Recent Advances in Molecular Breeding: The Example of Tomato Breeding for Flavor Traits

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Abstract

With the development of molecular markers, genetic maps have been constructed in plant species which allow for the localization of major loci and QTLs controlling agronomical trait variation. Molecular markers have been widely used for the introgression of major loci, but marker-assisted selection for quantitative trait breeding is used less. Both theoretical and applied aspects of marker-assisted back-crossing of quantitative traits are presented, with special emphasis on a program of tomato breeding for flavor traits. Improving organoleptic quality of fresh market tomato fruit has become an important objective for tomato breeders. The detection of QTLs controlling the variation of tomato quality traits was performed in the progeny of a cross between a cherry tomato chosen for its good flavor and a line with bigger but less tasty fruits. Both physical traits (fruit weight, color and firmness) and chemical traits (dry matter weight, titratable acidity, pH, and the contents of soluble solids, sugars, lycopene, carotene and 12 aroma volatiles) were evaluated. The lines were also evaluated by descriptive sensory profiling (taste, texture and aroma). A number of QTLs were detected for all the traits, some with major effects. Co-localizations of QTLs controlling several traits were found. Most of the favorable alleles came from the cherry tomato parent for chemical and sensory traits, showing the potential usefulness of this line for tomato organoleptic quality improvement. A marker-assisted selection scheme was thus initiated in order to transfer into elite lines the five regions carrying the most important QTLs involved in fruit quality. The backcross scheme was first optimised taking into account both theoretical and practical aspects. Three recurrent lines were chosen in order to study the effect of genetic background on QTL expression. Applications of the scheme are presented.

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INTRODUCTION

Many agricultural important loci have been mapped and tagged with molecular markers. Marker-assisted selection (MAS) has allowed breeders to drive the selection of genomic regions involved in the expression of traits of interest through these DNA markers. The efficiency and complexity of MAS depend on the genetic nature of the trait (monogenic or polygenic). For monogenic traits, marker-assisted backcross (MABC) is the most straightforward strategy, whereas for polygenic traits various strategies are available.

The principle of MABC for a single gene is quite simple. First, molecular markers tightly linked to the target gene must be identified, allowing assessment of the presence of the introgressed gene ("foreground selection"). Other markers are also used in order to accelerate the return to the recipient parent genotype at other loci ("background selection"). Background selection is based not only on markers located on the chromosomes carrying the gene to introgress (carrier chromosome), but also on non-carrier chromosomes. Markers devoted to background selection on a carrier chromosome allow the identification of individuals for which recombination events took place on one or both sides of the gene, in order to reduce the length of the donor type segment of genome dragged along with the gene (Young and Tanksley, 1989). Background selection on non-carrier chromosomes was investigated by Hospital et al. (1992). Visscher et al. (1996) investigated both foreground and background selection. In three generations of MABC, isogenicity is higher than that obtained by classical methods. By comparison, traditional approaches would require approximately two more generations to obtain such an isogenicity (Hospital et al., 1992).

THEORETICAL INVESTIGATIONS ON MAS FOR QTLs

Traits showing quantitative variation are usually controlled by a number of genes (quantitative trait loci, QTL), each with variable effect. Due to the genetic complexity of such traits, several QTLs with small effects must be simultaneously manipulated. Depending on their number, the nature and level of their effect, the origin of favorable alleles, different MAS strategies will be proposed.

As for monogenic traits, MABC is the most effective strategy when a small number of QTLs (less than five), coming all from the same parent, are transferred. Hospital and Charcosset (1997) determined the optimal number and positions of the markers needed to control the QTLs during the foreground selection step and the maximum possible number of QTLs that could be simultaneously monitored with realistic (a few hundred individuals) population sizes. They also investigated the use of markers for background selection. In practice, the position of the QTL is not precisely estimated and the true position of the QTL is unknown, but is supposed to be within a confidence interval. From this confidence interval length, Hospital and Charcosset (1997) deduced the number of markers and their position relative to the estimated position of the QTL, in order to insure an optimal control of the QTL. The optimal marker positions are not evenly spread over the confidence interval. On average, using at least three markers per QTL allows good control over several generations, providing low risk in having the donor type alleles at the markers without having the desired genotype at the QTL. However, as the minimum number of individuals that should be genotyped at each generation depends on (i) the confidence interval length, (ii) the number of markers and (iii) the number of QTLs, it seems illusive to transfer more than four or five QTLs with this simultaneous design unless a very large population can be considered, or the precision of the QTL location is very high.

The advanced backcross QTL analysis is another strategy tailored for the discovery and transfer of valuable QTL alleles from unadapted donor lines into established elite inbred lines (Tanksley and Nelson, 1996). The QTL analysis is delayed until an advanced generation (BC_3 or BC_4), and during the development of this generation, negative selection is pursued to reduce the frequency of deleterious donor alleles. The advantages of using BC_3/BC_4 populations include reducing linkage drag and

epistatic effects and decreasing the amount of time later needed to develop QTL-NILs (Fulton et al., 1997). Using this method it has been demonstrated that beneficial alleles can be identified in unadapted germplasm and simultaneously transferred into elite cultivars, thus exploiting the hidden value of exotic germplasm (Bernacchi et al., 1998).

When the number of QTLs to introgress becomes important, Hospital and Charcosset (1997) proposed to use a pyramidal design. QTLs are first monitored one by one by MABC, to benefit from a higher background selection intensity, and then the selected individuals are crossed, to accumulate favorable alleles at the QTLs in the same genotype. According to predictions, the pyramidal design should provide approximately the same efficiency as the simultaneous design with almost one third of the individuals. Moreover, a pyramidal design with large population size over three or four generations is preferable than simultaneous design when high isogenicity is required. When favorable alleles come from different sources, van Berloo and Stam (1998) proposed an index method to select among recombinant inbred lines for crossing, to obtain a single genotype containing as many favorable quantitative trait alleles as possible. The index is constructed for each pair of lines based on the genotype of the markers flanking the putative QTLs. Plants showing the optimal index are crossed together. This strategy was shown efficient to obtain transgression in offspring populations of Arabidopsis (van Berloo and Stam, 1999). Charmet et al. (1999) improved this approach by including interacting QTLs, and estimated the population size required to have a 95% probability of obtaining the best line from a given cross. They showed that a recurrent selection scheme is highly preferable for pyramiding many QTLs than a single cycle requiring very large populations.

The use of genetic markers to improve populations was proposed using a statistical approach based on an index combining phenotypic and marker information (Lande and Thompson, 1990). The efficiency of such a MAS was investigated either analytically (Lande and Thompson, 1990; Moreau et al., 1998) or by computer simulation (Whittaker et al., 1995; Hospital et al., 1997). This approach is primarily focused on population improvement rather than the fixation of extreme genotypes. The main conclusions are that MAS could be more efficient than purely phenotypic selection in quite large populations and for traits showing relatively low heritabilities. The study over several successive generations of the rate of fixation of QTLs (Hospital et al., 1997) showed that the higher efficiency of MAS than purely phenotypic selection on QTLs with major effects in early generations is balanced by a higher rate of fixation of unfavorable alleles at QTLs with small effects in later generations.

DETECTION OF QTLS FOR ORGANOLEPTIC QUALITY IN TOMATO

Tomato fruit quality is becoming of paramount importance for consumer acceptance. However, organoleptic quality is a complex characteristic, involving several components, some of them being antagonistic (e.g. fruit weight and sugar content). A program of QTL detection for fruit quality traits has been achieved. A range of 144 recombinant inbred lines derived from a cross between a cherry tomato line chosen for its good taste and aromatic intensity and a large-fruited line with unremarkable taste. An almost saturated map was constructed with RFLP, AFLP and RAPD markers (Saliba-Colombani et al., 2000). Each line was evaluated by physical (fruit weight, color and firmness) and chemical (dry matter weight, titratable acidity, pH, and the contents of soluble solids, sugars, lycopene, carotene and 12 aroma volatiles) measures. Trained panels performed a descriptive profile of each line. Taste was analyzed through sweetness and sourness, and aroma through the overall aroma intensity, together with candy, lemon, citrus fruit and pharmaceutical aromas. Firmness, meltiness, mealiness, juiciness and difficulty to swallow the skin characterized the texture. A wide range of overall variation was shown for all the traits and significant differences among lines were detected. The overall aroma intensity was positively correlated with sweetness and sourness, as well as with lemon, candy and citrus fruit aromas. It was negatively correlated with mealiness. A negative correlation was detected between fruit weight and dry matter weight.

Molecular markers were used to map QTLs (Saliba-Colombani et al., 2001; Causse et al., 2001a). One to six QTLs were detected per trait. The proportion of phenotypic variation explained by each QTL ranged from 8% to 45%. Several clusters of QTLs were identified, mainly on chromosomes 1, 2, 3, 4, 8, 9, 11 and 12. A total of 86 QTLs out of 130 (66%) mapped to about 14% of the map length. These co-localizations were compared to the correlations, as two related traits are expected to share common QTLs. QTL co-localizations were observed for related sensory and instrumental traits (Causse et al., 2002). For instance, QTLs for titratable acidity, sourness and lemon aroma were in the same regions on chromosomes 1, 2, 3 and 9. QTLs for sugar content and sweetness mapped in the same regions on chromosomes 2 (2 regions) and 11. A QTL for fruit weight but with an opposite effect was also detected in each of these three regions. Only one common QTL location, on chromosome 3 could be responsible for the negative correlation detected between sweetness and sourness. The contribution of sugars and acids not only to sweetness and sourness but also to the overall aroma intensity was confirmed. The QTLs for overall aroma intensity which mapped at the top of chromosomes 2, 9 and 12 were close to QTLs for sourness, while those which mapped at the bottom of chromosome 2 were close to QTLs for sweetness (Causse et al., 2002). On chromosome 4, QTLs for instrumentally measured firmness were co-localized with QTLs for mealiness and citrus fruit aroma. Only a few co-localizations between aroma descriptors and volatile content were observed. The strong correlation between pharmaceutical aroma and eugenol and ortho-methoxyphenol, two compounds with medicine odors, was corroborated by two co-localizations, one on chromosome 2 (pharmaceutical aroma with eugenol) and one on chromosome 9 (pharmaceutical aroma with eugenol and ortho-methoxyphenol). In both cases, unfavorable aroma was associated with the large-fruited parent.

FINE MAPPING OF A QTL-RICH REGION

The region characterized by the largest cluster of QTLs was the distal region of chromosome 2 (a region of 50 cM). QTLs with major effect for fruit weight, fruit elasticity, color, sourness, aroma intensity, candy aroma, mealiness, dry matter weight, soluble solids, sugar and eugenol content were localized in this cluster. Furthermore, for several traits, more than one QTL was detected in the region. Further genetic studies, such as fine mapping of this region were required to differentiate between closely linked multiple QTLs from the effect of pleiotropic genes. A substitution mapping experiment was thus performed and near isogenic lines differing only by a short region of this chromosome were evaluated for quality traits. It was thus possible to dissect the region around the CD035 locus and identify at least 4 different QTLs, one controlling locular number, one controlling sugar and soluble solids content and two controlling fruit weight (Lecomte et al., in preparation). On the contrary, in the bottom of chromosome 2, two QTLs for fruit weight and elasticity remained linked in an interval of 10 cM to QTLs for sugar content and acidity. Within this cluster where favorable alleles for physical and chemical traits are antagonistic, the fruit weight QTL could be allelic to the fw2.2 QTL controlling fruit weight variation in several genetic backgrounds (Frary et al., 2000).

SELECTION STRATEGY FOR THE TRANSFER OF QTLS FOR ORGANOLEPTIC QUALITY

Most of the favorable alleles for tomato organoleptic quality improvement came from the cherry tomato line (coded C). Consecutively, a MABC scheme has been set up in order to transfer five regions of the cherry tomato line with the largest effects on fruit quality into three recurrent lines (coded L, B and D) with large fruits and different levels of fruit firmness. The QTL regions were chosen according to the QTL effects and their involvement in complementary quality traits (Table 1). We retained the distal region of chromosome 2, as this region provided interesting alleles for quality traits, even though the cherry alleles controlled reduced fruit weight. Recurrent parent alleles (providing bigger fruits) were selected for the 4 other fruit weight QTLs on chromosome 2 (top), 3, 11 and 12.

The size of the regions to transfer was estimated relatively to the size of the confidence intervals evaluated by Mapmaker/QTL. A LOD decrease of 1.5 was chosen, approximately corresponding to a 5% type I risk (Mangin et al., 1994). In regions where many quality trait QTLs were detected, the regions to transfer were defined as the summary of overlapping QTL confidence intervals for the different traits. A single RIL with favorable alleles at all the five QTL regions was identified among the 144 RILs. It showed about 53% of its genome with "cherry" alleles (Fig. 1). It was crossed to the three recurrent lines and a second backcross (BC_2) was performed before marker-assisted selection began.

The optimization of the population size as well as the number and location of markers to be used at each generation was performed, based on the analytical formulas proposed by Hospital and Charcosset (1997). One to three markers controlled each QTL, with an average distance of 14 cM between markers. The probability to control each QTL varied from 0.95 to 0.99 and the overall probability was estimated at 0.86, leading to the analysis of 267 individuals to have a 5% risk of losing one QTL (Causse et al., 2001b).

A sequential elimination of the plants carrying the unwanted alleles was first performed on three regions, as a PCR marker was available for each of the three regions, and allowed a quick selection. Thus, for example in the second BC of the L progeny, the number of plants to be analyzed decreased from 267 to 38. The DNA of the remaining plants was then blotted to be analyzed by RFLP markers. By the end of the selection, three to five plants carried all the requested alleles at the QTLs, and were screened for markers of the genetic background. The selection process was repeated on BC_3. After three backcrosses by the recurrent parent, the average allele frequency of the donor parent is supposed to be 6% (in absence of selection). The three MABC were followed by selfing generations during which plants homozygous for the QTLs were selected. Two selfing generations were planned as the number of plants required to obtain all the five QTLs homozygous in one generation is about 3000, instead of 300 plants (for three homozygous QTLs and two heterozygous) the first generation and 50 the next one (for fixing the last two). The percentage of donor genome in the three selected plants was evaluated using 89 markers covering the whole genome. Table 2 shows the efficiency of marker-assisted selection. On one hand, the population size considered allowed us to successfully transfer all the five segments into one line. However, the MAS scheme allowed us to reduce the proportion of donor genome on the non-carrier chromosomes to a level under expected without selection. Background selection was not applied to markers linked to the QTL segments. Thus on chromosome 9, the whole chromosome remained with the C allele and on the other chromosomes, large pieces of donor genome were fixed. By chance, it was possible, within the D progeny, to select a BC_3S_1 plant homozygous for fw2.2 (around TG167) but segregating in all the five regions of interest. Breaking this unfavorable linkage would have theoretically required ten times more individuals.

GENETIC BACKGROUND EFFECT ON QTL EXPRESSION

In BC_3S_1, samples of the three segregating populations were evaluated in order to look at the QTL stability over the years and genetic backgrounds. Twenty five fruits from about 100 individual plants per progeny were collected and evaluated for fruit weight, color (L, a, b), firmness, locule number, and fruit composition (dry matter, soluble solids, sugars, carotene and lycopene contents, titratable acidity and pH). The plants were also scored with the ten markers used for the foreground selection. Eighteen QTLs (44%) were detected in both RIL and BC_3S_1-L populations, while about the same numbers (12 and 11, respectively) were specifically detected in the RILs or the BC_3S_1-L (Table 3). These discrepancies could be attributed to environmental effects, to the fixation of some QTLs in BC_3S_1, which allows for new ones to be detected, or to epistatic effects, which mask some effects due to that fixation. Indeed the population of 144 RILs was segregating for the whole genome whereas the BC_3S_1 population was segregating for only 35%. In the B and D progenies, the proportions of QTLs common to the L progeny were about 50 % (data not shown). The new effects may result from differences between the L, B and D

alleles when compared to the C.

QTL INTROGRESSION AND CUMULATIVE EFFECT

Plants carrying from one to five QTLs were selected in order to study their individual or combined effects. A phenotypic evaluation of the fruit quality of the selected material was performed. As three recurrent lines were used, the effect of the genetic background on QTL expression was evaluated. Fig. 2 illustrates the fruit weight variation in the NILs carrying each segment or the five segments, in the three genetic backgrounds. In L and D backgrounds, QTLs for fruit weight were detected on chromosome 1, 2 and 9a, with a major effect for the first two. In B background, each segment was significantly different from the recipient line, and the five lines exhibited approximately the same effect. The effects appeared overestimated, as when three or more segments were cumulated in the same genotype, the effect was always lower than expected by adding individual effects. Such less than additive effects have been attributed to epistatic interactions (Eshed and Zamir, 1996) and could constitute a limit to marker-assisted breeding.

CONCLUSION

The line carrying the five segments in L progeny was crossed to several other lines and the fruit quality of the hybrids was assessed by fruit composition and sensory evaluation. It appeared that although fruit size was reduced, hybrids had improved fruit quality, in comparison to parental lines, promising a potential improvement for the pleasure of consumers.

MAS has thus been shown particularly efficient for a trait as difficult and expensive to evaluate as fruit quality. Once molecular markers closely linked to the desirable alleles were identified, marker-assisted selection was performed in segregating populations and at early stages of plant development. It was thus possible to conduct several rounds of selection in a year. MABC was effective to quickly accumulate up to five QTLs in a single genotype. The availability of reliable PCR-based markers proved crucial for the success of such selection schemes. It seemed also important to re-evaluate QTL effects in advanced generations, as unexpected results may limit the success of MABC.

In the future, it seems important to explore the complementarity between marker-assisted selection and conventional breeding, and to develop overall strategies that tightly and interactively integrate the two approaches.

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Tables

Table 1. Characteristics of the five regions transferred into the recurrent tomato lines.

Chromosome region	Main QTLs (sensory trait)	R^2	Size of the region (cM)	Other QTLs
1	Sourness (+)	12.4	31	(-)[1] : Elasticity
2	Sweetness (+)	24.8	31	(+) : Candy, lemon, citrus fruit aromas, firmness, carotene content (-) : Elasticity, fruit weight
	Overall aroma intensity (+)	24.1		
4	Mealiness (+)	13.4	19	(+) : Content in various volatile compounds, embarrassing skin
	Firmness (+)	31.9		
9a	Sourness (+)	16.8	15	(+) : Lemon aroma, juiciness, dry matter weight, firmness
9b	Pharmaceutical aroma (+)	28.5	17	

[1](+) or (-) sign indicates that the cherry tomato line carries favorable (or unfavorable) alleles to the quality value.

Table 2. Percentage of the donor genome in the initial recombinant inbred line and in the three lines introgressed for the five segments in three different genetic backgrounds.

	LR	BC_3S_3 - L5 L background	BC_3S_3 - B_5 B background	BC_3S_3 - B_5 D background
Non-carrier chromosomes	23.5 %	3.9 %	4 %	0 %
Carrier chromosomes				
outside QTLs	16.5 %	15.8 %	11 %	6 %
within QTLs	13 %	13 %	13 %	13 %
Total	53 %	33 %	28 %	19 %

Table 3. Comparison of QTL effects in BC_3S_1 and RIL L progeny.

Segment	Trait	QTLs detected in the RIL population				QTLs detected in the BC_3S_1 population (L progeny)				
		Marker	LOD	Allele	R^2 (%)	Marker	P	Allele	Dominance[1]	R^2 (%)
1	Dry matter					TG430	0.0099	C	i+	6.5
	Titratable acidity	TG430	3.7	C	11.2	TG430	0.0027	C	a	8.7
	Carotene					TG116	0	C	a	17
2	Fruit weight	TG454	4.3	L	17.4					
		GC039	17.6	L	46.2	GC039	0	L	i-	50.2
	Locule Nb	ASC056	20.2	L	51	TG191	0	L	a	70.4
	Dry matter	TG191	7.4	C	25.6	TG454	0.0001	C	i-	13.5
		GC039	2.9	C	9.9	ASC056	0.001	C	d-	10
						TG250	0	C	a	17
	Soluble Solids	TG454	3.6	C	14.7	TG454	0	C	i-	14.8
		ASC056	4.6	C	18.6	ASC056	0.0001	C	d-	13.6
						TG250	0	C	a	21.1
	Sugars	TG454	2.7	C	11.9					
		ASC056	7.4	C	25.3	TG250	0.0056	C	a	7.5
	Titratable acidity	GC039	5.5	C	17.2	ASC056	0.008	C	d-	6.6
						TG250	0.0003	C	a	12.5
	pH					TG454	0.0049	C	a	7.5
	Carotene	TG167	3.9	C	14.1	GC039	0	C	a	22.5
	Firmness	TG191	2.8	C	9.3					
	L	ASC056	5.8	L	20.1					
	a	TG191	3.9	L	14.1	TG454	0	L	a	26.4
						ASC056	0	L	a	17.6
	b					TG454	0.0043	L	a	7.7
		GC039	5.1	L	15.7	ASC056	0.0093	L	a	6.3
4	Dry matter	CT192	3.11	L	9.5					

(Continued)

Table 3. (Continued)

Segment	Trait	QTLs detected in the RIL population				QTLs detected in the BC_3S_1 population (L progeny)				
		Marker	LOD	Allele	R^2 (%)	Marker	P	Allele	Dominance[1]	R^2 (%)
	Lycopene	TG457	3.9	C	11.7					
	Firmness	TG075	10.9	C	33.3	TG075	0	C	i-	17.5
	L	TG457	6.56	C	19.8	TG075	0.0098	C	d+	7.1
	a	TG457	10.4	C	30.8	TG457	0.0073	C	d-	7.3
	b	TG457	6.2	C	19.3					
9A	Dry matter	CT032	5.7	C	16.8	ASC021	0	C	a	19.5
	Soluble Solids	CT032	4.4	C	13.3	ASC021	0	C	a	19
	Sugars					ASC021	0.0049	C	i+	7.4
	Titratable acidity	CT032	7.8	C	22.4	CT032	0.001	C	a	10.2
	pH					ASC021	0.0014	C	d-	9.4
	Firmness	ASC021	12.7	C	41.1					
	L	CT032	5.2	L	16.5					
	a	CT032	2.7	L	8.3					
	b	CT032	8.8	L	26.5	CT032	0.0074	L	d-	6.8
9B	Fruit weight	TG008	3	L	8					
	pH					TG008	0	L	a	21.8
	Lycopene					TG008	0	L	a	21.1

[1] The dominance level indicates if the QTL effect is additive (a), intermediate unfavorable (i-) if $-1<d/a<-0.5$, intermediate favorable (i+) if $0.5>d/a>1$, recessive (d-) or dominant (d+).

Figures

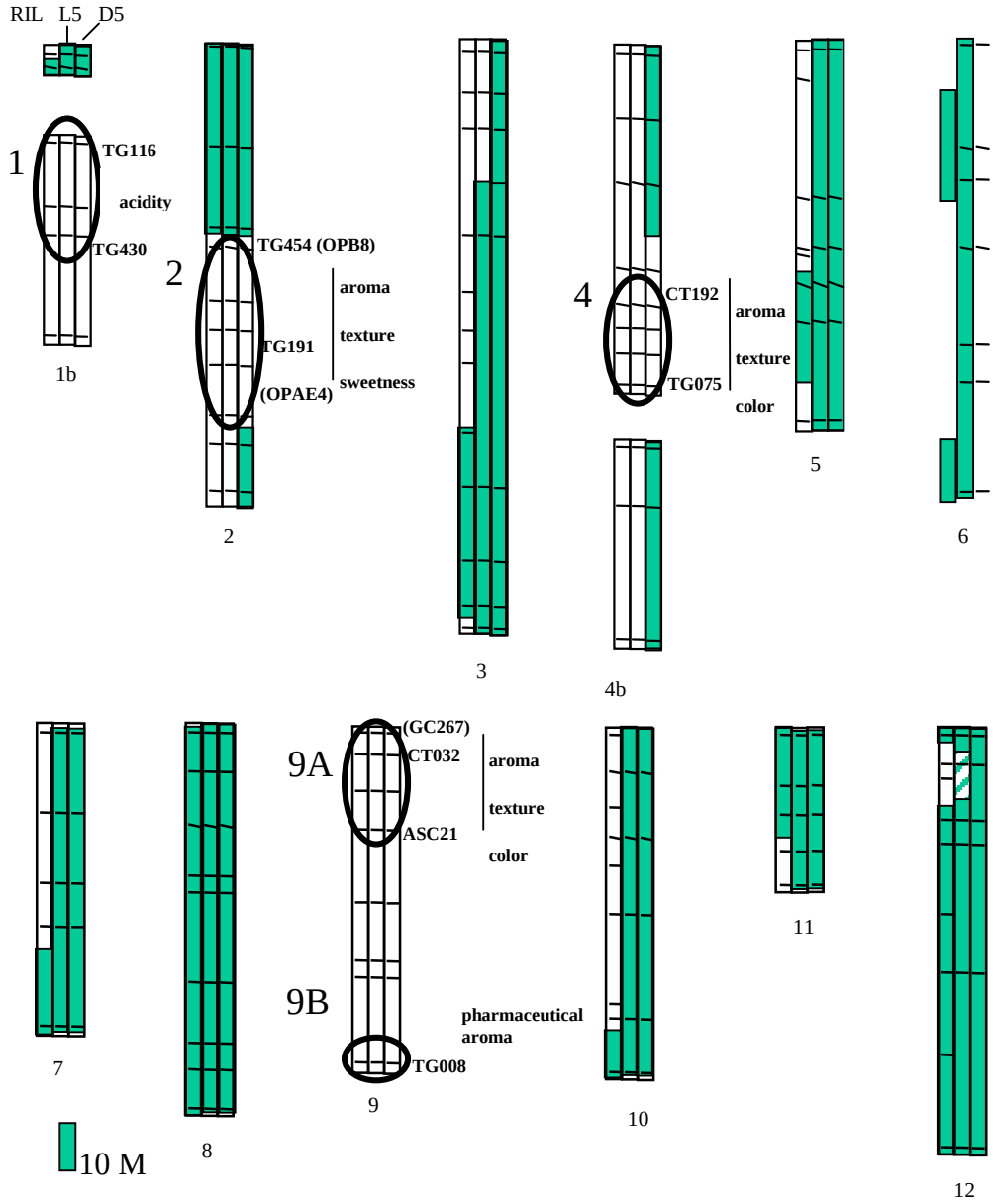

Fig. 1. Graphical genotypes of the recombinant line (on the left) and the two BC_3S_3 lines derived by backcrossing on the L background (L5 in the middle) and on the D background (D5 on the right), carrying C alleles at five regions of interest (circled). Linkage map of the tomato genome is based on an intraspecific RIL population derived from a cross betterave a cherry tomato line and a large-fruited line. Names of the markers used for selection, on the right of the chromosomes are described in Saliba-Colombani et al. (2000). Locations of markers used for background selection are indicated on the scale. Major traits for which QTLs were detected in the RIL population in the five regions are indicated.

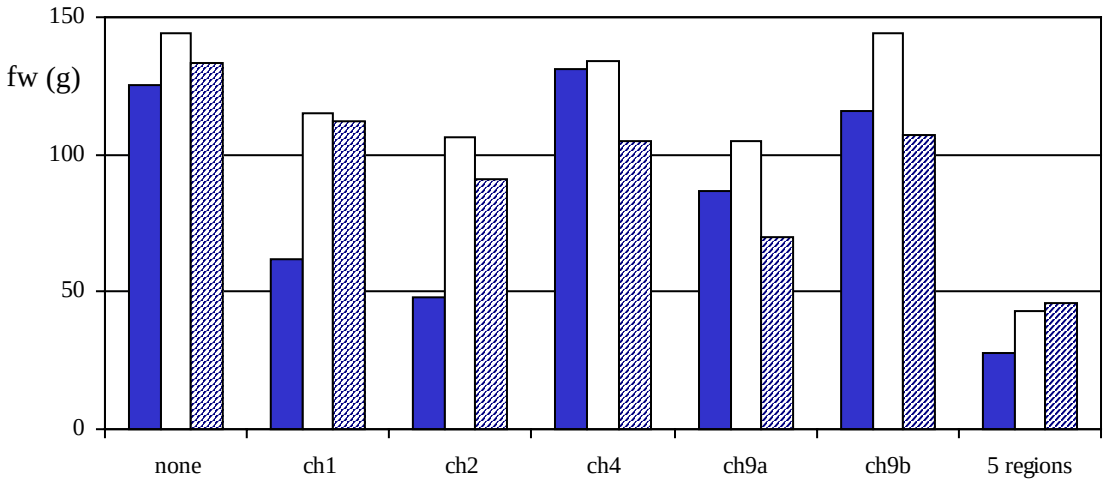

Fig. 2. Fruit weights of the lines derived by marker-assisted backcross that carry C alleles at just one region or at all five selected regions in the three genetic recurrent backgrounds (L in grey, D in white, and B in striped).