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TOMATO MOLECULAR BREEDING – A MINI-REVIEW OF LATEST ACHIEVEMENTS

HODOWLA MOLEKULARNA POMIDORA – MINIPRZEGLĄD OSTATNICH OSIĄGNIĘĆ

Abstract
Solanum lycopersicum L. is one the most widely grown vegetables in the world. Unfortunately, due to the domestication syndrome and intensive artificial selection this important crop has experienced severe genetic bottlenecks (so-called genetic erosion). The introduction of new alleles makes the basis for tomato improvement. However, it is difficult to introgress the targeted allele accurately, with favourable effect and eliminate unfavourable ones. It is a common problem in germplasm collection management and breeding programmes. Modern molecular techniques and pre-breeding (trait introgression from wild relatives) may help to increase the species diversity. Genome maps and PCR-based techniques are commonly used to identify, map and target the functional diversity of genes and QTLs encoding many biologically and agriculturally important traits of tomatoes. They are also used for germplasm screening, fingerprinting, and marker--assisted breeding. The aim of this mini-review was to summarise recent advances in tomato molecular breeding.

Keywords: introgression lines, molecular maps, QTLs

Introduction

The tomato (*Solanum lycopersicum* L.) is one of the most important and popular vegetables in the world (Corrado et al., 2014). This widely grown food crop has experienced severe genetic bottlenecks. Therefore, the introduction of new alleles is essential for tomato improvement (Corrado et al., 2013). Traditional introgression of genes from wild relatives and landraces has been accomplished through interspecific crosses, followed by phenotypic selection, and several backcrosses. Unlike for qualitative traits,

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this approach is ineffective for quantitative traits highly influenced by environmental conditions and by multiple interactions between a consistent number of genes (Hanson et al., 2007). The advent of molecular biology in the 1980s opened new possibilities to characterise the genetic diversity both in wild and cultivated tomatoes and to specify genomic regions involved in targeted traits (Bauchet and Causse, 2012). Modern molecular marker-based techniques and marker-assisted selection (MAS) have greatly improved the effectiveness of using tomato genetic resources and enabled identification of wild alleles improving both quantitative and qualitative traits and their rapid incorporation into elite cultivars (Hanson et al., 2007). A comprehensive review on tomato genome mapping and molecular breeding was published by Foolad in 2007. The aim of this mini-review was to summarise recent advances in tomato molecular breeding.

Tomato genetics

The species has been well investigated in terms of genetics, cytogenetics, genomics, and breeding (Foolad, 2007). Many genetic and genomic resources, including databases for sequencing, transcriptomic and metabolomic data are available today (Calafiore et al., 2016). Plant geneticists from 14 countries spent nine years mapping the tomato genetic material and discovered that the species had a small genome (2C = 1.90 pg of DNA; 9.5×10^5 Kb/1c = 950 Mb) with a high level of homozygosity and without gene duplication (El-Awady et al., 2012; Koo et al., 2008). The tomato contains 31,760 genes (The Tomato Genome Consortium, 2012). Like other *Lycopersicon* section species, *S. lycopersicum* is a diploid with 24 acrocentric to metacentric chromosomes (2n = 2x = 24) with large blocks of pericentric heterochromatin and distal euchromatic arms (except for chromosome 2, with a completely heterochromatic short arm including a distal nucleolus organiser region – NOR) (Anderson et al., 2010). Karyotype data indicate that 77% of the tomato genome is located in heterochromatin and 23% in euchromatin (Peterson et al., 1996). Tomato chromosomes can be easily identified by pachytene analysis. With the development of chromosome engineering, tomato cytogenetic research has become one of the most advanced areas in the field of agriculture. Moreover, the tomato has a relatively short life-cycle (70–90 days from sowing to fruit ripening). It can be grown under different conditions. It produces numerous seeds and its pollination/hybridisation can be easily controlled. The tomato can also be asexually propagated via grafting or tissue culture and it is capable of whole-plant *in vitro* regeneration from various explant types (Gerszberg et al., 2015; Passam et al., 2007). There are also efficient tomato transformation technologies and numerous genetic and genomic resources (Calafiore et al., 2016). Therefore, apart from its horticultural and economic importance, it is also a good model system both for basic and applied studies on plants (especially the ornamental dwarf 'Micro Tom' cultivar) (Kobayashi et al., 2014).

Molecular maps

The tomato is one of the first crop plants for which a genetic linkage map was developed (Foolad, 2007). Molecular linkage maps are used not only to identify the loca-

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tion of genes or chromosomal segments which are associated with the superior performance of wild tomato species, but also to identify causal mutations/exploiting induced genetic variability (Karp, 2002; Shirasawa et al., 2010). For example, genetic linkage maps enabled investigations of the chromosomal locations of quantitative trait *loci* (QTLs) genes to improve the yield and other complex traits of tomatoes (Frary et al., 2000). Currently there are several tomato molecular maps available, including a broad set of Expressed Sequenced Tag (EST) data, high-density genetic maps (with a total of more than 2200 *loci* detected by AFLP, CAPS, RFLP, RAPD and SSR markers), as well as comparative maps (with *Arabidopsis* of over 500 COS markers – a set of genes that are conserved throughout plant evolution in both sequence and copy number), which are linked to a physical map and eventually to the euchromatic genomic sequence (Foolad, 2007; Shirasawa et al., 2010; Van Deynze et al., 2007). Those maps resulted from mining the populations derived from crosses between commercial cultivars and wild tomato relatives (Van Deynze et al., 2007). In 2010 Shirasawa et al. developed the first intraspecific maps for *S. lycopersicum* with SNPs and other PCR-based co--dominant markers. In recent years, population genetics approaches, i.e. strategic sampling and germplasm genotyping without making crosses, enabled the discovery of allelic diversity by linkage disequilibrium mapping (association mapping) and selective sweep mapping (genome scanning) (Labate et al., 2009). Association mapping was conducted by van Berloo et al. (2008) within a collection of 94 accessions containing both old and elite (hybrids) European germplasm of cherry tomato (*S. lycopersicum* var. *cerasiforme*) and round-beef types. An extensive linkage disequilibrium (LD) was observed (15 cM average). Such maps provide a valuable tool for identification of QTLs in tomatoes. For example, Muños et al. (2011) successfully applied this technique to identify causal polymorphism of QTL controlling locule number (cavities containing seeds that are derived from carpels, affecting fruit shape and size) on chromosome 2.

QTLs

In the past few decades there have been efforts to identify the genes that influence the most important tomato traits (e.g. the synthesis of volatiles that positively affect the tomato flavour). The screening of genes encoding a certain trait and the knowledge of their DNA sequence simplify the classification of variation in the germplasm (Karp, 2002). Precise knowledge of map positions enables molecular cloning, especially in view of the fact that the tomato genome sequence has been available since 2012 (Mathieu et al., 2009; The Tomato Genome Consortium, 2012). Thereafter, high--throughput datasets and bioinformatic platforms, extremely valuable for the *Solanaceae* plant research community, were generated or implemented (Calafiore et al., 2016). Consequently, nowadays it is possible to purify valuable lines so that they will contain only a specific QTL. Classification of the sequence variants at a targeted *locus* can help to identify superior alleles and greatly reduce the amount of work required in breeding (Karp, 2002). QTL mapping techniques and genome mapping studies facilitate genetic characterisation of complex traits and germplasm management of both wild and cultivated tomatoes (Bauchet and Causse, 2012). However, due to the large number of QTLs molecular-assisted tomato breeding programmes are complex (Mathieu et al., 2009).

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The *fw2.2* gene that controls up to 30% of fruit weight variation was the first QTL that was identified by positional cloning (Frary et al., 2000). In the past few years several tomato candidate genes (CGs) and QTLs have been identified for fruit traits (shape, cracking and firmness), anti-oxidants, carotenoids, volatile aromas, non-volatile metabolites content (e.g. sugars and pigments, soluble solid content, semi-polar metabolites; the so-called metabolite QTL) and heterosis (Ballester et al., 2016; Bauchet and Causse, 2012; Calafiore et al., 2016; Capel et al., 2017; Yang et al., 2016). In 2015 a total of 13 QTLs and candidate genes associated to fruit quality traits was identified in a tomato genetic map composed of 353 molecular markers derived from *S. pimpinellifolium* L. – a wild relative of tomato (Capel et al., 2015). The following cloned genes controlling tomato fruit morphology are noteworthy: SUN and OVATE, which control the elongated fruit shape; FASCIATED (FAS) and LOCULE NUMBER (LC), which control the locule number, fruit size, and flat fruit shape (Muños et al., 2011). However, the use of QTLs in practical breeding is limited because of inherent difficulties implementing MAS for QTLs (Barrantes et al., 2016). Barrantes et al. (2016) reported that QTL stability across generations was trait-dependent. For example, it was very high for the fruit weight but low for organoleptic traits. Alseekh et al. (2015) observed that mQTLs (metabolic QTLs) of secondary metabolism were less affected by the environment than mQTLs of primary metabolism. This difference in QTL stability can be explained by the predominant additive gene action or epistatic and genetic background interactions for QTLs (Barrantes et al., 2016).

Introgression lines

Genetic libraries, which consist of marker-defined genomic regions taken from wild species and introgressed onto the background of elite crop lines, provide plant breeders with the material and knowledge which may help to improve the agricultural traits of modern tomato cultivars (Zamir, 2001). The set of introgression lines (ILs; i.e. near-isogenic lines derived from interspecific crosses and MAS, homozygous for one or several mapped wild DNA fragments/chromosome segments in a common recurrent parent) is a DNA library representing even 100% of the genome of the wild accession. The QTL detection by screening IL populations is the first step to identify (candidate) genes responsible for important traits. Reverse genetics is further required to clarify the function of candidate genes (Ballester et al., 2016). ILs enable fine mapping and positional cloning of genes and QTL of interest, studying QTL × environmental, QTL × genetic background and QTL × QTL interactions, analysis of the genetic basis of metabolome/transcriptome (and their correlation), enzyme activity, and eventually, evaluation of the agronomic performance of a specific QTL set (Barrantes, 2016). These libraries help to avoid complications arising from the segregation of multiple wild genes and epistasis (Hanson et al., 2007). Cornell University provides free access to a set of three ILs developed from *S. habrochaites, S. lycopersicoides* and *S. pennellii* accession through the TGRC (Hanson et al., 2007). IL lines facilitate the identification and incorporation of novel genetic variation from wild tomato species. Barrantes et al. (2016) studied the genomic library of ILs from the *S. pimpinellifolium* accession TO-937. They identified chromosomal regions associated with traits which were both vegetative (trich-

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ome density, plant vigour) and fruit-related (organoleptic quality, morphology, colour). There was low variability of the traits related with the fruit shape. Alseekh et al. (2015), on the other hand, detected 679 mQTLs across 76 *S. pennellii* ILs and investigated the genomic regions associated with secondary metabolism in the tomato fruit pericarp.

As the IL development process is normally time-consuming, Barrantes et al. (2014) conducted high-throughput SNP genotyping steps in early backcross generations in order to increase its accuracy and speed. Consequently, only five to seven generations were necessary to complete the final set of 53 ILs of *S. pimpinellifolium* accession TO-937. It showed that the introgressions present in the IL set covered 94% of the donor genome.

Conclusions

Many gene banks worldwide store tomato germplasm collections (Bauchet and Causse, 2012; Sharifova, 2013). For example, the Research Institute of Vegetable Crops, Skierniewice (Poland) maintains a working collection of 995 accessions, including 648 modern cultivars, 221 landraces, 74 breeding lines and 52 wild relatives (Kotlińska et al., 2007). These institutions are working on sustainable management of genetic resources of the species and reconstruction of its original genetic pool.

One of the main problems with transferring alleles is the fact that apart from desirable traits, wild tomato species also carry large numbers of undesirable ones. For example, landraces are characterised by high susceptibility to biotic stress (especially viruses), as compared with contemporary commercial cultivars (García-Martínez et al., 2013). Therefore, many backcross generations are traditionally required (Labate et al., 2009). Molecular studies can identify the genetic and physical position of the underlying QTLs and introgression breeding can transfer only the desirable traits and select against the undesirable ones (Ballester et al., 2016).

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HODOWLA MOLEKULARNA POMIDORA – MINIPRZEGLĄD OSTATNICH OSIĄGNIĘĆ

Abstrakt

Pomidor jest jednym z najważniejszych gatunków roślin warzywnych na świecie. Jednocześnie, na skutek udomowienia i intensywnej selekcji, sekcja *Lycopersicon* jest narażona na zjawisko ubożenia genetycznego (tzw. erozji genetycznej). Podstawowym sposobem poprawy cech użytkowych pomidora jest wprowadzanie nowych alleli, jednak introgresja dokładnie wyselekcjono-

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wanego allelu (determinującego korzystną cechę) bez jednoczesnego wystąpienia niepożądanych zmian jest bardzo trudna. Jest to powszechny problem w zarządzaniu kolekcjami zasobów genowych i programami hodowlanymi. Pomocne w zwiększaniu różnorodności gatunkowej *Solanum lycopersicum* mogą być nowoczesne techniki molekularne i hodowlane (introgresja cech pochodzących z dzikich gatunków spokrewnionych). Mapy genetyczne oraz techniki oparte na reakcji PCR są obecnie powszechnie wykorzystywane do identyfikacji, mapowania i detekcji genów oraz QTL kodujących wiele istotnych cech związanych z biologią i uprawą pomidora. Są one także podstawą hodowli molekularnej oraz badania bioróżnorodności tego gatunku. Celem niniejszego miniprzeglądu było podsumowanie ostatnich postępów w hodowli molekularnej pomidora.

Słowa kluczowe: krzyżowanie introgresywne, mapy molekularne, QTL

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