Gene Mapping in Tomato

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Abstract

Tomato is a model species for genetic analyses since a long time. Many mutations controlled by a single gene were discovered and the underlying genes were mapped first on the tomato genetic map. Most of these genes are involved in fruit colour and shape, in plant growth and architecture and in disease resistances. With the construction of high-density molecular genetic maps, many genes were located on the genome and subsequently several of them were fine-mapped and further identified by positional cloning. Today with the availability of the tomato genome sequence these genes are physically located on the genome and the identification of new ones is being considerably accelerated. The alignment of the physical and genetic maps allowed the identification of hot spots of recombination and of large regions where recombination is almost suppressed, whatever the progeny studied. The impact of this heterogeneity in recombination is discussed.

Keywords

Tomato · Gene mapping · Mutations · Resistance · Fruit quality

Introduction

Tomato has been a model species for genetic analyses for years. The diversity of its fruit colour, shape and size has interested geneticists since the early work of genetic mapping. Butler (1952) proposed one of the first genetic maps including more than 50 loci corresponding to phenotypic mutations. Nevertheless, until the discovery of molecular markers in the late 1980s, the location of mutations on genetic maps was not really precise as it was impossible to

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simultaneously map many loci. Molecular markers have enabled biologists to construct saturated linkage maps of the genome and to systematically localize mutations of interest on these maps. Over years, more and more markers were discovered and the genotyping cost decreased. Following isozymes, the first DNA markers, based on the detection of Restriction Fragment Length Polymorphisms (RFLP), allowed the construction of a reference map of the tomato genome (Tanksley et al. 1992). With more than 1000 loci, spread on the 12 chromosomes, this map allowed the precise localization of several mutations and of a few genes of interest. New mutations or genes of interest were subsequently mapped using either F_2 populations or pairs of near isogenic lines differing only in the region of the interesting gene (Laterrot 1996). Bulks of individuals were later used (following the Bulk Segregant Analysis method), together with markers based on PCR amplification of the DNA (RAPD or AFLP markers). Following the identification of PCR markers linked to the gene of interest, specific PCR markers were set up, simplifying the genotyping step for breeders. Nevertheless, PCR markers such as RAPD or AFLP are dominant and map for the most part close to the centromeres, reducing their potential efficiency for gene mapping in tomato (Grandillo and Tanksley 1996; Haanstra et al. 1999; Saliba-Colombani et al. 2000). Markers based on the variation in the number of small sequence repeats (microsatellites or SSR) were then discovered and mapped on the reference map or used for the construction of new maps (He et al. 2002; Liu et al. 2005). To increase the number of markers available and to use the microsynteny observed with the *Arabidopsis thaliana* genome, Fulton et al. (2002) proposed the use of Conserved Ortholog Sequences (COS) as markers.

The polymorphism revealed by RFLP markers among cultivated accessions was very low and only a few markers were polymorphic and thus useful for mapping genes in such genetic background (Saliba-Colombani et al. 2000). Interspecific progenies were much more polymorphic and maps based on progenies derived from crosses with every wild species related to tomato were constructed (Labate et al. 2007). A population of introgression lines derived from a cross with a *Solanum pennellii* accession (Eshed and Zamir 1995) was particularly useful to discover new genes and quantitative trait loci (QTL) involved in fruit colour, size and plant traits (Zamir 2001).

More recently, several tomato accessions were used to sequence fragments of expressed sequences and identify Expressed Sequence Tags (ESTs), allowing the first Single Nucleotide Polymorphism (SNP) markers to be discovered and mapped (Labate and Baldo 2005; Sim et al. 2009). With the access to the tomato genome sequence (Tomato Genome Consortium 2012), the increased throughput of sequencing and the advances in Next Generation Sequencing technologies, it has been possible to discover thousands of SNPs through RNA sequencing (RNAseq). The SolCAP consortium developed a SNP array carrying more than 8000 SNPs chosen to reveal polymorphisms among cultivated accessions (Sim et al. 2012). Another SNP array was developed by Víquez-Zamora et al. (2013). Today, thanks to the tomato genome sequence availability, several projects of resequencing whole genomes of tomato accessions allowed the discovery of several millions of SNP (Causse et al. 2013; Aflitos et al. 2014; Lin et al. 2014) and the construction of genetic maps at the intraspecific level is now possible (Shirasawa et al. 2010). Large SNP arrays permit the rapid mapping of new loci of interest (Viquez-Zamora et al. 2014).

Genes and Loci Involved in Morphological and Fruit Characteristics

Among the major mutations used in tomato, the self-pruning (*sp*) mutation was discovered about 100 years ago and confers the determinate growth behaviour. It was largely used in processing tomato for field grown production. The tomato *SELF-PRUNING* (*SP*) gene is the homolog of the *Antirrhinum majus CENTRORADIALIS* (*CEN*) and *Arabidopsis thaliana TERMINAL FLOWER1* (*TFL1*) genes (Pnueli et al. 1998).

Many mutations in genes related to the carotenoid pathway were identified and correspond to specific fruit colours (Hirschberg 2001). Among them the *B/ogc* locus has been shown to correspond to two mutations in the same gene responsible for either yellow or dark red colour of the fruit (Ronen et al. 2000). Recently the gene conferring the uniform ripening (*u*) phenotype was cloned and shown to correspond to a Golden 2-like (GLK) transcription factor, which determines the chlorophyll accumulation and distribution in developing fruit (Powell et al. 2012). The *y* locus, responsible for the pink fruit colour (due to a colourless peel which lacks the yellow flavonoid pigment naringenin chalcone), was also cloned. It corresponds to a MYB transcription factor (Adato et al. 2009; Ballester et al. 2010). Several alleles and their polymorphisms were identified at the *y* locus, thanks to the recent resequencing of more than 300 tomato accessions (Lin et al. 2014). Several mutations confer a long shelf life to the fruit. The most widely used, *rin* (for ripening inhibitor) corresponds to a deletion in a MADS BOX transcription factor (Vrebalov et al. 2002). Another important discovery was the mutation at the *Cnr* locus (Colourless non-ripening), which was one of the first epiallele discovered in tomato (Manning et al. 2006). Table 3.1 lists the genes involved in morphological and fruit mutations.

Disease Resistance Genes

Tomato is susceptible to many pathogens and all the resistance genes (R) were discovered in wild relatives. Many tomato disease resistance genes were mapped and characterized (Table 3.2). Since the first positionally cloned R gene (*Pto*, by Martin et al. 1993), more than 20 genes were cloned and characterized. Their structure and evolution was analyzed and the great conservation among genes conferring resistance to different types of pathogens revealed. The majority of R genes cloned so far encode proteins with a nucleotide-binding site (NBS) and a leucine-rich repeat (LRR) region (Ellis et al. 2000).

Mutant Collections

Many natural mutations were discovered in tomato. The Tomato Genetic Resources Center (TGRC, Davis, California, USA) collection encompasses more than 1000 monogenic mutants at over 600 loci, including spontaneous and induced mutations affecting many aspects of plant development and morphology, disease resistance genes, protein marker stocks, and other traits of economic importance (Chetelat 2005). Genetic data on individual stocks, including phenotypes, images, chromosome locations, etc. are available at the TGRC website (http://tgrc.ucdavis.edu/).

An additional series of provisional (i.e. less well-characterized) mutants is also available. The Hebrew University of Jerusalem developed an isogenic mutant library in the genetic background of cv. M82 (http://zamir.sgn.cornell.edu/mutants/index.html). A total of 13,000 M_2 families, generated by ethylmethane sulfonate (EMS) and fast-neutron mutagenesis, were phenotypically analyzed and catalogued into at least 3417 mutations (Menda et al. 2004). This series of mutations includes many previously described mutant phenotypes as well as many novel mutants, and multiple alleles per locus. Screening this collection allowed the discovery of interesting alleles which interact with the *SP* gene and whose mutation modify its expression and may allow optimization of crop productivity (Park et al. 2014). Other collections of mutants are available (Okabe et al. 2011). Together these mutant collections provide important tools for analyses of gene function either through forward or reverse genetic approaches (Chap. 5).

Recombination Heterogeneity

Many genes/mutations were mapped on a genetic map but not yet cloned (Table 3.3). The recent availability of the tomato genome sequence confirmed earlier observations that recombination is unevenly distributed along chromosomes and that large pieces of the chromosomes around the centromeres do not recombine at all

Table 3.1 Cloned genes with a phenotyped mutant mapped on the tomato genome assembly

ITAG gene model	Gene symbol	locus_name	Chromosome	Start	End	Phenotypic descriptors	References
Solyc01g008930	au	AUREA phytochromobilin synthase	1	2,948,574	2,955,890	Phytochrome-deficient	Muramoto et al. (2005)
Solyc01g056340	hp-2	De-etiolated 1	1	46,495,644	46,516,174	High pigment	Mustilli et al. (1999)
Solyc01g059870	phyB1	Apophytochrome B1	1	61,760,931	61,767,869	Red light reception	Weller et al. (2001)
Solyc01g079620	y	Colourless epidermis*	1	71,255,600	71,258,882	Pink epidermis	Ballester et al. (2010)
Solyc01g100490	chln	Chloronerva	1	82,262,052	82,263,287	Chlorophyll deficiency	Ling et al. (1999)
Solyc01g104340	gr	Green ripe	1	84,508,287	84,509,191	Reduces ethylene sensitivity in fruit	Barry and Giovannoni (2006)
Solyc02g021650	hp-1	UV damaged DNA binding protein 1	2	14,069,796	14,090,192	High pigment fruit pericarp	Lieberman et al. (2004); Liu et al. (2004)
Solyc02g077390	s	Compound inflorescence	2	36,913,957	36,915,889	Inflorescence branching	Lippman et al. (2008)
Solyc02g077920	Cnr	Colourless non-ripening	2	37,323,107	37,320,931	Inhibition of ripening	Manning et al. (2006)
Solyc02g080250	Wo	Wooly	2	39,094,298	39,095,666	High trichome density	Yang et al. (2011)
Solyc02g081120	Me	Knotted 2	2	39,767,063	39,773,953	Leaf complexity	Parnis et al. (1997)
Solyc02g081670	an	Anantha	2	40,120,235	40,121,602	Compound inflorescence, aborted flowers	Lippman et al. (2008)
Solyc02g089160	d	Dwarf	2	45,622,114	45,624,672	Dwarf plant, dpy	Bishop et al. (1996)
Solyc02g090890	hp-3	Zeaxanthin epoxidase	2	46,947,557	46,953,158	High pigment in fruits	Thompson et al. (2000)
Solyc03g007960	wf	Beta-carotene hydroxylase-2	3	2,447,949	2,450,014	White flower	Galpaz et al. (2006)
Solyc03g031860	r	Phytoene synthase 1	3	8,606,749	8,610,050	Yellow fruit	Fray and Grierson (1993)
Solyc03g063100	sft	Single flower truss	3	30,564,833	30,568,648	Single flower truss	Molinero-Rosales et al. (2004)

(continued)

Table 3.1 (continued)

ITAG gene model	Gene symbol	locus_name	Chromosome	Start	End	Phenotypic descriptors	References
Solyc03g083910	sucr	Sucrose accumulator	3	47,401,871	47,397,595	Accumulates predominantly sucrose in mature fruit, rather than glucose and fructose	Sato et al. (1993)
Solyc03g118160	fa	Falsiflora	3	61,162,449	61,164,404	Leafy inflorescence	Molinero-Rosales et al. (1999)
Solyc03g119060	div	Divaricata	3	61,827,331	61,831,038	Small squarrose plant with intercostally yellowish leaves and ventrally purple	van der Biezen et al. (1996)
Solyc03g119770	SlBrc1a	Branched1a	3	62,381,910	62,383,042	Shoot branching	Martín-Trillo et al. (2011)
Solyc04g051510	cu-3	Curl-3	4	49,870,634	49,874,257	Dwarf	Montoya et al. (2002)
Solyc04g074180	cry1a	Cryptochrome 1A	4	57,772,528	57,777,909	Blue light reception	Weller et al. (2001)
Solyc04g076850	e	Entire	4	59,354,677	59,358,365	Reduced leaf complexity	Zhang et al. (2007)
Solyc04g082520	cwp1	Cuticular water permeability 1	4	63,765,366	63,766,988	Microfissure/dehydration of fruits	Hovav et al. (2007)
Solyc05g005020	gwd	Alpha-glucan water dikinase	5	32,905	50,320	Starch excess phenotype and reduced pollen germination	Nashilevitz et al. (2009)
Solyc05g009380	lyr	Lyrate	5	3,536,207	3,540,567	Reduced leaf complexity	David-Schwartz et al. (2009)
Solyc05g012020	rin	Ripening inhibitor	5	5,217,073	5,230,708	Never ripening	Vrebalov et al. (2002)
Solyc05g012020	mc	Macrocalyx	5	5,217,073	5,230,708	Large sepals	Vrebalov et al. (2002)
Solyc05g053410	phyB2	Apophytochrome B2	5	62,648,223	62,653,411	Red light reception	Weller et al. (2001)
Solyc06g051550	fe	fe inefficient	6	31,547,361	31,549,010	Iron deficiency	Ling et al. (2002)
Solyc06g069240	SlBrc1b	Branched1b	6	39,396,681	39,398,027	Shoot branching	Martín-Trillo et al. (2011)
Solyc06g074240	B	Beta-carotene	6	42,288,127	42,289,623	Increased fruit beta-carotene	Ronen et al. (2000)
Solyc06g074350	sp	Self-pruning	6	42,361,623	42,363,883	Determinate plant habit	Pnueli et al. (1998)
Solyc06g074910	C	Potato leaf	6	42,804,036	42,806,196	Simple leaves	Busch et al. (2011)
Solyc07g056570	not	Notabilis	7	61,684,846	61,686,663	ABA deficiency. Wilty	Burbidge et al. (1999)

(continued)

Table 3.1 (continued)

ITAG gene model	Gene symbol	locus_name	Chromosome	Start	End	Phenotypic descriptors	References
Solyc07g062680	La	Lanceolate	7	62,593,583	62,594,785	Simple leaves	Ori et al. (2007)
Solyc07g062840	gob	Goblet	7	62,710,395	62,710,928	Shoot apical meristem terminates but occasionally partially recovers	Berger et al. (2009)
Solyc07g066250	ls	Lateral suppresser	7	64,958,148	64,959,434	Few or no axillary branches; corolla suppressed; partially male sterile	Schumacher et al. (1999)
Solyc07g066480	flacca	Flacca	7	65,118,760	65,130,514	Wilty	Sagi et al. (2002)
Solyc08g080090	Gr	Green flesh	8	60,582,066	60,579,438	Green fruit flesh	Barry et al. (2008)
Solyc09g075440	Nr	Never ripe	9	62,631,866	62,639,953	Not ripening	Wilkinson et al. (1995)
Solyc10g044670	phyA	Apophytochrome A	10	22,854,459	22,859,333	Far red light insensitive	Weller et al. (2001)
Solyc10g081650	t	Carotenoid isomerase	10	62,006,972	62,011,520	Orange fruit flesh	Isaacson et al. (2002)
Solyc10g081470	L-2	Lutescent-2	10	61,858,478	61,851,435	Altered chloroplast development and delayed ripening	Barry et al. (2012)
Solyc10g008160	*u*	Fruit ripening *(uniform ripening)*	10	2,293,088	2,295,824	Increased chlorophyl content	Powell et al. (2012)
Solyc11g010570	j	Jointless	11	3,640,857	3,645,766	No pedicel abscission zone	Mao et al. (2000)
Solyc11g011260	pro	Procera	11	4,303,769	4,305,535	Suppressed axillary bud development and altered branching architecture	Bassel et al. (2008)
Solyc11g011990	ghost	Plastid terminal oxidase	11	4,937,989	4,942,674	White seedlings	Josse et al. (2000)
Solyc11g069030	bl	Blind	11	50,686,745	50,688,284	Stem terminating in first inflorescence; midribs may develop adventitious shoots	Schmitz et al. (2002)
Solyc12g008980	Del	Del	12	2,285,372	2,290,327	Orange fruit	Ronen et al. (1999)
Solyc12g009470	Yg2	Heme oxygenase 1	12	2,726,504	2,729,459	Phytochrome-deficient	Terry and Kendrick (1996)
*	ht-a	HT-A	12	47,894,134	47,896,625	Self incompatibility gene from *S. peruvianum*	Kondo et al. (2002)
*	ht-b	HT-B	12	47,896,590	47,896,869	Self incompatibility gene from *S. peruvianum*	Kondo et al. (2002)

*indicate loci that do not have a corresponding Solyc gene

Table 3.2 Disease resistance genes cloned

ITAG gene model	Gene symbol	locus_name	Chromosome	Start	End	Phenotypic descriptors	References
*	cf-9	Cladosporium fulvum resistance-9	1	3,972,616	3,975,213	Defense responses to specific races of *Cladosporium fulvum*	Jones et al. (1994)
Solyc02g062560	tm-1	Tobacco mosaic virus resistance-1	2	28,856,001	28,864,037	TMV resistance	Ishibashi et al. (2007)
Solyc03g005870	pot	Eukaryotic translation initiation factor 4E (eIF4E)	3	590,087	59,328	Potyvirus immunity	Piron et al. (2010)
Solyc03g114600	asc	Alternaria stem canker resistance	3	58,592,692	58,594,435	Alternaria stem canker resistance	Mesbah et al. (1999)
*	Hero	Heterodera rostochiensis resistance	4	1,795,425	1,799,656	Cyst nematode resistance	Ernst et al. (2002)
Solyc05g013280	pfr	Pseudomonas resistance	5	6,379,823	6,385,909	Pseudomonas resistance	Salmeron et al. (1996)
Solyc05g013290	Fen	Fenthion	5	6,387,418	6,388,380	Confers sensitivity to the insecticide Fenthion	Martin et al. (1994)
Solyc05g013300	pto	Pseudomonas syringae pv tomato resis.	5	6,404,160	6,405,095	Resistance to bacterial speck disease	Martin et al. (1994)
Solyc05g052620	coi1	Coronatine-insensitive 1	5	61,968,745	61,974,317	Jasmonate signalling in *Pseudomonas syringae* response	Katsir et al. (2008)
Solyc05g007850	bs-4	Bacterial spot disease resistance protein 4	5	62,136,023	62,140,081	Mediates HR against *Xanthomonas campestris pv. vesicatoria*	Schornack et al. (2004) and Ballvora et al. (2001)
Solyc06g008270	Cf2.2	Cladosporium fulvum resistance 2.2	6	2,139,526	2,142,150	*Cladosporium fulvum* resistance	Dixon et al. (1996)
Solyc06g008300	cf2	Cladosporium fulvum resistance 2.1	6	2,164,746	2,161,344	*Cladosporium fulvum* resistance	Dixon et al. (1996)

(continued)

Table 3.2 (continued)

ITAG gene model	Gene symbol	locus_name	Chromosome	Start	End	Phenotypic descriptors	References
*	Mi-1.1	Mi-1.1	6	2,327,468	2,331,298	Unknown	Bhattarai et al. (2007)
*	Mi-1.2	Mi-1.2	6	2,354,799	2,358,629	*Meloidogyne incognita* resistance	Kaloshian et al. (1998)
Solyc06g051170, Solyc06g051180, and Solyc06g051190	Ty-1/Ty-3	TYLCV	6	30,862,817	30,879,542	Tomato yellow leaf curl virus	Verlaan et al. (2013)
Solyc09g005080	Ve2	Verticillium wilt disease resistance	9	48,645	52,064	verticillium wilt disease resistance	Kawchuk et al. (2001)
Solyc09g005090	Ve1	Verticillium wilt disease resistance	9	55,478	58,639	Verticillium wilt disease resistance	Kawchuk et al. (2001)
*	Tm-2	Tobacco mosaic virus resistance-2	9	13,621,396	13,623,981	TMV resistance	Lanfermeijer et al. (2003)
Solyc09g098130	Sw-5	Spotted wilt resistance-5	9	67,301,675	67,305,412	Spotted wilt resistance	Brommonschenkel et al. (2000)
Solyc09g092280-Solyc09g092310	Ph-3	Phytophtora infestans	9L	66,764,694	66,795,551	Late blight resistance	Zhang et al. (2013, 2014)
Solyc11g071430	I-2	Immunity to Fusarium wilt race 2	11	51,992,917	51,996,706	Fusarium resistance	Ori et al. (1997)

*indicate loci that do not have a corresponding Solyc gene

Table 3.3 Genes mapped on a genetic map with a phenotype but not yet cloned

Gene symbol	Phenotypic descriptors	Chromosome	References
S	Self incompatibility	1	Tanksley and Loaiza-Figueroa (1985) and Rivers et al. (1993)
ms-10	Male sterility	2	Tanksley et al. (1992)
af	Anthocyanin free	5	Rick 1980 (cited by Tanksley et al. 1992)
tf	Trifoliate	5	Rick 1980 (cited by Tanksley et al. 1992)
ae	Entirely anthocyaninless	8	Rick 1980 (cited by Tanksley et al. 1992)
h	Hairs absent	10	Rick 1980 (cited by Tanksley et al. 1992)
ag	Anthocyanin gainer	10	Rick 1980 (cited by Tanksley et al. 1992)
hl	Hairless	11	Rick 1980 (cited by Tanksley et al. 1992)
a	Anthocianinless	11	Rick 1980 (cited by Tanksley et al. 1992)
alb	Albescent	12	Rick 1980 (cited by Tanksley et al. 1992)
alc	Fruit ripening *(alcobaca)*	10	Kinzer et al. (1990)
nor	Fruit ripening *(non-ripening)*	10	Moore et al. (2002)
j-2	Jointless	12	Budiman et al. (2004)
Disease resistance genes mapped but not yet cloned			
Cf-4	Cladosporium fulvum (leaf mold)	1	Thomas et al. (1997)
Cf-1	Cladosporium fulvum (leaf mold)	1	Jones et al. (1993)
rx-1, rx-2,	Hypersensitive reaction	1	Yu et al. (1995)
Cf-ECP2, Cf-ECP3	Cladosporium fulvum (leaf mold)	1	Haanstra et al. (1999) and Yuan et al. (2002)
Cf-ECP5	Cladosporium fulvum (leaf mold)	1	Haanstra et al. (2000)
Cf-ECP1, Cf-ECP4	Cladosporium fulvum (leaf mold)	1	Soumpourou et al. (2007)
I-5,	*Fusarium oxysporum f. sp.lycopersici* (race 2)	2	Sela-Buurlage et al. (2001)
Xv4	*Xanthomonas campestris pv. vesicatoria (race T3*	3	Astua-Monge et al. (2000)
pot-1	*Potato virus Y* (PVY) and *Tobacco etch virus* (TEV)	3S	Parrella et al. (2002a, b) and Ruffel et al. (2005)
py-1	*Pyrenochaeta lycopersici (corky root)*	3S	Doganlar et al. (1998)
ol-2	*Oidium neolycopersici (Powdery Mildew)*	4C	De Giovanni et al. (2004) and Bai et al. (2008)
rx-3	*Xanthomonas campestris* pv. *vesicatoria*	5	Yu et al. (1995)
Ol-1	*Oidium neolycopersici (Powdery Mildew)*	6L	Huang et al. (2000a) and Bai et al. (2005)
Ol-3	*Oidium neolycopersici (Powdery Mildew)*	6L	Huang et al. (2000b) and Bai et al. (2005)
Ol-4	*Oidium neolycopersici (Powdery Mildew)*	6	Bai et al. (2004, 2005)
Ol-5	*Oidium neolycopersici (Powdery Mildew)*	6L	Bai et al. (2005)
Am	Alfalfa Mosaic Virus (AMV)	6S	Parrella et al. (2004)

(continued)

Table 3.3 (continued)

Gene symbol	Phenotypic descriptors	Chromosome	References
Cf-5	Cladosporium fulvum (leaf mold)	6S	Dixon et al. (1998)
Mi-9	*Meloydogine* spp. nematode (root-knot)	6S	Jablonska et al. (2007)
I-3	*Fusarium oxysporum f. sp.lycopersici (race 3) (fusarium wilt)*	7L	Hemming et al. (2004) and Lim et al. (2008)
I-1	*Fusarium oxysporum f. sp.lycopersici* (race 1) (fusarium wilt)	7	Sarfatti et al. (1991) and Scott et al. (2004)
Frl	*Fusarium oxysporum* f. sp. *radici-lycopersici (root rot)*	9	Vakalounakis et al. (1997)
I-6	*Fusarium oxysporum f. sp.lycopersici (race 2) (fusarium wilt)*	10	Sela-Buurlage et al. (2001)
Ph-2	*Phytophtora infestans (late blight)*	10L	Moreau et al. (1998)
aI	*Fusarium oxysporum* f. sp. *lycopersici* (race 1) (fusarium wilt)	11S	Scott et al. (2004)
Sm	*Stemphyllium spp. (grey leaf spot)*	11	Behare et al. (1991)
Cmr	Cucumber Mosaic Virus (CMV)	12	Stamova and Chetelat (2000)
Lv	*Leveillula taurica*	12C	Chunwongse et al. (1994, 1997)
Mi-3, Mi-5	*Meloidogyne* spp (nematode)	12S	Yaghoobi et al. (1995)

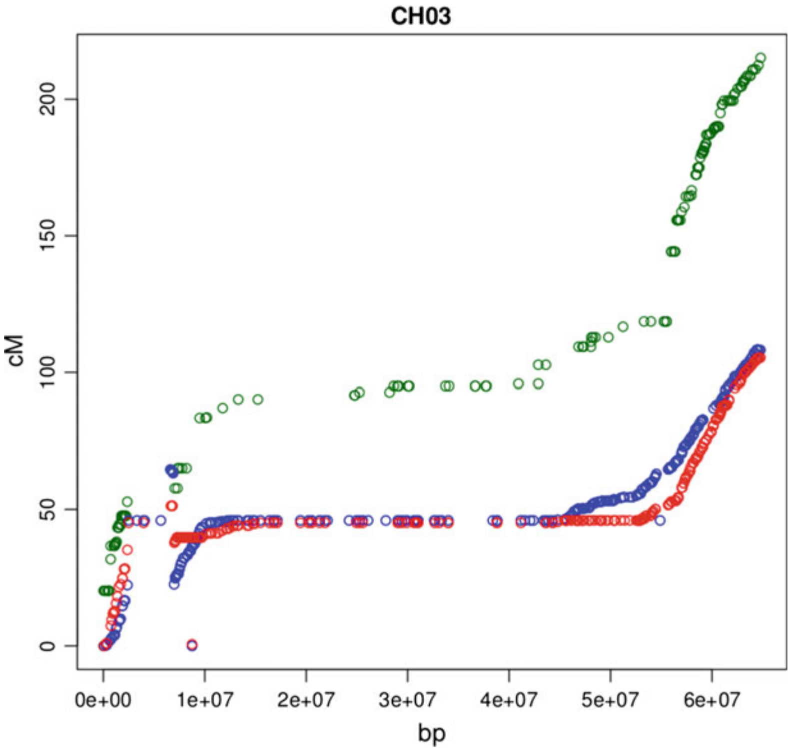

Fig. 3.1 Relationships between physical and genetic distances: example of chromosome 3

(Sim et al. 2012; Tomato Genome Consortium 2012). If the recombination frequencies may vary from one progeny to the other (Fig. 3.1), these regions do not recombine more in any. The ratio of kb per cM thus greatly varies hampering the characterization of some mutations due to the lack of recombination. Hopefully, these regions of low recombination also correspond to regions with lower gene density.

Many genes involved in morphological traits or disease resistances remain to be characterized. The high-quality genome sequence and millions of SNPs available today constitute unique resources to rapidly identify new genes of interest. High throughput genotyping technologies combined to the information on gene annotation and expression in various tissues should make the task much easier.

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