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QTL mapping for the cooking time of common beans

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Abstract The decrease in the per capita consumption of beans has been partially attributed to their lengthy cooking time and the aggregated capital costs of their preparation. The aim of this study was to map microsatellite (SSR) markers linked to quantitative trait loci (QTLs) that govern the cooking time of common beans. An F_2 generation consisting of 140 families was generated from a cross between lines CNFM7875 and Laranja. The cooking time of the $F_{2:4}$ and $F_{2:5}$ generations was then evaluated, and the latter generation was tested in two environments. The analysis of variance found a significant effect for the interactions between the families ($P < 0.01$) in both the $F_{2:4}$ and $F_{2:5}$ generations, as well as for the group analyses performed in the two environments. The experimental coefficient of variation varied from 9.42 to 17.94%. The Pearson's correlation test indicated no significant association between water absorption and cooking time. The heritability coefficients had values of 0.532 and 0.739 for the $F_{2:5}$ families evaluated at the two different locations, and the group analysis of the $F_{2:5}$ generation indicated that there was a significant genotype × environment interaction. Of the 105 polymorphic SSRs evaluated, 91 mapped to 12 linkage groups with an estimated map size of 1,303.7 cM. Six significant QTLs were detected in both environments, and the percentage of the phenotypic variation that was explained by these loci ranged from 11.54 to 21.63%. As the genetic control was oligogenic, the identification of QTLs should serve as an optimal starting point for the implementation of a selection program.

Keywords *Phaseolus vulgaris* · Grain quality · Linkage map · QTL · SSR markers

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Introduction

The development of common bean cultivars through genetic improvement programs has contributed to increases in crop production. The focus of such programs has been the development of new common bean cultivars with greater production potential, increased tolerance to biotic and abiotic stress, and favorable agronomic attributes (Miklas et al. 2006;

Ramalho and Abreu 2006). In terms of consumer preference, the most desirable traits are those related to the technical and nutritional qualities of the bean, such as the ease of cooking, a good taste, a soft tegument texture, the ability to produce a thick sauce after cooking, and a high protein and mineral content (Santos and Gavilanes 2006). According to data from the Brazilian Institute of Geography and Statistics (BIGE), the average consumption of beans has decreased 27% in the last 5 years, from 12.4 to 9.1 kg. These data do not directly reflect a decrease in per capita consumption because the Brazilian population beans constitute an important part of the diet and are consumed daily with meals [Brazilian Bean Institute (BBI)]. However, cooking time is certainly considered to be one of the factors that limit the consumption of beans at home, and a reduction in cooking time could significantly increase the consumer's interest in the common bean as a food product and have direct and favorable consequences on both production and the commercial market. Furthermore, prolonged cooking times may lead to structural changes at the cellular level and nutrient loss (Ribeiro et al. 2007), as well as an increased capital cost for the process (Mesquita et al. 2007).

Cooking time is believed to be an oligogenic trait (Jacinto-Hernandez et al. 2003) and is influenced by a number of factors, such as planting time, cultivation practices, high temperature, high or low humidity during bean growth, harvest time, post-harvest handling, storage conditions, and processing technology (Rodrigues et al. 2005; Bertoldo et al. 2008; Coelho et al. 2008). Studies have shown a high genetic variability in cooking time and also that beans generally lose their commercial value rapidly after harvest due to decreased re-hydration capacity, increased cooking time, and tegument darkening (Bressani 1993). Therefore, the genotypic and environmental interactions that determine the culinary traits of beans (Carbonell et al. 2003) are important components of the inheritance of cooking time. Quantitative trait loci (QTLs) analysis may lead to the identification of a number of loci that are linked to this trait, and this type of analysis could also determine the specific favorable alleles for each bean cultivation environment.

In the last 10 years, a growing number of microsatellite markers have become available for the common bean (Yu et al. 2000; Blair et al. 2003; Grisi et al. 2007; Garcia et al. 2011), which has facilitated the construction of molecular maps with high genomic saturation. Repetitive sequence mining techniques and expressed sequence tag (EST) databases have been successfully used for bean species (Hanai et al. 2007; Blair et al. 2009a; Garcia et al. 2011). A new linkage map for the common bean that integrated single nucleotide polymorphism (SNP) marker information was recently described by Galeano et al. (2009); this was followed by the development of transcription maps (Hanai et al. 2010; Garcia et al. 2011). QTL detection studies for bean quality have been frequently reported in the literature for many legumes (Panthee et al. 2005; Burstin et al. 2007). Pérez-Vega et al. (2010) identified a group of QTLs distributed throughout the bean genome that were associated with phenological traits and bean size and quality in different environments, while Blair et al. (2010) identified QTLs that were associated with the nutrient levels in the seeds. However, studies to identify QTLs that are linked to common bean seed qualities, such as cooking time, are rare or nonexistent. In addition, QTL data are difficult to validate, which results in the pressing need for larger and more consistent studies in different population structures and in diverse environments and genetic backgrounds.

The aim of this study was to map microsatellites that are linked to QTLs for cooking time in a population of the common bean.

Materials and methods

Experimental population

A segregating population derived from a cross between the parental CNFM 7875 and Laranja strains was used for the mapping. CNFM 7875 is an elite line from the Embrapa rice and bean improvement program and was derived from crossing A 252/BAT 258/IPA 7419/EMP 97. It is a commercial type of mottled bean that is resistant to common diseases, is highly productive, and has a reduced cooking time. The Laranja cultivar was developed by the Pato Branco CEFET improvement program and was derived by crossing IAPAR 14/IAPAR 31. This parent strain is representative of the Carioca commercial group, producing beans with a yellow shell and a long cooking time. It has the favorable traits of tolerance to bacterial blight, rust, anthracnose, and common mosaic virus and has a

moderate susceptibility to angular leaf spot. The F_2 generation from the study population was expanded individually in a greenhouse to create 140 $F_{2:3}$ families. These were then planted in one-row parcels that were 3 m wide. The tests were carried out in 2004 during the dry season at the Federal University of Lavras (914 m a.s.l.; 21°14′30″S, 45°00′10″W), which is located in the southern region of the state of Minas Gerais (MG). The plants from each $F_{2:3}$ family were collected in bulk to produce generations $F_{2:4}$ and $F_{2:5}$.

Phenotypic characterization

The 140 families from generation $F_{2:4}$ as well as the parental lines and two outgroups (cvs. BRS Requinte and BRS Pontal) were evaluated in 2005 during the winter season (June to September) using a randomized block design with two replicates at Embrapa Rice and Beans (823 m a.s.l.; 16°28′00″S, 49°7′00″W), which is located in the municipality of Santo Antônio de Goiás [State of Goiás (GO)]. Generation $F_{2:5}$ was evaluated in 2006 during the dry season (February to May) at the experimental plot in Ponta Grossa [State of Paraná (PR); 975 m a.s.l.; 25°05′42″S, 50°09′43″W], and this generation was evaluated during the winter (June to September) at Embrapa Rice and Beans. These two experiments were conducted using a 12 × 12 triple lattice experimental design with three replicates and two-row parcels that were 4 m wide. These experiments also included the CNFM 7875 and Laranja genitors and the BRS Requinte and BRS Pontal outgroups. Two replicates that contained samples of 25 common bean grains were used for the cooking time analysis for each experimental plot of the $F_{2:4}$ (Santo Antônio de Goiás) and $F_{2:5}$ generations (Ponta Grossa and Santo Antônio de Goiás). Prior to cooking, grain samples were soaked in distilled water for 18 h at 25°C, and the water absorption ratio of grains from generation $F_{2:5}$ was estimated by the proportional difference in the mass of the beans before and after water soaking, which occasionally doubled bean mass (shown as a percentage). After absorption, each sample (25 hydrated bean grains) was placed in a 25-plunger Mattson cooker (Proctor and Watts 1987). This cooker utilized 25 stainless steel, cylindrical, piercing tip rods in contact with the surface of the bean. The cooker was then placed into a 2 l-beaker containing 1,000 ml of boiling distilled water on a hot plate. Bean grains were judged as "cooked" when the 2-mm-diameter tip of the brass rods passed through the beans. The determination of cooking time (measured in minutes with a chronometer) began when the water reached 100°C and ended when the 13th rod fell (50% plus one). The cooking time was therefore reported as the time required for 52% of the grains to be cooked, as indicated by plungers dropping and penetrating individual beans. An analysis of variance (ANOVA) was performed using the Genes ver. 7.0 software program (Cruz 2006). The genetic and phenotypic variances and the genetic parameters, including overall heritability, the coefficient of genetic variation, and the ratio between the coefficient of genetic variation and the coefficient of experimental variation (CVg/CVe), were estimated from the expected means squared value (Vencovsky and Barriga 1992). For the $F_{2:5}$ generation, an analysis of group variance was performed for the two experimental testing locations (Ponta Grossa and Santo Antônio de Goiás). The Pearson correlation between cooking time and water absorption was calculated.

Microsatellite loci screening

A group of 944 microsatellite (SSR) loci, including 459 (53.10%) that were derived from ESTs and 485 (46.90%) that were derived from genomic sequences (Yu et al. 2000; Blair et al. 2003, 2009a, 2009b; Buso et al. 2006; Grisi et al. 2007; Garcia et al. 2011), were evaluated for the quality of the amplified product and the polymorphism between the genitors of the segregant populations. The amplification reactions were performed in a total volume of 15 µl consisting of 0.3 µM of each primer, one unit of *Taq* DNA polymerase, 0.25 mM of each dNTP, 10 µM Tris–HCl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$, 1.3 µl of DMSO (50%), and 15 ng of the template DNA. The reactions were amplified using an initial cycle of 94°C for 1 min that was followed by 30 cycles of 94°C for 1 min, primer-specific annealing temperature for 1 min, 72°C for 1 min, and a final extension at 72°C for 7 min. The amplified products were visualized in a high-resolution 6% polyacrylamide denaturing gel and were stained with silver nitrate using the protocol described by Creste et al. (2001).

Genetic map construction and QTL analysis

The genetic map was constructed based on the segregation data obtained from the 140 individuals of the F_2 population using the MapDisto program version 1.7b (http://mapdisto.free.fr/). The chi-squared test (χ^2) was performed for each marker to estimate the deviation from the expected Mendelian segregation value (1:2:1; $P < 0.05$), and this was followed by the administration of the false discovery rate (FDR) test on the distribution of the observed P values to correct for multiple comparisons by controlling for false positives (Benjamin and Hocheberg 1995). The stringency parameters utilized for the mapping analysis were a limit of detection (LOD) equal to three and a maximum recombination frequency (θ) of 0.3. The commands "order sequence" and "ripple" were used to order the markers within the linkage groups. The distances between the markers were estimated in centiMorgans (cM) using the Kosambi mapping function. The QTL analysis was performed using composite interval mapping (CIM) and multiple interval mapping (MIM) as implemented in the QTL Cartographer 2.5 for Windows program (Wang et al. 2005). The precision interval was 2 cM, and a distance of 10 cM was used to control for interference from multiple QTLs in the forward–backward regression models. The most probable location of the QTL was estimated by the verisimilitude maximum function. The significance limits for the declaration of a QTL were determined for each trait with 1,000 permutations ($P < 0.05$) (Churchill and Doerge 1994). The proportion of phenotypic variance (R^2) explained by each QTL, which indicates the contribution of each specific locus to the trait as well as the additive, dominance, and epistatic effects of the QTLs, was also estimated using Cartographer 2.5. The mean cooking time and water absorption values obtained in the individual experiments on the $F_{2:4}$ (Santo Antônio de Goiás) and $F_{2:5}$ (Ponta Grossa and Santo Antônio de Goiás) generations as well as the overall means of the populations (calculated from the averages of the $F_{2:4}$ and $F_{2:5}$ at the two study locations) were used for the analysis. The QTL × environment interaction was also performed using least square means from two environments by the multiple-trait analysis (MTA) method of QTL Cartographer 2.5 for Windows program (Wang et al. 2005).

Results

Phenotypic analysis

The ANOVAs for cooking time found significant effects for the interaction between families ($P < 0.01$) in both the individual analyses performed on the $F_{2:4}$ (Santo Antônio de Goiás) and $F_{2:5}$ families in each location (Santo Antônio de Goiás and Ponta Grossa) (Table 1) and for the group analysis performed on the $F_{2:5}$ families in each location (Table 2). For the trait of water absorption that was evaluated for the $F_{2:5}$ families, the ANOVA found a significant effect for the interaction between families only for the experiment conducted in Ponta Grossa (Table 1). In the group analysis, the interaction effect between families was significant only for cooking time ($P < 0.01$), while the effect of the interaction between families and the environment [genotype × environment (G × E)] was significant for both cooking time ($P < 0.01$) and water absorption ($P < 0.05$) (Table 2). For cooking time, the experimental coefficients of variation (CVs) were 9.51% for the $F_{2:4}$ generation in Santo Antônio de Goiás, 17.94% for the $F_{2:5}$ generation in Ponta Grossa, and 9.42% for the $F_{2:5}$ generation in Santo Antônio de Goiás (Table 1). The estimated CVs for water absorption were 5.84 and 5.85% for the experiments in Ponta Grossa and Santo Antônio de Goiás, respectively.

For the three experiments that were performed on the two generations ($F_{2:4}$ and $F_{2:5}$), the cooking time for each of the bean families ranged from 18 to 41 min. For the CNFM 7875 line and Laranja cultivar, the minimum and maximum cooking times were 19 and 29 min (average 21 min) and 29 and 31 min (average 27 min), respectively (Table 1). For the families within each generation, the cooking time varied from 19 to 34 min for the $F_{2:4}$ generation that was evaluated in Santo Antônio de Goiás, from 18 to 41 min for the $F_{2:5}$ generation that was evaluated in Ponta Grossa, and from 22 to 36 min for the $F_{2:5}$ generation that was evaluated in Santo Antônio de Goiás (Table 3). None of the families at either location or from either generation had a cooking time that was significantly less than that of the parental CNFM 7875 line, although the BRS Requinte and BRS Pontal outgroups had average cooking times that were greater (30 and 28 min, respectively) than those of the optimal families of the $F_{2:4}$ generation in Santo Antônio de

Table 1 Summary of the analysis of variance for the cooking time and water absorption traits in common beans evaluated from the $F_{2:4}$ families in Santo Antônio de Goiás and the $F_{2:s}$ families in Ponta Grossa and Santo Antônio de Goiás

Sources of variation	$F_{2:4}$ STA		$F_{2:5}$ PG			$F_{2:5}$ STA		
	df	Cooking time Mean square	*df*	Cooking time Mean square	Water absorption	*df*	Cooking time Mean square	Water absorption
Replications	1	12.087	2	110.318	604.997	2	47.687	2,242.845
Blocks	–	–	33	55.519	2,133.325	33	16.053	53.384
Genotypes	143	17.300**	143	35.893**	5,702.383**	143	19.938**	34.774 ns
Error	143	5.128	253	19.417	74,689.009	253	7.556	29.982
GV		6.09		5.49	3.45		4.13	1.60
PV		8.65		11.96	13.29		6.65	11.60
Heritability (%)		70.35		45.90	25.97		62.10	13.78
CVe (%)		9.41		17.94	5.84		9.42	5.85
CVg (%)		10.25		9.54	1.99		6.96	1.35
CVg/CVe		1.089		0.532	0.342		0.739	0.231
Mean range		19–34 (min)		18–41 (min)	78–112%		22–36 (min)	81–113%
CNFM 7875		20 (min)		19 (min)	95%		29 (min)	94%
Laranja		31 (min)		29 (min)	102%		31 (min)	94%
Total mean		25 (min)		24 (min)	93%		29 (min)	94%

df degrees of freedom, *GV* genotypic variance, *PV* phenotypic variance, *CVe* experimental coefficient of variance; *CVg* genetic CV, *CVg/CVe* ratio of genetic CV to experimental CV, *ns* not significant

** Statistical significance of the *F* test ($P < 0.01$)

Table 2 An analysis of group variance for the cooking time and water absorption traits in common beans from the $F_{2:5}$ families studied in Ponta Grossa and Santo Antônio de Goiás, and the estimates of Pearson's correlation for cooking time and water absorption obtained in Ponta Grossa and Santo Antônio de Goiás with their respective *P* values

Sources of variation	*df*	Cooking time		Water absorption	
		Mean square	*F*	Mean square	*F*
Genotypes	143	28.871	2.141**	33.054	1.111 ns
Environment	1	4.608.450	341.70**	80.661	2.711 ns
G × E	143	26.959	1.999**	41.598	1.398*
Effective error	506	13.487		29.752	
Mean range		17–35 (min)		78–94%	
CNFM 7875		21 (min)		97%	
Laranja		27 (min)		100%	
Total mean		25 (min)		92%	
Traits correlations	Pearson correlation	*P* Value			
CT_PG × WA_PG	0.139	0.09			
CT_PG × WA_STA	−0.085	0.31			
CT_STA × WA_PG	0.025	0.77			
CT_STA × WA_STA	0.025	0.76			

G × *E* genotype × environment, *CT* cooking time, *WA* water absorption, *PG* Ponta Grossa, *STA* Santo Antônio de Goiás, *ns* not significant

*, ** Statistically significant at $P < 0.05$ and $P < 0.01$, respectively, according to the *F* test

Goiás and the $F_{2:5}$ generation in Ponta Grossa (29 and 29 min, respectively) (Table 3). Based on the results of the group analysis of the experiments performed on the $F_{2:5}$ generation in Ponta Grossa and Santo Antônio de Goiás, the mean cooking times ranged from 17 to 35 min.

The water absorption capacity of the beans in the $F_{2:5}$ generation ranged from 78 to 112% in Ponta Grossa and from 81 to 113% in Santo Antônio de Goiás (Table 1). The Pearson's correlation test did not find a significant association between water absorption and cooking time (Table 2). Moreover, as shown in Table 3, the bean families with the shortest cooking times did not have greater proportional changes in mass, i.e., greater water absorption.

For the $F_{2:4}$ families that were evaluated in Santo Antônio de Goiás, the coefficient of heritability and the estimated CVg/CVe ratio were 70.35 and 1.089%, respectively. The water absorption capacity had heritability values that ranged from 13.78% in Santo Antônio de Goiás to 25.97% in Ponta Grossa, while the estimates obtained for the cooking time trait ranged from 45.90% in Ponta Grossa to 62.10% in Santo Antônio de Goiás ($F_{2:5}$) (Table 1). The coefficient of overall heritability of the $F_{2:5}$ generation had a value of 0.532 and 0.739 for cooking time and 0.342

Table 3 The average cooking times of the two generations studied in each environment and their respective water absorption capacity values

$F_{2:4}$ STA		$F_{2:5}$ PG			$F_{2:5}$ STA			Joint analysis		
Family	CT (min)	Family	CT (min)	WA (%)	Family	CT (min)	WA (%)	Family	CT (min)	WA (%)
116	19	108	18	93	32	22	94	108	17	78
79	21	107	18	90	3	23	96	85	20	95
121	21	90	19	96	87	24	93	96	20	96
100	21	28	19	93	21	24	96	112	20	92
70	21	48	20	94	121	25	90	111	20	89
111	21	81	20	95	80	25	95	19	20	91
78	21	99	20	90	123	25	92	94	20	92
7	21	16	20	90	22	25	95	30	21	93
115	22	55	20	92	112	26	91	124	21	92
77	22	10	20	92	16	26	93	117	21	90
21	30	101	30	88	26	34	95	2	29	97
14	30	121	30	90	49	34	93	138	29	95
109	30	37	31	92	64	34	92	41	29	93
57	30	138	31	95	94	34	91	29	29	93
113	30	86	32	90	10	34	91	73	29	102
43	30	70	32	83	125	34	100	125	29	91
4	31	69	32	112	56	34	88	22	29	91
30	32	22	33	94	39	35	94	25	30	94
37	32	25	36	97	4	36	92	66	32	93
54	34	62	41	89	1	30	97	62	35	94
BRS Requinte	30	BRS Requinte	29	94	BRS Requinte	28	92	BRS Requinte	30	95
BRS Pontal	28	BRS Pontal	29	96	BRS Pontal	27	94	BRS Pontal	31	97
CNFM 7875	20	CNFM 7875	19	95	CNFM 7875	29	94	CNFM 7875	21	97
Laranja	32	Laranja	29	102	Laranja	31	94	Laranja	27	100

The first ten lines depict the optimal families and are followed by the families with poorer performance. The average values for the outgroups (BRS Requinte and BRS Pontal) and the estimates obtained for the parental lines (CNFM 7875 and Laranja) are listed from the group analysis that was performed as part of the experiments on the $F_{2:5}$ generation in Ponta Grossa (PG) and Santo Antônio de Goiás (STA)

and 0.231 for water absorption in Ponta Grossa and Santo Antônio de Goiás, respectively.

Analysis of linkage and QTL mapping

Once the amplification reaction conditions had been determined, 922 SSRs (97.66%) had good amplification quality and 22 (2.33%) demonstrated nonspecific amplification. Of the 922 SSRs with good amplification quality, 105 (11.39%) were polymorphic between the parental lines and subsequently used to genotype 140 F_2 plants from the CNFM 7875 by Laranja cross; 54 (51.43%) SSRs were derived from the genomic sequence, and 51 (48.57%) were derived from gene sequences. Of the 105 polymorphic SSRs, 12 (11.43%) significantly deviated from the expected Mendelian ratios for the F_2 generation (1:2:1) by the χ^2 and FDR test ($P < 0.05$).

The segregation data for the 105 SSRs were used in the linkage analysis. Of these, 91 (86.66%) mapped to 12 linkage groups, which was greater than the number of chromosomes of *Phaseolus vulgaris* ($n = 11$) (Fig. 1). The identification of the chromosomes that corresponded to the location of each linkage group was performed based the nomenclature established by Pedrosa-Harand et al. (2008) and by comparing each group with the *Phaseolus* reference map (Garcia et al. 2011) and the available *Phaseolus* SSR data from the Bean Improvement Cooperative (BIC, http://www.css.msu.edu/bic/Genetics.cfm). The extra chromosome obtained from the mapping analysis corresponded to the top point of chromosome 3. The total size of the map was 1,303.7 cM, and the average distance between the markers was estimated to be 14.3 cM. The number of markers in the linkage groups was between 3 (chromosomes 3A, 4, and 11) and 15 (chromosome 2). Among the markers that differed from the expected segregation ratios, ten were mapped and only one cluster on chromosome 6 was observed (IAC01, PV163, PV198, and BM187), very likely located nearby the centromeric region. The markers that were derived from gene sequences mapped throughout the genome to each of the chromosomes.

A comparative analysis of the SSR markers that were common between the current map and three previously developed maps for beans derived from the BAT93 by Jalo EEP558 (BJ) cross population revealed a high level of conservation for the linkage of common markers: 26 (95%) and 50 (94%) of the markers were found at identical chromosomal positions on the BJ maps developed by Grisi et al. (2007) and Garcia et al. (2011), respectively. With regards to the maps developed by Hanai et al. (2007, 2010), only four of the SSR markers mapped coincided with the locations on our map, and these published maps had the PvM12 marker positioned on a different chromosome. Two markers (PVBR149 and PVBR131) mapped to different chromosomes on our map when compared to the BJ population map (Grisi et al. 2007), and three markers (PVBR149, PVBREST258, and PVBR078) did not maintain the same position on our map when compared to the map by Garcia et al. (2011). One marker (PVBR078) was located on a different chromosome on our map compared with the BJ map developed by Garcia et al. (2011), although its location on our map was coincident with that on the BJ map by Grisi et al. (2007).

From the CIM analysis, six significant QTLs with an LOD $\geq$ 3.0 (Table 4; Fig. 1) were found for the cooking time of the $F_{2:4}$ and $F_{2:5}$ generations that were evaluated in Santo Antônio de Goiás. No QTLs were detected for the traits of water absorption or cooking time in the $F_{2:5}$ generation from Ponta Grossa or for the group averages of the $F_{2:5}$ generation from either location. Among the QTLs, two of those detected in the same marker interval were considered as only one (*ct1.1*), although they were detected in different generations. The *ct1.1* QTL explained 21.36% of the phenotypic variation in $F_{2:4}$ and the *ct1.1* QTL explained 12.34% of this variation in $F_{2:5}$. The *ct1.3* QTL, which was also detected on chromosome 1 and was adjacent to the *ct1.1* QTL, explained 11.54% of the phenotypic variation. Two QTLs were also identified in adjacent regions on chromosome 9 for the two generations evaluated in Santo Antônio de Goiás (*ct9.1* in $F_{2:4}$ and *ct9.2* in $F_{2:5}$), and these explained 14.47 and 19.24% of the phenotypic variation, respectively. The additive effects of these loci were negative for the identified QTLs, which indicated that the reduction in cooking time was due to allelic substitution at these loci. Based on MIM analysis, one QTL was confirmed (*ct1.1*) and a new one was detected on chromosome 9, namely as *ct.9.3* detected in the $F_{2:5}$ generation, in the experiment of Ponta Grossa (Table 4; Fig. 1). The MTA allowed QTLs within the same regions to be located as QTLs *ct1.1* (36 cM), *ct1.2* (130 cM), and

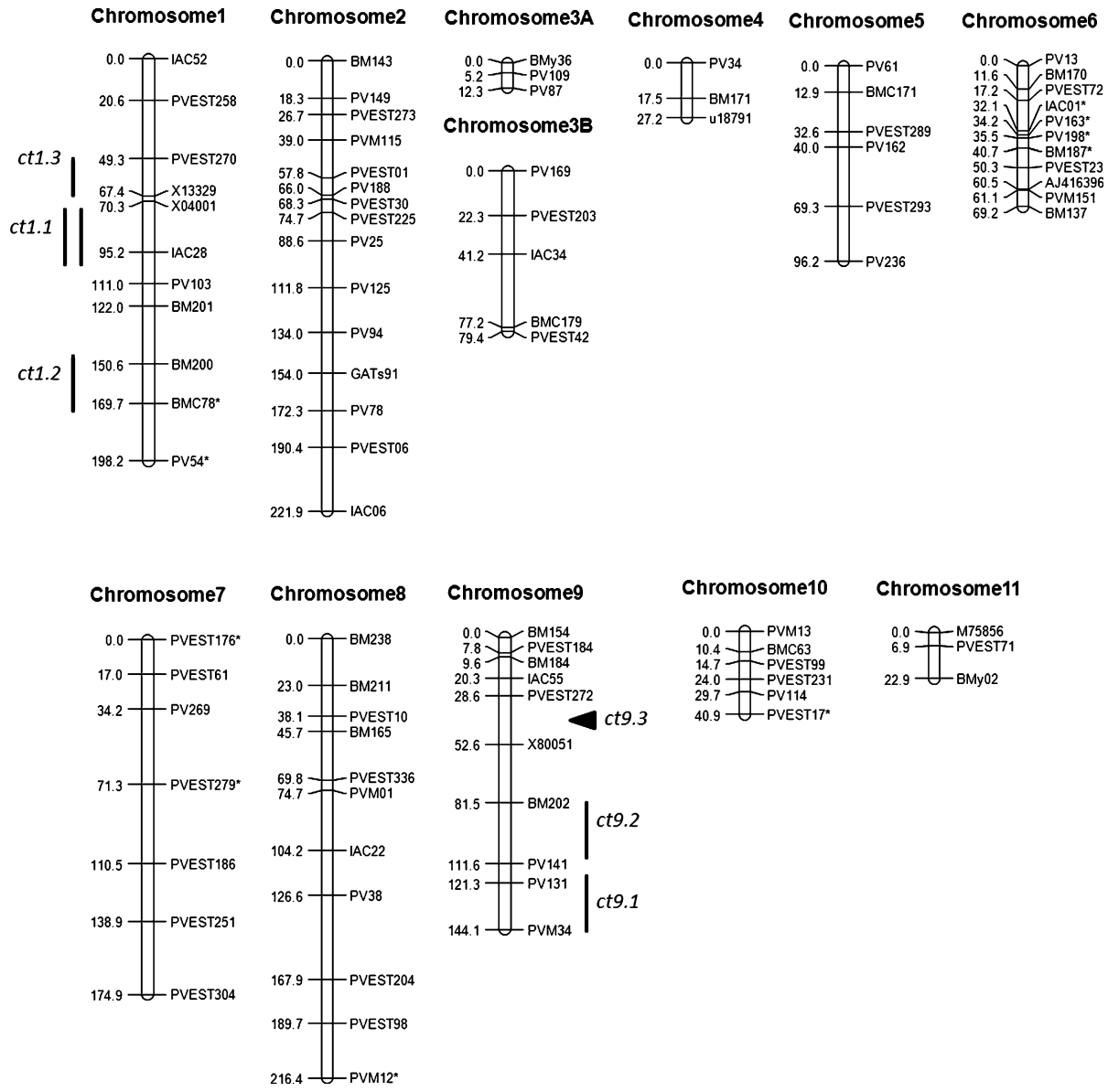

Fig. 1 A linkage map derived from the cross CNFM 7875 × Laranja based on microsatellite markers and locations of the quantitative trait loci (QTLs) associated with the cooking time indicated in the chromosomes. *Bars* indicate the confidence intervals of QTLs detected by composite interval mapping, *arrows* indicate the QTLs detected by multiple interval mapping in the Ponta Grossa environment. Markers that showed segregation distortions denoted with an *asterisks* ($P < 0.05$)

ct9.1 (125 cM) (Table 4). In addition, one of the QTLs detected by MIM was located on a position close to the QTL *ct9.3* located in Ponta Grossa by MIM (40 and 34.8 cM, respectively). However, MTA revealed that the genomic regions linked to cooking time were not stable across the environments, and most QTLs were detected only in one location for both generations.

Discussion

Phenotypic analysis

The experimental CVs that were estimated for the cooking times of the common beans in Santo Antônio de Goiás (9.41% in $F_{2:4}$ and 9.42% in $F_{2:5}$) were within the range of the coefficients estimated by previous

Table 4 Descriptions of the QTLs that were identified using composite interval mapping and multiple interval mapping for the cooking time of common beans

Analysis type	Evaluation site	Generation	QTL	Chromosome	QTL interval (cM)	QTL peak (cM)	LOD score/LR	R^2 (%)	Additive
CIM	Santo Antônio de Goiás	F2:4	*ct1.1*	1	70.0–95.8	82.0	5.1	21.36	−1.964
			ct1.2	1	149.0–169.9	169.0	3.0	10.40	−1.344
			ct9.1	9	120.9–142.2	121.0	3.0	14.47	−0.924
		F2:5	*ct1.3*	1	48.9–69.9	59.0	3.2	11.54	−1.351
			ct1.1	1	70.2–95.2	84.0	4.4	12.34	−1.486
			ct9.2	9	81.2–111.0	94.0	5.5	19.24	−1.984
MIM	Santo Antônio de Goiás	F2:4	*ct1.1*	1	–	88.5	18.1	–	−1.544
		F2:5	*ct1.1*	1	–	70.0	11.2	–	−1.177
	Ponta Grossa	F2:5	*ct9.3*	9	–	34.8	8.6	–	−1.144

CIM composite interval mapping, *MIM* multiple interval mapping

The R^2 coefficient (%) shows the proportion of the total variation that can be explained by the QTL, estimated by CIM. The term "additive" refers to the additive effect of the alleles at the loci estimated by CIM and MIM. The QTLs detected by MIM have a likelihood ratio (LR) statistical value

studies for the same trait [10.70% by Bertoldo et al. (2008), 8.18 and 12.91% by Baldoni and Santos (2005), and 8.0 and 11.7% by Carbonell et al. (2003)]. However, the estimated CV for the $F_{2:5}$ generation in Ponta Grossa had a comparatively high value (17.94%), which indicated the lower experimental precision of the experiments conducted at this location. This may be attributed to irregular rain patterns, as the dry season in Ponta Grossa is characterized by irregular rainfall. During the period of the experiment in Ponta Grossa, there was a decrease in water availability during the swelling and physiological maturation of the beans. The water shortage during this developmental phase may explain the higher estimated CV, the lower heritability levels, and the CVg/CVe ratio at this location. In Santo Antônio de Goiás, the experiment was conducted during the winter and irrigation was performed during the entire growth cycle, which could have led to the lower CV values.

The major factors that affect the cooking time for a specific genotype include the harvest weather conditions (dry or rainy), the bean handling, the G × E interaction, and the conditions and time of storage (Bertoldo et al. 2008). As the beans in the three experiments were evaluated soon after harvest and were not stored, the variance differences can be attributed to the G × E interactions and the harvest weather conditions. Ponta Grossa and Santo Antônio de Goiás are geographically distant (latitude 25°05′42″S, longitude 50°09′43″W; latitude 16°28′00″S, longitude 49°17′00″W, respectively) and have very different environmental conditions. The group analysis between experiments demonstrated a significant interaction between genotype and environment (G × E) for both the cooking time and the water absorption, which indicated that the performance of the families in the two locations was not equal (Table 1). The estimated overall heritability values were very high for the two study environments, which suggests that the determination of cooking time may be under the control of multiple genes. These estimates indicate that there is sufficient genetic variability between the two families for the successful selection of plants with beans that have reduced cooking times (Melo et al. 2002). However, the fact that the heritability estimate was relatively low for the experiment conducted in Ponta Grossa indicates that the predictive value for shorter cooking time is also low, suggesting that the phenotypic value may not be a good indication of the genetic value. More favorable conditions for the selection of reduced cooking times were observed in Santo Antônio de Goiás because the estimated CVg/CVe ratio at this location was greater than 1 for the $F_{2:4}$ generation (1.089) and was close to 1 for the $F_{2:5}$ generation (0,729), indicating that the genetic variability would be sufficient for selection.

The water absorption capacity of beans is considered to be a relevant factor when the aim is to study cooking time. Studies on soybeans and common beans have shown that pre-hydration with salted water

significantly decreases the cooking time of stored beans (Khetarpaul et al. 2005; Vale et al. 2010) due to changes in cotyledon structure (Paredes-Lopez et al. 1991). However, this practice may promote an increase in salt consumption, which is not desirable. In testing hydration without salt, Coelho et al. (2008) demonstrated that increasing the water temperature could differentially increase the water uptake of the studied genotypes of beans. Similarly, Bertoldo et al. (2008) demonstrated a negative correlation between water absorption and cooking time (i.e., greater water absorption meant a shorter cooking time). However, a significant correlation between water absorption and cooking time ($P < 0.05$) was not detected in our study. Our result is consistent with previous ones that have found low correlation coefficients, such as −0.26 (Baldoni and Santos 2005) and 0.22 (Carbonell et al. 2003), for these traits, indicating that the correlation between water absorption and cooking time is less than would be expected. In practical terms, the absence of this correlation demonstrates that soaking beans in water to accelerate the cooking process is unnecessary. However, our results strongly indicate that cooking time is more strongly influenced by environmental factors that are related to genotypic interactions than by the capacity of the beans to absorb water.

The majority of the SSR loci studied in the CNFM 7875 by Laranja cross populations had a satisfactory amplification pattern (89.17%), which highlights the availability of this set of microsatellite markers for genetic analyses in common bean strains. However, only 11.39% (105) of these loci were polymorphic due to the low genetic divergence (or contrast) between the genitors of the cross, as previously demonstrated in studies involving lines from a common origin (Garcia et al. 2011). Greater polymorphism levels have been identified in parents derived from divergent genetic pools, such as the reference population of the common bean from the cross between BAT93 (Mesoamerican Period) and Jalo EEP558 (Andean Period), which has polymorphism levels of >40% (Yu et al. 2000; Grisi et al. 2007). In our study, both the genomic and gene loci had similar polymorphism levels and were randomly and representatively distributed throughout the genome. This result indicates that markers derived from transcribed sequences (ESTs) represent a valuable source of markers that could be used to improve genomic studies in the common bean. Of the 105 polymorphic loci used for the construction of the genetic map, 12 (11.43%) differed from the expected Mendelian segregation ratios, which could have been due to one or more of many factors related to the distribution of distorted markers along linkage groups. These factors can be divided into two main types, as described by Xian-Liang et al. (2006). One type originates from deviations from Mendelian ratios at individual loci directed towards either parental class and widespread between chromosomes, resulting from errors in marker genotyping or mutation within the binding site for a DNA marker. The other type occurs when a block of markers is distorted in the same direction; this is usually regarded to be related to existence of segregation distortion loci (SDLs), as widely reported in different crop species (Lu et al. 2002; Song et al. 2005). In our study, one small cluster of four markers was formed, and the remaining skewed markers were located at the end of the linkage groups, The clustering of markers at centromeric, and possibly telomeric, areas has being reported for several crops (Tanksley et al. 1992; Qi et al. 1996) and may be due to genetic processes related to position near centromeres. In addition, the block of four markers skewed toward the same genitor (Laranja) gives support to the hypothesis that the distortion had a biological basis, i.e., as genes subject to gametic or zygotic selection, and that these genotypes had/have some evolutionary advantage and are selected for at the developmental processes (Xu et al. 1997; Xu 2008; Xu and Hu 2010). Comparative mapping is a useful tool to estimate the effects of segregation distortion on linkage and is usually performed among different populations to determine how much the map is affected (Xian-Liang et al. 2006). In previous studies, deviating markers were mapped and did not affect the quality of the generated maps (Blair et al. 2003; Grisi et al. 2007; Garcia et al. 2011). The effect of distortion on the determining power to detect a QTL occurs when the QTL and SDLs are close, but in general, this distortion will not produce more false QTLs, nor will distortion have a significant impact on the estimation of QTL position if the distortion is not extremely serious (Zhang et al. 2010). In addition, QTLs under the additive model are favorably affected when segregation distortion of a locus is a random event (Xu 2008). Of the 91 markers located on the map, 31 mapped to novel positions. The formation of 12 linkage groups (common bean has 11 chromosomes)

indicates that a greater number of molecular markers need to be integrated into the analysis. Only by increasing the number of markers will we be able to overcome the limitations of reduced genetic diversity among the parental lines selected by the breeding programs and increase the resolution of the maps generated. The prospects for increasing the number of markers are promising, and the recently developed second-generation sequencing strategies are facilitating the discovery of SNP markers in *P. vulgaris* (Hyten et al. 2010, Souza et al. 2011) that can be used for large-scale studies on genetic diversity.

A CIM analysis revealed that the same position on chromosome 1 (*ct1.1*) was associated with cooking time for two generations ($F_{2:4}$ and $F_{2:5}$). Although this QTL was detected at the same study location (Santo Antônio de Goiás), it was consistently identified in the analysis of the cooking time during different years of the study, which indicates the robust presence of this QTL across generations. This QTL was also detected by the MIM analysis, showing that it is a strong candidate for marker-assisted selection. Two regions on chromosome 9 were detected for generations $F_{2:4}$ and $F_{2:5}$ in Santo Antônio de Goiás and one for generation $F_{2:5}$ in Ponta Grossa. These QTLs were located in three different regions of chromosome 9. The non-coincidence of the QTLs found in Santo Antônio de Goiás and Ponta Grossa corroborates the G × E interaction that was indicated by the phenotypic data and the MTA analysis. The small number of QTLs identified and the identification of a region on chromosome 1 strongly associated with cooking time corroborates previous observations and suggests that this trait is predominantly oligogenic, i.e., is controlled by only a few genes that mediate a large effect. Jacinto-Hernandez et al. (2003) evaluated cooking time in a population of pure recombinant common bean lines and suggested that two dominant genes control this trait. Later, Silva and Santos (2005) also studied the genetic control of cooking time using 175 markers and a bulk segregant analysis (BSA) strategy and found an association between this trait and only one molecular marker. Together, these results strongly indicate that genetic control of the trait is in fact oligogenic (few QTLs with large effects) and, as for any quantitative trait, that the main purpose of QTL analysis is to identify molecular markers linked to the majority of major genes to provide the opportunity to improve for the desired trait through marker-assisted selection (MAS). In addition, the QTLs identified were affected by environmental conditions and the cooking time was found to be a trait of late evaluation; according to Lande and Thompson (1990), this means that MAS promises to be a superior breeding approach than conventional phenotypic selection.

The QTL on chromosome 1 was stably detected in the two generations, but at the same location, Santo Antônio de Goiás, while the QTL detected in Ponta Grossa was located on a different region on chromosome 9, not coincident with any other QTL. The differences in the observed variation between the two locations could be attributed to differences in the environmental conditions during the growth period (dry in Ponta Grossa vs. irrigation in Santo Antônio de Goiás), as discussed previously, as well as the effects of the interactions between genotype and the environment. The influence of environmental factors on the expression of this trait can also be explained by the proportion of the estimated variation for the QTLs. The *ct1.1* QTL had the greatest effect of any QTL and still only explained 20.26% of the phenotypic variation. This is a small proportion considering that the trait is oligogenic and highly heritable, as was observed in this study. However, the additive effects in the loci were negative, which indicates that the reduction in cooking time may be due to allelic substitution, i.e., the alleles of the CNFM 7875 founder resulted in a reduced cooking time when these were substituted for the alleles of the Laranja parent. Therefore, when performing MAS for beans with reduced cooking times, the alleles from the CNFM 7875 line should be selected for at these loci.

Conclusion

As trait characterization is a slow and laborious process and because cooking time is controlled by only a few genes, an understanding of the genetic control over the cooking time of common beans will provide relevant information for improvement programs that aim to facilitate genetic selection. In addition, based on the results of this study, we conclude that this trait is significantly affected by environmental conditions during bean swelling, which makes the choice of location for family selection an important consideration in this process. Furthermore, the map constructed for the population resulting from

the CNFM 7875 by Laranja cross contributes to a better understanding of the control over this trait and also provides a novel group of mapped microsatellite markers that will increase the amount of information available for genetic and genomic studies in *P. vulgaris*. The identification of QTLs, which statistically define the location of genes that govern the target trait in this study, represents the first step towards the artificial selection of new alleles of interest into elite common bean lines.

The common bean is a species of emerging social and economic interest worldwide, and it will undoubtedly assume a position of importance alongside agricultural species whose complete genetic sequences will soon be available, such as the soybean (Schmutz et al. 2010). The QTL information generated from sequenced genomes will be available for exploration and will reveal novel genes as well as alleles of known genes that have been identified in specific genetic backgrounds under predetermined environmental conditions (Mace and Jordan 2011). Therefore, these novel QTLs that were identified in isolation represent a valuable genetic pool that will allow for the detailed analysis of this trait and the efficient facilitation of MAS in the near future.

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