



Review

Tomato proteomics: Tomato as a model for crop proteomics

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ABSTRACT

The understanding of plant stress response is essential to develop crops that are capable of withstanding adverse conditions. The development of proteomics led to the characterization of many of the metabolic pathways involved in plant resistance and adaptation to abiotic stresses. Mass spectrometry has been a popular tool for the study of plant protein expression under special environmental conditions due to its high throughput capacity and sensitivity. Recent studies have applied proteomics methodologies, such as phosphoproteomics, to understand metabolic dynamics and regulations. Isobaric tags, such as iTRAQ, have been used to obtain more precise and less time-consuming quantitative analysis. Although these proteomic strategies have been successfully applied to studies with tomato (*Solanum lycopersicum*), a major challenge of crop proteomics is the lack of genetic functional information when compared to the model plant, *Arabidopsis thaliana*. Still, tomato has been the model crop for genetic and molecular research of the Solanaceae family due to its attributes of diploidy, easy genetic transformation, and many genetic resources. The necessity of better strategies to increase the genetics and proteomics resources of tomato is in high demand. Here, we explore the various proteomics methodologies used in studies on tomato plants, and we discuss the present challenges of crop proteomics data interpretation.

1. Introduction

Proteomics allows for the study of global gene products in various tissues and cell physiological states. With the advancement of genomic sequencing and mapping of proteins, proteomics has become one of the largest areas to study functional genomics (Park, 2004), with the most publications of any omics field for a few years (Sanchez-Lucas et al., 2016). Most of the proteomics studies have focused on humans and, the majority, on cancer research. Although agriculture development has been a frequent topic when discussing food security (Godfray et al., 2012; Wheeler and Braun, 2013), plant research funding has not yet achieved the same level as human proteomics, making the access to new technologies limited. The importance of using proteomics to study the dynamic and complex plant proteomes relies on the identification of proteins and its modifications in stress conditions to develop crop improvement (Hu et al., 2015; Kilambi et al., 2016). In this review, we address the proteomics studies related to stress conditions on tomato plants, due to the rising importance of tomato as a model plant in crop proteomics and the importance of agricultural development for crop improvement.

2. The tomato genome and proteome databases

Tomato is the most intensively studied member of the *Solanaceous*

family (Barone et al., 2008), mainly due to its short generation time, elementary diploid genetics, a well-known genetic transformation methodology, inbreeding tolerance, and a vast well-characterized genetic resource (Barone et al., 2008; Van der Hoeven et al., 2002). Many datasets have been gathered regarding the tomato genome: collections of wild tomato species and mutant germplasm collections; marker collections; F2 synteny and permanent recombinant inbred (RI) mapping population; BAC libraries and an advanced physical map; TILLING populations, tomato microarrays, gene silenced tomato lines; and VIGS libraries (for transient silencing) (Barone et al., 2008).

The whole genome sequencing of tomato (*Solanum lycopersicum*) was completed in 2012 as an initiative of the Tomato Genome Consortium, formed with more than 90 research institutions (Tomato Genome Consortium, 2012). The genome of cultivar Heinz 1706 (H1706) comprises 12 chromosome pairs with a size of 950 Mb, and a total of 35,000 genes (Van der Hoeven et al., 2002). In contrast to the genome of *Arabidopsis* and sorghum, tomato presents fewer high-copy, full-length long terminal repeat (LTR) retrotransposons with an older average insertion age (2.8 compared to 0.8 million years ago) and fewer high-frequency k-mers (Tomato Genome Consortium, 2012). Amongst tomato relatives, as the wild tomato (*Solanum pimpinellifolium*), only 0.6% of nucleotide divergence is seen. Compared to the genome of another member of the Solanaceae family, the tomato and the potato (*Solanum tuberosum*) genomes present only 8% nucleotide divergence

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and signs of recent admixture, presenting nine large and many small inversions (Tomato Genome Consortium, 2012).

Proteome databases contain the protein sequences diverged from predicted genomic gene models and unigene transcripts. The latter is determined either by applying Hidden Markov models to find coding regions, through EstScan (Iseli et al., 1999), determining the probable translation initiation by NetStart (Pedersen and Nielsen, 1997), or by the reading of the longest open reading frame (Bombarely et al., 2011). The last version update of the tomato database (v.3.2), maintained by the international tomato annotation group (iTAG), contained 30,868 annotated genes, from which 2,300 genes were user curated. Other proteomics and genomics databases are available by Phytosome (<https://phytozome.jgi.doe.gov/phytozome/results.do?trail=%7Cquery>), Plant Genome and Systems Biology (PGSB) (<http://pgsb.helmholtzmuellenchen.de/plant/tomato>), and the Tomato Genomic Resources Database (TGRD) (<http://59.163.192.91/tomato2>). As for the functional annotation of the genome, 56.6% of the genes are associated with Gene Ontology (GO) terms. The FASTA files compatible with Mascot (Hirosawa et al., 1993), basic local alignment search tool (BLAST) (Altschul et al., 1990), and Protein Pilot (Applied Biosystems) (<https://scienc.com/products/software/proteinpilot-software>) can be obtained via file transfer protocol (FTP). Today, numerous search algorithms, such as MASCOT, SEQUEST (Eng et al., 1994), Comet (Eng et al., 2013), X!Tandem (Craig and Beavis, 2004), MS Amanda (Dorfer et al., 2014), OMSSA (Geer et al., 2004), and others are currently used. These algorithms are implemented by various software, and have the role to assign the protein identification to the spectra, and therefore, are essential in all proteomics pipelines. There are various softwares for proteomics dataset analysis available nowadays, some of the most popular software are: Proteome Discoverer (Thermo Fischer Scientific), MassLynx MS (Waters, Inc.), ProteinPilot (Applied Biosystems), Byonic (Protein Metrics Inc.), Scaffold (Proteome Software), MaxQuant (Cox and Mann, 2008) (free), and Searchgui (Compomics) (free). They differ in the input file format required and in the pipeline possibilities, such as using two different search engines, performing iterative searches; data visualization options (graphics, tables), and others optional parameters.

Sol Geonomics Network (SGN) has created an initiative to map the tomato secretome. The *Secretom* (<https://solgenomics.net/secretom>) was created to aid the study of proteins of the cell wall, proteins secreted in the exterior of the plasma membrane, and that are part of the secretory pathway. Secretome proteins are important because of their role in communication, responses to stress, and plant development (Krause et al., 2013). For fleshy fruits, the secretome is especially important due to the relationship of the mechanical and chemical characteristics of the cell wall and the fruit texture (Konozy et al., 2013). The SGN has also developed SecreTary, a tool for accurate computational prediction of proteins of the secretome. Secretom datasets are available through FTP on the Secretom website.

3. Plant proteomics from stress conditions

The development of stress tolerant plants is an important step in the context of food security. An in-depth investigation of gene networks and regulons that are involved in plant response is essential to precisely balance energy, adaptation, and plant development (Godfray et al., 2012; Mittler and Blumwald, 2010). Plant stress response has been a topic explored in various scientific reviews (Cramer et al., 2011; Knight and Knight, 2001; Komatsu and Hossain, 2013; Mittler, 2002; Rodziewicz et al., 2014). This paper will review the emerging studies that applied proteomics methodologies to characterize and analyze, in depth, stress responses from tomato. Tomato has emerged as the model plant for the Solanaceae family, and here we argue its role as a model

for crop proteomics. Table 1 resumes important publications of the last 15 years of proteomics studies on tomato.

Stress conditions are commonly categorized as biotic (plant-pathogen interactions), or abiotic (extreme temperatures and light intensity, drought, salinity, and toxicity). The stress responses present some interaction level on the signaling pathways. This cross-talk has been reviewed in abiotic stresses (Knight and Knight, 2001), and resulted in the generation of a “stress matrix”. In the stress matrix, the positive or the negative impact of different stress interactions are presented in a matrix format (Fig. 1). The knowledge of the interactions amongst stresses is used as a guide for crop improvement research, through a wider and applied view of how simultaneous stresses (as ozone and UV) can result in potential positive interactions.

3.1. Abiotic stress

Plants cope with abiotic stress by either avoiding it or acclimating to it. Avoidance is the survival of the plant during unfavorable conditions as mature seeds. Acclimation to stress concerns the modification of plant metabolism, which is caused by significant changes at the gene-expression level (Kosová et al., 2011). Both mechanisms affect plant growth and yield, causing a major constraint faced by agriculture and a negative impact on global crop production (Hossain et al., 2012; Rockström and Falkenmark, 2000).

The usual approach to studying crop abiotic stress is to compare plants under different stress environments to an optimal condition (control). Another strategy is the comparison of different genotypes (tolerant vs. control). These two approaches aim to establish correlations between protein dynamics with phenotypic changes (Abreu et al., 2013). The aim of this review is to discuss recent studies on tomato plants of different abiotic stress conditions responses that utilize these strategies and to present the latest proteomics methodologies applied in the field.

3.1.1. Temperature

High-temperature stress was found to cause starch depletion in tomato leaves as a result of enhanced hydrolysis and reduced biosynthesis reactions (Zhang et al., 2014). At the chloroplast level, high-temperature stress results in changes to grana stacking or swelling, modifications in the thylakoids structural organization and reduction of PSII antenna (Zhang et al., 2014). All photosynthesis reactions are susceptible to heat stress (Shaheen et al., 2015). PSII and the oxygen evolving complexes are notably affected, thylakoid membrane carbon metabolism and stroma photochemical pathways are the first reactions to be damaged (Gerganova et al., 2016).

The suppression of Rubisco activase and S-adenosyl-L-homocysteine hydrolase has been reported in heat-induced modifications in the whole proteome of tomato leaves of different heat-tolerant cultivars (Yamamoto et al., 1981). The authors also identified the differential expression of the glyoxylate shunt, carbohydrate metabolism, photosynthesis and cell defense reactions. They determined the tomato regulatory molecular mechanism for temperature coping, offering to plant geneticists many opportunities to develop heat tolerant plants. Furthermore, similarly to heat stress conditions, rubisco activase has been reported to be repressed in tomato infected with the cucumber mosaic virus (Di Carli et al., 2010). However, it was found to be upregulated during drought, salinity stress, and mineral toxicity (Salekdeh and Komatsu, 2007). Another protein, S-adenosyl-L-homocysteine hydrolase has been reported to be upregulated on the resistant line of wild tomato inoculated with *C. michiganensis* ssp (Afroz et al., 2011).

A proteomics study conducted by Muneer et al. (2016) on graft unions of three tomato genotypes revealed a high activity of peroxide

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