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QTL analysis of fertility restoration in cytoplasmic male sterile pepper

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Abstract Fertility restoration of Peterson's cytoplasmic male-sterility in pepper (*Capsicum annuum* L.) is quantitative and environment-dependent. QTL analysis of fertility restoration was performed based on the test-cross progeny of 77013A (a strict cytoplasmic-genetic male sterile line) and a doubled haploid population of 114 lines obtained from an F_1 hybrid between Yolo wonder (a sterility maintainer line) and Perennial (a fertility-restorer line). The fertility of the test-crossed lines was assessed under greenhouse and open field conditions using three criteria related to pollen or seed production. One major QTL for fertility restoration was mapped to chromosome P6. It was significant in all the environments and for all the traits, accounting for 20–69% of the phenotypic variation, depending on the trait. Four additional minor QTLs were also detected on chromosomes P5, P2, and linkage groups PY3 and PY1, accounting for 7–17% of the phenotypic variation. Most of the alleles increasing fertility originated from the restorer parent, except for two alleles at minor QTLs. Phenotypic analysis and genetic dissection indicated that breeding pepper for complete sterility of female lines and high hybrid fertility requires complex combinations of alleles from both parents and a strict control of the environment.

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Introduction

Male-sterility in pepper was first documented by Martin and Grawford (1951) for nuclear genetic male-sterility, and Peterson (1958) for cytoplasmic male-sterility (CMS). Genetic male-sterility is monogenic and controlled by recessive *ms* alleles. Several spontaneous or induced *ms* mutants have been characterised (for review, see Shifriss 1997) and some are presently used for hybrid seed production. However this genetic sterility has not been widely used, due to the segregation of fertile plants resulting from the sib-maintenance of the female parent. CMS is maternally inherited and occurs in many plant species (Laser and Lersten 1972). CMS has been shown to result from defects in the mitochondrial genome that are suppressed by nuclear restorer genes named *Rf* genes (Schnable and Wise 1998). Because of its maternal inheritance, cytoplasmic sterility ensures 100% sterility in the female parent, and remains the best system for hybrid seed production if sterility is stable and restorer genes are available.

In pepper, CMS lines have been obtained from interspecific crosses but the search for restorer genes has remained unsuccessful (Shifriss 1997). Only the CMS source from Peterson (1958), originating from an Indian *Capsicum annuum* accession (USDA PI 164835), has been successfully restored. Dominant restorer alleles have been found in several hot and small-fruited pepper genotypes whereas many sweet and large-fruited genotypes have been shown to possess recessive maintainer alleles (Peterson 1958; Novak et al. 1971; Woong 1990; Zhang et al. 2000). Depending on the authors, fertility restoration was checked as a quantitative or a qualitative trait and was reported to be governed by dominant alleles at one or two nuclear (*Rf*) genes, or by a major dominant allele with modifier genes. Using bulked segregant analysis of the extreme plants from an F_2 progeny, Zhang et al. (2000) identified two RAPD markers tightly linked to a major restorer gene (*Rf*). However, the F_2 segregation was quantitative and the intermediate phenotypes (i.e. partially sterile) were not taken into account. Intermediate pheno-

types can either result from interactions with the environment or from quantitative genetic control. Peterson (1958) and Shifriss (1997) reported that CMS in pepper was unstable and temperature sensitive, with the sterile lines producing a few pollen grains when temperatures dropped below the optimal. In a doubled haploid (DH) segregation, Wang et al. (submitted) gave evidence for a quantitative segregation resulting from an oligogenic control. Breeders must select both maintainer and restorer lines for extreme phenotypes to guarantee a completely sterile female parent, but a fully fertile hybrid. Moreover, breeding is complicated by interactions between modifier genes and temperature. In order to assist selection, a more detailed genetic analysis of the suspected major and minor restorer genes must be performed using QTL analysis.

In this paper, we report the first map of the fertility-restorer loci for CMS in pepper. The CMS line was test-crossed to the 114 DH lines derived from the F_1 hybrid between a maintainer line (Yolo Wonder) and a restorer line (Perennial). The linkage map previously constructed in this DH progeny (Lefebvre et al. 2002) allowed to map one major and several minor QTLs governing fertility restoration, evaluated through pollen and seed production under different environmental conditions.

Materials and methods

Plant material and genetic map

The inbred line 77013A (77A) is a strict cytoplasmic male sterile pepper line developed in the Institute of Vegetables and Flowers (IVF, Beijing, China) from the male sterile accession of Peterson (1958). Perennial (Per), a fertility-restorer inbred line was obtained from J. Singh (Punjab University, Ludhiana, India). Yolo Wonder (YW) is a bell pepper inbred line from California maintaining sterility. The F_1-derived DH progeny consists of 114 DH lines that were developed with in vitro androgenesis (Dumas de Vaulx et al. 1981). Each DH line and the parental lines were crossed with the CMS line 77013A as the female parent to produced 116 F_1 hybrids (test-cross progeny) that were evaluated for their fertility phenotypes. A linkage map was obtained from the DH progeny including 630 molecular markers with a minimum LOD score of 5.0 and a maximum recombination fraction of 0.3. A set of 150 markers was selected for their uniform distribution over the genome, based on the integrated pepper map (Lefebvre et al. 2002). This core map included 50 RFLPs, 46 AFLPs, 27 RAPDs, 38 known genes and PCR-based markers, and two phenotypic markers distributed in 22 linkage groups spanning a total map length of 1,770 Haldane cM with an average inter-marker distance of 11.8 cM (±9.0). Alignment with the pepper integrated map assigned 17 of the 22 linkage groups to the 12 pepper chromosomes.

Experimentation and fertility assessment

The 116 test-cross hybrids and the 77013A line were planted and evaluated for their fertility at the IVF under greenhouse conditions in the spring of 2000, and in an open field in the spring of 2001. Twenty plants of each test-cross hybrid were planted in a single block design. Insecticide treatments were performed periodically in the greenhouse to prevent pollination by insects. Three methods were used to evaluate fertility. The pollen index (PIG for pollen index in the glasshouse, PIF for pollen index in the field) was assessed by visually scoring the pollen quantity using a 0–4 semi-quantitative scale in comparison with the fertile control (the YW inbred line). Two flowers per plant and ten plants per genotype (20 flowers) were independently scored at anthesis, with 0 representing no visible pollen in the anthers, 1; only a few pollen grains, 2; many pollen grains but <50% of the fertile control, 3; many pollen grains up to or above 50% of the fertile control, 4; anther full of pollen grains as for the fertile control. In the second method, the number of stained pollen grains (PNG for pollen number in the glasshouse and PNF for pollen number in the field) was evaluated by microscopy. Ten plants per genotype were individually sampled, with ten anthers from two flower buds (white bud stage) per plant. The ten anthers from each plant were transferred into a tube and stocked in a dessicator with silica gel. After 3 days, 100 µl of 0.1% acetocarmine in distilled water was added to every tube and the pollen number was counted using an haemacytometer. In the third method, two green-mature fruits per plant were harvested from ten plants, the seeds were extracted and numbered independently for every fruit (SNG for seed number per fruit in the glasshouse, SNF for the seed number per fruit in the field).

Data analysis

Phenotypic data were first submitted to a two-factor variance analysis according to the model $Y=\mu + g_I + b_j + (g_I{*}b_j) + e_{ij}$ with Y = phenotype of the test-cross hybrid, μ = mean of the progeny, g_I = genotype effect, b_j = cultivation method (glasshouse or open field), $g_I{*}b_j$ = interaction genotype × cultivation method and e_{ij} = error. Because of the significant effects of the cultivation method and of the interaction on the pollen index, pollen number and seed number, the data from the field and glasshouse studies were further analysed separately using the model $Y = \mu + g_I + e_I$. The heritability of the genotypic mean values for each trait was computed using the formula $h^2 = \sigma^2_g/(\sigma^2_g + n\sigma^2_e)$ were σ^2_g is the genotypic variance, σ^2_e the environmental variance (error effects) and n is the number of repeats.

The QTL detection was performed using linear regression (LR), simple interval mapping (IM) and composite interval mapping (CIM) with the QTL Cartographer software, version 1.15 (Basten et al. 1999) on the mean values of each genotype (traits PIG, PIF, PNG, PNF, SNG,

SNF). Significance threshold in LR was fixed to $P<10^{-3}$. For IM and CIM, significance thresholds were computed by 1,000 permutation tests. Depending on the fertility trait, empirical LOD score thresholds varied from 2.41 to 2.59 for IM and 2.56 to 2.74 for CIM (type I error = 0.1). A maximum of five markers, selected by a forward-backward stepwise regression analysis, were used as cofactors in the CIM procedure, with a window size of 10 cM and a walking speed of 2 cM. The magnitude of the marker-associated phenotypic effect is described by the coefficient of determination of the model (r^2). Digenic interactions between markers linked to the additive QTLs was tested using two-way ANOVA with an interaction component as described in Lefebvre and Palloix (1996). The percentage of phenotypic variation explained by all the QTLs for a given trait was obtained by multiple regression on the flanking markers of the QTLs.

Results

Inheritance of fertility restoration and relationships between traits

The parental and progeny values for the six quantitative traits analysed are presented in Table 1. The CMS line 77A displayed a completely male sterile phenotype, except for PNG with a few pollen grains being observed, particularly in the field-grown plants. The F_1 hybrid (77A × YW) was partially fertile, indicating that YW is not a stable maintainer of sterility. The test-cross progeny with the DH lines displayed a continuous segregation with a few test-cross hybrids displaying a higher sterility than the (77A × YW) hybrid (three completely sterile hybrids, data not shown). These transgressions were reciprocal with a few lines displaying a higher fertility than the (77A × Per) hybrid. Variance analysis showed that the effect of the genotypes and cultivation method was highly significant ($P<10^{-6}$) for all the traits. Comparing the two cultivation methods, both the PNF and SNF were significantly higher than the PNG and SNG, whatever the genotype. The heritability values are high (0.67–0.92) indicating that the phenotypic values are poorly affected by uncontrolled environmental effects, except for the PNG (0.38).

The Pearson correlation coefficients between traits ranged from 0.55 to 0.84 and all were highly significant ($P\leq10^{-6}$), indicating that the different traits did not segregate independently.

Mapping of fertility-restorer loci

Five genomic regions, distributed over three distinct chromosomes and two small linkage groups, displayed significant effects on fertility restoration (Table 2, Fig. 1). When several linked markers were significantly associated with fertility traits, the overall region was considered as a single QTL. The three models of QTL analyses (LR, IM and CIM) were convergent for three of the QTLs detected, which were located on chromosomes P5, P6 and in linkage group PY3, for which CIM results only are given in Table 2. Two QTLs, located on chromosome P2 and in linkage group PY1, were significant by LR and IM only, but were below the detection threshold with CIM ($2.1 < LOD < 2.5$), and the IM results only are given in Table 2.

One major QTL on chromosome P6 was highly significant for all six traits analysed, with r^2 values ranging from 20 to 69% depending on the traits. The maximum LOD scores of the different traits were grouped in an interval of 6 cM, and the overlap of confidence intervals of the different traits did not allow us to dissect this region into trait-specific QTLs. The QTL in PY3 was detected for PNF and SNF only, with lower r^2 values. The QTL on chromosome P5 was significant for PIG only, but it was considered as a putative QTL for both the PNF and SNF , with LOD values close to the CIM and IM thresholds (LOD values between 2.3 and 2.4) and P values close to the LR threshold ($P=10^{-2}$). The P2 QTL significantly affected the PNG and the SNF traits in both the IM and LR analyses. This same QTL was putative by CIM analysis of the SNF (LOD=2.41), and LR analysis of PIF, PIG and PNG ($10^{-3} < P < 10^{-2}$). The PY1 linkage group displayed a significant effect on PNF with a low r^2 value and a putative effect on PIG and SNG.

Most of the QTLs detected were significant and/or putative for both pollen and seed traits and for traits measured in the glasshouse as well as in the field, except for the PY3 QTL that was field-specific. Most of the alleles increasing fertility originated from the Perennial parent, except in P5 and PY1, where the YW alleles increased fertility for the significant QTLs (PIG and PNF

Table 1 Means and heritabilities of the fertility traits in the CMS parental line and the test-cross progeny. Trait code: pollen index in glasshouse (*PIG*) or in field (*PIF*), pollen number in glasshouse (*PNG*) or in field (*PNF*), seed number per fruit in glasshouse (*SNG*) or in field (*SNF*). h^2 is the heritability of the trait evaluation

Trait	77A	F1(77A × YW)	F1(77A × Per)	Mean progeny (standard deviation)	h^2
PIG	0.00	1.70	4.00	3.17 (1.07)	0.92
PIF	0.00	0.20	4.00	2.19 (1.12)	0.82
PNG	1.92	51.30	112.20	68.12 (51.81)	0.67
PNF	3.10	72.90	126.50	79.35 (42.49)	0.74
SNG	0.00	35.90	89.20	89.20 (53.23)	0.38
SNF	23.00	76.70	165.00	165.00 (94.73)	0.76

Table 2 QTLs for fertility restoration in the test-cross progeny. Trait code: pollen index in glasshouse (*PIG*) or in field (*PIF*), pollen number in glasshouse (*PNG*) or in field (*PNF*), seed number per fruit in glasshouse (*SNG*) or in field (*SNF*). Marker indicates the nearest upper flanking marker to the QTL. Markers with an asterisk (*) were putative with composite interval analysis but significant with IM and LR analyses, hence for those QTLs, IM data are given. Position is the position of the LOD max of the QTL from the upper part of the chromosome in centiMorgans. r^2 is the proportion of variance accounted for by the QTL

Trait	Chromosome	Marker	Position	LOD value	r^2	Restorer allele	Additive effect	Phenotypic variance explained by the QTLs (%)
PIG	P5	E41 M49-134y	113.5	2.722	0.103	YW	0.735	50.4
	P6	E39 M48-Dp	16.0	14.252	0.475	Per	−1.533	
PIF	P6	E40 M55-210p	20.9	23.6214	0.692	Per	−1.88	70.1
PNG	P6	E39 M48-Dp	16.0	10.658	0.337	Per	−60.40	49.8
	P2	E45 M58-HP*	97.2	2.572	0.123	Per	−35.55	
PNF	PY1	R19 0.75*	0.0	2.441	0.084	YW	24.36	47.1
	PY3	CT 114 A	2.0	3.917	0.163	Per	−36.06	
	P6	E40 M55-210p	18.9	6.965	0.269	Per	−44.79	
SNG	P6	E39 M48-Dp	14.0	4.924	0.202	Per	−25.94	33.2
SNF	P2	E45 M58-HP*	97.2	3.213	0.169	Per	−42.79	68.2
	PY3	CT 114 A	2.0	2.892	0.077	Per	−28.14	
	P6	E39 M48-Dp	14.0	23.795	0.660	Per	−81.30	

respectively) as well as the putative QTLs (PNF and SNF, PIG and SNF respectively). No significant digenic interactions were detected between the additive QTLs.

With multiple regression, the five additive QTLs accounted for 33–70% of the phenotypic variance (Table 2), and 55–90% of the heritability, depending on the traits. Seed traits were slightly better explained by the QTLs than pollen traits.

Discussion

To our knowledge, this study is the first report of QTLs for fertility restoration of CMS in pepper. One major QTL on chromosome P6 and four additional minor-effect QTLs were mapped in the pepper genome. The fertility-restorer QTLs were directly mapped in the first crossing generation, thanks to the test-cross of DH lines segregating for sterility maintenance/restoration. Because the fertile phenotype was evaluated in F_1 hybrids, we were able to detect only dominant and additive restorer alleles. The literature

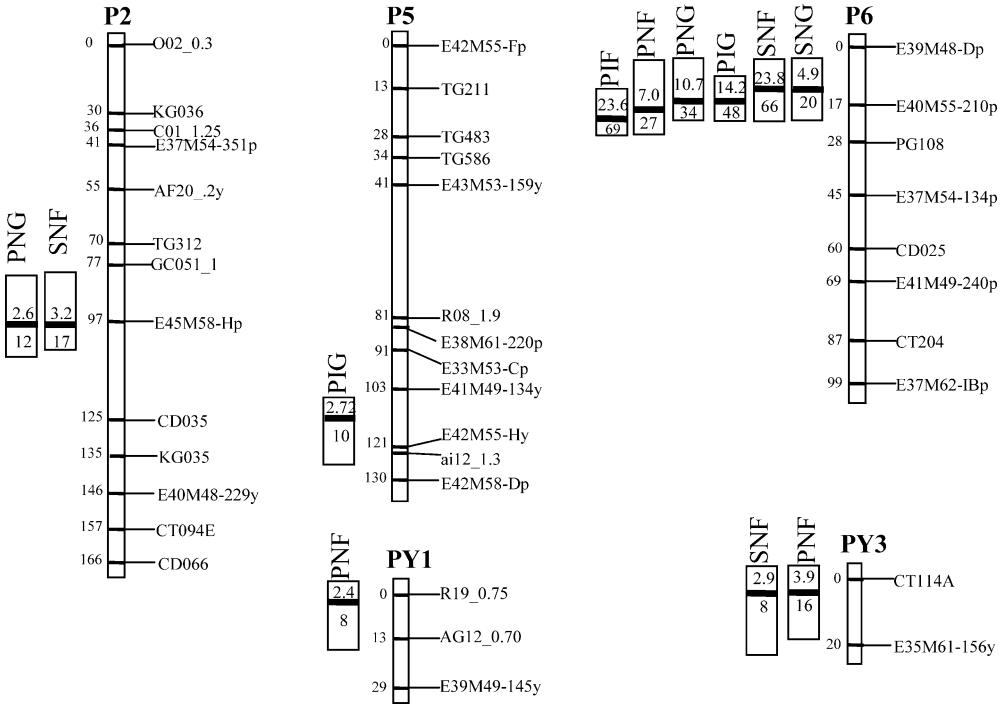

Fig. 1 Map location of the QTLs for fertility restoration components: pollen index in glasshouse (*PIG*) or in field (*PIF*); pollen number under glasshouse conditions (*PNG*) or in field trials (*PNF*); seed number per fruit in the glasshouse (*PNG*) or in the field (*PNF*). Only linkage groups containing QTLs associated with the traits are shown. Marker names refer to Lefebvre et al. (2002). Distances (in centiMorgans) are to the *left* of each linkage group. QTLs are presented as *large vertical bars* to the *left* of the linkage group with the *upper number* in each bar being the LOD value and the *lower value* being the r^2 value from Table 2. The *dark horizontal bar* in the QTL indicates the position of the LOD peak (Table 2) and the length of the QTL indicates the LOD-1 support interval (obtained in IM) from the LOD peak

consistently supports the hypothesis that most, if not all, the genes restoring cytoplasmic sterility display a dominant expression (Schnable and Wise 1998).

The distinct components of fertility were evaluated in the progeny in order to compare the genetic control of pollen and seed production under field and glasshouse growth conditions. The significance of the correlation coefficients between the fertility components were confirmed by the QTL analysis: the major QTL on chromosome P6 was significant for all six traits, while the minor QTLs were either significant or putative for pollen as well as seed quantities. No component-specific QTLs were clearly detected. In the field trial, a higher number of pollen grains and seeds were detected compared to those seen in plants grown in the glasshouse. We hypothesise that seed production was increased by the presence of insect pollinators in the field, however, the pollen number was also higher in the field-grown plants. The minor PY3 QTL appeared to be field-specific for pollen as well as seed number and this field effect more probably results from temperature differences. Pepper sterility has been shown to be unstable at low temperatures (Peterson 1958) and meiotic breakdown, causing microspore abortion, is affected at temperatures below 24°C (Shifriss 1997). This temperature threshold was frequently reached in the field but not in the glasshouse. This indicated that part of the variation in the expression of pepper CMS is caused by a minor QTL interacting with the environment.

The major QTL on chromosome P6 explains the major part of this variation. This QTL probably corresponds to the major restorer gene reported by several authors after phenotypic evaluation (Peterson 1958; Novak et al. 1971; Woong 1990) and has been flanked by RAPD markers by using bulked segregant analysis (Zhang et al. 2000). We did not succeed in mapping these markers that were not polymorphic in the DH progeny. Quantitative restoration of CMS has been subjected to QTL analysis in only a few crops including coffee (Coulibaly et al. 2003), sugar beet (Hjerdin-Panagopoulos et al. 2002), wheat (Ahmed et al. 2001), winter rye (Miedaner et al. 2000) and also resulted in the detection of one major QTL determining more than 50% of the phenotypic variation and a few minor QTLs. In sugar beet, the major QTL was further dissected into two tightly linked QTLs. The LOD peaks are very close on pepper chromosome P6 and the confidence intervals overlap. Further fine mapping will require a larger progeny and a high density map of chromosome P6. New markers may also be obtained by using a candidate gene strategy: the recent cloning of fertility-restorer genes in *Petunia* (Bentolila et al. 1999), which also belongs to the Solanaceae family, and in *Brassica* (Desloire et al. 2003) has demonstrated the functional role of the pentatricopeptide-repeat gene family. Mapping the sequences of this gene family and looking for co-segregation with the major QTL is necessary to address this hypothesis for pepper.

Four additional QTLs with low effects were also detected. The QTL on chromosome P2 overlapped with the *C* gene (governing pepper pungency) that has been mapped between the markers CD035 and TG312 by Ben Chaim et al. (2001). This linkage confirms previous observations that pungent lines are generally more efficient in fertility restoration (Novak et al. 1971; Woong 1990; Zhang et al. 2000). With regard to the four minor QTLs, the alleles increasing fertility originated either from the restorer parent Perennial in P2 and PY3, or from the maintainer parent YW in P5 and PY1. This explains why the test-cross between 77013A and YW was not completely sterile and why transgressions for sterility and fertility occurred in the DH progeny. In sugar beet one minor fertility-restorer allele has also been detected in the maintainer parent, and displays an epistatic effect with the major QTL. In pepper, complete sterility and high fertility depends on minor QTLs which may differ in distinct maintainer and restorer lines, and whose expression is environment-dependent.

Because of these minor QTLs, breeding pepper for CMS remains a challenge: complete sterility is required to avoid inbred seeds in commercial hybrids and a high fertility is required for fruit production of F_1 hybrids. In conclusion, our results will permit testing for the favourable allele at the major QTL as soon as the plantlet stage, which is an advantage for a late-expressed characteristic (flowering stage). However, screening for extreme sterile versus fertile genotypes will depend on control of the environment and on further selection for a complex combination of alleles from both parents.

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