University of São Paulo
"Luiz de Queiroz" College of Agriculture

Redefining the hormonal control of tomato (*Solanum lycopersicum* cv. Micro-Tom) fruit development

Ignacio Achon Forno

Thesis presented to obtain the degree of Master in Science. Area: Plant Physiology and Biochemistry

Piracicaba
2017

Ignacio Achon Forno
Agronomist

Redefining the hormonal control of tomato (*Solanum lycopersicum* cv. Micro-Tom) fruit development

Advisor:
Prof. Dr. LAZARO EUSTAQUIO PEREIRA PERES

Thesis presented to obtain the degree of Master in Science. Area: Plant Physiology and Biochemistry

Piracicaba
2017

Dados Internacionais de Catalogação na Publicação
Divisão de Biblioteca – DIBD/ESALQ/USP

Achon Forno, Ignacio

Redefining the hormonal control of tomato (*Solanum lycopersicum cv.* Micro-Tom) fruit development / Ignacio Achon Forno. - - Piracicaba, 2017.

69 p.

Dissertação (Mestrado) - - USP/Escola Superior de Agricultura “Luiz de Queiroz”.

1. Tomato 2. Hormones 3. Fruit development. I. Título

RESUMO

Redefinindo o controle hormonal do desenvolvimento do fruto do tomateiro (*Solanum lycopersicum* cv. Micro-Tom)

O controle hormonal do desenvolvimento do fruto do tomateiro (*Solanum lycopersicum* cv. Micro-Tom) já foi extensamente estudado, principalmente no amadurecimento. No entanto, ainda existem consideráveis lacunas em nosso conhecimento da função e distribuição espaço-temporal dos hormônios durante o desenvolvimento do fruto. Foram realizados ensaios histoquímicos com cinco linhas transgênicas de tomate *cv.* Micro-Tom que carregavam o gene repórter GUS fusionado a cinco diferentes promotores responsivos aos hormônios, auxina, citocinina (CKs), giberelina (GAs), ácido abscísico (ABA) e etileno, com o fim de redefinir a distribuição espaço-temporal deles ao longo do desenvolvimento do fruto, desde estágios iniciais pre-anteses até o estágio red ripe (RR). Os níveis de CKs foram altos na fase pre-anteses, inicialmente na placenta e posteriormente nos óvulos, indicando um papel importante deste hormônio no crescimento do ovário, pre- fertilização. Nos estágios inicias, post-fertilização, o conteúdo de CKs foi alto nas sementes e depois nas camadas epidérmicas e subepidérmicas internas e externas do pericarpo. Alto conteúdo de auxina foi observado, durante todos o desenvolvimento do fruto, no pedicelo, sugerindo o transporte basípeto de auxina para a planta mãe. Os níveis de etileno aumentaram durante o crescimento do ovário antes da anteses. Interessantemente, o nível de etileno não diminuiu imediatamente post-fertilização. Os conteúdos de GA e ABA foram baixos prévios a anteses e nos estágios inicias pre-fertilização, especificamente na placenta e pericarpo. Inversamente, o conteúdo desses hormônios aumentou na fase de expansão celular do crescimento do fruto. Os grãos de pólen que chegaram ao stigma, post deiscência das anteras, apresentaram altos níveis de ABA e auxina. Além disso, reportamos um antagonismo entre conteúdo de etileno e giberelina durante o desenvolvimento do fruto, onde o nível de etileno começou a decrescer durante a fase de expansão celular do crescimento do fruto, momento em que o nível de giberelina começou a aumentar na placenta e pericarpo.

Palavras-chaves: 1. Tomate 2. Desenvolvimento do fruto 3. Hormônios 4. Gene reporter GUS L.

ABSTRACT

Redefining the hormonal control of tomato (*Solanum lycopersicum* cv. Micro-Tom) fruit development

The hormonal control of tomato (*Solanum lycopersicum*) fruit development have been extensively studied, mainly during ripening. Notwithstanding, considerable gaps still exist in our understanding of the function and spatial-temporal distribution of hormones during fruit development. Here, we performed histochemical analysis of tomato *cv.* Micro-Tom transgenic lines harboring the gene reporter *GUS* fused to five different promoter responsive to the hormones, auxin, cytokinins (CKs), gibberellins (GAs), abscisic acid (ABA) and ethylene, in order to redefine their spatial-temporal distribution during tomato fruit development, from early pre-anthesis stages to red ripe (RR) stage. CKs levels were high during pre-anthesis, initially in placental tissues and subsequently in ovule, indicating a major function of this hormone during pre-fertilized ovary growth. At early post-fertilization stages, CKs contents were high in seeds, and afterward in the outer and inner epidermical and subepidermical layer of pericarp. High auxin content was observed, during all pre-anthesis and fruit development stages, in pedicel, suggesting a basipetal transport to the mother plant. Ethylene contents increased during pre-anthesis ovary growth. Interestingly, ethylene contents did not decrease, immediately, post-fertilization. The content of GAs and ABA was low at pre-anthesis and early post-fertilization stages, specific in placental tissues and pericarp. Conversely, these hormones accumulated mainly during cell expansion phase of fruit growth. Pollen grains that reached the stigma, post anther dehiscence, showed high content of auxin and ABA. In addition, we reported an antagonism between ethylene and GAs contents during tomato fruit development, where the level of ethylene started to decrease during the cell expansion phase of the fruit growth, moment when the level of GAs started to increase in placental tissues and pericarp.

Key-words: 1. Tomato 2. Fruit development 3. Hormones 4. Gene reporter GUS L.

1. INTRODUCTION

In angiosperms, embryonic development occurs concomitantly with the development of the ovary into a specialized organ, the fruit (Gillaspy et al., 1993). In tomato, a multicarpelar berry that is considered as a model system for fleshy climacteric fruit development (Azzi et al., 2015), fruit develops from the ovary, which consist in two or more carpels forming the locules, separated by a septum that fuses with each of the carpels, and ovules are attached to the central septum via placental tissue (Gasser and Robinson-Beer, 1993; Pattison et al., 2015).

Tomato fruit development is usually divided in four phases; fruit set, growth, maturation and ripening. The fruit set, defined as the transition of a quiescent ovary to a rapidly growing young fruit, depends on the successful completion of pollination and double fertilization, when one sperm fuses with the eggs cell to form the embryo and the other sperm fuses with the two haploid polar nuclei in the central cell to give rise to the endosperm (Raghavan, 2003). The fruit growth is divided in two stages: a very active period of cell division within the pericarp, mainly in the outer layer, which last about 7 to 10 days after successful fertilization, whereas after cell division phase during the following days until the fruit reach it final size, the fruit growth depend mainly on cell expansion. Fruit growth is followed by the fruit maturation, where it acquire the prerequisite competence to enter into the final development stage, ripening. Fleshy fruit such as tomato undergo a ripening process in which the biochemistry, physiology, and structure of the organ are developmentally altered to influence appearance, texture, flavor and aroma (Gillaspy et al., 1993; Giovannoni, 2004; de Jong et al., 2009a; McAtee et al, 2013; Kumar et al, 2014; Liu et al, 2015). It is worth noting that the four phases described above are well accepted by most author, although they do not take into account the initial ovary development before anthesis, where important events, such as the definition of the number of carpels, and thus the number of locules and the final size of the fruit, take place (Xu et al., 2015).

New evidences suggest that functions of plant hormones are not limited to a restricted phase in fruit development, and that there exists a complex crosstalk between them during the whole fruit development (Kumar et al., 2014; McAtee et al., 2013; Pattison et al., 2015). Increase of auxin contents upon pollination, mostly synthesized in the embryo and exported to pericarp, plays a major role in the regulation of fruit set and growth (Gillaspy et al., 1993; Serrani et al., 2008, 2007; Vriezen et al., 2008; de Jong et al., 2009a; Mariotti et al., 2011; Pattison and Catala, 2012; McAtee et al., 2013;). This induction of fruit set and growth by increased auxin post-fertilization is, at least partially, due to an increase in gibberellins (GAs) biosynthesis (Serrani et al., 2008). Exogenous applications of either auxin or GAs induce parthenocarpic fruits that present, respectively, increased cell layers or greater cell expansion (Serrani et al., 2007), suggesting that auxin contributes to cell division in fruit, while gibberellin to cell expansion.

Application of synthetic cytokinins (CKs) induces parthenocarpic fruit through promotion of cell division (Ding et al., 2013). Additionally, the cytokinin transduction pathway is active in cell division phase of fruit development, but the first peak of cytokinin accumulation occurs during anthesis (Matsuo et al., 2012). These evidences suggest that cytokinin might be involved in the growth of ovaries until pollination and afterwards in the cell division period post-pollination.

Acid abscisic (ABA) and ethylene biosynthesis genes expression is attenuated post-pollination, which suggest an antagonist role of these two plant hormones in fruit set (Vriezen et al., 2008; Shinozaki et al., 2015). In climacteric fruit, such as tomato, ethylene production reaches its maximum at the onset of ripening, which indicates a main role of this hormone at this phase of fruit development (Liu et al., 2015). On the other hand, the facts that the expression of ethylene biosynthesis genes (*SlACS2*, *SlACS4* and *SlACO1*) is induced by exogenous ABA, and that

ABA maximum precedes ethylene release, reveals an ABA/ethylene interaction acting at the level of ethylene biosynthesis (Liu et al., 2015). These evidence imply that ABA may function as a trigger for the initiation of fruit ripening by inducing ethylene-mediated pathway and other ethylene-independent processes (Zhang et al., 2009; Mou et al., 2016). Moreover, Jones et al. (2002) and Trainotti et al. (2007) suggests a crosstalk between ethylene and auxin during onset of ripening.

Although the importance of hormones in fruit development is well known (Zhang et al., 2016), considerable gaps in our knowledge about hormonal networks and crosstalk between different hormones still exist (Kumar et al., 2014). Moreover, the spatial-temporal distribution of hormones and expression of genes related to hormonal metabolism and signaling during the entire fruit development, from pre-anthesis to red ripe stages, is poorly understood (Zhang et al., 2016). The aim of this work was to redefines the hormonal control of fruit development by using transgenic plant harboring the gene reporter GUS fused to five different promoter responsive to auxin, CKs, GAs, ABA and ethylene. Through histochemical analysis, we demonstrates the spatial-temporal distribution of the five classics plant hormones from 12 days before anthesis, referred to here as -12 days post anthesis (-12 DPA), to the red ripe (RR) stage in tomato *cv.* Micro-Tom fruit. According to our results, GAs and ABA have its main functions in the cell expansion phase of fruit development, reaching its maximum production at mature green stage and cell expansion phase, respectively, and presenting apparently no activity during fruit set and early fruit growth. Surprisingly, an increase in the ethylene contents was observed, during the ovary growth, at pre-anthesis stages without diminishing during early post-fertilization stages. Furthermore, CKs show a major role during ovary growth at pre-anthesis stages in placenta and ovules. We additionally, proposes an interplay between ethylene and GAs during the transition from cell division to cell expansion phase of fruit growth.

2. CONCLUSIONS

Taken together, the results presented here redefined the hormonal balance during tomato fruit development. In this working hypothesis, auxin and cytokinin are the main hormones in stimulating ovary/fruit development during pre-anthesis and early post-fertilization cell division phase, whereas GAs and ABA are responsible for fruit growth during cell expansion phase. On the other hand, ethylene may presents a role in cell division phase, suppressing GAs metabolism, giving that an antagonist temporal and spatial distribution of *EBS*::GUS and *GA2OX*::GUS was noticed, and that *Nr* fruits showed a higher *GA2Ox::GUS* expression in placenta and pericarp compared to WT. The decrease of ethylene content during cell expansion phase may release ethylene repressed GAs metabolism, which in turns, promotes cell expansion. In seeds (ovules), the hormones balance, in general, parallels the pericarp, with the notable exception of ethylene, which seems not to accumulate in seeds, and the more persistent accumulation of auxin, probably reflecting their further role in germination.

BIBLIOGRAPHIC REFERENCE

ALBA, R.;PAYTON, P.; FEI, Z.; MCQUINN, R.; DEBBIE, P.; MARTIN, G.B.; TANKSLEY, S.D.; GIOVANNONI, J.J. Transcriptome and selected metabolite analyses reveal multiple points of ethylene control during tomato fruit development. **The Plant Cell**, Baltimore, v. 17, p. 2954-2965, Nov. 2005.

ALONI, R.; ALONI, E.; LANGHANS, M.; ULLRICH, C.I. Role of auxin in regulating Arabidopsis flower development. **Planta**, New York, v. 223, p. 315-328, Oct. 2006.

AZZI, L.; DELUCHE, C.; GÉVAUDANT, F.; FRANGNE, N.; DELMAS, F.; HERNOULD, M.; CHEVALIER, C. Fruit growth-related genes in tomato. **Journal of Experimental Botany**, Oxford, v. 66, p. 1075-1086, Jan. 2015.

BASSEL, G. W.; MULLEN, R. T.; BEWLEY, J. D. *procera* is a putative DELLA mutant in tomato (*Solanum lycopersicum*): effects on the seed and vegetative plant. **Journal of Experimental Botany**, Oxford, v. 59, p. 585-593, Feb. 2008.

BARRY, C. S.; LLOP-TOUS, M. I.; GRIERSON, D. The regulation of 1-aminocyclopropane-1-carboxylic acid synthase gene expression during the transition from system-1 to system-2 ethylene synthesis in tomato. **Plant Physiology**, Minneapolis, v. 123, p. 979-986, Jul. 2000.

BERGERVOET, J. H.; BERHOEVEN, H. A.; GILISSEN, L. J.; BINO, R. J. High amounts of nuclear DNA in tomato (Lycopersicon esculentum Mill.) pericarp. **Plant Science**,Limerick, v. 116, p. 141-145, May. 1996.

BLEECKER, A. B.; KENDE, H. Ethylene: a gaseous signal molecule in plants. **Annual Review of Cell and Developmental Biology**, Palo Alto, v. 16, p. 1-18, Jan. 2000.

BOHNER, J.; BANGERTH, F. Effects of fruit set sequence and defoliation on cell number, cell size and hormone levels of tomato fruits (*Lycopersicon esculentum* Mill.) within a truss. **Plant Growth Regulation**, Boston, v. 7, p. 141-155, Mar. 1988.

BRUKHIN, V.; HERNOULD, M.; GONZALEZ, N.; CHEVALIER, C; MOURAS, A. Flower development schedule in tomato Lycopersicon esculentum cv. sweet cherry. **Sexual Plant Reproduction**, Berlin, v. 15, p. 311-320, Mar. 2003.

BRUMOS, J.; ALONSO, J. M.; STEPANOVA, A. N. Genetic aspects of auxin biosynthesis and its regulation. **Physiologia Plantarum**, Lund, v. 151, p. 3-12, May. 2014.

CAMPOS, M. L.; CARVALHO, R. F.; BENEDITO, V. A; PERES, L. E. P. Small and remarkable: the Micro-Tom model system as a tool to discover novel hormonal functions and interactions. **Plant signaling & Behavior**, Georgetown, v. 5, p. 267-270, Mar. 2010.

CARA, B.; GIOVANNONI, J. J. Molecular biology of ethylene during tomato fruit development and maturation. **Plant Science**, Limerick, v. 175, p. 106-113, Apr. 2008.

CARVALHO, R. F.; CAMPOS, M. L.; PINO L. E.; CRESTANA, S. L.; ZSOGON, A.; LIMA, J. E.; BENEDITO,V. A.; PERES, L. E. P. Convergence of developmental mutants into a single tomato model system: Micro-Tom as an effective toolkit for plant development research. **Plant Methods**, London, v. 7, p. 1-14, Jun. 2011.

CARRARI, F.; FERNIE, A .R.; IUSEM, N. D. Heard it through the grapevine? ABA and sugar cross-talk: the ASR story. **Trends in Plant Science**, Oxford, v. 9, p. 57-59, Feb. 2004.

CECCHETTI, V.; ALTAMURA, M. M.; FALASCA, G.; COSTANTINO, P.; CARDARELLI, M. Auxin regulates Arabidopsis anther dehiscence, pollen maturation, and filament elongation. **The Plant Cell**, Baltimore, v. 20, p. 1760-1774, Jul. 2008.

CHANDLER, J. The hormonal regulation of flower development. **Journal of Plant Growth Regulation**, New York, v. 30, p. 242-254, Oct. 2011.

CHENG, Y.; DAI, X.; ZHAO, Y. Auxin biosynthesis by the YUCCA flavin monooxygenases controls the formation of floral organs and vascular tissues in Arabidopsis. **Genes & Development**, New York v. 20, p. 1790-1799, Apr. 2006.

CHENICLET, C.; RONG, W.Y.; CAUSSE, M.; FRANGNE, N.; OLLING, L.; CARDE, J. P.; RENAUDIN, J. P. Cell expansion and endoreduplication show a large genetic variability in pericarp and contribute strongly to tomato fruit growth. **Plant Physiology**, Minneapolis, v. 139, p. 1984-1994, Dec. 2005.

CHHUN, T.; AYA, K.; ASANO, K.; YAMAMOTO, E.; MORINAKA, Y.; WATANABE, M.; KITANO, H.; ASHIKARI, M.; MATSUOKA, M.; UEGUCHI-TANAKA, M. Gibberellin regulates pollen viability and pollen tube growth in rice. **The Plant Cell**, Baltimore, v. 19, p. 3876-3888, Dec. 2007.

CHRISTMANN, A.; HOFFMANN, T.; TEPLOVA, I.; GRILL, E.; MÜLLER, A. Generation of active pools of abscisic acid revealed by in vivo imaging of water-stressed Arabidopsis. **Plant Physiology**, Minneapolis, v. 137, p. 209-219, Jan. 2005.

CUCINOTTA, M.; COLOMBO, L.; ROIG-VILLANOVA, I. Ovule development, a new model for lateral organ formation. **Frontier in Plant Science**, Lausanne, v. 5, p. 117, Mar. 2014.

CZEREDNIK, A.; BUSSCHER, M.; BIELEN, B. A.; WOLTERS-ARTS, M.; DE MAAGD, R.A.; ANGENENT, G.C. Regulation of tomato fruit pericarp development by an interplay between CDKB and CDKA1 cell cycle genes. **Journal of Experimental Botany**, Oxford, v. 63, p. 2605-2617, Jan, 2012.

D'AGOSTINO, I. B.; DERUERE, J.; KIEBER, J. J. Characterization of the response of the Arabidopsis response regulator gene family to cytokinin. **Plant Physiology**, Minneapolis, v. 124, p. 1706-1717, Dec. 2000.

DAYAN, J.; VORONIN, N.; GONG, F.; SUN, T. P.; HEDDEN, P.; FROMM, H.; ALONI, R. Leaf induced gibberellin signaling is essential for internode elongation, cambial activity, and fiber differentiation in tobacco stems. **The Plant Cell**, Baltimore, v. 24, p. 66-79, Jan. 2012.

DE JONG, M.; MARIANI, C.; VRIEZEN, W. H. The role of auxin and gibberellin in tomato fruit set. **Journal of Experimental Botany**, Oxford, v. 60 (5), p. 1523-1532, Mar. 2009a.

DE JONG, M., M. WOLTERS-ARTS, R. FERON, C. MARIANI, AND W. H. VRIEZEN, W. H. The Solanum lycopersicum auxin response factor 7 (*SlARF7*) regulates auxin signaling during tomato fruit set and development. **The Plant Journal**, Oxford, v. 57, p. 160-170, Jan. 2009b.

DE JONG, M.; WOLTERS-ARTS, M.; GARCÍA-MARTÍNEZ, J.L.; MARIANI, C.; VRIEZEN, W. H.; The *Solanum lycopersicum* AUXIN RESPONSE FACTOR 7 (*Sl*ARF7) mediates cross-talk between auxin and gibberellin signalling during tomato fruit set and development. **Journal of Experimental Botany**,Oxford, v. 62, p. 617-626, Feb. 2011.

DHARMASIRI, N.; DHARMASIRI, S.; ESTELLE, M. The F-box protein TIR1 is an auxin receptor. **Nature**, London, v. 435, p. 441-445, May. 2005.

DORCEY, E.; URBEZ, C.; BLÁZQUEZ, M.A.; CARBONELL, J.; PEREZ-AMADOR, M.A. Fertilization dependent auxin response in ovules triggers fruit development through the modulation of gibberellin metabolism in Arabidopsis. **The Plant Journal**, Oxford, v. 58, p. 318-332, Jan. 2009.

EGEA, I., W. BIAN, C. BARSAN, A. JAUNEAU, J.-C. PECH, A. LATCHÉ, Z. LI, AND C. CHERVIN, 2011, Chloroplast to chromoplast transition in tomato fruit: spectral confocal microscopy analyses of carotenoids and chlorophylls in isolated plastids and time-lapse recording on intact live tissue. **Annals of Botany**, London, v. 108 p. 291-297, Apr. 2011.

EXPÓSITO-RODRÍGUEZ, M.; BORGES, A. A.; BORGES-PÉREZ, A.; PÉREZ, J. A. Gene structure and spatiotemporal expression profile of tomato genes encoding YUCCA-like flavin monooxygenases: the ToFZY gene family. **Plant Physiology and Biochemistry**, Paris, v. 49, p. 782-791, Mar. 2011.

GARCIA-HURTADO, N.; CARRERA, E.; RUIZ-RIVERO, O.; LOPEZ-GRESA, M. P.; HEDDEN, P.; GONG, F.; GARCIA-MARTINEZ, J. L. The characterization of trangenic tomato overexpressing gibberellin 20-oxidase reveals induction of parthenocarpic fruit growth, higher yield, and alteration of gibberellin biosynthetic pathway. **Journal of Experimental Botany**, Oxford, v. 66, p. 5803-5813, Set. 2012.

GASSER, C. S.; ROBINSON-BEERS, K. Pistil development. **The Plant Cell**, Baltimore, v. 5, p. 1231-1239, Oct. 1993.

GILLASPY, G.; BEN-DAVID, H.; GRUISSEM, W. Fruits: a developmental perspective. **The Plant Cell**, Baltimore, v. 5, p. 1439-1451, Oct. 1993.

GOETZ, M.; HOOPER, L. C. JOHNSON, S. D.; RODRIGUES, J. C. M.; VIVIAN-SMITH, A.; KOLTUNOW, A.M. Expression of aberrant forms of AUXIN RESPONSE FACTOR8 stimulates parthenocarpy in Arabidopsis and tomato. **Plant Physiology**, Minneapolis, v. 145, p. 351-366, Oct. 2007.

GONZÁLEZ, R. M.; IUSEM, N. D. Twenty years of research on Asr (ABA-stress-ripening) genes and proteins. **Planta**, New York, v. 239, p. 941-949, Feb. 2014.

GUSTAFSON, F. G. Inducement of fruit development by growth-promoting chemicals. **Proceedings of the National Academy of Sciences**, Washigton, v. 22, p. 628-636, Oct. 1936.

GUZMAN, P.; ECKER, J. R. Exploiting the triple response of Arabidopsis to identify ethylene-related mutants. **The Plant Cell**, Baltimore, v. 2, p. 513-523, Jun. 1990.

HIRANO, K.; AYA, K.; HOBO, T.; SAKAKIBARA, H.; KOJIMA, M.; SHIM, R. A.; HASEGAWA, Y.; UEGUCHI-TANAKA, M.; MATSUOKA, M. Comprehensive transcriptome analysis of phytohormone biosynthesis and signaling genes in microspore/pollen and tapetum of rice. **Plant and Cell Physiology**, Oxford, v. 49, p. 1429-1450, Aug. 2008.

HU, J.; MITCHUM, M. G.; BARNABY, N.; AYELE, B. T.; OGAWA, M.; NAM, E.; LAI, W. C.; HANADA, A.; ALONSO, J. M.; ECKER, J. R. Potential sites of bioactive gibberellin production during reproductive growth in Arabidopsis. **The Plant Cell**, Baltimore, v. 20, p. 320-336, Feb. 2008.

INZÉ, D.; DE VEYLDER, L. Cell cycle regulation in plant development. **Annual Review of Genetics**, Palo Alto, v. 40, p. 77-105, Sept. 2006.

JI, K.; KAI, W.; ZHAO, B.; SUN, Y.; YUAN, B.; DAI, S.; LI, Q.; CHEN, P.; WANG, Y.; PEI, Y. SlNCED1 and SlCYP707A2: key genes involved in ABA metabolism during tomato fruit ripening. **Journal of Experimental Botany**, Oxford, v.65, p.5243-5255, Jul. 2014.

KARLOVA, R.; CHAPMAN, N.; DAVID, K.; ANGENENT, G. C.; SEYMOUR, G. B.; DE MAAGD, R. A. Transcriptional control of fleshy fruit development and ripening. **Journal of Experimental Botany**, Oxford, v. 65, p. 4527-4541, Jul. 2014.

KLEE, H. J.; GIOVANNONI, J. J. Genetics and control of tomato fruit ripening and quality attributes. **Annual Review of Genetics**, Palo Alto, v. 45, p. 41-59, May. 2011.

KONG, X.; ZHANG, L.; DING, 2016, Z. 26S Proteasome. Hunter and Prey in Auxin Signaling. **Trends in Plant Science**, Oxford, v. 21 (7), p. 546-548, Jul. 2016.

KUMAR, R.; KHURANA, A.; SHARMA, A. K. Role of plant hormones and their interplay in development and ripening of fleshy fruits. **Journal of Experimental Botany**, Oxford, v. 65, p. 4561-4575, Jul. 2014.

LEMAIRE-CHAMLEY, M.; PETIT, J.; GARCIA, V.; JUST, D.; BALDET, P.; GERMAIN, V.; FAGARD, M.; MOUASSITE, M.; CHENICLET, C.; ROTHAN, C.; Changes in transcriptional profiles are associated with early fruit tissue specialization in tomato. **Plant Physiology**, Minneapolis, v. 139, p. 750-769, Oct. 2005.

LENG, P.; YUAN, B.; GUO, Y.; CHEN, P. The role of abscisic acid in fruit ripening and responses to abiotic stress. **Journal of Experimental Botany**, Oxford, v. 65, p. 4577-4588, Jul. 2014.

LIU, M.; PIRRELLO, J.; CHERVIN, C.; ROUSTAN, J. P.; BOUZAYEN, M. Ethylene control of fruit ripening: revisiting the complex network of transcriptional regulation. **Plant Physiology**, Minneapolis, v. 169, p. 2380-2390, Dec. 2015.

LIU, Z.; FRANKS, R. G. Molecular basis of fruit development. **Frontiers in Plant Science**, Lausanne, v. 6, p. 28-31, Feb. 2015.

LUDWIG-MÜLLER, J.; GEORGIEV, M.; BLEY, T. Metabolite and hormonal status of hairy root cultures of Devil's claw (Harpagophytum procumbens) in flasks and in a bubble column bioreactor. **Process Biochemistry**, London, v. 43, p. 15-23, Oct. 2008.

MATSUO, S.; KIKUCHI, K.; FUKUDA, M.; HONDA, I.; IMANISHI, S. Roles and regulation of cytokinins in tomato fruit development. **Journal of Experimental Botany**, Oxford, v. 63, p. 5569-5579, Aug. 2012.

MCATEE, P.; KARIM, S.; SCHAFFER, R. J.; DAVID, K. A dynamic interplay between phytohormones is required for fruit development, maturation, and ripening. **Frontiers in Plant Science**, Lausanne, v. 4, p. 79, Apr. 2013.

MINTZ-ORON, S.; MANDEL, T.; ROGACHEV, I.; FELDBERG, L.; LOTAN, O.; YATIV, M.; WANG, Z.; JETTER, R.; VENGER, I.; ADATO, A. Gene expression and metabolism in tomato fruit surface tissues. **Plant Physiology**, Minneapolis, v. 147, p. 823-851, Jun. 2008.

MOU, W.; LI, D.; BU, J.; JIANG, Y.; KHAN, Z. U.; LUO, Z.; MAO, L.; YING, T. Comprehensive Analysis of ABA Effects on Ethylene Biosynthesis and Signaling during Tomato Fruit Ripening. **Plos One**, San Francisco, v. 11, p. 1-30, Apr. 2016.

MOUNET, F.; MOING, A.; KOWALCZYK, M.; ROHRMANN, J.; PETIT, J.; GARCIA, V.; MAUCOURT, M.; YANO, K.; DEBORDE, C.; AOKI, K. Down-regulation of a single auxin efflux transport protein in tomato induces precocious fruit development. **Journal of Experimental Botany**, Oxfrod, v. 63, p. 4901-4917, Jul. 2012.

NISHIO, S., MORIGUCHI, R.; IKEDA, H.; TAKAHASHI, H.; TAKAHASHI, H.; FUJII, N.; GUILFOYLE, T. J.; KANAHAMA, K.; KANAYAMA, Y. Expression analysis of the auxin efflux carrier family in tomato fruit development. **Planta**, New York, v. 232, p. 755-764, Jun. 2010.

NITSCH, L.; KOHLEN, W.; OPLAAT, C.; CHARNIKHOVA, T.; CRISTESCU, S.; MICHIELI, P.; WOLTERS-ARTS, M.; BOUWMEESTER, H.; MARIANI, C.; VRIEZEN, W. ABA-deficiency results in reduced plant and fruit size in tomato. **Journal of Plant Physiology**, Oxford, v. 169, p. 878-883, Feb. 2012.

NITSCH, L. M. C.; OPLAAT, C.; FERON, R.; MA, Q.; WOLTERS-ARTS, M.; HEDDEN, P.; MARIANI, C.; VRIEZEN, W. H. Abscisic acid levels in tomato ovaries are regulated by LeNCED1 and SlCYP707A1. **Planta**, New York, v. 229, p. 1335-1346, Mar. 2009.

ORTEGA-MARTÍNEZ, O.; PERNAS, M.; CAROL, R. J.; DOLAN, L. Ethylene modulates stem cell division in the Arabidopsis thaliana root. **Science**, Washington, v. 317, p. 507-510, Jul. 2007.

OSORIO, S.; SCOSSA, F.; FERNIE, A. Molecular regulation of fruit ripening. **Frontiers in Plant Science**, Lausanne, v. 4, p. 198, Jun. 2013.

OZGA, J. A.; VAN HUIZEN, R.; REINECKE, D. M. Hormone and seed-specific regulation of pea fruit growth. **Plant Physiology**, Minneapolis, v. 128, p. 1379-1389, Apr. 2002.

PANDOLFINI, T.; ROTINO, G. L.; CAMERINI, S.; DEFEZ, R.; SPENA, A. Optimisation of transgene action at the post-transcriptional level: high quality parthenocarpic fruits in industrial tomatoes. **BMC Biotechnology**, London, v. 2, p. 1-11, Jan. 2002.

PATTISON, R. J.; CATALÁ, C. Evaluating auxin distribution in tomato (*Solanum lycopersicum*) through an analysis of the PIN and AUX/LAX gene families. **The Plant Journal**, Oxford, v. 70, p. 585-598, Feb. 2012.

PATTISON, R. J.; CSUKASI, F.; ZHENG, Y.; FEI, Z.; VAN DER KNAAP, E.; CATALÁ, C. Comprehensive Tissue-Specific Transcriptome Analysis Reveals Distinct Regulatory Programs during Early Tomato Fruit Development. **Plant Physiology**, Minneapolis, v. 168, p. 1684-1701, Jun. 2015.

PESARESI, P.; MIZZOTTI, C.; COLOMBO, M.; MASIERO, S. Genetic regulation and structural changes during tomato fruit development and ripening. **Frontiers in Plant Science**, Lausanne, v. 5, p. 124-138, Apr. 2014.

PHARIS, R. P.; KING, R. W. Gibberellins and reproductive development in seed plants. **Annual Review of Plant Physiology**, Palo Alto, v. 36, p. 517-568, Jul. 1985.

PINO, L. E.; CRESTANA, S.; AZEVEDO, M. S.; SCOTTON, D. C.; BORGO, L.; QUECINI, V.; FIGUEIRA, A.; PERER, L. E. P. The Rg1 allele as a valuable tool for genetic transformation of the tomato Micro-Tom model system. **Plant Methods**, London, v. 6, p. 1-11, Oct. 2010.

PLACKETT, A. R.; THOMAS, S. G.; WILSON, Z. A.; HEDDEN, P. Gibberellin control of stamen development: a fertile field. **Trends in Plant Science**, Oxford, v. 16, p. 568-578, Oct. 2011.

RAGHAVAN, V. Some reflections on double fertilization, from its discovery to the present. **New Phytologist**, London, v. 159, p. 565-583, May. 2003.

RAGHAVENDRA, A. S.; GONUGUNTA, V. K.; CHRISTMANN, A.; GRILL, E. ABA perception and signalling. **Trends in Plant Science**, Oxford, v. 15, p. 395-401, May. 2010.

REBERS, M.; KANETA, T.; KAWAIDE, H.; YAMAGUCHI, S.; YANG, Y. Y.; IMAI, R.; SEKIMOTO, H.; KAMIYA, Y. Regulation of gibberellin biosynthesis genes during flower and early fruit development of tomato. **The Plant Journal**, Oxford, v. 17(3), p. 241-250, Nov. 1999.

ROSSI, M.; CARRARI, F.; CABRERA-PONCE, J.; VÁZQUEZ-ROVERE, C.; HERRERA-ESTRELLA, L.; GUDESBLAT, G.; IUSEM, N. Analysis of an abscisic acid (ABA)-responsive gene promoter belonging to the Asr gene family from tomato in homologous and heterologous systems. **Molecular Genetics and Genomic**, Berlin, v. 258, p. 1-8, Nov. 1998.

RUAN, Y. L.; PATRICK, J. W.; BOUZAYEN, M.; OSORIO, S.; FERNIE, A. R. Molecular regulation of seed and fruit set. **Trends in Plant Science**, Oxford, v. 17, p. 656-665, Nov. 2012.

SAKAKIBARA, H. Cytokinins: activity, biosynthesis, and translocation. **Annual Review of Plant Biology**, v. 57, p. 431-449, Feb. 2006.

SANTNER, A.; CALDERON-VILLALOBOS, L. I. A.; ESTELLE, M. Plant hormones are versatile chemical regulators of plant growth. **Nature Chemical Biology**, New York, v. 5, p. 301-307, May. 2009.

SANTNER, A.; ESTELLE, M. Recent advances and emerging trends in plant hormone signalling. **Nature**, London, v. 459, p. 1071-1078, Jun. 2009.

SERRANI, J. C.; CARRERA, E.; RUIZ-RIVERO, O.; GALLEGO-GIRALDO, L.; PERES, L. E. P.; GARCIA-MARTINEZ, J. L. Inhibition of auxin transport from the ovary or from the apical shoot induces parthenocarpic fruit-set in tomato mediated by gibberellins. **Plant Physiology**, Minneapolis, v. 153, p. 851-862, Jun. 2010.

SERRANI, J. C.; FOS, M.; ATARÉS, A.; GARCÍA-MARTÍNEZ, J. L. Effect of gibberellin and auxin on parthenocarpic fruit growth induction in the cv Micro-Tom of tomato. **Journal of Plant Growth Regulation**, New York, v. 26, p. 211-221, Sept. 2007.

SERRANI, J. C.; RUIZ-RIVERO, O.; FOS, M.; GARCÍA-MARTÍNEZ, J. L. Auxin-induced fruit-set in tomato is mediated in part by gibberellins. **The Plant Journal**, Oxford, v. 56, p. 922-934, Sept. 2008.

SERRANI, J. C.; SANJUÁN, R.; RUIZ-RIVERO, O.; FOS, M.; GARCÍA-MARTÍNEZ, J. L. Gibberellin regulation of fruit set and growth in tomato. **Plant Physiology**, Minneapolis, v. 145, p. 246-257, Sept. 2007.

SEYMOUR, G. B.; ØSTERGAARD, L.; CHAPMAN, N. H.; KNAPP, S.; MARTIN, C. Fruit development and ripening. **Annual Review of Plant Biology**, Palo Alto, v. 64, p. 219-241, Feb. 2013.

SHINOZAKI, Y.; HAO, S.; KOJIMA, M.; SAKAKIBARA, H.; OZEKI-IIDA, Y.; ZHENG, Y.; FEI, Z.; ZHONG, S.; GIOVANNONI, J. J.; ROSE, J. K. Ethylene suppresses tomato fruit set through modification of gibberellin metabolism. **The Plant Journal**, Oxford, v. 83, p. 237-251, May. 2015..

SRIVASTAVA, A.; HANDA, A. K. Hormonal regulation of tomato fruit development: a molecular perspective. **Journal of Plant Growth Regulation**, New York, v. 24, p. 67-82, Sept. 2005.

STEPANOVA, A. N.; YUN, J.; LIKHACHEVA, A. V.; ALONSO, J. M. Multilevel interactions between ethylene and auxin in Arabidopsis roots. **The Plant Cell**, Baltimore, v. 19, p. 2169-2185, Jul. 2007.

SUN, L.; SUN, Y.; ZHANG, M.; WANG, L.; REN, J.; CUI, M.; WANG, Y.; JI, K.; LI, P.; LI, Q. Suppression of 9-cis-epoxycarotenoid dioxygenase, which encodes a key enzyme in abscisic acid biosynthesis, alters fruit texture in transgenic tomato. **Plant Physiology**, Minneapolis, v. 158, p. 283-298, Jan. 2012.

SUN, X.; SHANTHARAJ, D.; KANG, X.; NI, M. Transcriptional and hormonal signaling control of Arabidopsis seed development. **Current Opinion in Plant Biology**, London, v. 13, p. 611-620, Sept. 2010.

TANKSLEY, S. D. The genetic, developmental, and molecular bases of fruit size and shape variation in tomato. **The Plant Cell**, Baltimore, v. 16, p. 181-189, May. 2004.

TRAINOTTI, L.; TADIELLO, A.; CASADORO, G. The involvement of auxin in the ripening of climacteric fruits comes of age: the hormone plays a role of its own and has an intense interplay with ethylene in ripening peaches. **Journal of Experimental Botany**, Oxford, v. 58, p. 3299-3308, Oct. 2007.

ULMASOV, T.; HAGEN, G.; GUILFOYLE, T. J. Dimerization and DNA binding of auxin response factors. **The Plant Journal**, Oxford, v. 19, p. 309-319, Aug. 1999.

ULMASOV, T.; MURFETT, J.; HAGEN, G.; GUILFOYLE, T. J. Aux/IAA proteins repress expression of reporter genes containing natural and highly active synthetic auxin response elements. **The Plant Cell**, Baltimore, v. 9, p. 1963-1971, 1997.

VAN DEN HEUVEL, K.; BARENDSE, G.; WULLEMS, G. Effect of gibberellic acid on cell division and cell elongation in anthers of the gibberellin deficient gib-1 mutant of tomato. **Plant Biology**, Stuttgart, v. 3, p. 124-131, 2001.

VAN DOORN, W. G.; KAMDEE, C. Flower opening and closure: an update. **Journal of Experimental Botany**, Oxford, v. 65, p. 5749-5757, Aug, 2014.

VANNESTE, S.; FRIML, J. Auxin: a trigger for change in plant development. **Cell**, Cambridge, v. 136, p. 1005-1016, Mar. 2009.

VRIEZEN, W. H.; FERON, R.; MARETTO, F.; KEIJMAN, J.; MARIANI, C. Changes in tomato ovary transcriptome demonstrate complex hormonal regulation of fruit set. **New Phytologist**, London, v. 177, p. 60-76, Aug. 2008.

WANG, H.; JONES, B.; LI, Z.; FRASSE, P.; DELALANDE, C.; REGAD, F.; CHAABOUNI, S.; LATCHE, A.;PECH, J. C.; BOUZAYEN, M. The tomato Aux/IAA transcription factor IAA9 is involved in fruit development and leaf morphogenesis. **The Plant Cell**, Baltimore, v. 17, p. 2676-2692, Oct. 2005.

WANG, H.; C.-E. TIAN, C.E.; DUAN, J; WU, K. Research progresses on GH3s, one family of primary auxin-responsive genes. **Plant growth regulation**, New York, v. 56, p. 225-232, Aug, 2008.

WENG, L.; ZHAO, F.; LI, R.; XIAO, H. Cross-talk modulation between ABA and ethylene by transcription factor SlZFP2 during fruit development and ripening in tomato. **Plant signaling & Behavior**, v. 10, p. e1107691. Oct. 2015.

WENG, L.; ZHAO, F.; LI, R.; XU, C.; CHEN, K.; XIAO, H. The zinc finger transcription factor *Sl*ZFP2 negatively regulates abscisic acid biosynthesis and fruit ripening in tomato. **Plant Physiology**, Georgetown, v. 167, p. 931-949, Mar. 2015.

WILKINSON, J. Q.; LANAHAN, M. B.; YEN, H. C.; GIOVANNONI, J. J.; KLEE, H. J. An ethylene-inducible component of signal transduction encoded by *Never ripe*. **Science**, Washington, v. 270, p. 1807-1810. Dec. 1995.

WILSON, Z. A.; SONG, J.; TAYLOR, B.; YANG, C. The final split: the regulation of anther dehiscence. **Journal of Experimental Botany**, Oxford, v. 62, p. 1633-1649, Feb. 2011.

XIAO, H.; RADOVICH, C.; WELTY, N.; HSU, J.; LI, D.; MEULIA, T.; VAN DER KNAAP, E. Integration of tomato reproductive developmental landmarks and expression profiles, and the effect of SUN on fruit shape. **BMC Plant Biology**, London, v. 9, p. 1-21, May. 2009.

YADEGARI, R.; DREWS, G. N. Female gametophyte development. **The Plant Cell**, Baltimore, v. 16, p. 133-141, Jun. 2004.

YAMAGUCHI, S. Gibberellin metabolism and its regulation. **Annual Review of Plant Biology**, Palo Alto, v. 59, p. 225-251, 2008.

ZDARSKA, M.; DOBISOVÁ, T.; GELOVÁ, Z.; PERNISOVÁ, M.; DABRAVOLSKI, S.; HEJÁTKO, J. Illuminating light, cytokinin, and ethylene signalling crosstalk in plant development. **Journal of Experimental Botany**, Oxford, v. 66(16), p. 4913-4931, May. 2015.

ZHANG, M.; YUAN, B.; LENG, P. The role of ABA in triggering ethylene biosynthesis and ripening of tomato fruit. **Journal of Experimental Botany**, Oxford, v. 60, p. 1579-1588, Feb. 2009.

ZHANG, S.; XU, M.; QIU, Z.; WANG, K.; DU, Y.; GU, L.; CUI, X. Spatiotemporal transcriptome provides insights into early fruit development of tomato (*Solanum lycopersicum*). **Scientific Reports**, London, v. 6, p. 23173, Mar. 2016.