

A BRIEF OVERVIEW OF ETHYLENE MANAGEMENT TO EXTEND THE SHELF LIFE OF TOMATOES

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Abstract

Tomato (Lycopersicon esculentum Mill.) is one of the most important vegetable crops in the world of horticultural economy, being commercially valuable worldwide, both for fresh and for processing markets. In addition, tomato represent a major research plant material, thus results obtained from its study can be applied to other plants of the Solanaceae family. It is a climacteric fruit, with a respiratory peak during their ripening process. Ethylene is one of the most important natural plant hormones that regulates fruit ripening. Thus, ethylene biosynthesis management, especially during postharvest period allow producers more time for shipment and increase the shelf life of tomato fruit for consumers. Maximum tomato loss in quality and quantity occurs from harvesting to consumption. The problem of loss can be controlled by adapting suitable scientific methods of packing and storage and by establishment properly postharvest management. One of the first and simplest conditions to influence the postharvest production of ethylene refers to the handling practices and storage temperature. Some classical treatments as for instance, postharvest application of 1-methylcyclopropene (1-MCP) as one of ethylene action inhibitor is also successfully used. There are also recent functional genomic studies in tomato. Integrating molecular approaches with conventional breeding may enhance fruit quality and could significantly improve the postharvest shelf life of tomato.

Key words: *Lycopersicon esculentum*, postharvest, ripening, shelf life.

INTRODUCTION

The postharvest losses of fruits and vegetables in the developing countries account for almost 50% of the production (Meli et al., 2010).

Tomato (*Lycopersicon esculentum* Mill.) is one of the most important vegetable crop in the world of horticultural economy (Upendra et al., 2003), being commercially valuable worldwide (Kimura and Sinha, 2008), both for fresh and for processing markets (Opiyo and Ying, 2005), not only because of its volume, but also because of its overall contribution to nutrition, and its important role in human health (Agrawal and Rao, 2000; Martinez-Madrid et al., 2007; Me et al., 2007). The nutrient value of tomato fruit is related to its composition in carbohydrates, organic acids, minerals, vitamins and pigments (Helyes, 1999; Nasrin et al., 2008; Mutari and Debbie, 2011). It is the second most widely grown vegetable crop in the world other than the white potato (Hanson et al., 2001; Panthee and Chen, 2010).

In addition, the tomato belongs to the extremely large family *Solanaceae* and is closely related to many commercially important

plants such as potato, eggplant, peppers, tobacco, and petunias. Knowledge obtained from its studies can be easily applied to these plants, which makes tomato important research material. So, tomato serves as a model organism for the family *Solanaceae*, also a model system for studying many aspects of fruit biology, including development and metabolism (Kimura and Sinha, 2008; Okabe et al., 2011; Xu et al., 2012), in part due to the availability of well characterized ripening mutants (Zhang et al., 2009). Tomato is a climacteric, perishable vegetable fruit, with a very short life span, usually 2-3 weeks. An increase in the storage life and improvement of tomato fruit quality is really desirable (Sammi and Masud, 2007). Ethylene synthesized by all higher plants tissues is involved in regulating many growth and developmental processes in plants (Yang, 1985; Abeles et al., 1992) and constitute an important regulator of fruit ripening (Behboodan et al., 2012). Delaying the fruit ripening process would allow producers more time for shipment and increase

the shelf life of the fruit for consumers (Opiyo and Ying, 2005).

Even if in the past appearance quality has been emphasized, consumers buy tomatoes on the basis of appearance and firmness, their satisfaction and repeat purchases depend upon good flavor quality (Kader, 1986).

MATERIALS AND METHODS

A literature search strategy was used, mainly on the most recent scientific papers on the relationship between ethylene and fruit quality of tomato, especially during post harvest, using online database Science Direct.

RESULTS AND DISCUSSIONS

GENERAL ASPECTS OF ETHYLENE BIOSYNTHESIS MANAGEMENT DURING FRUIT RIPENING

Fruit ripening has received considerable attention due to its commercial importance (Yokotani et al., 2009). The control of fruits ripening is often achieved through early harvest, by controlling the postharvest storage atmosphere and by genetic selection for slow or late ripening varieties (Oms-Oliu et al., 2011).

It is known that ethylene function to promote many aspects of ripening of many climacteric fruits, including tomato (Abeles et al., 1992; Yokotani et al., 2009; Barry and Giovannoni, 2007) and modulating its levels in the transgenic plants, as regard as many biotic or abiotic stress factor is readily attainable for a variety of plants [(Stearns and Glick, 2003).

Ethylene biosynthesis starts from methionine via S-adenosyl-L-methionine (AdoMet) having as an intermediate the non-protein amino acid 1-aminocyclopropane-1-carboxylic acid (ACC) (Adams and Yang, 1979). The conversion of AdoMet to ACC and of ACC to ethylene is assured by ACC synthase and ACC oxidase, respectively (Kende, 1993).

Ethylene regulation in climacteric and non-climacteric fruits is under control of two distinct ethylene producing system defined by McMurchie et al. (1972): system 1 (autoinhibitory) and system 2 (autocatalytic). System 1 control the low ethylene production rate and represent basal ethylene in unripe fruit and vegetative tissues, while system 2 is associated with the autocatalytic rise in

ethylene production as is the case of mature climacteric fruits, too (Oetiker and Yang, 1995). Fruit ripening and the role of ethylene in its regulation is complex. Therefore, understanding what controls these processes in non climacteric ripening may prove pertinent to gaining full understanding of climacteric fruit ripening and vice versa (Alexander and Grierson, 2002).

Recently, Yokotani et al. (2009) proposed a model to explain the transition from system 1 to system 2. System 1 is produced via *LeACS1A* and *LeACS6*, which are regulated by a negative feedback system, in the case of absence of exogenous ethylene and stress, via the limited expression of *LeACS2* and *LeACS4*, thus registering a limited increase of ethylene biosynthesis. In a such situation, limited ethylene would play a role as a trigger to stimulate an ethylene burst due to the ethylene-dependent expression of *LeACS2* and *LeACS4*, inducing fruit ripening. System 1 decreases with the onset of system 2, as *LeACS6* is regulated by a negative feedback system; therefore, system 2 in tomato fruit consists of both ethylene-dependent (autocatalytic) and ethylene-independent (non-autocatalytic) systems. Even when the effect of system 1 ethylene is eliminated, fruit can initiate system 2, leading to fruit ripening.

Moreover, responses to this hormone is realized by a signal transduction pathway in which Ethylene Responsive Element Binding Proteins (EREBPs) are transcription factors that help regulate the ethylene response by regulating transcription and gene expression. For example, Zhang et al. (2012) have cloned the gene Tomato LeERF1, indicated its location at the cellular level in the nucleus, nucleolus and plastids, and little signal was detected in the cell wall and vacuole. They have established relationship of LeERF1 with the ripening of tomato fruit.

MEANS TO EXTEND TOMATO SHELF LIFE

Maximum loss in quality and quantity of tomato occurs from harvesting to consumption (Kader, 1986), so, the problem of loss can be controlled by adapting suitable scientific methods of packing and storage and by establishment proper post harvest management (Rahman et al., 2010).

One of the first and simplest conditions to influence ethylene production refers to the handling practices and storage temperature. When matter plants in general are subjected to physical or biological stress the result may be a tissue damage, which implies the production of the ethylene, either as a defense response or to repair the damage tissues. So, an increase of respiration and softening are registered (Mutari and Debbie, 2011). Tomato sealed in plastic films had an extended marketable life and it affects the gaseous atmosphere around the fruit. The use of KMnO₄ contributed to the production of CO₂ and water in the package atmosphere which helped in lowering the respiration and ripening processes (Sammi and Masud, 2007). Post-harvest packing methods, such as storage in perforated (0.25%) polythene bags under ambient conditions (temperature of 20^o-25^o C and relative humidity of 70-90%) extended up to 17 days tomato shelf life without excessive quality decay (Nasrin et al., 2008). The use of black perforated polythene bags (Rahman et al., 2010), treating fruits with chloride and calcium chloride, and treatment of 0.1% gibberellic acid and 0.4 nM salicylic acid (Pila et al., 2010) have been shown to decrease fruit decay and weight loss.

There are also used some treatments in relation to ethylene management. For instance, post-harvest application of 1-methylcyclopropene (1-MCP) as one of ethylene action inhibitor (Sisler, 2006) delayed tomato fruit ripening in relation to the used concentration (Moretti et al., 2002). Response of various climacteric species, including tomato is variable and depends also on internal levels of ethylene (Zhang et al., 2009; Zhang et al., 2010). It should be considered that ingress and accumulation in tomato fruit of gaseous 1-MCP applied as gaseous or aqueous formulation is rapidly. The post-exposure fate is due in relation to multiple factors: inherent sorption-capacity, surface properties (e.g., waxes, stoma), volume and continuity of gas-filled intercellular spaces, and tissue hydration (Dong et al., 2013). In addition, Su and Gubler (2012) showed that reducing post-harvest decay by 1-MCP is also associated with a reduction of economic loss caused by diseases. There is also a positive interaction between jasmonates resulting from treatment with methyl jasmonate (MeJA) and ethylene. MeJA

application causes increased jasmonates concentration, which regulate LOX activity associated with the production of superoxide anion, which has an impact on ethylene production (Yu et al., 2009). JA-ethylene cross-talk in the ethylene synthesis pathways is based on their synergistic interaction, as for example the JA-ethylene responsive antifungal defensin *PDF1.2* (Spoel et al., 2003) regulation by the simultaneously activation of JA and ethylene response pathways (Abeles et al., 1992). Kim et al. (2013) obtained contradictory results. They noticed that JA has also an inhibitory effect on ethylene signaling, which may involve an EIN2 (a key protein in ethylene signaling)-independent pathway. JA antagonistic and ethylene independently function was also registered during lycopene biosynthesis in tomato fruits (Liu et al., 2012).

Respiration rate may be also controlled by influence its proper molecular mechanism. Alternative oxidase (AOX) and ethylene mediate fruit ripening of tomato. Xu et al. (2012) used tomato plants with reduced *LeAOX* (*Le* alternative oxidase) levels and results were retarded ripening; reduced carotenoids, respiration, and ethylene production; and the down-regulation of ripening-associated genes. On the other hand, the fruit that over expressed *LeAOX1a* accumulated more lycopene, and they displayed a similar pattern of ripening to wild-type fruit.

Zhang et al. (2009) described a *relationship between ABA and ethylene* during tomato fruit ripening and senescence as followings: (i) the expression of the ABA biosynthetic gene (*LeNCEDI*) (which encode 9-*cis*-epoxy carotenoid dioxygenase (NCED) as a key enzyme in ABA biosynthesis) occurs before that of ethylene biosynthesis genes; (ii) ABA content also preceded the climacteric increase in ethylene production; (iii) ABA may induce ethylene biosynthesis via the regulation of ACS and ACO gene expression; (iv) exogenous ABA accelerates fruit ripening, and fluridone or nordihydroguaiaretic acid treatment delayed fruit ripening by inhibition of ABA; and (v) ethylene plays a key role in the later stages of fruit ripening.

Delaying ripening and enhancing resistance to a post-harvest fungal pathogens can be also assure by NO treatments (Lai et al., 2011)

which suppress ethylene biosynthesis, stimulate the activity of antioxidant enzymes and regulate the expression of age-related genes.

Tomato is a suitable system for studying unique biological phenomena not harbored by *Arabidopsis* (Okabe et al., 2011). As Me et al. (2007) noticed, in molecular technologies, using molecular markers in plants breeding programs is a common procedure. Unfortunately, gene *modification techniques* introduced into tomato crop improvement, greatly altered tomato variety characteristics. Studies performed by Rodríguez et al. (2011) emphasized that polymorphic polypeptides from fruit pericarp associated with quality fruits traits and fruit shelf life can be such useful tomato breeding programs, as protein molecular markers.

The tomato genome was entirely sequenced by The International Solanaceae Genomics Project (SOL), and many of the gene sequences can be retrieved from databases (Mueller et al., 2009). Also, recently (2012) The Tomato Genome Consortium presented a high-quality genome sequence of domesticated tomato, a draft sequence of its closest wild relative, *Solanum pimpinellifolium*, and compared them to each other and to the potato genome (*Solanum tuberosum*). Although the tomato is completely sequenced, its genomic resources have not been fully exploited. Few studies have reported the detection of quantitative trait loci (QTLs) using simple sequence repeat (SSR) markers for fruit quality traits in tomato, in the recent studies carried out by Yogendra and Gowda (2013). Xu et al. (2013) presented a complete analysis of the RNA helicases (a class of molecular motor proteins) gene family, including the chromosomal locations, phylogenetic tree, and gene structure analysis and expression profile under various growth conditions.

Twenty years ago Klee (1993) noticed that biochemical analysis of transgenic tomato fruits line expressing 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase enzyme emphasized no significant differences from controls in the levels of ACC oxidase or polygalacturonase. Also, transgenic fruit were significantly firmer than the control, so, the author conclusion was that other enzymes may have a significant role in fruit softening. Meli et al. (2010) identified and targeted two ripening-specific *N*-glycoprotein modifying enzymes (α -

mannosidase (α -Man) and β -D-*N*-acetylhexosaminidase (β -Hex) and also demonstrated that genetic manipulation of *N*-glycan processing can be of strategic importance to enhance fruit shelf life, without any negative effect on phenotype, including yield.

To accelerate functional genomic research in tomato, Okabe et al. (2011) developed a Micro-Tom TILLING (Targeting Induced Local Lesions In Genomes) platform and to be used for efficient mutant isolation, six ethylene receptor genes in tomato (*SlETR1–SlETR6*) were screened. The identification of two novel *Sletr1* mutant alleles that are distinguished by the level of ethylene sensitivity and the characterization of their associated phenotypes could provide insight into the ethylene-mediated fruit ripening mechanism in tomato.

Behboodan et al. (2012) were employed RNA interference (RNAi) technology to silence the genes involved in ethylene biosynthetic pathway, by blocking the expression of specific gene encoding the ACC oxidase. The obtained results have successfully demonstrated that several transgenic lines of lowland tomato cv. MT1, harboring an hpRNA-ACO1 (ACC oxidase) construct, showed lower ethylene production because the transgenic fruits displayed delayed post-harvest life with no phenotypic changes and similar amounts of soluble solids content, titratable acidity and ascorbic acid as compared to wild type fruits. They proposed that, hpRNAi ACO1 could effectively be used to delay post-harvest damage, especially in climacteric fruits.

Research carried out by Xie et al. (2006) emphasized that Virus-induced gene silencing (VIGS) technology combined with vacuum infiltration can silence *LeACS2* gene function for a certain time and is an efficient way to postpone the post-harvest senescence of tomato fruit. In the same time, vacuum infiltration is an easy and inexpensive method at room temperature, so, a potential method to maintain the quality of detached tomato fruit. The syringe infiltration method of VIGS [tobacco rattle virus (TRV)-LeRIN: the transcription factor RIN (Ripening Inhibitor) belongs to the MADS box family and regulates tomato ripening] was successfully applied to silence the LeRIN, LeACS2, LeACS4 and LeACO1 genes in tomato fruits. There were identified also, the target genes

of RIN transcription factor in ethylene biosynthesis in tomato fruit (Li et al., 2011).

Integrating molecular approaches with conventional breeding to enhance fruit quality could significantly improve the post-harvest shelf life of tomato. Recently, tomato hybrids with enhanced shelf life were developed using ripening mutants and agronomically superior Indian cultivars, and hybrids from all possible line x tester crosses were screened for shelf life, yield, and other fruit qualities (Yogendra and Gowda, 2013).

CONCLUSIONS

Tomatoes are one of the most important vegetables worldwide and are used both for fresh consumption, as well as processed, considering their nutritional value and health benefits to people.

Always, there have been major concerns for the improvement of tomato characteristics feature, including those regarding the ripening dynamics, with a view to reduce the post-harvest loss and to extend shelf life.

Ethylene is one of the most important plant hormone, which regulates tomato ripening. So, ethylene management by integrating molecular approaches with conventional breeding could significantly improve the post-harvest shelf life of tomato.

In addition to breeders focus to increase tomato production and to extend the fruits shelf life, flavor improvement still remains one of the major challenges (Klee and Tieman, 2013).

REFERENCES

- Abeles F.B., Morgan P.W., Salveit Jr. M.E., 1992. Ethylene in plant biology. New York: Academic Press. Adams, D.O., Yang, S.F. 1979. Ethylene biosynthesis: identification of 1-aminocyclopropane-1-carboxylic acid as an intermediate in the conversion of methionine to ethylene. *Proc. Nat. Acad. Sci, USA*, 76, p. 170-174.
- Agarwal S., Rao A.V., 2000. Tomato lycopene and its role in human health and chronic diseases. *Canadian Medical Association*, 163, p. 739-744.
- Alexander L., Grierson D., 2002. Ethylene biosynthesis and action in tomato: a model for climacteric fruit ripening. *J. Exp. Bot.*, 53, p. 2039-2055.
- Barry C.S., Giovannoni J.J., 2007. Ethylene and fruit ripening. *J. Plant Growth Regul.* 26, p.143-159.
- Behboodian B., Ali Z.M., Ismail I., Zainal Z., 2012. Postharvest Analysis of Lowland Transgenic Tomato Fruits Harboring hpRNAi-ACO1 Construct. *The Scientific World Journal*, Article ID 439870, 9 pages, doi:10.1100/2012/439870 Research Article.
- Dong X., Ramirez-Sánchez M., Huber D.J., Rao J., Zhang Y., Choi S.T., Lee J.H., 2013. Postharvest Biology and Technology, 78, p. 40-47.
- Hanson P., Chen J.T., Cou C.G., Morris R., Opena R.T., 2001. Tomato production. *Asian Vegetable Research Development Center*.
- Helyes L., 1999. *A paradicsom és termesztése*. Syca Szakkönyvszolgálat, Budapest, Hungary.
- Kader A.A., 1986. Effects of postharvest handling procedures on tomato quality. *Acta Hort.* 190, p.209-221.
- Kende, H., 1993. Ethylene biosynthesis. *Annu. Rev. Plant Physiol. Plant. Mol. Biol.*, 44, p. 283-307.
- Kimura S., Sinha N., 2008. Tomato (*Solanum lycopersicum*) : A Model Fruit-Bearing Crop. *Cold Spring Harb Protoc*; doi:10.1101/pdb.emo 105.
- Kim J., Patterson S.E., Binder B.M., 2013. Reducing jasmonic acid levels causes ein2 mutants to become ethylene responsive. *FEBS Letters*, 587, p. 226-230.
- Klee H.J., 1993. Ripening physiology of fruit from transgenic tomato (*Lycopersicon esculentum*) plants with reduced ethylene synthesis. *Plant Physiology*, 102, p. 911-916.
- Klee H.J., Tieman D.M., 2013. Genetic challenges of flavor improvement in tomato. *Trends in Genetics* xx 1-6.
- Lai T., Wang Y., Li B., Qin G., Tian S., 2011. Defence response of tomato fruit to exogenous nitric oxide during postharvest storage. *Postharvest Biology and Technology*, 62, p. 127-133.
- Li L., Zhu B., Fu D., Luo Y., 2011. RIN transcription factor plays an important role in ethylene biosynthesis of tomato fruit ripening. *J. Sci Food Agric.*, 91, p. 2308-2314.
- Liu L., Wei J., Zhang M., Li C., Wang Q., 2012. Ethylene independent induction of lycopene biosynthesis in tomato fruits by jasmonates. *J. Exp. Bot.* doi: 10.1093/jxb/ers224.
- Martinez-Madrid M.C., Egea M.I., Sánchez-Bel P., 2007. Effect of combined 1-MCP and cold storage on the shelf life and postharvest quality of tomato. In *Advances in Plant Ethylene Research*.
- McMurchie E.J., McGlasson W.B., Eaks I.L., 1972. Treatment of fruit with propylene gives information about the biogenesis of ethylene. *Nature*, 237, p. 235-236.
- Me B.B., Be L.K., Be J.J., Ying T.Y., 2007. Fruit quality of transgenic tomatoes with suppressed expression of LeETR1 and LeETR2 genes. *Asia Pac. J. Clin. Nutr.*, Vol. 16, p.122-126.
- Meli V.S., Ghosh S., Prabha T.N., Chakraborty N., Chakraborty S., Datta A., 2010. Enhancement of fruit shelf life by suppressing N-glycan processing enzymes. *PNAS*, 107, p. 2413-2418.
- Mueller L.A., Lankhorst R.K., Tanksley S.D., Giovannoni J.J., White R., Vrebalov J., 2009. A snapshot of the emerging tomato genome sequence. *Plant Genome*, 2, p.78-92.
- Moretti C.L., Araújo A.L., Maurouelli W.A., Silca W.L.C., 2002. 1-Methylcyclopropene delays tomato fruit ripening. *Horticultura Brasileira*, 20, p. 65-663.

- Mutari A., Debbie R., 2011. The effects of postharvest handling and storage temperature on the quality and shelf life of tomato. *African Journal of Food Science*, 5, p. 446-452.
- Nasrin T.A.A., Molla M.M., Hossain M.A., Alam M.S., Yasmin L., 2008. Effect of postharvest treatments on shelf life and quality of tomato. *Bangladesh J. Agri. Res.*, 33, p. 579-585.
- Oetiker J.H., Yang S.F., 1995. The role of ethylene in fruit ripening. *Acta Horticulturae*, 398, p.167-178.
- Okabe Y., Saito T., Matsukura C., Ariizumi T., Bres C., Rothan C., Mizoguchi T., Ezura H., 2011. Tomato TILLING Technology: Development of a Reverse Genetics Tool for the Efficient Isolation of Mutants from Micro-Tom Mutant Libraries. *Plant Cell Physiology*, 52, p. 1994-2005.
- Oms-Oliu G., Hertog M.L.A.T.M., Vande Poel B., Ampofo-Asiama J., Geeraerd A.H., Nicolai B.M., 2011. metabolic characterization of tomato fruit during preharvest development, ripening, and postharvest shelf-life. *Postharvest Biology and Technology*, Vol.62, p.7-16.
- Opiyo A.M., Ying T.J., 2005. The effects of 1-methylcyclopropane treatment on the shelf life and quality of cherry tomato (*Lycopersicon esculentum* var. cerasiforme) fruit. *International Journal of Food Science and Technology*, 40, p. 665-673.
- Panthee D.R., Chen F., 2010. Genomics of Fungal Disease Resistance in Tomato. *Curr Genomics*, 11, p. 30-39.
- Pila N., Gol N.B., Rao T.V.R., 2010. Effect of post harvest treatments on physicochemical characteristics and shelf life of tomato (*Lycopersicon esculentum* Mill.) fruits during storage. *American-Eurasian J. Agric. & Environ. Sci.*, 9, p. 470-479.
- Rahman M.M., Islam M.N., Wazed M.A., Arfin M.S., Hossain F.B., 2010. Determination of post harvest losses and shelf life of tomato as influenced by different types of polythene at refrigerated condition (100 C). *Int. J. Sustain., Crop Prod.*, 5, p. 62-65.
- Rodríguez G.R., da Costa J.H.P., Tomat D.D., Pratta G.R., Zorzoli R., Picardi L.A., 2011. Pericarp total protein profiles as molecular markers of tomato fruit quality traits in two segregating populations. *Scientia Horticulturae*, 130, p. 60-66.
- Sammi S., Masud T., 2007. Effect of different packing systems on storage life and quality of tomato (*Lycopersicon esculentum* var. Rio Grande) during different ripening stages. *Internet Journal of Food Safety*, p. 37-44.
- Sisler E.C., 2006. The discovery and development of compounds counteracting ethylene at the receptor level. *Biotechnol Adv.*, 24, p. 357-367.
- Spoel S.H., Koornneef A., Claessens S.M.C., Korzelius J., Van Pelt J.A., Mueller M.J., Buchala A.J., Métraux J.P., Brown R., Kazan K., Van Loon L.C., Dong X., Pieterse C.M.J., 2003. NPR1 modulates cross talk between salicylate-and jasmonate-dependent defense pathways through a novel function in the cytosol. *Plant Cell*, p. 760-770.
- Spoel S.H. et al., 2003. NPR1 modulates cross-talk between salicylate-and jasmonate-dependent defense pathways through a novel function in the cytosol. *Plant Cell*, 15, p. 760-770.
- Stearns J.C., Glick, B.R., 2003. Transgenic plants with altered ethylene biosynthesis or perception. *Biotechnology Advances*, 21, p. 193-210.
- Su H., Gubler W.G., 2012. *Postharvest Biology and Technology*, Vol. 64, p.133-137.
- Upendra M.S., Dris R., Bharat S., 2003. Mineral nutrition of tomato. *Journal of Food Agriculture and Environment*, 1, p.176-183.
- Xie Y.H., Zhu B.Z., Yang X.L., Zhang H.X., Fu D.Q., Zhu H.L., Shao Y., Gao H.Y., Luo Y., 2006. Delay of postharvest ripening and senescence of tomato fruit through virus-induced LeACS2 gene silencing. *Postharvest Biology and Technology*, 42, p. 8-15.
- Xu F., Yuan S., Zhang D.W., Lv X., Lin H.H., 2012. The role of alternative oxidase in tomato fruit ripening and its regulatory interaction with ethylene. *J. Exp. Bot.* doi: 10.1093/jxb/ers226.
- Xu R., Zhang S., Lu L., Cao H., Zheng C., 2013. A genome-wide analysis of the RNA helicase gene family in *Solanum lycopersicum*. *Gene*, 513, p. 128-140.
- Yang S.F., 1985. Biosynthesis and action of ethylene. *HortScience*, 20, p. 41-45.
- Yogendra K.N., Gowda P.H.R., 2013. Phenotypic and molecular characterisation of a tomato (*Solanum lycopersicon* L.) F2 population segregation for improved shelf life. *Gen. Mol. Res.*
- Yokotani N., Nakano R., Imanishi S., Nagata M., Inaba A., Kubo Y., 2009. Ripening-associated ethylene biosynthesis in tomato fruit is autocatalytically and developmentally regulated. *J Exp Bot.*, 60, p.3433-3442.
- Yu M., Shen L., Fan B., Zhao D., Zheng Y., Sheng J., 2009. The effect of MeJA on ethylene biosynthesis and induced disease resistance to *Botrytis cinerea* in tomato. *Postharvest Biology and Technology*, 54, p. 153-158.
- Zhang M., Yuan B., Leng P., 2009. The role of ABA in triggering ethylene biosynthesis and ripening of tomato fruit. *J Exp Bot.*, 60, p. 1579-1588.
- Zhang Z., Huber D.J., Hurr B.M., Rao J., 2009. Delay of tomato fruit ripening in response to 1-methylcyclopropene is influenced by internal ethylene levels. *Postharvest Biology and Technology*, 54, p.1-8.
- Zhang Z., Huber D.J., Rao J., 2010. Short-term hypoxic hypobaric transiently decreases internal ethylene levels and increases sensitivity of tomato fruit to subsequent 1-methylcyclopropene treatments. *Postharvest Biology and Technology*, 56, p.131-137.
- Zhang H., Zhu B., Luo Y., Xie Y., 2012. The research of subcellular localization of ethylene response factor LeERF1 in tomato fruit. *Procedia Environmental Sciences*, 12, p.1187 - 1196.
- The Tomato Genome Consortium. 2012. The tomato genome sequence provides insights into fleshy fruit evolution. *Nature*, 485, p.635-641