

TOMATO MOLECULAR MARKERS

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Summary

Tomato (*Solanum lycopersicum* L.) is one of the most popular vegetable grown in many regions of the world. Due to its high taste quality and nutritional value increase interest in the cultivation of this species and its consumption. Using the latest achievements in fields of genetics, molecular biology and biotechnology, breeders can create new varieties with improved useful traits. Introduction of DNA markers, especially those based on the polymerase chain reaction (PCR) has led to breakthrough in the plants genetic research, including tomato. They are successfully used for plant genomes mapping, phylogenetics studies, selection of parental forms in plant breeding, and above all to identify the genes of important traits. For tomato have been identified and mapped 9309 molecular markers. High-density genetic maps development gives an opportunity to use them in genetic research and breeding programs. Identification of DNA markers closely linked to studied gene can significantly facilitate the identification of desirable traits in material breeding, or accelerate the plants selection for elimination of genotypes with undesirable genes. Material breeding selection using molecular markers, defined as MAS (marker-assisted-selection) is increasingly being used in tomato breeding programs, contributing to facilitated identification of genes or QTL and their transfer into the cultivated species from wild form.

key words: tomato, molecular markers, molecular breeding, Marker-Assisted Selection (MAS)

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the main vegetable in the world (Foolad 2007a). Originating in the region covered by present day Chile, Bolivia, Ecuador, Columbia, Peru, they were brought to Europe in the fifteenth century. It belongs to the *Solanaceae* family, includes over

3000 species (Yuling & Lindhout 2007). It occupies the second place on the list of the most frequently consumed vegetable. The large popularity of tomatoes is its nutritional value, high content of vitamins, mainly A, C, micro, macro elements and phenolic compounds with strong antioxidant properties, mainly lycopene. In the diet it occurs as a fresh vegetable,

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ingredient in sauces, juices and dried (Foolad 2007a). The tomato is also one of the more intensively investigated *Solanaceous* species due to the simple diploid genome. The tomato genome, 950 Mb, contains 35 000 genes located on 12 chromosomes. The part of tomato genome, 730 Mb exist as a pericentromeric heterohromatin, remaining 220 Mb consist of the distal euchromatic segments of the chromosomes. The order BAC (Bacterial Artificial Chromosome) approach was chosen for sequencing the tomato genome and was based on the F2-2000 map – www.sgn.cornell.edu (Mueller *et al.* 2005a). For a better understanding the structure and functioning of tomato genome researchers uses highly efficient methods such as: molecular marker analysis, protein-protein interaction, transcripts, proteins and post-translational modification analysis. Many *Solanaceous* species such as tomato, potato, pepper, petunia, tobacco, play a significant role as a model organisms (Mueller *et al.* 2005b).

The SOL (The International Solanaceae Genome Project) project is an important element of research on the *Solanaceae* family. It was established to create a scientific network on the *Solanaceae* and to coordinate research carried out by different groups of scientists from around the world (Mueller *et al.* 2005a, Barone *et al.* 2008). The SOL was initiated at the meeting near Washington and the aim of this project is two significant question: how can deeper understanding of the genetic basis of plant diversity and how a common genes and proteins give rise to a wide range of morphologically and ecologically distinct

organisms (Mueller *et al.* 2005a). One of the works of SOL project is an Internet database SGN (Solanaceae Genomics Network) designed to integrate information about the tomato genome and later all *Solanaceous* species (Barone *et al.* 2008). Currently SGN houses maps and markers data from *Solanaceae* species, expressed sequence tag collection, database of phenotypic information for a mutagenized tomato populations and some tools such as real-time quantitative trait loci (Mueller *et al.* 2005b).

The DNA markers are sequences showing polymorphism between individuals or between species (Foolad 2007a). The beginning of the use of molecular markers in plant breeding dates back to 1980 when it was used isozyme to accelerate monogenic traits introgression (Tanksley & Rick 1980, Tanksley 1983, Xu & Crouch 2008). The use of isozymes as a marker has some limitations, as limited number, specific of the tissues and detected by specific staining (Winter & Kahl 1995). In contrast to the isozymes, DNA markers are not limited by number, their expression is not necessary for detection and all may be detected by one technique (Beckmann & Soller 1986, Melchinger 1990, Winter & Kahl 1995). Several years later Beckmann & Soller (1986) described a method using RFLP (Restriction Fragment Length Polimorphism) markers to improve crops quality and drew up the issues of Marker-Assisted Selection Backcrossing - MABC (Xu & Crouch 2008). MABC proved to be ideal solution where we have many good varieties that need to be corrected by one trait for example resistance to pest or disease (Cregan *et al.* 1999,

Cahill & Schmidt 2004, Johnson 2004, Crosbie *et al.* 2006, Miklas *et al.* 2006, Dwivedi *et al.* 2007, Ragot & Lee 2007, Xu & Crouch 2008).

The use of molecular markers associated with interesting trait for material breeding selection are called MAS (Marker-Assisted Selection). This is an ideal tool for breeders, since it lowers costs, improves precision and efficiency of material selection, and eliminates impact of environmental conditions (Foolad 2007a). Marker-assisted selection appeared in the literature for the first time more than two decades ago (Beckmann & Soller 1986, Xu & Crouch 2008). In order to establish a connection between marker and locus of useful trait are used four approaches: the markers search using genetic map, associative mapping, search candidate gene and direct sequences test (Masojc 2009). Molecular markers are used to accelerate introgression of resistance gene for bacteria, fungi, viruses, nematodes and insects, gene pyramiding, and to improve commercial traits such as yield, proteins content, tolerance to drought and low temperature (Winter & Kahl 1995). These markers for which the procedure are expensive and long are not useful in breeding programs (Foolad 2007a). RFLP analysis requires large quantities and high quality of DNA and detection by Southern hybridization is a long and laborious. The development of PCR (Polymerase Chain Reaction) technique in 90s of the twentieth century contributed to creation of many methods for DNA polymorphism detection (Mullis & Faloona 1987). Tanksley and Mutschler (1990) needed three

years for published a map of 162 RFLP markers, the authors, which testifies difficulty and labor intensity of this method.

Another advantage of the DNA markers are their use in interspecific crosses, for example to transfer potato gene into tomato (Stevens & Robbins 2007). By 2008, more than 2500 markers, including RFLP, EST (Expressed Sequence Tag polymorphism), SSR (Simple Sequence Repeat) and COS (Conserved Orthologue Set) were mapped on 12 tomato chromosomes (Frary *et al.* 2005, Barone *et al.* 2009). They are intensively used for the identification and mapping of QTL (Quantitative Trait Loci) associated with important biological and agronomical traits, fingerprinting and MAS. The use of Marker-Assisted Selection in tomato breeding has been limited by number of polymorphic marker in the species and for economical reason. The work is continuing on the development of high efficiency and resolution markers, such as SNP (Single Nucleotide Polimorphism). Development of the tomato EST database (currently 214 000 sequences), DNA microarray and genomes sequencing will contribute to emergency of new more practical markers. Tomato euchromatin sequencing paves the way for a comparison of important genes and QTL (Foolad 2007a). The DArT (Diversity Array Technology), is another technique with carrying high hopes for search of useful markers. It is rapid analysis of multiple loci in the genome. This technique allows discovery and mapping hundreds of polymorphic markers in a single experiment (Stevens & Robbins 2007).

Molecular markers in studies of biotic stresses (Table 1)

Table 1. List of disease and insect resistance genes/QTL, DNA markers and isozyme marker mapped on tomato chromosome

Disease	Pathogen	QTL/Gene	Marker	Chromosome	Reference
Root-Knot	<i>Meloidogyne</i> spp.	<i>Mi</i> , <i>Mi-1.2</i>	Isozyme, CAPS, SCAR	6	Rick et al. 1974; Gilbert et al. 1955; Williamson et al. 1994; Garcia et al. 2007
Nematode (potato cyst)	<i>Globodera rostochiensis</i>	<i>Hero</i>	RFLP	4	Ganal et al. 1995
Alternaria stem canker	<i>Alternaria alternata</i> f. sp. <i>lycopersici</i>	<i>Asc</i>	RFLP	3	Scott et al. 2007; Grogan et al. 1975; Van der Biezen et al. 1995; Mesbah et al. 1999
Blackmold	<i>Alternaria alternata</i>	QTL	RFLP, CAPS	2, 3, 9, 12	Robert et al. 2001
Early Blight	<i>Alternaria solani</i>	7 QTL	RFLP	3, 4, 5, 6, 8, 10, 11	Zhang et al. 2003
Fusarium wilt	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> race 1, race 2	<i>I1</i> , <i>I2</i> , <i>I3</i>	RFLP, CAPS, SCAR	7, 11	Sarfatti et al. 1991; Staniaszek et al. 2007; Sarfatti et al. 1989; Lim et al. 2006; Barillas et al. 2008
Fusarium crown and root rot	<i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i>	<i>Frl</i>	RAPD	9	Fazio et al. 1999
Gray leaf spot	<i>Stemphylium</i> spp.	<i>Sm</i>	RFLP	11	Behare et al. 1991
Late blight	<i>Phytophthora infestans</i> (Mont.) deBary	<i>Ph-2</i> <i>Ph-3</i>	RFLP, RAPD, SCAR	10, 7	Moreau et al. 1998, YiPeng et al. 2009, PueHee et al. 2010
Anthraxnose ripe rot	<i>Colletotrichum coccodes</i>	QTL	RAPD	several chromosomes	Stommel et al. 1998
Verticillium wilt	<i>Verticillium dahliae</i>	<i>Ve</i>	SCAR, RFLP	9	Kawchuk et al. 1998; Diwan et al. 1999
Powdery mildew	<i>Oidium lycopersici</i>	<i>Ol-1</i> , <i>Ol-2</i>	RAPD, RFLP, SCAR, CAPS	6	Van der Beek et al. 1994; Huang et al. 2000; Bai et al. 2003
	<i>Leveillula taurica</i>	<i>Lv</i>	RFLP, RAPD	12	Chunwongse et al. 1994
Leaf mold in tomato	<i>Cladosporium fluvum</i>	<i>Cf-2</i>	RFLP	6	Dickinson et al. 1993
Bacterial spot	<i>Xanthomonas euvesicatoria</i> , <i>X. vesicatoria</i> , <i>X. peronans</i> , <i>X. gardneri</i>	QTL: <i>Rx1</i> , <i>Rx2</i> , <i>Rx3</i> , <i>Bs4</i>	RFLP, CAPS, STS	1, 5	Yang et al. 2007; Yu et al. 1995

Bacterial speck	<i>Pseudomonas syringae</i> pv. <i>Tomato</i> (Pst)	<i>Pto</i>	RFLP, RAPD	5	Martin et al. 1991; Martin et al. 1993
Bacterial canker	<i>Clavibacter michiganensis</i> ssp. <i>michiganensis</i>	QTL (Rcm5.0, Rcm7.1, Rcm9.0, Rcm2.0, Rcm5.1)	RFLP, SCAR	2, 5, 7, 9	Vn Heusden et al. 1999; Kabelka et al. 2002
Cucumber mosaic virus	CMV	<i>Cmr</i>	RFLP	12	Stamova et al. 2000
Tomato spotted wilt virus	TSWV	<i>Sw-5</i>	RAPD, RFLP, SCAR	9	Stevens et al. 1995; Stevens et al. 1996
Tabaco mosaic virus	ToMV	<i>Tm-1</i> , <i>Tm-2a</i>	RFLP, SCAR	2, 9	Ohmori et al. 1996; Young et al. 1988; Schroeder et al. 1967; Tanksley et al. 1992
Tomato yellow leaf curl virus	TYLCV	<i>Ty-1</i> , <i>Ty-2</i> , <i>Ty-3</i>	RFLP, CAPS	6, 11	Zamir et al. 1994; Hanson et al. 2000; Hanson et al. 2006; Yuanfu et al. 2006; Castro et al. 2007

Nematodes

The identification of molecular markers associated with disease resistance of tomato, began in 1970. The pioneer was Charles M. Rick and his co-worker. They have identified a link between resistance to root-knot caused by nematodes (*Meloidogyne* spp.) and form of isozyme, acid phosphates, *Asp-1* (Rick & Fobes 1974). This resistance is controlled by a single dominant gene, *Mi*, located on the long arm of chromosome 6 (Gilbert & McQuire 1955). Williamson *et al.* (1994) created CAPS (Cleaved Amplification Polymorphic Sequences) marker REX-1 useful in material selection with resistance to nematode (*Meloidogyne* spp). Garcia *et al.* (2007) developed co-dominant SCAR (Sequence Characterized Amplified Region) marker Mi23 linked with *Mi-1.2* gene (Godzina *et al.* 2010). Kaloshian *et al.* (1995) reported that *Mi* gene conferring to nematode re-

sistance is tightly linked with *Meu-1* gene responsible for resistance to potato aphid (*Macrosiphum euphorbiae*) in tomato.

Globodera rostochiensis are other nematode on tomato. Resistance gene *Hero* has been introgressed from wild species *Lycopersicon pimpinellifolium* into the cultivated tomato. Ganai *et al.* (1995) mapped *Hero* gene between the RFLP markers H293 and CT229. The RFLP marker HR1 is closely linked to *Hero* gene.

Fungal disease

Disease caused by *Alternaria alternata* f. sp. *lycopersici* was first described in California by Grogan *et al.* (1975). Infected plants have dark brown to black cankers with concentric zonation on the stems near the soil line or aboveground (Scott & Gardner 2007). Van der Biezen *et al.* (1995) and Mesbah *et al.* (1999) were reported that *Asc* gene was linked to RFLP

markers TG422 and TG134 on the long arm of chromosome 3.

Alternaria alternata causing blackmold is a major disease of ripe tomato fruits. Robert *et al.* (2001) used RFLP and CAPS markers and mapped QTLs responsible for resistance to *A. alternata*. They are located on chromosomes 2, 3, 9, 12. In their studies as a source of resistance used a wild species *L. cheesmanii*.

Alternaria solani causes the EB (Early Blight) is one of the most common and destructive pathogen of tomato, causing symptoms throughout the plant and in all stages of development. Zhang *et al.* (2003) using RFLP markers and resistance gene analogs (RGA) found 7 QTL associated with resistance to *A. solani*, one in each of chromosomes 3, 4, 5, 6, 8, 10, and 11. Location of some RGA overlap with location of known genes or QTLs of resistance to the EB, which may suggest link between RGA and resistance to *Alternaria solani*.

Fusarium oxysporum f. sp. *lycopersici* (*Fol*) is another fungal pathogen causing severe disease in warmer regions of the world. Sarfatti *et al.* (1989) showed that a dominant *I2* gene confers in tomato resistance to *Fusarium oxysporum* f. sp. *lycopersici* race 2, is linked with the RFLP marker TG105B on the chromosome 11. Authors, using RFLP markers, mapped the *I1* gene on chromosome 7 between TF20 and TG128 markers, responsible for resistance to race 1 (Sarfatti *et al.* 1991). Staniaszek *et al.* (2007) have developed CAPS marker TAO1₉₀₂ that is useful to identify tomato genotypes with *I2* gene. Lim *et al.* (2006) reported the use of CAPS CT226 marker to detection the *I3*

gene responsible for resistance to race 3. The SCAR marker P7-43DF3/R1 was found to be closely linked to the *I3* gene in tomato. This marker can be used for selection of inbreds with *Fol* race 3 resistance in tomato breeding programs (Barillas *et al.* 2008).

Fusarium crown and root rot of tomato is causing by *Fusarium oxysporum* f. sp. *radicis-lycopersici* (FORL). Fazio *et al.* (1999) identified three RAPD (Random Amplified Polymorphic DNA) markers - UBC 116, UBC 194 and UBC 655, linked to *Frl* gene, located on chromosome 9, responsible for resistance to pathogen. UBC 194 marker would be the most useful for selecting *Frl* because it is the most tightly linked.

Gray leaf spot of tomato, reflected in a gray spots on the leaves, is causing by four different species of *Stemphylium*: *S. solani* Weber, *S. floridanum* Hannon and Weber, *S. botryosum* Wallr., *S. vesicarium* (Wallr.) Simmons (Bashi *et al.* 1973). Andrus *et al.* (1942) showed that resistance donor is a species with red fruits *L. pimpinellifolium*, while Hendrix & Frazier (1949) reported that it is conditioned by monogenic inheritance of *Sm* gene. Behare *et al.* (1991) mapped *Sm* gene on chromosome 11, linked with RFLP T10 marker at a distance of 6,8cM.

The late blight on tomato caused by *Phytophthora infestans* (Mont.) deBary is a common disease which occurs in cool and moist areas, causing large losses in field and in greenhouses. Moreau *et al.* (1998) using RFLP and AFLP (Amplified Fragment Length Polymorphism) markers have located *Ph-2* gene contributing to the partial resistance. This gene is

locating on the end of long arm of chromosome 10 between RFLP markers CP105 and TG233. YiPeng *et al.* (2009) identified RAPD marker for resistance to late blight in tomato. This marker was designed as the CCPB272-03₇₄₀ and it was tightly linked to resistant *Ph-3* gene. The AFLP marker L87 was successfully converted to SCAR marker which is linked to *Ph-3* gene, and can be used for selection of tomato plant resistant to *Phytophthora infestans* (Mont.) deBary (PueHee *et al.* 2010).

Stommel & Zhang (1998) using RAPD markers found QTLs responses for resistance to *Colletotrichum coccodes* causing anthracnose ripe rot. They are located on several chromosomes. This fungus can grow through the stem which results in vascular darkening. However, *C. coccodes* does not cause major losses in yield, because pathogen attacks later and developed slowly (Ślusarski 2000).

Kawchuk *et al.* (1998) developed co-dominant, allele specific SCAR marker useful in the selection of tomato for resistance to *Verticillium dahliae*. Linkage analysis showed that genetic distance between marker and locus *Vr* is less than 0,67cM $\pm$ 0,49 cM. Diwan *et al.* (1999) mapped this gene on the short arm of chromosome 9. It is strongly linked with RFLP marker, GP39.

Tomato is highly susceptible to *Oidium lycopersici*, a fungus belonging to the *Erysiphales* causing powder mildews. Resistance to this pathogen is controlling by one incompletely-dominant gene *Ol-1*. The *Ol-1* gene was mapped on chromosome 6. RAPD marker RAPD17 was amplified in the susceptible plants but was

not amplify in resistance. Localization of this marker is close to the *Asp-1* locus. Further analysis suggested that *Ol-1* locus is close to RFLP marker TG135 (Van der Beek *et al.* 1994). Another gene responsible for resistance to *O. lycopersici*, *Ol-3* was found on chromosome 6, and he is associated with several RFLP and SCAR markers, TG25/SCAF10 and H9A11 (Huang *et al.* 2000). Bai *et al.* (2003) reported that resistance to *O. lycopersici* in *L. parviflorum* G1.1601 was controlled by three QTLs: *Ol-qt1* on chromosome 6 in the same region as the *Ol-1*, *Ol-qt2* and *Ol-qt3* on chromosome 12. Authors developed two SCAR markers: B432U, tg111 and seven CAPS markers: Aps1, dc21, tg25, dct136, ct129, ct99 Y258 which can be use to monitoring of the target QTL genomic regions in marker-assisted selection.

Another fungus caused powdery mildew on tomato is *Leveillula taurica*. Chunwongse *et al.* (1994) localized *Lv* gene, responsible for resistance to this pathogen, between RFLP markers CT211 and CT219 on chromosome 12.

Leaf mold in tomato caused by *Cladosporium fulvum* occurs on major crops in greenhouse around the world. The *Cf-2* gene, conferring to resistance to this pathogen, was mapped on chromosome 6 between RFLP markers TG232 and H2D1 (Dickinson *et al.* 1993).

Bacterial disease

The initial work on identification of molecular markers linked to the loci conferring resistance to bacterial diseases started in early 1990. MAS has not be widely applied in breeding for resistance to bacterial canker, bac-

terial spot and bacterial wilt (Yang & Francis 2007).

Bacterial speck caused by *Pseudomonas syringae* pv. *tomato* (*Pst*) can be present in all stages of development and in all parts of above-ground plant. The three RAPD markers S47, R110, RS120 (Martin *et al.* 1991) and seven RAPD R-S7, R-Q14, R-X6, R-150n, R-151n, R174n, R-DD5 (Carland & Staskawicz 1993) were found to be linked to *Pto* locus. Martin *et al.* (1993) developed RFLP marker TG538 cosegregated with *Pto* on chromosome 5.

Clavibacter michiganensis ssp. *michiganensis* causes bacterial canker on tomato occurs at the tropical and subtropical areas. The disease manifests itself by the wilting of leaves, reduced fruit production and early plants death (Sandbrink *et al.* 1995). Van Heusden *et al.* (1999) using RFLP and SCAR markers mapped three QTLs: *Rcm5.0*, *Rcm7.1*, *Rcm9.0* located on chromosome 5, 7 and 9. Kabelka *et al.* (2002) using RFLP markers, found two QTL: *Rcm2.0* on chromosome 2 and *Rcm5.1* on chromosome 5.

Bacterial spot, causes by *Xanthomonas euvesicatoria*, *X. vesicatoria*, *X. peronars*, *X. gardneri*, was first reported in South Africa (Doidge 1921). Maximum infection occurs under warm, moist conditioned with the incident especially high when night temperature are also warm (Yang & Francis 2007). Two loci, *Rx1*, *Rx2* on chromosome 1 and one *Rx3* on chromosome 5, were described based on linkage to RFLP markers (Yu *et al.* 1995, Yang & Francis 2007). Ballvora *et al.* (2001) converted two AFLP markers: P11M6, P15M1 and four

RFLP markers: CT242, TG432, TG441, TG598 linked to *Bs4* locus, into locus-specific PCR markers. The CAPS P11M6 marker and STS (Sequence Tagged Site) TG432 marker are suitable for use in large scale screen.

Viral disease

Cucumber mosaic virus (CMV) infects many crops including tomato, causing large economic losses in many regions of the world especially in the Mediterranean. The results of RFLP and isozymes analysis showed the presence of *Cmr* gene facilitated resistance to CMV. This gene is located on chromosome 12 and it is linked to TG68 and CT79 markers (Stamova & Chetelat 2000).

Tomato spotted wilt virus (TSWV) contributes to a significant yield and fruit quality reduction due to the presence of necrotic or chlorotic spots on fruits (Paterson *et al.* 1989). Stevens *et al.* (1995) using a near isogenic line developed a RAPD marker of the size of 2200bp (base pair) linked to *Sw-5* gene. They determined the location of the gene for resistance to TSWV to be between the RFLP CT71 and CT220 markers, near the telomere on the short arm of chromosome 9. Stevens *et al.* (1996) also developed SCAR421 marker linked to the *Sw-5* gene conferring to resistance on TSWV.

Mosaic of tomato caused by tomato mosaic virus (ToMV) is a major diseases and leads to heavy losses in tomato breeding (Ohmori *et al.* 1996). ToMV is very stable and moves mechanically or with the seed, causing severe distortion of leaves, stunted plants, discoloration and distortion of fruit (Pospieszny *et al.*

2009). Tanksley *et al.* (1992) using RFLP markers, located the *Tm-1* gene on the short arm of chromosome 2 near the rDNA region. Ohmori *et al.* (1996) developed SCAR markers: SCA15₁₀₀₀, SCB10₁₃₀₀, SCG12₉₀₀, SCI10₁₁₀₀, SCN09₁₁₀₀ and SCN20₁₄₀₀ based on the sequence of RAPD markers. Young *et al.* (1988) created a RFLP markers linked with *Tm-2a* gene.

Tomato yellow leaf curl virus belongs to begomoviruses and is transmitted by whitefly; manifested itself in chlorosis between the veins of leaves, distortion of young leaves and reduced plant growth. Resistance to this pathogen was found in some wild tomato species such as: *S. pimpinellifolium*, *S. peruvianum*, *S. chilense*, *S.*

habrochaites, *S. cheesmaniae* (Pico *et al.* 1996). Zamir *et al.* (1994) mapped the dominant *Ty-1* gene responsible for resistance to TYLCV on chromosome 6, near the RFLP marker TG36. Another gene *Ty-2* responsible for resistance to this virus, originally from *S. habrochaites*, was located on chromosome 11 between RFLP markers TG393 and TG36 (Hanson *et al.* 2000, Hanson *et al.* 2006). Ji & Scott (2006) mapped *Ty-3* gene on the long arm of chromosome 6, between cLED-31-P16 and T1079 markers. Castro *et al.* (2007) developed a CAPS marker JB-1 associated with the *Ty-1* gene and this marker is useful in MAS to identify resistant plant.

Molecular markers in studies of abiotic stresses (Table 2)

Table 2. List of abiotic stress resistance/tolerance QTL, DNA markers and isozyme markers mapped on tomato chromosomes

Stress	QTL/Gene	Markers	Chromosome	Reference
Cold tolerance	QTL	RFLP	1, 3, 5, 6, 7, 9, 11, 12	Truco <i>et al.</i> 2000; Vallejos <i>et al.</i> 1983
Salt	QTL	RFLP, Isozyme	1, 3, 5, 6, 11	Foolad 2007; Foolad <i>et al.</i> 2001; Zamir <i>et al.</i> 1987; Rush <i>et al.</i> 1981; Tal <i>et al.</i> 1983
Drought	QTL	RFLP	1, 9, 8, 12	Foolad <i>et al.</i> 2003

Current world agricultural production is largely limited by environmental stresses (Boyer 1982). It is estimated that only 10% of the world's arable land may be free of stress (Dudal 1976). Extreme temperatures, drought, soil salinity, and nutrient imbalances are the main environmental constraints worldwide to crop production. Most plant breeding programs have focused on the development of cultivars with high yield potential in favorable environments (Foolad 2007b).

Tomato is sensitive to low temperature: growth and development are inhibited in about 10°C, while temperatures below 6°C lead to irreversible damage (Truco *et al.* 2000). Three species of the genus *Lycopersicon* - *L. chilense*, *L. hirsutum* and *L. peruvianum* - are characterized by tolerance to low temperatures. Vallejos & Tanksley (1983) identified three QTL responsible for growth at low temperatures. They were located on chromosome 6, 7, 12. Truco *et al.* (2000), working with the BC1 generation and using RFLP mark-

ers mapped ten QTL associated with tolerance to low temperature.

Researchers have undertaken the identification of QTLs responsible for tolerance to salinity stress at different stages of plant development: germinating seeds, vegetative growth, mature plant (Foolad 2007a). Foolad *et al.* (2001), using RFLP markers, located five QTL on chromosomes 1, 3, 5, 6, 11, associated with tolerance to salinity stress. The source of tolerance was *L. pimpinellifolium* (Jusl.) Mill. LA722. Salt tolerant species (*L. pennellii*, *L. peruvianum*, *L. cheesmanii*) are able to accumulate more potassium and sodium ions than sensitive species (Rush & Epstein 1981, Tal & Shannon 1983). Zamir & Tal (1987) using isoenzymatic markers identified four loci associated with the uptake of Na^+ and Cl^- (enzymes *Prx-1*, *Prx-2*, *Tpi-2*, *Pgm-2*, *Aco-1*) and two loci responsible for uptake of K^+ (enzymes *Asp-1*, *Got-2*).

Drought is another important factor limiting the viability of crops and the stability of yield in the world. It leads to disturbances in the plants development and is defined as a deficit of water in the soil or atmosphere (Ceccarelli & Grando 1996, Foolad *et al.* 2003). Many plants, including tomato, are susceptible to drought at any stage of ontogeny (Hsiao 1973; Foolad *et al.* 2003). Therefore, it is important to understand the genetic basis of tolerance to desiccation and its application in obtaining of resistant cultivars. Using RFLP markers, four QTL responsible for this trait have been mapped: two of them, located on chromosome 1 and 9 (derived from *L. pimpinellifolium*) showed a stronger effect than the other two QTL (chromosome 8 and 12) derived from *L. esculentum* (Foolad *et al.* 2003).

Molecular markers in studies of quality traits (Table 3)

Table 3. List of agronomical traits DNA markers, isozyme markers and their chromosomal localization

Traits	QTL/Gene	Markers	Chromosome	Reference
Antioxidant capacity	5 QTL	RFLP	3, 6, 7, 10	Rousseaux et al. 2005
Ascorbic acid	6 QTL	RFLP	3, 5, 10, 12	Rousseaux et al. 2005
β -carotene	2 QTL	RFLP	6	Rousseaux et al. 2005
Citric acid	7 QTL	RFLP	4, 5, 7, 8, 9, 10	Causse et al. 2004
Malic acid	5 QTL	RFLP	3, 4, 8, 12	Causse et al. 2004
Fructose content	4 QTL	RFLP	4, 5, 7, 9	Causse et al. 2004
Glucose content	4 QTL	RFLP	4, 5, 9, 12	Causse et al. 2004
Fruit weight	3 QTL	RFLP	3, 10, 12	Frary et al. 2004
Fruit size	4 QTL	RFLP	2, 3, 10, 12	Frary et al. 2004
Fruit shape	4 QTL	RFLP	2, 8, 10, 12	Frary et al. 2004
Fruit color (external)	2 QTL	RFLP	5, 12	Frary et al. 2004
Self incompatibility	<i>S</i>	RFLP	1	Bernatzky 1993
Male sterility, Functional male sterility	<i>ms-10</i> <i>ps-2</i>	Isozyme CAPS	2 4	Tanksley et al. 1984 Staniaszek et al. 2010
Jointless	<i>j, j-2</i>	RFLP, RAPD	11, 12	Zhang et al. 1994; Wing et al. 1994; Zhang et al. 2000

The quality of fresh tomato sold in the market is determined by appearance, firmness and flavor: in tomato used for processing the quality is determined mainly by total soluble solids content, color, pH and firmness. In both areas the parameters that influence these positive attributes are often the same. Sugars and organic acids are the major components of dry matter - but they also markedly influence the flavor of the product. Inheritance of fruit quality components has been extensively reviewed by Davies & Hobson (1981), Stevens (1986) and Causse *et al.* (2007).

Antioxidants compounds contained in vegetables are an important factor in the prevention of heart disease, arthritis, cancer, and also oxidative stress. The major compounds belonging to this group are: ascorbic acid, tocopherol, lycopene, β -carotene. Five QTL: *ao-6-2*, *ao7-2*, *ao10-1*, *ao6-3*, *ao-3-3* have been mapped as being responsible for the make-up of TACW (total antioxidant capacity of the water-soluble fraction); they are located on chromosome 3, 6, 7 and 10. In turn, for the synthesis of ascorbic acid, six corresponding QTLs *aa3-3*, *aa3-4*, *aa10-1*, *aa5-3*, *aa12-3*, *aa12-4* were mapped on chromosome 3, 5, 10, 12, while two QTLs *bc6-2*, *bc6-3* for β -carotene were located on chromosome 6. In all of these cases, the QTL donor was a wild species *L. pennellii* (Rousseaux *et al.* 2005).

In ripe tomato fruits, the main sugars present are glucose and fructose and the main organic acids, citric and malic. Inheritance of these traits are quantitative, with a large influence of adverse environmental conditions.

In order to locate the QTLs responsible for these traits the candidate gene approach with RFLP markers was used. Seven QTL: *ca-4F*, *ca-5E*, *ca-7B*, *ca-8E*, *ca-9F*, *ca-10B*, *ca-10E*, are responsible for the synthesis of citric acid, for malic acid five QTLs: *ma-3FG*, *ma-4G*, *ma-4I*, *ma-8E*, *ma-12D*, for fructose four QTLs: *fru-4I*, *fru-5G*, *fru-7F*, *fru-9D* and for glucose four QTLs: *glu-4I*, *glu-5G*, *glu-9D*, *glu-12D* (Causse *et al.* 2004).

Using an AB-QTL mapping strategy (Backcross Advanced QTL mapping) and RFLP markers the quantitative traits loci responsible for quality of tomato fruit (size, weight, shape and color) have been identified. Tanksley & Nelson (1996) were the first to apply AB-QTL to tomato. They found three QTLs: *fw3.1*, *fw10.1*, *fw12.1* to be responsible for the fruit weight, four QTLs: *fsz2b.1*, *fsz3.1*, *fsz10.1*, *fsz12.1* for fruit size. Three of these QTLs are closely linked to the loci of fruit weight. Four QTLs: *fs2b.1*, *fs8.1*, *fs10.1*, *fs12.1* were associated with fruit shape and two QTLs: *ec5.1*, *ec12.1* with external fruit color (Frary *et al.* 2004).

Abscission is a universal process, whereby plants shed organs such as fruit, flowers, leaves and thus regulate their growth and development (Zhang *et al.* 1994). In tomato two loci have been identified that suppress flower formation and fruit pedicel abscission zone. These genes are *j* and *j-2* (Zhang *et al.* 1994, Butler 1936, Rick 1957). A jointless locus (*j*) was mapped between two RFLP markers TG523 and TG194 in a F₂ population of crosses between *L. esculentum* and *L. pennellii*. Additionally, five RAPD markers were mapped on chromo-

some 11. One of these, RPD158, was mapped to the opposite side of a *jointless* relative to TG523 (Wing *et al.* 1994). Authors identified RAPD marker RPD140 linked to *j-2* gene. For a chromosomal location of this locus, researchers converted RPD140 marker to RFLP marker, then mapped it on chromosome 12 (Zhang *et al.* 2000).

Self-incompatibility is a mechanism that prevent self-fertilization in a large number of plants. This trait is controlled by a single multiallelic locus *S* lying on chromosome 1 and is closely linked to CD15 marker (Bernatzky 1993).

Male-sterility is an important trait in vegetable crop because eliminate manual emasculation. In tomato genetic male-sterility is determined by recessive alleles *ms-10*. Tanksley *et al.* (1984) tested two enzyme marker loci: *Est-1* and *Prx-2* located on chromosome 2. The linkage intensity of *ms-10* gene and *Prx-2* (1,5cM) suggested that this enzyme marker might provide a selection tool for male-sterility. Staniaszek *et al.* (2010) created CAPS marker designated as C4-30₁₀₀₀ which is linked to *ps-2* gene responsible for functional male sterility in tomato and it can be useful for selection of male sterile tomato plants. These marker was developed based on a conserved ortholog set II (COSII) sequence C2_At3g20020 located on tomato chromosome 4.

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MARKERY MOLEKULARNE POMIDORA

Streszczenie

Pomidor (*Solanum lycopersicum* L.) należy do najpopularniejszych warzyw uprawianych w wielu regionach świata. Ze względu na wysokie walory smakowe i wartości odżywcze, wzrasta zainteresowanie zarówno uprawą tego gatunku jak i jego spożyciem. Wykorzystując najnowsze osiągnięcia z dziedziny genetyki, biologii molekularnej i biotechnologii hodowcy mogą tworzyć nowe odmiany o lepszych cechach użytkowych. Wprowadzenie markerów DNA, zwłaszcza tych generowanych przy zastosowaniu łańcuchowej reakcji polimerazy (PCR, ang. polymerase chain reaction), doprowadziło do przełomu w badaniach genetycznych roślin, w tym również dla pomidora. Są one z powodzeniem wykorzystywane między innymi do mapowania genomów roślinnych, badań filogenetycznego pokrewieństwa gatunków, doboru form rodzicielskich w hodowli roślin, a przede wszystkim do identyfikacji genów ważnych cech użytkowych. Dla pomidora zidentyfikowano i zmapowano 9309 markerów molekularnych. Opracowanie map genetycznych o dużym zagęszczeniu markerami stwarza szansę na ich wykorzystanie, zarówno w badaniach genetycznych jak i w pracach hodowlanych. Identyfikacja markerów DNA, silnie i trwale sprzężonych z badanym genem może w znacznym stopniu ułatwić identyfikację pożądanej cechy w materiałach hodowlanych, bądź przyspieszyć selekcję roślin pod kątem eliminacji genotypów z genami niepożądanymi. Selekcja materiałów hodowlanych z wykorzystaniem markerów molekularnych, określona jako MAS (ang. marker-assisted-selection), znajduje coraz szersze zastosowanie w programach hodowlanych pomidora, przyczyniając się do ułatwienia identyfikacji genów lub QTL oraz ich transferu do gatunków hodowlanych z form dzikich.