the "6(1)"), and 24 genes, 19 SSR markers, 51 RFLP markers, 388 BAC clones within 97.15–124.53 cM of chromosome 6 (hereinafter the "6(2)"). We used marker number per Centimorgan (cM) to show their densities, and the SSR marker had a lower density, with a distance of more than

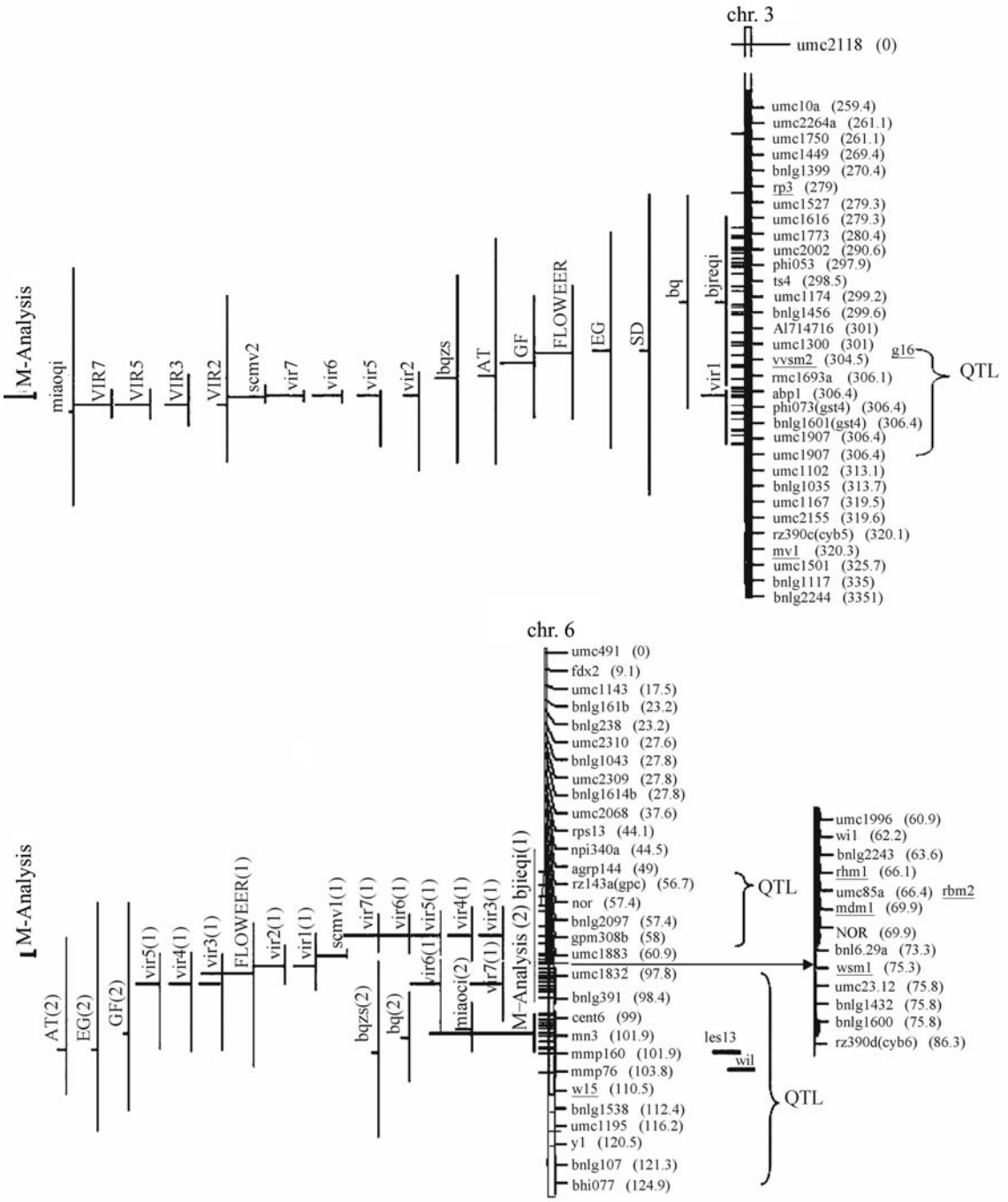

Fig. 1 The integrated QTL map for SCMV resistance on chromosomes 3 and 6

Note: The length of the vertical lines on the left of the map represents the confidence interval of each QTL, and the length of the horizontal lines represents the LOD score value. Markers and their coordinates are located on the right of the map.

Table 1 Three "consensus QTLs" for resistance to SCMV on the IBM2 2005 Neighbors map identified by meta-analysis

chromosome	*AIC* value	map position and adjacent marker/cM	*C.I.*/cM	map distance/cM	QTL number integrated	mapping population involved	left adjacent marker	right adjacent marker
3	162.62	305.60(umc1693a)	302.38–308.82	6.44	19	7	bnlg1456	umc1102
6	203.84	56.18(rz143a)	53.10–59.26	6.16	21	8	umc2068	umc1883
		110.84(gpm725)	97.15–124.53	27.48			umc2313	umc1517

Table 2 Marker numbers within the "consensus QTL" for SCMV resistance according to IBM2 2005 Neighbors

chromosome	map position	total marker	gene		SSR		RFLP marker		BAC clone	
			no.	gene/cM	no.	marker/cM	no.	marker/cM	no.	clone/cM
3	302.38–308.82	62	7	1.09	4	0.62	13	2.02	38	5.90
6	53.1–59.26	15	0	0.00	1	0.16	10	1.62	4	0.65
6	97.15–124.53	385	24	0.88	19	0.69	51	1.86	388	14.17

1 cM between markers; the RFLP marker had higher density, and a distance of around 0.5 cM between markers. Therefore, region mapping by using only SSR markers can not achieve fine gene mapping (< 1 cM). The RFLP marker possesses a relatively higher density, but is also limited within 0.5 cM and has low practical usage. The BAC clone is better in this aspect, but how to develop it into a practical PCR marker still needs to be solved in the future.

Our results showed that there were one resistant gene *wsm2* and two resistance-related genes *gl6*, *abp1* within the consensus-resistant QTL on chromosome 3, and 4 resistant genes *rhm1*, *rhm2*, *wsm1*, *mdm1* close to the map coordinates at 53.10–59.26 cM on chromosome 6, by comparing them with the maize IBM2 2005 Neighbors genetic map and trait linkage map (Fig. 1). In addition, we selected 62 markers within the consensus-resistant QTL on chromosome 3, and downloaded the related EST, gene or DNA sequences from the website MaizeGDB, identified their sequences based on gene sequence homology comparisons in the genome data base, and obtained 4 resistance-related sequences that are highly homologous with rice and maize (Table 3). Analysis showed that the sequences such as CG366993 and CC738247 contained ORF and code-resistant protein, and we concluded that they were the positional candidate genes of SCMV-resistant QTLs.

4 Discussion

4.1 Comparative mapping of maize SCMV-resistant gene/QTL

Up to now, a large amount of QTLs have been detected under different genetic backgrounds and environments, but the number of applicable effective markers in plant breeding is very limited. The main reason is that QTL mapping is liable to be affected by experimental conditions such as accuracy of phenotype evaluation, sampling error of progeny, marker density, size of population and QTL effect and so forth, which leads to the positional variance of QTLs mapped in different studies. Through the integration of several experimental results, carrying out meta-analysis of QTLs clustered in the identical segment of the same chromosome, and digging the consensus interval within the QTL confidence interval, the QTLs in this interval are very likely related with one certain gene locus.

Meta-analysis provides a new channel for comparing existent QTL information and digging for the consensus QTL. In this paper, an integrated QTL map for Sugarcane mosaic virus (SCMV) resistance in maize was constructed by compiling a total of 81 QTL loci from 8 mapping populations, with the high density genetic map IBM2 2005 Neighbors as reference. By using the method of meta- analysis, we identified one and two "consensus QTLs" on chromosomes 3 and 6, respectively. These three QTLs were found located on 305.6 cM (302.38–308.82 cM) of chromosome 3, and 56.18 cM (53.1–59.26 cM) and 0.84 cM (97.15–124.53 cM) of chromosome 6, and cover the genetic distances of 6.44 cM, 6.16 cM and 27.48 cM on the genetic map IBM2 2005 Neighbors, respectively. Based on the collinearity of the genetic materials among different species (Wang et al., 2005), further research needs to be conducted on gene sequence homology comparisons in the genomic data base between markers with primitive sequences within the consensus QTL and resistance-related genes, from which we can determine the positional resistant candidate gene.

Table 3 Homologous genes relevant to disease resistance identified within the "consensus QTL" for SCMV resistance on chromosome 3

IBM marker	originated EST/ DNA code	ORF	domain	homologous gene code	gene source	coding protein
Mmp80	CG366993	1 (107–592 bp)	NB-ARC	AP008218, AL713908, NM001073575, NM001074172	rice chr.12	family protein for disease resistance
IDP1433	BM339617	1 (236–541 bp)	unknown	CT830408, NM001073487	rice chr.12	seryl-tRNA synthetase
bnlg1601	CC738247	2 (453–575 bp, 645–812 bp)	unknown	AY574035	maize	gene conferring resistance to common rust
IDP401	AW574477	2 (416–823 bp, 891–1253 bp)	unknown	BT019283	maize	protein relevant to disease infection

Finally, adopting genetic analysis and genetic transformation techniques to validate the function of positional candidate gene and obtain resistant genes and markers can be done.

This method of comparative mapping can reduce the prophase investment of molecular breeding, and provide the foundation for identifying the main gene and linkage markers of complex quantitative traits and for further cloning QTG.

4.2 Exploring and using the resistant candidate gene

Reverse genetics provides new strategies for unknown gene locations and separations, as follows: First, in the searching and locating of the homologous gene according to existing resistant gene sequences of the same or different species; Second, in designing primers according to similarity of genetic structure, obtaining the resistant gene analog (RGA), and in identifying the resistant candidate gene; Third, according to resistant candidate gene-related EST, in obtaining total length transcription information of the objective gene through bioinformatics tools. The recent rapid increase in the EST database raises the possibility of searching new genes from EST.

Obtaining the consensus QTL based on comparative mapping of objective traits, then searching and locating homologous genes according to the EST and DNA sequences within the consensus QTL will be another effective method for identifying resistant candidate genes. In our study, four positional candidate resistant genes were identified within the consensus QTL on chromosome 3. These candidate genes pave the way for further exploration of the resistant genes and markers.

4.3 Clustering and evolution of resistant gene

The clustering distribution phenomenon of resistant genes was identified by comparing the maize genetic map and the trait linkage map. For instance, there are 1 resistant gene *wsm2* and 2 resistance-related genes *gl6*, *abp1* on the consensus resistant QTL of chromosome 3. Wang and Paigen (2002) discovered a positional overlap between QTL and the gene that controlled the HDL cholesterin level of murine. Wong et al. (2004) discovered that QTLs controlling carotenoid synthesis are overlapped with related genes *y1* and *vp9*; Zhang et al. (2003a) reported one QTL controlling the globulin level of maize capillament overlapped with candidate genes *p1* and *p2*. This kind of overlapping phenomenon may be taken from multieffect genes or gene linkages, and needs to be identified by cloning the resistant genes. Yet no matter what the real reason is, the linkage of different resistant genes is helpful for the breeding of multi-resistant crops. Further analysis of gene overlapping will be valuable for resistance breeding of crops.

What is more, we conducted the sequence homology comparison of the 62 marker primitive sequences within the consensus resistant QTL of chromosome 3, and discovered that the primitive sequences of 2 markers (Mmp80 and IDP1433) showed some resistant homologous sequences on rice chromosome 12. This indicates that resistant genes of maize and rice may share the same origin, and provides a clue for cloning the maize gene using rice genome sequence information.

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