Botanica SERBICA 39 (2): (2015) 95-102

Review Article

Tomato: a model species for fruit growth and development studies

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ABSTRACT: Because of its specific biochemical and molecular properties and nutrient importance, tomato (*Solanum lycopersicum*) is an established model to study fruit growth and development. This review paper addresses several aspects of tomato fruit growth and development including its specific phases, control by water regime, cell wall enzymes, plant hormones and metabolic processes.

Keywords: tomato, fruit, growth, development

Received: 12 March 2015 Revision accepted 29 May 2015

UDK: 581.1:582.951.4

INTRODUCTION

Fruits are a major component of the human diet contributing a large portion of the vitamins, minerals and fiber. Among them tomato (*Solanum lycopersicum* L.) fruits are of special importance both as a fresh vegetable and as a component for the food processing industry. Moreover, tomato fruits contribute more nutrients to the diet than any other fruit or vegetable, as they contain relatively large amounts of lycopene, vitamins C and A, potassium, folic acid and many other metabolites. The importance of tomato as an agricultural commodity has resulted in significant breeding efforts to produce tomato cultivars with increased fruit quantity and quality and therefore the assessment of fruit growth and development is of special interest. Furthermore, due to the relatively small genome size, with a haploid set of 12 chromosomes (950 Mb, around 33,000 genes have been predicted and some 5000 genes are preferentially expressed in fruits), and specific visible metabolic changes that occur during fruit development and ripening (differentiation of the initial green color to red with the dominance of carotenoids and lycopene), and availability of well-characterized ripening mutants, tomato is often used as a representative model species for studies of fruit development and ripening. Recent progress in "omics" methods (proteomics, metabolomics), identification of the role of several key genes and molecular analyses of hormone signaling pathways have greatly improved the assessment of fruit development.

The aim of this paper is to briefly review some of the recent advances in our understanding of the complex processes that regulate tomato fruit growth and ripening with emphases on physiological and biochemical aspects. In this review we have not considered effects of different environmental factors (especially abiotic and biotic stress factors) which may significantly change fruit growth and development. As the large number of genes associated with fruit development now identified have been reviewed recently by Ariizumi *et al*. 2013), genetic aspects of fruit set, development and ripening will not be discussed here. For tomato germplasm information the following web sites are recommended: Tomato Genetic Resource Center [http:// tgrc.ucdavis.edu/] and Hebrew University [http:// zamir.sgn.cornell.edu/mutants/]). Another database (http://solgenomics.net) is recommended for molecular genetics and genomics for plants in the *Solanaceae* family (tomato, potato, pepper, tobacco, petunia etc.).

PHASES OF FRUIT GROWTH AND DEVELOPMENT

Fruit typically develops from the ovary after flower pollination and fertilization. In the fruits, cells in

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the ovary wall undergo a long series of divisions and expansion, which gives the fruit its final size before the onset of ripening. In spite of the complexity of these developments, the growth and development involve three or four distinct phases. According to Gillaspy *et al.* (1993) in phase I, the ovary differentiates from the floral meristem and after fertilization cell division (phase II) starts and continues for 10 to 14 days. In phase III cell expansion occurs due to increasing cell volume, until the fruit reaches its final size. Phase III is the longest phase of fruit development, continuing for six to seven weeks and lasting up to one week before the onset of ripening. In phase IV the fruits reach their final phase and the process of ripening starts. Other authors, contrary to Gillaspy *et al.* (1993), have distinguished three major periods in the growth of tomato fruit: cell division, the growth phase and ripening (Guichard *et al.* 2001). During these early phases of fruit development, the carpel differentiates into the pericarp and the placenta develops into a jelly-like substance that consists of highly vacuolated cells.

There is a dilemma on whether the final fruit size is determined by the duration and/or frequency of the cell division phase, or by the cell elongation phase alone. According to Cheniclet *et al.* (2005), larger fruits contain more cells than smaller fruits due to a longer period of cell division. The pericarp cell volume of ripe red fruit is between 2,000 and 220,000 times larger than that of the pre-anthesis ovary wall.

Very recent results of Pećinar (2015) showed that 22-31% of pericarp cells of the tomato cultivar Ailsa Craig reach their final size during the phase of cell division, while 69 to 78% due to the cell elongation phase. The final area of the pericarp cells was increased more than 390 times.

Usually, for physiological or biochemical investigations the fruit growth rate is presented in the form of a sigmoid or "S"-shaped curve, where increase in fruit diameter is plotted against a function of time. Analysis of this curve shows three distinct regions indicating the first phase of growth (cell division), a phase of cell elongation and a steady phase when growth is stopped. The middle region of the curve shows the period of exponential growth where fruits exhibit maximal rate of growth (Fig.1A).

Fruit growth rate could also be presented in the form of symmetrical, bell-shaped curves (Monselise *et al.* 1978) obtained by fitting the changes in fruit growth rate (FGR) with a third order regression line. Presented in such a way, the FGR profile also shows that the initial short lag phase of growth is followed by a phase of rapid fruit expansion, after which FGR declines and, as the fruit finally ripens, FGR reaches near zero (Fig.1B).

Figure 1 presents both types of curves obtained during investigations of the effect of drought on the growth rate of the tomato fruit cultivar Sunpak (Savić *et al.* 2008). These results showed that the smaller diameter of fruits exposed to drought (D) compared with optimally irrigated (FI) fruits (Fig.1A) was not the result of a smaller maximal fruit growth rate (2.8 mm day^{-1} for D and 3.0 mm day^{-1} for FI), but was the result of a shorter period of cell elongation (Fig.1B). In drought-treated plants, the maximal fruit growth rate was accomplished 15 days after fruit initiation, and 22 days after initiation in the FI treatment.

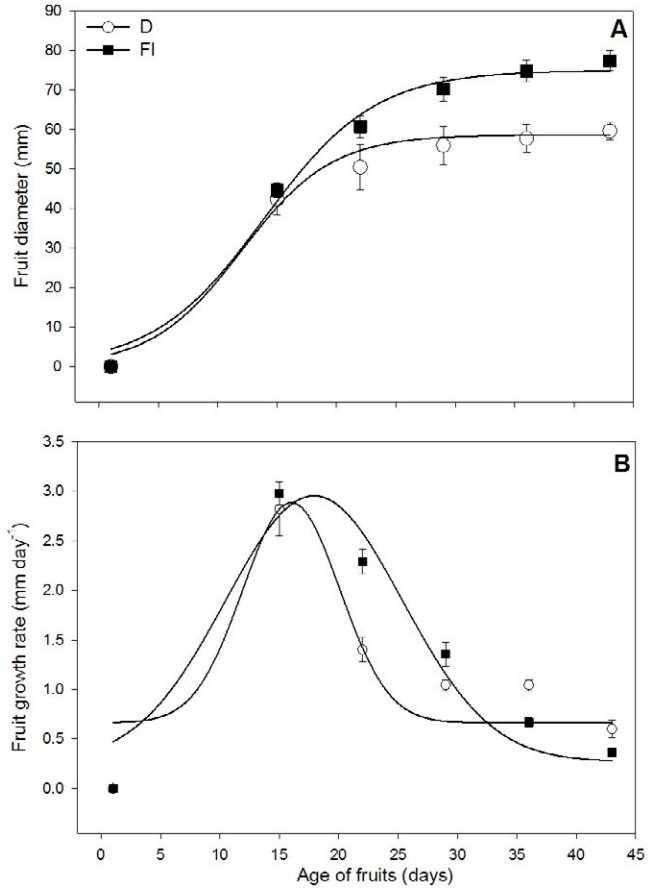

Figure 1. The effects of drought (D) and optimal irrigation (FI) on fruit diameter (A) and fruit growth rate (B) during tomato fruit development (modified from Savić *et al.* 2008).

WATER REGIME AND FRUIT DEVELOPMENT

The cell wall is one of the key determinants of plant cell and organ shape. The growth of a plant's cells is determined by the plastic response of the wall to the mechanical force induced by the internal turgor pressure. The enlargement of fruit cells, similarly to other cells is affected by the cell turgor pressure and properties of the cell wall, which may facilitate or restrict cell enlargement (Lockhart 1965). The properties of the cell wall can be modulated by enzymatic alteration of the degree of cross-linking

between existing cell wall polymers or by the addition of new cell wall material. New cell wall material can rigidify the wall, for example through an increase of its thickness or through the incorporation of mechanically-stable polymers such as cellulose microfibrils or lignin (Cosgrove 2000).

The period of cell enlargement is characterized by a large accumulation of water by the fruits and the ripe tomato fruits contain more than 90% water (Ho *et al.* 1987). Water for the fruit is supplied by the phloem as well as the xylem, and is lost through transpiration. Fruit transpiration represents also the key driver for accumulation of xylem-born minerals, while the growth of the fruit depends on the phloem stream. The diurnal variations in fruit transpiration (maximum at midday) and in xylem water potential of the stem (minimum at midday) induce a negative fruit water balance between the morning and mid-afternoon and variation in fruit volume (Montanaro *et al.* 2010).

According to the Morandi *et al.* (2010) model, when water loss occurs during the day the fruit water potential decreases (becomes more negative) *via* an increase in the osmotic concentration and a decrease in the turgor pressure. At the same time, the xylem import of water to the fruit is low (mainly because water is directed to transpiring leaves), and because of water losses by transpiration, fruit shrinking and decrease of their turgor pressure occur. This facilitates translocation and import of water from the phloem. However, environmental conditions, related to the time of day, and stem/fruit water potential gradients, may affect fruit inflows.

Tomato, like other species, can be exposed to physiological disorders. It is well-known that Ca^{2+} is a xylem mobile and phloem immobile ion. Because ion transport occurs mostly via the phloem during fruit development, the phloem immobility of Ca^{2+} partly explains why fruits are generally low-Ca^{2+} organs. However, other factors such as hormones, nutrient or metabolic demand may also influence partitioning and transport of Ca^{2+} between plant organs (Montanaro *et al.* 2012).

FRUIT GROWTH AND CELL WALL ENZYMES

Growth and development requires modulation of cell size and shape, which is accomplished by regulated changes in wall plasticity. Mechanical properties and plasticity of the cell wall can be modulated by enzymatic alteration of the degree of cross-linking between existing cell wall polymers or by the addition of new cell wall material. Biochemical investigations showed that three groups of wall-bound enzymes such as xyloglucan endotransglycosylase (XET), expansins and cell wall-associated peroxidase are involved in the regulation of the expansion of fruit cells (reviewed by Brummell 2006). Expansins were first identified in cell wall protein fractions able to catalyze the irreversible extension of cell walls (McQueen-Mason & Cosgrove 1995). Application of auxins has been demonstrated to increase expansin expression in tomato fruits (Catala *et al.* 2000). The exact mechanism by which expansins affect cell wall plasticity is still unknown and one hypothesis is that they disrupt hydrogen bonding between cellulose microfibrils and the matrix glucans (Cosgrove 2000).

Xyloglucan endotransglycosylase (XET) is an enzyme capable of cleaving and rejoining xyloglucan chains (Cosgrove 2000). In dicotyledonous plants, cellulose microfibrils are thought to be hydrogen-bonded to xyloglucans; cleavage of xyloglucans may therefore allow the cell wall to expand. Thompson *et al.* (1998) and Rose *et al.* (1997) demonstrated that the activity of XET and expansins is also correlated with fruit growth.

Peroxidases (EC.1.11.1.7), as heme-containing enzymes, catalyze many diverse reactions in plants. These reactions also include cross-linking in cell walls as a result of the formation of diferuloyl bridges between pectin residues, and isodityrosine bridges between hydroxyproline-rich extensin molecules (Hatfield *et al.* 1999).

In this way, cell wall peroxidases have been implicated in "locking" together cellulose microfibrils during cell growth by forming phenolic cross-linkages between cell wall components and thereby decreasing the ability of the cell wall to expand (Passardi *et al.* 2004).

Many studies have shown increases in peroxidase activity or in its different isoforms during maturation or cessation of tomato fruit growth (Thompson *et al.* 1998; Andrews *et al.* 2002). Similarly to the analyses of leaf growth (Jovanovic *et al.* 2004), our results also confirmed that drought significantly affects cell wall peroxidase activities in the fruits of Sunpak cultivar (Savić *et al.* 2008). These results showed that the activity

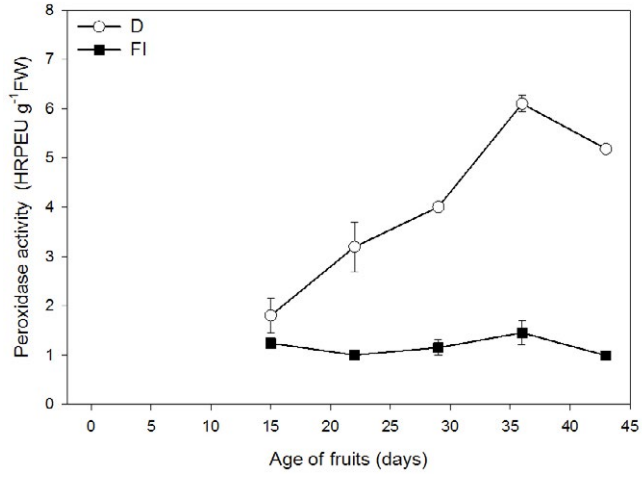

Figure 2. The effect of drought (D) and optimal irrigation (FI) on cell wall peroxidase activity in exocarp during tomato fruit development (modified from Savić *et al.* 2008).

of peroxidase was significantly higher in the fruits of plants exposed to drought (D) than in control FI plants (Fig.2). Comparison of these results on a temporal scale with the fruit growth data (Fig 1A and B), showed differences between D and FI treatments. During the measurement period (from 15th to 43rd day after fruit initiation), no significant differences in peroxidase activity in fruits of FI plants were found, because fruits of these plants continued to grow throughout the whole experimental period. In the fruits of D plants, peroxidase activity began to increase from the 15th day and this phase coincided with the phase when fruit growth started to decline. This significantly-increased enzyme activity of the fruit exocarp consequently caused the reduction of fruit diameter in Sunpak plants exposed to drought.

HORMONES AND FRUIT GROWTH

Fruit set and development is also under the control of plant hormones (reviewed in detail by Srivastava & Handa 2005; Ariizumi *et al.* 2013). Plant hormones auxin and gibberellic acid (GA) increase in the tomato ovary upon pollination (Mapelli *et al.* 1978). Treatment of tomato flowers or flower buds with exogenous auxin or gibberellins (GA) can induce parthenocarpic fruits (De Jong *et al.* 2009). Ariizumi *et al.* (2013) proposed a schematic model for the regulation of parthenocarpic fruit formation by components of hormonal signaling pathways. In this model, parthenocarpy is induced by the action of several components involved in the signaling pathway of various hormones, especially ethylene, auxin, gibberellin and cytokinin. The identification of genes associated with hormone signaling pathways has improved our understanding of the formation of parthenocarpic fruit in tomato.

It is well-known that the plant hormone auxin (indoleacetic acid - IAA) triggers fruit set in tomato by activating cell division in the pericarp (i.e., phase II). Also, increases in endogenous levels of cytokinins (CK) have been linked with fruit growth (Gillaspy *et al.* 1993) and are critically involved in the regulation of early fruit growth through regulation of cell division by D-type cyclin expression (Baldet *et al.* 2006). Increases in GA concentrations have been found during tomato fruit set and early fruit development. The plant hormone abscisic acid (ABA) also regulates development and ripening of tomato fruit. In addition, ABA could control, at least in part, the production and effects of ethylene in climacteric tomato fruit (Zhang *et al.* 2009). Very recent results indicate that *SlNCED1* and *SlCYP707A2* are key genes in the regulation of ABA synthesis and catabolism, and are involved in fruit ripening (Ji *et al.* 2014).

Progression in ripening induces the degradation of cell wall components, and this leads to changes of cell wall metabolism and softening of the fruit. Our preliminary results showed that an ABA increase in tomato fruit pericarp coincides with the beginning of the ripening phase. The results of Sun *et al.* (2012) provide direct evidence at the molecular level for a physiological role of ABA in cell wall catabolism related to fruit ripening. According to these results, ABA directly participates in the cell wall catabolism involved in fruit ripening *via* regulation of the expression of a suite of important genes during this process in tomato.

Another aspect of ABA action is in interactions with other hormones. Transcriptome analysis of pollinated as well as GA-treated ovaries revealed that the expression of ABA biosynthesis genes is high prior to pollination, while that of ABA catabolism genes is induced upon pollination and GA treatment, suggesting that ABA induces and maintains the dormant state of ovaries, repressing the transition to the fruit by acting as an antagonist of GA or auxin. The formation of small fruits by ABA-deficient mutants which show a significant increase in ethylene production during fruit development, suggests that ABA promotes cell expansion in the pericarp by suppressing ethylene production (Ariizumi *et al.* 2013). ABA can also be considered as the ripening control factor, because the ABA content is very low in unripe fruit but increases during the process of fruit ripening (Zhang *et al.* 2009).

Ethylene production is closely associated with ripening of many fruits. Fruits, in general, show two distinct respiratory patterns during ripening and on this basis they are categorized into climacteric and non-climacteric groups. In fruits classified as *climacteric*, the respiration rate increases, followed by an increase of ethylene production. The major rise in ethylene production may take place before, just after or close to the respiration peak. *Non-climacteric* fruits do not show such changes. Respiration rate either remains unchanged or shows a steady decline until senescence intervenes, with no increase in ethylene production. Table 1 presents examples of both classes of fruits. However, there are many variations between the two types of fruits. For example, kiwi (climacteric fruit) progresses through most of the ripening changes in the absence of any rise in ethylene and respiration, though this occurs only towards the end of ripening and softening.

According to Alexander & Grierson (2002), two systems of ethylene regulation have been proposed to operate in climacteric plants. System 1, that is functional during normal vegetative growth, is ethylene autoinhibitory (meaning that exogenous ethylene inhibits any further synthesis of ethylene) and is responsible for producing basal ethylene levels that are detected in all tissues including those of non-climacteric fruits. System 2 operates during the ripening of climacteric fruit and senescence of some petals when ethylene production is autocatalytic. Autocatalitic means that exogenous ethylene when applied to climacteric fruits (at the mature stage) stimulates ethylene biosynthesis and generally induces rapid fruit ripening. Ripening usually commences

Table 1. Climacteric (CL) and non-climacteric (NC) fruits.

Plant species (Latin and common name)	Type
Actinidia delicious (kiwi)	CL
Carica papaya (papaya)	CL
Cucumis (melon)	CL
Ficus carica (fig)	CL
Lycopersicon esculentum (tomato)	CL
Malus domestica (apple)	CL
Mangifera indica (mango)	CL
Musa sp. (banana)	CL
Persea sp. (avocado)	CL
Prunus sp. (peach, apricot, plum)	CL
Pyrus sp. (pear)	CL
Ananas comosus (pineapple)	NC
Capsicum sp. (pepper)	NC
Citrus limon (lemon)	NC
Citrus paradise (grapefruit)	NC
Citrus sinensis (orange)	NC
Cucumis (cucumber)	NC
Fragaria sp. (strawberry)	NC
Olea (olive)	NC
Prunus sp. (cherry)	NC
Vitis sp. (grape)	NC

in one region of a fruit, spreading to neighboring regions as ethylene diffuses freely from cell to cell and integrates the ripening process throughout the fruit. However, although ethylene is the dominant trigger for ripening in climacteric fruit, it has been suggested that both ethylene-dependent and ethylene-independent gene regulation pathways coexist to co-ordinate the process in climacteric and non-climacteric fruits.

Ripe climacteric fruits are soft and delicate and these fruits are often harvested hard and green, but fully mature, and are ripened near consumption areas. A small dose of ethylene is used to induce the ripening process under controlled conditions of temperature and humidity. To improve the external skin color and market acceptance, citrus fruits like orange or lemon, can be treated with ethylene, as a de-greening agent. Ethylene treatment breaks down the green chlorophyll pigment in the exterior part of the peel and allows the yellow or orange carotenoid pigments to be expressed.

METABOLIC CONTROL OF FRUIT DEVELOPMENT

During development, fruits of tomato shift from partially photosynthetic to heterotrophic metabolism. This is a result of the differentiation of photosynthetically active chloroplasts into chromoplasts, coupled with a decline in the expression and activity of carbon assimilation enzymes. Also, this occurs simultaneously with changes of cell wall composition and climacteric ripening. However, the role of fruit photosynthesis in fruit metabolism and development is not fully understood. There are results indicating that fruit photosynthesis can contribute between 10% and 15% of the carbohydrate required for fruit growth, and that the remaining photoassimilates are imported from source leaves. On the contrary, lowered fruit chlorophyll levels and photosynthetic activity were associated with almost no differences in fruit size and weight (Pesaresi *et al.* 2014).

Fruit development and growth are dependent on photosynthesis in the leaves and the translocation of sucrose, amino acids and organic acids to fruit cells. These assimilates are required to sustain cell division and growth of the fruit embryo and fruits act as sink organs for assimilates. During the third phase of development, the tomato fruit enters into the mature green (MG) stage and attains its final size. After reaching the MG stage, significant metabolic changes occur in the fruits leading to the breaking (BR) and final ripening (RG) stages. During this period, visual symptoms occur as fruit color changes from green (MG) to orange (BR) and red (RG). This change is followed by chlorophyll degradation and carotenoid accumulation (Gillaspy *et al.* 1993).

Carotenoids, especially β-carotene and lycopene, are the main ripe fruit pigments of tomato, and gene expression for the rate-limiting enzyme in the carotenoid pathway, i.e. phytoene synthetase (PSY), is regulated by ethylene (Fray & Grierson 1993). Fruit ripening is a genetically programmed process that is modified by both endogenous and exogenous signaling systems. Specific factors influencing ripening include developmental signals, hormones, light, temperature and nutrient status. The role of the plant hormone ethylene and a number of recently-described ripening transcription factors have been well characterized at the molecular level (Giovannoni 2004).

The transition from chloroplast to chromoplast involves extensive exchange of information between the nucleus and the plastids to regulate the plastid proteome and ensure that the organelle can meet the changing metabolic and energy demands of the cell. An example that supports this view is mutation of the tomato *lutescent2* locus (*l2*), encoding a chloroplast-targeted zinc metalloprotease, which delays fruit ripening, thereby implying the existence of a chloroplast-derived signal that stimulates ripening (Pesaresi *et al.* 2014).

Fruit ripening is a very complex, genetically-programmed process that results in changes in fruit color, texture and aroma. During ripening, biochemical changes include the production of various secondary metabolites and volatile compounds, softening of the cell wall, increase in ascorbic acid and the content of total soluble solids (Carrari & Fernie 2006).

Investigation of carbon metabolism showed that sucrose, glucose and fructose are the major sugars found in tomato fruits. During the phases of cell expansion and seed development and maturation, most fruits accumulate high levels of carbohydrates in the form of either sugars or starch and, therefore, are typical storage sinks. Carbohydrate contents vary depending on the environmental conditions during development and ripening, stage of development and the investigated cultivar. High hexose accumulation (sucrose, glucose and fructose) is characteristic of domesticated tomato (*Solanum lycopersicum*) whereas some wild tomato species (i.e. *S. chmielewskii*) accumulate mostly sucrose. Together with quinic and citric acid, these compounds are the principal quality components for "ketchup" tomatoes, determining the soluble solid content or Brix index. The variance in relative levels of sucrose and hexoses is most likely due to the relative activities of enzymes responsible for the degradation of sucrose - invertase and sucrose synthase (Carrari *et al.* 2007).

However, information about the TCA cycle, glycolysis and conversion of hexose phosphates into organic acids in the fruits is insufficient. The detailed analyses of metabolic regulation underlying tomato fruit development done by Carrari & Fernie (2006) revealed an up-regulation of glycolysis prior to the onset of ripening, together with an increase in ethylene biosynthesis rates, as the main features that distinguish climacteric and non-climacteric fruits. Biochemical evidence also suggests that ethylene production may be influenced or regulated by interactions between its biosynthesis and other metabolic pathways.

Nitrogen metabolism in tomato fruits is also important in ripening and is closely related to the central carbon metabolism. At earlier stages of development GABA (gamma-aminobutyric acid), glutamine, alanine, asparagine, arginine, valine and proline were found as predominant amino acids and their concentrations decreased at later stages of development. In contrast, glutamate, cysteine, aspartate, tryptophan, methionine and putrescine increased at the later stage of fruit development and ripening (Carrari *et al.* 2007).

Recent technological advances in "omics" and genomic tools allow investigations of changes in metabolites, transcripts and proteins during tomato growth and development. Analysis of transcript changes focused on the cell expansion phase in different fruit cell types showed that the expansion of locular cells is concomitant with the expression of genes controlling water flow, organic acid synthesis, sugar storage, and photosynthesis and suggest that hormones (mainly auxin and gibberellin) regulate this process (Lemaire-Chamley *et al.* 2005).

Proteomic analysis was also used for the investigation of biochemical mechanisms of tomato growth (Faurobert *et al.* 2007). Extensive proteome analyses done during tomato fruit development and ripening demonstrated changes in a large number of proteins during fruit development: 15 proteins associated with carbohydrate metabolism, 5 with photosynthesis and respiration, 9 with amino acid metabolism, 5 with secondary metabolism, and 1 with vitamin and lipid metabolism (Faurobert *et al.* 2007).

We performed similar analyses of growing tomato fruits of cultivar Ailsa Craig under mild drought stress conditions (partial root-zone drying - PRD) and in optimal water regime (FI). T understand better the effects of PRD on fruit growth, we focused our proteomic research on 15 dpa (days post-anthesis), which corresponds to the stage of full expansion and rapid growth of fruit cells, and on 30 dpa (days post-anthesis), which is the stage close to the beginning of the ripening process (Marjanovic *et al.* 2012). In total, we identified 46 proteins from 52 spots (Fig.3). At the proteome level, the expression of proteins related to carbon and amino acid metabolism mirrored the fruit growth rate and indicated that slower metabolic flux in PRD fruits may be the cause of a slower growth rate compared with FI fruits. The increase in expression of proteins related to cell wall, energy, and stress defense could allow PRD fruits to increase the duration of fruit growth compared with FI fruits. Up-regulation of some of the antioxidative enzymes during the cell expansion phase of PRD fruits appears to be related to their role in protecting fruits against the mild stress induced by PRD.

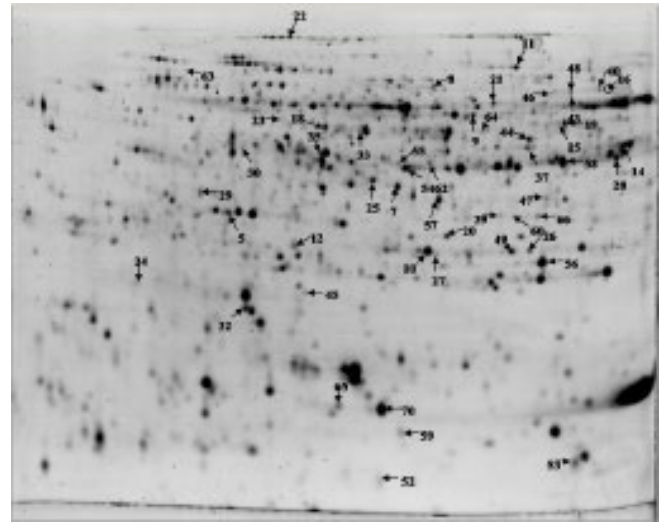

Figure 3. Two-dimensional electrophoresis gel of tomato pericarp proteins (modified from Marjanović *et al.* 2012).

Various secondary metabolites are responsible for the nutrient value, aroma and flavor of tomato fruits. The most common carotenoids, lycopene and provitamin A (β-carotene) increase between 10–14-fold during ripening and this is caused by the increased expression of genes involved in isoprenoid biosynthesis. There is special interest in tomato fruit production of alkaloids, flavonoids and other phenolics which can contribute to a healthy diet. Volatile organic compounds (VOCs) are also present in tomato fruits. These compounds are sensed orally and nasally and they are of special importance because they directly influence the consumers' choice of fruits. In ripe tomato fruits, 16 volatile compounds were shown to contribute to the flavor of the fruits. More information on secondary metabolites can be found in the recent review of Tohge *et al.* (2014).

CONCLUSION

In this paper we reviewed some of the recent results important for understanding the biochemical and physiological processes during fruit growth. Results were presented for tomato which is usually used as the fruit model system. Although not detailed, recent genetic research also significantly improves our understanding of fruit growth processes. Similarly to other fruit crops, yield of tomato is predominantly determined by the efficiency of fruit growth and therefore this increased understanding is also of applicative importance.

Acknowledgements — This study was supported by the EU Commission (FP7 REGPOT project AREA, No 316004) and Serbian Ministry of Education, Science and Technological Development (project TR 31005).

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REZIME

Paradajz: model biljka za ispitivanje rastenja i razvića plodova

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U ovom radu dat je pregled najnovijih rezultata koji su od značaja za razumevanje biohemijskih i fizioloških procesa u toku rastenja plodova. Rezultati su predstavljeni za paradajz kao model biljku za ispitivanje plodova. Iako nisu detaljno predstavljena, genetska istraživanja takođe doprinose poznavanju rastenja i razvića plodova. Prinos paradajza, kao i drugih kultura, u značajnoj meri zavisi od efikasnosti rastenja plodova te su stoga stečena znanja i od praktičnog značaja.

Ključne reči: paradajz, plodovi, rastenje, razviće