

Erratum

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Advanced back-cross QTL analysis of tomato. II. Evaluation of near-isogenic lines carrying single-donor introgressions for desirable wild QTL-alleles derived from *Lycopersicon hirsutum* and *L. pimpinellifolium*

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Due to a technical error, the tables 1–6 were unfortunately not included in the above-mentioned article.

We apologize for this error and print the missing tables.

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Abstract Improved-processing tomato lines were produced by the molecular breeding strategy of advanced backcross QTL (AB-QTL) analysis. These near-

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isogenic lines (NILs) contained unique introgressions of wild alleles originating from two donor wild species, *Lycopersicon hirsutum* (LA1777) and *L. pimpinellifolium* (LA1589). Wild alleles targeted for trait improvement were selected on the basis of previously published replicated QTL data obtained from advanced backcross populations for a battery of important agronomic traits. Twenty three NILs were developed for 15 genomic regions which were predicted to contain 25 quantitative trait factors for the improvement of seven agronomic traits: total yield, red yield, soluble solids, brix × red yield, viscosity, fruit color, and fruit firmness. An evaluation of the agronomic performance of the NILs in five locations worldwide revealed that 22 out of the 25 (88%) quantitative factors showed the phenotypic improvement predicted by QTL analysis of the BC₃ populations, as NILs in at least one location. Per-location gains over the elite control ranged from 9% to 59% for brix × red yield; 14% to 33% for fruit color; 17% to 34% for fruit firmness; 6% to 22% for soluble-solids content; 7% to 22% for viscosity; 15% to 48% for red yield, and 20% to 28% for total yield. The inheritance of QTLs, the implementation of the AB-QTL methodology for characterizing unadapted germplasm and the applicability of this method to other crops are discussed.

Key words Molecular breeding · Germplasm · Quantitative traits

Table 1 Targeted quantitative factors from *L. hirsutum* LA1777 (H) and *L. pimpinellifolium* LA1589 (PM) and corresponding NILs. Targeted QTL are in lower case italics and targeted quantitative factors identified at subthreshold significance are in capitals (trait affected and *marker locus*) (Bernacchi et al. 1997b; Tanksley et al. 1996).

Chr = chromosome. NIL = near isogenic line. SSC = soluble solids; BOS = viscosity Bostwick; YDT = total yield; YDR = red yield; BYR = brix red yield; FC = fruit color and FIR = fruit firmness. See Fig. 1 for cM lengths of introgressed fragments

Targeted factor	Chr	Donor	NIL
SSC-TG260/CT267	1	H	TA523
<i>ssc3.2/BOS-TG417</i>	1	H	TA1257
<i>ydt4.1/YDR-CD59/BYR-CD59</i>	3	H	TA1276
<i>fc4.2/byr4.1/BOS-CT50/SSC-TG163/YDR-TG163</i>	4	H	TA1133
<i>fc5.1/BOS-TG441</i>	4	H	TA517
<i>BYR-TG574/FIR-TG574/YDR-TG574</i>	4	H	TA1284
<i>fc5.1/BOS-TG441</i>	5	H	TA1138
<i>ssc5.1/FC-TG60/CT138</i>	5	H	TA1116
<i>fc11.2</i>	5	H	TA1292
<i>fir3.1</i>	5	H	TA1291
<i>byr3.1/ssc3.1</i>	5	H	TA1293
<i>SSC-CT101</i>	5	H	TA1118
<i>vis9.1</i>	5	H	TA1117
<i>fc11.2</i>	5	H	TA1297
<i>fir3.1</i>	11	H	TA1347
<i>byr3.1/ssc3.1</i>	3	PM	TA515
<i>SSC-CT101</i>	3	PM	TA524
<i>vis9.1</i>	3	PM	94T872-13
<i>FC-TG393</i>	5	PM	94T868-24
<i>fc11.2</i>	9	PM	TA514
<i>fir3.1</i>	9	PM	94T873-30
<i>byr3.1/ssc3.1</i>	9	PM	TA534
<i>FC-TG393</i>	11	PM	TA516

Table 2 Number of QTL/factors for which the corresponding NILs showed the expected phenotypic effect in at least one location. SSC = soluble solids; BOS = viscosity Bostwick; YDT = total yield; YDR = red yield; BYR = brix red yield; FC = fruit color; FIR = fruit firmness

	SSC	BOS	YDT	YDR	BYR	FC	FIR
Total # QTL/factors tested as NILs	6	4	1	3	4	5	2
# showing expected effect at $P \leq 0.1$	4	4	1	2	4	5	2
# showing expected effect at $P \leq 0.05$	4	3	0	1	3	4	2

Table 4 QTL/factors classified according to significance of BC_3 detection and significance of NIL best representing the predicted effects. P = significance level of single point analysis (QTL) and of linear contrast between NIL and control (NIL Δ%). Names of QTL/factors are described in Table 1

Significance of NIL Δ%					
Significance of QTL/factor detection in BC_3	ns	0.1 ≤ P < 0.01	0.01 ≤ P < 0.001	0.001 ≤ P < 0.0001	
0.1 ≤ P < 0.01	<i>ssc5.1</i>	SSC-TG260/CT267 <i>ydt4.1</i> YDR-CD59 BYR-CD59 BOS-CT50 FC-TG60/CT138 BYR-TG574	SSC-CT101	BOS-TG441	
0.01 ≤ P < 0.001	YDR-TG574	YDR-TG163 FIR-TG574 <i>fc5.1</i>	BOS-417 FC-TG393 <i>byr3.1</i>	SSC-TG163	
0.001 ≤ P < 0.0001	<i>ssc3.1</i>	<i>fc4.2</i> <i>vis9.1</i>	<i>ssc3.2</i> <i>byr4.1</i> <i>fir3.1</i> <i>fc11.2</i>		

Table 3 QTL-allelic effect ($\Delta\%$) predicted for the NILs based on BC₃ data compared with observed performance of the NILs. Grouped data are QTL/factors statistics from BC₃ mapping (first row, in italics) and corresponding NIL/s statistics (subsequent rows). If QTL/factor did not reach the threshold significance in BC₃ only the trait affected is described (Bernacchi et al. 1997b). Statistics for QTL are $\Delta\%$ = percent phenotypic change associated with the *L. hirsutum* (H) or *L. pimpinellifolium* (PM) allele; P = significance of the association (Bernacchi et al. 1997b). Statistics for NIL evaluation are $\Delta\%$ = percent phenotypic difference relative to *L. esculentum* control E6203; P = significance of contrast NIL-E6203. Markers, in *italics*, are RFLP loci associated with QTL/factor. Introgression indicates the segments of H DNA contained in the NIL. IS = Israel; SP = Spain; CAP = California, Woodland; CAH = California, Stockton and JP = Japan. ns = not significant ($P > 0.1$). na = not available in a given location. Avg. $\Delta\%$ = average phenotypic effect associated to the H or PM allele, considering only deviations at $P \leq 0.1$ irrespective of the direction of the difference. none sig = none of the contrasts were significant at $P \leq 0.1$. The NILs selected for best performance in the case of QTL/factors represented by more than one NIL are indicated in bold

Trait, QTL (BC ₃) NIL	Donor	Marker Introgression	IS		SP		CAP		CAH		JP		Avg. $\Delta\%$	
			$\Delta\%$	P	$\Delta\%$	P	$\Delta\%$	P	$\Delta\%$	P	$\Delta\%$	P		
<i>Soluble solids</i>	H	<i>TG260/CT267</i>	6	0.03	5	0.07	7	0.07						6.0
TA523		<i>TG260-CT190</i>	9	0.01	-3	ns	-3	ns	6	0.06	7	0.08		7.5
TA1257		<i>CT190</i>	2	ns	-4	ns	4	ns	1	ns	4	ns		ns
<i>Soluble solids, ssc3.2</i>	H	<i>TG417/CT243</i>	11	0.0009	12	0.0006	5	ns						11.5
TA1276		<i>TG417-CT243</i>	5	ns	-1	ns	1	ns	8	0.015	5	ns		8.3
<i>Viscosity (Bostwick)</i>	H	<i>TG417</i>			-2	0.013								-14.6
TA1276		<i>TG417-CT243</i>			2	ns	-9	0.1	-11	0.013	-22	no rep		-9.9
<i>Total Yield, ytd4.1</i>	H	<i>CD59</i>	16	0.03	20	0.078	9	0.1						14.8
TA1133		<i>CD59</i>	-12	0.1	-10	ns	20	0.1			28	0.1		12.0
<i>Red yield</i>	H	<i>CD59</i>	15.4	0.09	26	0.05	2	ns						20.7
TA1133		<i>CD59</i>	-14.2	0.02	3.5	ns	20	0.1	19.1	0.04	48.2	0.03		18.2
<i>Brix red yield</i>	H	<i>CD59</i>	17	0.03	15	ns	-5	ns						17.2
TA1133		<i>CD59</i>	-20	0.005	-5	ns	13	ns	11	ns	42	0.04		10.7
<i>Red yield</i>	H	<i>TG163</i>	-1	ns	-12	ns	33	0.006						32.5
TA517		<i>TG305-CT50-TG163</i>	-14	0.03	15	0.1	5	ns	-12	ns	1	ns		0.5
TA1284	H	<i>CT50-TG163</i>	-1	ns	-19	0.08	-32	0.02	-2	ns				-25.2
<i>Soluble solids</i>	H	<i>TG163</i>	3	ns	10	0.004	5	ns						9.6
TA517		<i>TG305-CT50-TG163</i>	9	0.01	10	0.008	6.31	0.014	22	<0.0001	13.8	0.002		12.2
TA1284		<i>CT50-TG163</i>	13	0.001	9	0.01	0.14	ns	5.5	0.1				9.2
<i>Brix red yield, bry4.1</i>	H	<i>TG163</i>	3	ns	6	ns	41	<0.0001						41.0
TA517		<i>TG305-CT50-TG163</i>	-7	ns	267	0.01	13	ns	8	ns	16	ns		26.5
TA1284		<i>CT50-TG163</i>	11	0.1	-11	ns	-32	0.02	4.	ns				-10.2
<i>Fruit color, fc4.2</i>	H	<i>TG163</i>	46	0.0003	14	0.06	-3	ns						29.7
TA517		<i>TG305-CT50-TG163</i>	7	ns	0	ns	23	0.05	-14	0.1	33	0.03		14.0
TA1284		<i>CT50-TG163</i>	-9	ns	0	ns	-2	ns	7	ns				ns
<i>Viscosity</i>	H	<i>CT50</i>			12	0.04								12.1
TA517		<i>TG305-CT50-TG163</i>			-4	ns	-3	ns	-15	0.001				-15.3
TA1284		<i>CT50-TG163</i>			-13	0.02	-13	0.02	-6	ns				-12.8
<i>Red yield</i>	H	<i>TG574</i>	14	0.08	3	ns	37	0.007						26.5
TA1138		<i>TG264-TG574-CT50</i>	-3	ns	3	ns	16	ns						ns
<i>Brix red yield</i>	H	<i>TG574</i>	12	0.08	9	ns	34	0.01						22.7
TA1138		<i>TG264-TG574-CT50</i>	-1	ns	7	ns	24	0.08	12	0.1	13	ns		18.2

Table 3 Continued

Trait, QTL (BC_3) NIL	Donor	Marker Introgression	IS		SP		CAP		CAH		JP		Avg. Δ%
			Δ%	P	Δ%	P	Δ%	P	Δ%	P	Δ%	P	
Firmness TA1138	H	TG574 TG264-TG574-CT50	-9 17	ns 0.06	17 4	0.01 ns	13 2	ns ns	34	0.04	25 0.1	17.0 25.3	
Fruit color, fc5.1 TA1116	H	TG441 TG441-CT167-CD64	42 7	0.01 ns	15 17	0.06 0.04	2 -2	ns ns	-1	ns	8 ns	28.4 16.7	
TA1291		TG441			0	ns	-2	ns	-1	ns		ns	
TA1292		TG441			6	ns						ns	
TA1293		CD64	7	ns	17	0.04	18	0.1	-1	ns		17.4	
Viscosity TA1116	H	TG441 TG441-CT167-CD64			-12 -3	0.05 ns			-23	< 0.0001		-11.8 -22.5	
TA1291		TG441			6	ns	5	ns	15	0.001		14.7	
TA1292		TG441			-7	ns						ns	
TA1293		CD64			-11	0.053	1	ns	5	ns		-10.6	
Soluble solids, ssc5.1 TA1118	H	TG69 TG69-CT138	12 3	0.01 ns	8 3	0.08 ns	13 -2	0.02 ns	4	ns	-1 ns	11.0 ns	
TA1117		TG69-CT138	1	ns	-4	ns	-5	0.03	-1	ns	-1 ns	-5.4 -5.4	
TA1297		CT138	2	ns	-8	ns	-5	0.03	3	ns	1 ns	-5.4	
Fruit color TA1118	H	TG60/CT138 TG69-CT138	31 -4	0.06 ns	5. 0	0.01 ns	6 13	0.052 ns	11	ns	25 8	0.1 ns	14.0 25.0
TA1117		TG69-CT138	7	ns	6	ns	18	0.1	7	ns		18.0	
TA1297		CT138	-9	ns	-11	0.1	3	ns	-10	ns	8	ns	-11.1
Fruit color, fc11.2 TA1347	H	TG393 TG393	46 14	0.0002 0.02	-3 3	ns ns	2 0	ns ns	-20	0.02	8 ns	46.2 -2.6	
Soluble solids ssc3.1/3.2 TA524	PM	TG129/CD51/TG388 TG246-TG129-CD51-TG388	7 -2	0.04 ns	7 -4	0.0007 ns	7 -8	< 0.0001 0.002	-4	ns	-1 ns	7.1 -7.9	
94T872-13		TG246-TG129-CD51	3	ns	-11	0.03	na	na	-3	ns	-5 ns	-10.8	
94T868-24		TG388	2	ns	-6	0.1	-5	0.04	-3	ns	-1 ns	-5.4	
Brix red yield, byr3.1 TA524	PM	CD51-TG388 TG246-TG129-CD51-TG388	5 9	ns 0.1	18 2	0.001 ns	-8	ns	9	ns	59 0.005	18.2 34.1	
94T872-13		TG246-TG129-CD51	25	0.001	-15	ns			0	ns	-7 ns	24.7	
94T868-24		TG388	7	ns	-3	ns	-19	0.1	6	ns	8 ns	-19.4	
Firmness, fir3.1 TA515	PM	TG525 TG114-TG525-CT141-TG66	40 22	0.0001 0.01	4	ns	2	ns	34	ns	-17 ns	40.0 22.2	
Soluble solids TA514	PM	CT101	-1 2.1	ns ns	1 11	ns 0.005	5.2	0.04	-7	0.04	5 ns	5.2 1.70	
Viscosity, vis9.1 TA534	PM	TG421 TG421			-13 -8	0.0003 0.1			-3	ns	-36 no rep	-13 -7.5	
94T873-30		TG421-CT74-TG551			-3	ns	-5	ns	-5	ns	-28 no rep	ns	
Fruit color TA516	PM	TG393-I2-TG36-TG546	11 18	ns ns	23 25	0.009 0.002	1 17	ns 0.1	-15	0.07	25 0.07	2.3 12.9	

Table 5 QTL/factors classified according to the number of locations of BC₃ detection and the number of locations where corresponding NIL showed the predicted effect (NIL Δ%) ($P \leq 0.1$). Names of QTL/factors are described in Table 1

Number Loc. QTL/factor detection in BC ₃	Number Loc. significant NIL Δ% in predicted direction				
	0	1	2	3	5
1		<i>fir3.1</i> SSC-CT101 BOS-TG441 <i>fc11.2</i> BYR-CD59 <i>byr4.1</i>	<i>byr3.1</i> YDR-TG163 BOS-CT50 <i>fc5.1</i> <i>ssc3.2</i>	FIR-TG574 FC-TG393	SSC-TG163
2		YDR-TG574	<i>BYR-TG574</i> <i>fc4.2</i>		YDR CD59
3	<i>ssc3.1</i> <i>ssc5.1</i>	FC-TG60/CT138	<i>ydt4.1</i>		SSC-TG260/CT267

Table 6 Percent phenotypic differences between NILs and the *L. esculentum* control for traits other than those predicted by QTL analysis results. Δ% = percent phenotypic difference. Only the best performing NIL for each target are considered. IS = Israel; SP = Spain; CAP = California; Woodland; CAH = California, Stockton and JP = Japan. FC = fruit color; BYR = brix × red yield; YDR = red yield; FIR = fruit firmness; AFW = average fruit weight; SSC = soluble solids; BOS = viscosity Bostwick; YDT = total yield. Loc = location. The original association

NIL	Trait	NIL deviations from E6203 at $P < 0.1$								BC ₃ mapping
		Loc	Δ%	Loc	Δ%	Loc	Δ%	Loc	Δ%	
TA253	FC	IS	+15	JP	+48	SP	-22	SP	+11	<i>fc1.3</i> -33%, (-CAP) (-CAP) (-IS, -CAP)
	BYR	CAH	+22							
	YDR	JP	+38							
	FIR	CAH	+46							
	AFW	CAH	-10							
TA1276	FC	CAP	-4	JP	-10	IS	-15	SP	+11	(+SP, +CAP) (-SP) (-IS, -SP, -CAP) (-IS, -SP)
	FIR	CAH	-23	SP	-12					
	YDR	IS	-11							
	AFW	CAH	-15	CAP	-12					
TA1133	BOS	CAH	-9	CAP	-8	SP	-20	SP	-7	(-CAP)
	SSC	CAH	-7	CAP	-6	IS	-6			
	AFW	CAH	-14	IS	-15	SP	-18			
TA517	pH	SP	+2	JP	+1.5	IS	-21	SP	-20	(-SP, -CAP) (-SP)
	YDT	IS	-16							
	FIR	SP	-12	JP	-23					
	AFW	CAH	-25	CAP	-21					
TA1284	YDT	CAP	-31	IS	-15	SP	-16	SP	-20	(-SP)
	AFW	CAH	-15							
TA1138	BOS	CAH	+12	CAP	+13	JP	+21	SP		(+SP) ^a (+SP) ^a (-SP, -CAP)
	SSC	CAH	+7	CAP	+6					
	AFW	CAH	-12	CAP	-12					
	FC	SP	-8							
TA1116	SSC	CAH	+9	IS	+8	JP	+25	SP	-32% (-SP) ^a (-IS, -SP)	
	FIR	CAH	+53	IS	+22					
	AFW	CAH	-20	SP	-21					
TA1117	FIR	JP	-23	SP	-17	SP	-20	SP	-32% (-SP) ^a (-IS, -SP)	
	BYR	IS	-20	SP	-20					

between the introgressed markers and any given trait are given under BC₃ association (Bernacchi et al. 1997b) as follows: if a QTL was detected with significance in the BC₃, its name is given as well as the estimated phenotypic effect associated with the wild allele; if an association failing to reach QTL significance was detected, the location in which it was detected is given in brackets, preceded by a negative sign (-) if the H or PM allele was associated with inferior performance or a positive sign (+) if H or PM allele improved the trait

NIL	Trait	NIL deviations from E6203 at $P < 0.1$								BC ₃ mapping
		Loc	Δ%	Loc	Δ%	Loc	Δ%	Loc	Δ%	
TA253	FC	IS	+15	JP	+48	SP	-22	SP	+11	<i>fc1.3</i> -33%, (-CAP) (-CAP) (-IS, -CAP)
	BYR	CAH	+22							
	YDR	JP	+38							
	FIR	CAH	+46							
	AFW	CAH	-10							
TA1276	FC	CAP	-4	JP	-10	IS	-15	SP	+11	(+SP, +CAP) (-SP) (-IS, -SP, -CAP) (-IS, -SP)
	FIR	CAH	-23	SP	-12					
	YDR	IS	-11							
	AFW	CAH	-15	CAP	-12					
TA1133	BOS	CAH	-9	CAP	-8	SP	-20	SP	-7	(-CAP)
	SSC	CAH	-7	CAP	-6	IS	-6			
	AFW	CAH	-14	IS	-15	SP	-18			
TA517	pH	SP	+2	JP	+1.5	IS	-21	SP	-20	(-SP, -CAP) (-SP)
	YDT	IS	-16							
	FIR	SP	-12	JP	-23					
	AFW	CAH	-25	CAP	-21					
TA1284	YDT	CAP	-31	IS	-15	SP	-16	SP	-20	(-SP)
	AFW	CAH	-15							
TA1138	BOS	CAH	+12	CAP	+13	JP	+21	SP		(+SP) ^a (+SP) ^a (-SP, -CAP)
	SSC	CAH	+7	CAP	+6					
	AFW	CAH	-12	CAP	-12					
	FC	SP	-8							
TA1116	SSC	CAH	+9	IS	+8	JP	+25	SP	-32% (-SP) ^a (-IS, -SP)	
	FIR	CAH	+53	IS	+22					
	AFW	CAH	-20	SP	-21					
TA1117	FIR	JP	-23	SP	-17	SP	-20	SP	-32% (-SP) ^a (-IS, -SP)	
	BYR	IS	-20	SP	-20					

Table 6 Continued

NIL	Trait	NIL deviations from E6203 at P < 0.1								BC ₃ mapping
		Loc	Δ%	Loc	Δ%	Loc	Δ%	Loc	Δ%	
TA1347	FIR	CAH	+27							(-SP) (+IS) (-IS, -SP)
	BYR	JP	+53	SP	-24					
	YDR	JP	+51							
	BOS	CAH	-15							
	SSC	CAP	-7	SP	-7	IS	+5			
	FC	CAP	-21							
TA524	AFW	CAH	-11							
	BOS	CAH	+10							(-SP)
	YDR	JP	+60	IS	+11					(+SP)
	FIR	JP	+33							(-CAP, -IS, -SP)
TA516	AFW	CAH	-15	SP	-16					
	BYR	SP	-24							(+IS)
	SSC	CAP	-5							(+CAP, +SP)
TA514	AFW	CAH	-8	CAP	-25	IS	-16	SP	+12	(-CAP, -IS, -SP)
	BYR	IS	+18							
	FC	IS	+36							(+SP)
	FIR	JP	+34							
TA534	FIR	SP	-12	JP	-33					
	YDR	JP	+30	SP	+29					(+ IS) ^a
	BYR	SP	+18							
	FIR	CAH	+34	SP	+13					
	SSC	SP	-8							(-SP) ^a
TA515	FC	CAH	-22	CAP	-16	SP	-11			(-SP)
	FIR	CAH	+53	CAP	-23					(+IS)
	AFW	SP	+20	CAH	-13	CAP	-32			(-IS)

^aA QTL or a subthreshold association was detected for the RFLP marker adjacent to introgressed segment