

**University of São Paulo
“Luiz de Queiroz” College of Agriculture**

Mutations affecting tomato (*Solanum lycopersicum* L. cv. Micro-Tom) response to salt stress and their physiological meaning

Versão simplificada

Ariadne Felício Lopo de Sá

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

**Piracicaba
2016**

Ariadne Felício Lopo de Sá
Bachelor in Biological Sciences

**Mutations affecting tomato (*Solanum lycopersicum* L. cv. Micro-Tom) response to
salt stress and their physiological meaning**
versão revisada de acordo com a resolução CoPGr 6018 de 2011

Advisor:
Prof. Dr. **LÁZARO EUSTÁQUIO PEREIRA
PERES**

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

Piracicaba
2016

RESUMO

Mutações afetando a resposta ao estresse salino em tomateiro (*Solanum lycopersicum* L. cv. Micro-Tom) e seu significado fisiológico

A salinidade é um desafio para a produtividade agrícola, uma vez que plantas expostas à salinidade tem o crescimento vegetativo e reprodutivo reduzido devido aos efeitos adversos de íons específicos no metabolismo e nas relações hídricas. A fim de lidar com a salinidade, as plantas desempenham mecanismos fisiológicos baseados em três principais características: *i*) relações fonte-dreno; *ii*) alocação de reservas e *iii*) alterações nos níveis endógenos de hormônios. Nesse trabalho, investigamos a relação entre os processos de desenvolvimento e de regulação hormonal com a resposta à salinidade. Para tanto foram usados genótipos de tomateiro com alteração em diferentes vias de desenvolvimento e de produção ou sinalização de hormônios vegetais. Os seguintes genótipos foram usados: *Galapagos dwarf (Gdw)*, *Lanata (Ln)*, *lutescent (l)*, *single flower truss (sft)*, *sft heterozygous (sft/+)*, *diageotropica (dgt)*, *entire (e)*, *Never ripe (Nr)*, *epinastic (epi)*, *procera (pro)*, *notabilis (not)*, *anti sense Dioxigenase cloroplastídica de carotenoide 7 (35S::asCCD7)* e *Salicilato hidroxilase (35S::nahG)*. Entre os genótipos de desenvolvimento estudados, *sft* e *l*, relacionados à menor indução floral e senescência respectivamente, foram os menos afetados quando expostos à salinidade. O genótipo *l* acumulou maior biomassa e área foliar, apesar de ser considerado deletério devido à senescência precoce. As plantas heterozigotas, *sft/+*, cuja maior produtividade foi recentemente relacionada a um melhor balanço vegetativo/reprodutivo, alteraram esse balanço sob salinidade e reduziram sua produtividade mais que o controle MT sob estresse salino. Na análise dos genótipos com alteração hormonais foram observados quatro tipos de respostas à salinidade: *i*) elevado crescimento da parte aérea, apesar da razão Na:K ser alta no genótipo *CCD7* cujo transgene induz deficiência de estrigolactona e excessiva ramificação; *ii*) elevado crescimento e acúmulo reduzido de Na nos tecidos (devido provavelmente a diluição) apresentada pelo mutante de resposta constitutiva a auxina *e*; *iii*) o oposto da resposta anterior foi apresentado pelo mutante pouco sensível à auxina, *dgt*; *iv*) inibição do crescimento combinado com nível reduzido de Na e alto acúmulo de K apresentada pelo mutante *not* que produz menos ácido abscísico. Considerados em conjunto, os resultados apresentaram temas para novos mecanismos de desenvolvimento, como a promoção moderada de senescência e do crescimento vegetativo além dos desbalanços hormonais, para serem explorados na busca de culturas resistentes ao estresse salino.

Palavras-chave: Ácido abscísico; Ácido salicílico; Auxina; Crescimento vegetativo/reprodutivo; Estrigolactona; Etileno; Giberelina; Heterose; Hormônios vegetais; Indução floral; Mutante; Produtividade; Resistência; Salinidade; Senescência; Tolerância

ABSTRACT

Mutations affecting tomato (*Solanum lycopersicum* L. cv. Micro-Tom) response to salt stress and their physiological meaning

Salinity is a challenge for crop productivity. Hence, plants exposed to saline environments reduce their vegetative and reproductive growth due to adverse effects of specific ions on metabolism and water relations. In order to cope with salinity, plants display physiological mechanisms based on three main aspects: *i*) source-sink relationships, *ii*) resource allocation and *iii*) alterations in endogenous hormone levels. The roles of developmental and hormonal mechanisms in salt response were investigated here. We employed mutants and transgenic tomato plants affecting different aspects of plant development and hormone response in the same genetic background (cultivar Micro-Tom). The following genotypes were used: *Galapagos dwarf* (*Gdw*), *Lanata* (*Ln*), *lutescent* (*l*), *single flower truss* (*sft*), *sft heterozygous* (*sft/+*), *diageotropica* (*dgt*), *entire* (*e*), *Never ripe* (*Nr*), *epinastic* (*epi*), *procera* (*pro*), *notabilis* (*not*), *anti sense Chloroplastic carotenoid cleavage dioxygenase 7* (*35S::asCCD7*) and *Salicylate hydroxylase* (*35S::nahG*). Among the developmental genotypes studied, *sft* and *l*, involved in flower induction and senescence, respectively, were less affected when exposed to salt stress. Although *l* is considered deleterious due to its precocious senescence, it presented greater shoot biomass and leaf area during salinity. The heterozygous *sft/+*, whose high productivity was recently linked to an improved vegetative-to-reproductive balance, changed this balance and lowered its yield more than the control MT upon salt treatment. In the analysis of genotypes affecting hormonal status/signaling four kinds of salt responses among the genotypes were observed: *i*) High shoot growth in spite of high Na:K ratio presented by the strigolactone deficient and high branching *CCD7* transgene; *ii*) High shoot growth and reduced accumulation of Na in tissues (probably due to dilution) presented by the auxin constitutive response *e* mutant; *iii*) The opposite response observed in “*ii*” presented by the low auxin sensitivity *dgt* mutant and *iv*) growth inhibition combined with reduced levels of Na and higher accumulation of K presented by the *not* mutant, which produces less ABA. Taken together, the results presented here points to novel developmental mechanisms, such as the promotion of moderate senescence and vegetative growth, and hormonal imbalances to be explored in the pursuing of crops resistant to salt stress.

Keywords: Abscisic acid; Auxin; Ethylene; Flower induction; Gibberellin; Heterosis; Mutant; Plant hormones; Productivity; Resistance; Salicylic acid; Salinity; Senescence; Strigolactone; Tolerance; Vegetative-to-reproductive growth

1 INTRODUCTION

Salinity was probably not a problem at the beginning of agriculture about 12,000 year ago (SNIR et al., 2015), but it emerged with the sophistication of plant cultivation and the demand to obtain more food due to rapid population growth. Hence, salinity is mainly a side effect of irrigation, one of the most revolutionary techniques invented at Sumerian's times to improve productivity (VARGAS; GALLEGOS, 1990). There are archeological evidences that salinity gradually reduced the yield of the salt-sensitive wheat, which was replaced by the salt-tolerant barley in Mesopotamia (modern Iraq and part of Syria, Iran and Kuwait). However, after seven centuries, the ongoing salinization also decreased the average yield of barley (GOLDSMITH; HILDYARD, 1984) leading to the decline of the Mesopotamia civilization (JACOBSEN; ADAMS, 1958). At present times, 20% of the 230 millions hectares irrigated around the world are in salinization process, decreasing the productivity and preventing the cultivation of several crops (FAO, 2005), which is a challenge to our own civilization.

Plants grown under salinity show impaired of water and nutrient, limited stomatal conductance, increased production of reactive oxygen species, ionic imbalance and altered enzyme activity. All these events restrain plant growth and, in extreme conditions, cause plant death. In order to cope with salinity, plants exhibit complex responses that involve biochemical, physiological and morphological mechanisms.

Plant hormones are considered the major players in salt response. Thus hormones are involved in the control of various mechanisms of acclimation to adverse environments, extending their effects from the operation of ion channels to the control of organ formation and differentiation (FAHAD et al., 2015; RYU; CHO, 2015).

In general, salinization induces hormone status alterations that mediate the rapid inhibition of shoot growth and the preferential partitioning of biomass to roots, increasing survival and maintaining plant growth, although in a lower rate (ALBACETE et al., 2008). This novel source-sink relation leads to yield reduction. As reported by Pérez-Alfocea et al. (2010), salt injury and shoot development is not directly limited by carbohydrate availability but by the changes in distribution and use of assimilates. Therefore, it is expected that plants with different architectures have different degrees of resistance to salinity.

The plant architecture is determined by meristematic activity, which in tomato is partially regulated by the rate of *SINGLE FLOWER TRUSS* (*SFT*) and *SELF PRUNING* (*SP*) regulatory genes. The *SFT* gene is considered the long-sought florigenic signal that induces

flowering, while *SP* inhibits the action of *SFT*, being required to maintain the vegetative stage (MOLINERO-ROSALES et al., 2004; SHALIT et al., 2009). Together, *SFT* and *SP* affect many aspects of plant architecture, such as the development and the identity of meristems, leaves and flowers initiation, sympodium formation, and radial expansion of the stem (SHALIT et al., 2009). However, the effect of *sft* dosage alteration in salt response remains unknown.

In the last two decades, the understanding of the molecular mechanisms involved in salinity resistance broadened with the use of transgenic and mutant plants, especially on identification of cell-based mechanisms related to transmembrane channels. The three main classes of Na^+ transporters for cellular homeostasis are *HIGH-AFFINITY K⁺TRANSPORTER1* (*HKT1*), *SALT OVERLY SENSITIVE1* (*SOS1*) and *Na⁺/H⁺EXCHANGER* (*NHX*) (YAMAGUCHI; HAMAMOTO; UOZUMI, 2013). The impact of these channels on plant performance is impressive. Introgression of *TmHKT;5-A* into commercial durum wheat varieties (*Triticum turgid* ssp. *durum*) promotes effective Na^+ exclusion of root xylem vessel, leading to enhanced grain yield by 25% on saline soils (JAMES et al., 2012; MUNNS et al., 2012; MUNNS; TESTER, 2008). *SOS* pathway was first described in the *sos1* Arabidopsis mutant. The protein kinase complex, *SOS3/SOS2*, senses changes in Ca^{2+} signal induced by high Na^+ cytosolic concentration, which then stimulates the *SOS1* exchange activity (Na^+/H^+ antiporter) prompting the efflux of excess Na^+ ions (JI et al., 2013; ZHU, 2002). Overexpression of *NHX1* in different plant species, including tomato, promotes Na^+ compartmentalization into the vacuole, minimizing the toxic accumulation of this ion in the cytosol and enhancing salt resistance (APSE et al., 1999; ZHANG; BLUMWALD, 2001; ZHANG et al., 2001).

Complementary to plant membrane manipulations, alterations in plant development and hormonal signalling/synthesis are likely to play a role in the salinity resistance. However, the knowledge about these two aspects in salt response remains limited. In order to determine their roles in the response to salinity, we used tomato genotypes that exhibit alterations on plant development and hormonal status in the same genetic background (*Solanum lycopersicum* L. cultivar Micro-Tom). The following genotypes were used: *Galapagos dwarf* (*Gdw*), *Lanata* (*Ln*), *lutescent* (*l*), *single flower truss* (*sft*), *sft heterozygous* (*sft/+*), *diageotropica* (*dgt*), *entire* (*e*), *Never ripe* (*Nr*), *epinastic* (*epi*), *procera* (*pro*), *notabilis* (*not*), *anti sense Chloroplastic carotenoid cleavage dioxygenase 7* (*35S::asCCD7*) and *Salicylate hydroxylase* (*35S::nahG*). The growth performance, chlorophyll fluorescence, nutritional and hormonal status and productivity of genotypes were evaluated.

The present work was organized in two chapters. The first presents the results of developmental genotypes under salinity and a discussion about the prospect to use such developmental processes in the pursuit of salinity resistance. The second chapter displays the hormonal influence in growth performance and ionic homeostasis under salinity.

2 CONCLUSIONS

The salt treatment tends to influence flower induction, leading to an alteration of reproductive-to-vegetative balance. As reported by Vicente et al. (2015), the heterosis of *sft/+* (KRIEGER; LIPPMAN; ZAMIR, 2010) influences this same growth balance. In this work, we observed that the vegetative and reproductive growth pattern of *sft/+* was broken under salinity. Therefore, the use of this pseudoheterosis in order to achieve higher yield must be used with care in areas subjected to salinity as demonstrated in this work. On the other hand, the precocious senescence of *lutescent*, although considered deleterious at a first glimpse, may be advantageous as a novel acclimatory mechanism under salinity.

Based on the results of genotypes that exhibit alterations on hormonal status, we observed four kinds of salt response among the genotypes were observed: *i*) High shoot growth in spite of high Na:K ratio presented by the strigolactone deficient and high branching *CCD7* transgene; *ii*) High shoot growth and reduced accumulation of Na in tissues (probably due to dilution) presented by the auxin constitutive response *e* mutant; *iii*) The opposite response observed in “*ii*” presented by the low auxin sensitivity *dgt* mutant and *iv*) growth inhibition combined with reduced levels of Na and higher accumulation of K presented by the *not* mutant, which produces less ABA. Such specific behaviors point to novel levels of salt response regulation, suggesting a role for auxin in Na dilution in tissues and specific mechanisms of ABA and strigolactones in the control of growth under salinity.

References

ACHARD, P.; CHENG, H.; DE GRAUWE, L.; DECAT, J.; SCHOUTTETEN, H.; MORITZ, T.; STRAETEN, D. van der; PENG, J.; HARBERD, N.P. Integration of plant responses to environmentally activated phytohormonal signals. **Science**, New York, v. 311, n. 5757, p. 91–94, 2006.

ACHARD, P.; GONG, F.; CHEMINANT, S.; ALIOUA, M.; HEDDEN, P.; GENSCHIK, P. The cold-inducible CBF1 factor-dependent signaling pathway modulates the accumulation of the growth-repressing DELLA proteins via its effect on gibberellin metabolism. **The Plant Cell**, Rockville, v. 20, n. 8, p. 2117–2129, 2008.

ADAM, Z. Emerging roles for diverse intramembrane proteases in plant biology. **Biochimica et Biophysica Acta (BBA) Biomembranes**, Amsterdam, v.1828, n. 12, p. 2933–2936, 2013.

ALBACETE, A.; GHANEM, M.E.; MARTÍNEZ-ANDÚJAR, C.; ACOSTA M.; SÁNCHEZ-BRAVO, J.; MARTÍNEZ, V.; LUTTS, S.; DODD, I.C.; PÉREZ-ALFOCEA, F. Hormonal changes in relation to biomass partitioning and shoot growth impairment in salinized tomato (*Solanum lycopersicum* L.) plants. **Journal of Experimental Botany**, Oxford, v. 59, n. 15, p. 4119–4131, 2008.

ALMEIDA, J.; ASÍS, R.; MOLINERI, V.N.; SESTARI, I.; LIRA, B.S.; CARRARI, F.; PERES, L.E.P.; ROSSI, M. Fruits from ripening impaired, chlorophyll degraded and jasmonate insensitive tomato mutants have altered tocopherol content and composition. **Phytochemistry**, New York, v. 111, n. 1, p. 72–83, 2015.

APSE, M.P.; AHARON, G.S.; SNEDDEN, W.A.; BLUMWALD, E. Salt tolerance conferred by overexpression of a vacuolar Na⁺/H⁺ antiport in Arabidopsis. **Science**, New York, v. 285, n. 5431, p. 1256–1258, 1999.

ASENSI-FABADO, M.A.; AMMON, A.; SONNEWALD, U.; MUNNÉ-BOSCH, S.; VOLL, L.M. Tocopherol deficiency reduces sucrose export from salt-stressed potato leaves independently of oxidative stress and symplastic obstruction by callose. **Journal of Experimental Botany**, Oxford, v. 66, n. 3, p. 957–971, 2015.

BARRY, C.S.; ALDRIDGE, G.M.; HERZOG, G.; MA, Q.; MCQUINN, R.P.; HIRSCHBERG, J.; GIOVANNONI, J.J. Altered chloroplast development and delayed fruit ripening caused by mutations in a zinc metalloprotease at the *lutescent* locus of tomato. **Plant Physiology**, Lancaster, v. 159, n. 3, p. 1086–1098, 2012.

BARRY, C.S.; FOX, E.A.; YEN, H.; LEE, S.; YING, T.; GRIERSON, D.; GIOVANNONI, J.J. Analysis of the ethylene response in the *epinastic* mutant of tomato. **Plant Physiology**, Lancaster, v. 127, n. 1, p. 58–66, 2001.

BARRY, C.S.; MCQUINN, R.P.; CHUNG, M.Y.; BESUDEN, A.; GIOVANNONI, J.J. Amino acid substitutions in homologs of the STAY-GREEN protein are responsible for the green-flesh and chlorophyll retainer mutations of tomato and pepper. **Plant Physiology**, Lancaster, v. 147, n. 1, p. 179–187, 2008.

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, n. 3, p. 585–593, 2008.

BORSANI, O.; VALPUESTA, V.; BOTELLA, M.A. Evidence for a role of salicylic acid in the oxidative damage generated by NaCl and osmotic stress in Arabidopsis seedlings. **Plant Physiology**, Lancaster, v. 126, n. 3, p. 1024–1030, 2001.

BRADFORD, K.J.; YANG, S.F. Stress-induced ethylene production in the ethylene-requiring tomato mutant *diageotropica*. **Plant Physiology**, Lancaster, v. 65, n. 2, p. 327–330, 1980.

BRADING, P.A.; HAMMOND-KOSACK, K.E.; PARR, A.; JONES, J.D.G. Salicylic acid is not required for Cf-2- and Cf-9-dependent resistance of tomato to *Cladosporium fulvum*. **The Plant Journal**, Malden, v. 23, n. 3, p. 305–318, 2000.

BURBIDGE, A.; GRIEVE, T.M.; JACKSON, A.; THOMPSON, A.; MCCARTY, D.R.; TAYLOR, I.B. Characterization of the ABA-deficient tomato mutant *notabilis* and its relationship with maize Vp14. **The Plant Journal**, Malden, v. 17, n. 4, p. 427–431, 1999.

CAO, Y.; ZHANG, Z.-W.; XUE, L.-W.; DU, J.-B.; SHANG, J.; XU, F.; YUAN, S.; LIN, H.-H. Lack of salicylic acid in Arabidopsis protects plants against moderate salt stress. **Journal of Biosciences: Zeitschrift für Naturforschung**, Tubingen, v. 64, n. 3/4, p. 231–238, 2009.

CARRERA, E.; RUIZ-RIVERO, O.; PERES, L.E.P.; ATARES, A.; GARCIA-MARTINEZ, J.L. Characterization of the *procera* tomato mutant shows novel functions of the *SIDELLA* protein in the control of flower morphology, cell division and expansion, and the auxin-signaling pathway during fruit-set and development. **Plant Physiology**, Lancaster, v. 160, n. 3, p. 1581–1596, 2012.

CARVALHO, R.F.; CAMPOS, M.L.; PINO, L.E.; CRESTANA, S.L.; ZSÖGÖN, 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, n. 1, p. 1-14, 2011.

CHEN, G.; BI, Y.R.; LI, N. *EGY1* encodes a membrane-associated and ATP-independent metalloprotease that is required for chloroplast development. **The Plant Journal**, Oxford, v. 41, n. 3, p. 364–375, 2005.

CHENG, H.; QIN, L.; LEE, S.; FU, X.; RICHARDS, D.E.; CAO, D.; LUO, D.; HARBERD, N.P.; PENG, J. Gibberellin regulates Arabidopsis floral development via suppression of DELLA protein function. **Development**, Cambridge, v. 131, n. 5, p. 1055–1064, 2004.

CORBESIER, L.; LEJEUNE, P.; BERNIER, G. The role of carbohydrates in the induction of flowering in *Arabidopsis thaliana*: comparison between the wild type and a starchless mutant. **Planta**, New York, v. 206, n. 1, p. 131–137, 1998.

CORRALES, A.-R.; NEBAUER, S.G.; CARRILLO, L.; FERNÁNDEZ-NOHALES, P.; MARQUÉS, J.; RENAU-MORATA, B.; GRANELL, A.; POLLMANN, S.; VICENTE-CARBAJOSA, J.; MOLINA, R.-V.; MEDINA, J. Characterization of tomato Cycling Dof Factors reveals conserved and new functions in the control of flowering time and abiotic stress responses. **Journal of Experimental Botany**, Oxford, v. 65, n. 4, p. 995–1012, 2014.

CUARTERO, J. Increasing salt tolerance in the tomato. **Journal of Experimental Botany**, Oxford, v. 57, n. 5, p. 1045–1058, 2006.

CUYPER, C.; FROMENTIN, J.; YOCGO, R.E.; KEYSER, A.; GUILLOTIN, B.; KUNERT, K.; BOYER, F.D.; GOORMACHTIG, S. From lateral root density to nodule number, the strigolactone analogue GR24 shapes the root architecture of *Medicago truncatula*. **Journal of Experimental Botany**, Oxford, v. 66, n. 1, p. 137–146, 2015.

DEMIDCHIK, V.; CUIN, T.A.; SVISTUNENKO, D.; SMITH, S.J.; MILLER, A.J.; SHABALA, S.; SOKOLIK, A.; YURIN, V. Arabidopsis root K⁺-efflux conductance activated by hydroxyl radicals: single-channel properties, genetic basis and involvement in stress-induced cell death. **Journal of Cell Science**, London, v. 123, n. 9, p. 1468–1479, 2010.

DENGLER, N.G. Comparison of leaf development in normal (+/+), *Entire (ele)*, and *Lanceolate (Lal/+)* plants of tomato, *Lycopersicon esculentum* "Ailsa Craig". **Botanical Gazette**, Chicago, v. 145, n. 1, p. 66–77, 1984.

DING, H.; LAI, J.; WU, Q.; ZHANG, S.; CHEN, L.; DAI, Y.S.; WANG, C.; DU, J.; XIAO, S.; YANG, C. Jasmonate complements the function of Arabidopsis lipoxygenase3 in salinity stress response. **Plant Science**, Cambridge, v. 244, n. 1, p. 1–7, 2016.

DORP, K. von.; HÖLZL, G.; PLOHMANN, C.; EISENHUT, M.; ABRAHAM, M.; WEBER, A.P.M.; HANSON, A.D.; DÖRMANN, P. Remobilization of phytol from chlorophyll degradation is essential for tocopherol synthesis and growth of Arabidopsis. **The Plant Cell**, Rockville, v. 27, n. 10, p. 2846–2859, 2015.

EL-BASSIOUNY, H.M.S.; SADAK, M.S. Impact of foliar application of ascorbic acid and α -tocopherol on antioxidant activity and some biochemical aspects of flax cultivars under salinity stress. **Acta Biológica Colombiana**, Bogotá, v. 20, n. 2, p. 209–222, 2015.

ESSINGTON, M.E. **Soil and water chemistry: an integrative approach**. 2.ed. Boca Raton: CRC Press, 2015. 656 p

FAHAD, S.; HUSSAIN, S.; MATLOOB, A.; KHAN, F.A.; KHALIQ, A.; SAUD, S.; HASSAN, S.; SHAN, D.; KHAN, F.; ULLAH, N.; FAIQ, M.; KHAN, M.R.; TAREEN, A. K.; KHAN, A.; ULLAH, A.; ULLAH, N.; HUANG, J. Phytohormones and plant responses to salinity stress: a review. **Plant Growth Regulation**, Dordrecht, v. 75, n. 2, p. 391–404, 2015.

FAO. **Global network on integrated soil management for sustainable use of salt-affected soils**. Rome: FAO, Land and Plant Nutrition Management Service, 2005. Disponível em: <<http://www.fao.org/ag/agl/agll/spush>>. Acesso em: 30 maio 2016.

FLEISHON, S.; SHANI, E.; ORI, N.; WEISS, D. Negative reciprocal interactions between gibberellin and cytokinin in tomato. **The New Phytologist**, London, v. 190, n. 3, p. 609–617, 2011.

FLOWERS T. J. Improving crop salt tolerance. **Journal of Experimental Botany**. Oxford, v. 55, n. 396, p. 307–319, 2004.

FLOWERS, T.J.; GALAL, H.K.; BROMHAM, L. Evolution of halophytes: Multiple origins of salt tolerance in land plants. **Functional Plant Biology**, Victoria, v. 37, n. 7, p. 604–612, 2010.

FRACETTO, G.G.M.; PERES, L.E.P.; MEHDY, M.C.; LAMBASIS, M.R. Tomato ethylene mutants exhibit differences in arbuscular mycorrhiza development and levels of plant defense-related transcripts. **Symbiosis**, Philadelphia, v. 60, n. 3, p. 155–167, 2013.

FRANCO-NAVARRO, J.D.; BRUMÓS, J.; ROSALES, M.A.; CUBERO-FONT, P.; TALÓN, M.; COLMENERO-FLORES, J.M. Chloride regulates leaf cell size and water relations in tobacco plants. **Journal of Experimental Botany**, Oxford, v. 67, p. 873–891, 2016.

FRICKE, W.; AKHIYAROVA, G.; VESELOV, D.; KUDOYAROVA, G. Rapid and tissue-specific changes in ABA and in growth rate in response to salinity in barley leaves. **Journal of Experimental Botany**, Oxford, v. 55, n. 399, p. 1115–1123, 2004.

FUJINO, D.W.; BURGER, D.W.; YANG, S.F.; BRADFORD, K.J. Characterization of an ethylene overproducing mutant of tomato (*Lycopersicon esculentum* Mill. Cultivar VFN8). **Plant Physiology**, Lancaster, v. 88, n. 3, p. 774–779, 1988.

GARCIA-ABELLAN, J.O.; FERNANDEZ-GARCIA, N.; LOPEZ-BERENGUER, C.; EGEE, I.; FLORES, F.B.; ANGOSTO, T.; CAPEL, J.; LOZANO, R.; PINEDA, B.; MORENO, V.; OLMOS, E.; BOLARIN, M.C. The tomato res mutant which accumulates JA in roots in non-stressed conditions restores cell structure alterations under salinity. **Physiologia Plantarum**, Copenhagen, v. 155, n. 3, p. 296–314, 2015.

GHANEM, M.E.; ALBACETE, A.; MARTÍNEZ-ANDÚJAR, C.; ACOSTA, M.; ROMERO-ARANDA, R.; DODD, I. C.; LUTTS, S.; PÉREZ-ALFOCEA, F. Hormonal changes during salinity-induced leaf senescence in tomato (*Solanum lycopersicum* L.). **Journal of Experimental Botany**, Oxford, v. 59, n. 11, p. 3039–3050, 2008.

GOLDSMITH, E.; HILDYARD, N. **The social and environmental effects of Large Dams**. Cornwall: Worthyvale Manor Camelford, 1984. 404 p.

GOLLDAK, D.; LI, C.; MOHAN, H.; PROBST, N. Tolerance to drought and salt stress in plants: Unraveling the signaling networks. **Frontiers in Plant Science**, Lausanne, v. 5, n. April, p. 1-10, 2014.

GOMEZ-ROLDAN, V.; FERMAS, S.; BREWER, P.B.; PUECH-PAGÈS, V.; DUN, E.A.; PILLOT, J.-P.; LETISSE, F.; MATUSOVA, R.; DANOUN, S.; PORTAIS, J.-C.; BOUWMEESTER, H.; BÉCARD, G.; BEVERIDGE, C.A.; RAMEAU, C.; ROCHANGE, S.F. Strigolactone inhibition of shoot branching. **Nature**, London, v. 455, n. 7210, p. 189–194, 2008.

GRATÃO, P.L.; MONTEIRO, C.C.; CARVALHO, R.F.; TEZOTTO, T.; PIOTTO, F.A.; PERES, L.E.P.; AZEVEDO, R. A. Biochemical dissection of *diageotropica* and *Never ripe* tomato mutants to Cd-stressful conditions. **Plant Physiology and Biochemistry**, Paris, v. 56, p. 79–96, 2012.

GUPTA, B.; HUANG, B. Mechanism of Salinity Tolerance in Plants: Physiological, Biochemical, and Molecular Characterization. **International Journal of Genomics**, New York, v. 2014, n. 2014, p. 1–18, 2014.

GURMANI, A.R.; BANO, A.; ULLAH, N.; KHAN, H.; JAHANGIR, M.; FLOWERS, T.J. Exogenous abscisic acid (ABA) and silicon (Si) promote salinity tolerance by reducing sodium (Na⁺) transport and bypass flow in rice (*Oryza sativa*). **Australian Journal of Crop Science**, Lismore, v. 7, n. 9, p. 1219–1226, 2013.

HA, C. Van; LEYVA-GONZÁLEZ, M.A.; OSAKABE, Y.; TRAN, U.T.; NISHIYAMA, R.; WATANABE, Y.; TANAKA, M.; SEKI, M.; YAMAGUCHI, S.; DONG, N. Van; YAMAGUCHI-SHINOZAKI, K.; SHINOZAKI, K.; HERRERA-ESTRELLA, L.; TRAN, L.-S.P. Positive regulatory role of strigolactone in plant responses to drought and salt stress.

Proceedings of the National Academy of Sciences of the United States of America, Washington, v. 111, n. 2, p. 851–856, 2014.

HAMILTON, A.J.; LYCETT, G.W.; GRIERSON, D. Antisense gene that inhibits synthesis of the hormone ethylene in transgenic plants. **Nature**, London, v. 346, n. 6281, p. 284–287, 1990.

HAN, Y.; YIN, S.; HUANG, L. Towards plant salinity tolerance-implications from ion transporters and biochemical regulation. **Plant Growth Regulation**, Dordrecht, v. 76, n. 1, p. 13–23, 2015.

HASEGAWA, P.M.; BRESSAN, RAY A; BOHNERT, J.-K. Z.H.J. Plant Cellular Andmolecular Responses To High Salinity. **Annual Review of Plant Physiology and Plant Molecular Biology**, Palo Alto, v. 51, p. 463–499, 2000.

HICHRI, I.; MUHOVSKI, Y.; CLIPPE, A.; ŽIŽKOVÁ, E.; DOBREV, P.I.; MOTYKA, V.; LUTTS, S. *SIDREB2*, a tomato dehydration-responsive element-binding 2 transcription factor, mediates salt stress tolerance in tomato and Arabidopsis. **Plant, Cell & Environment**, New York, v. 39, n. 1, p. 62–79, 2016.

HORTENSTEINER, S.; FELLER, U. Nitrogen metabolism and remobilization during senescence. **Journal of Experimental Botany**, Oxford, v. 53, n. 370, p. 927–937, 2002.

HU, Z.L.; DENG, L.; YAN, B.; PAN, Y.; LUO, M.; CHEN, X.Q.; HU, T.Z.; CHEN, G.P. Silencing of the *LeSGR1* gene in tomato inhibits chlorophyll degradation and exhibits a stay-green phenotype. **Biologia Plantarum**, Praha, v. 55, n. 1, p. 27–34, 2011.

HUANG, P.C.; PADDOCK, E.F. The Time and Site of the Semidominant Lethal Action of “*Wo*” in *Lycopersicon esculentum*. **American Journal of Botany**, Baltimore, v. 49, n. 4, p. 388–393, 1962.

ISCHEBECK, T.; ZBIERZAK, A.M.; KANWISCHER, M.; DÖRMANN, P. A salvage pathway for phytol metabolism in *Arabidopsis*. **The Journal of Biological Chemistry**, Baltimore, v. 281, n. 5, p. 2470–2477, 2006.

JACOBSEN, T.; ADAMS, R.M. Salt and silt in ancient Mesopotamian agriculture. **Science**, New York, v. 128, n. 3334, p. 1251–1258, 1958.

JAMES, R.A.; BLAKE, C.; ZWART, A.B.; HARE, R.A.; RATHJEN, A.J.; MUNNS, R. Impact of ancestral wheat sodium exclusion genes *Nax1* and *Nax2* on grain yield of durum wheat on saline soils. **Functional Plant Biology**, Victoria, v. 39, n. 7, p. 609–618, 2012.

JAYAKANNAN, M.; BOSE, J.; BABOURINA, O.; RENGEL, Z.; SHABALA, S. Salicylic acid improves salinity tolerance in Arabidopsis by restoring membrane potential and preventing salt-induced K⁺ loss via a GORK channel. **Journal of Experimental Botany**, Oxford, v. 64, n. 8, p. 2255–2268, 2013.

JESUS, F.A. de, ZSÖGÖN, A.; PERES, L.E.P. Physionomics. In: BORÉM, A.; FRITSCHENETO, R. (Ed.). **Omics in Plant Breeding**. New Jersey: John Wiley, 2014. chap. 6, p. 104–126.

- JESUS, F.A. de. **Caracterização de uma variação genética natural de *Solanum galapagense* controlando o comprimento do entrenó e arquitetura foliar em tomateiro.** 2015. 70 p. Tese (Doutorado em Fisiologia e Bioquímica de Plantas) – Escola Superior de agricultura “Luiz de Queiroz”, Universidade de São Paulo, Piracicaba, 2015. Disponível em: <<http://www.teses.usp.br/teses/disponiveis/11/11144/tde-28032016-135123/en.php>>. Acesso em: 30 maio 2016.
- JI, H.; PARDO, J.M.; BATELLI, G.; OOSTEN, M.J. van; BRESSAN, R.A.; LI, X. The Salt Overly Sensitive (SOS) pathway: established and emerging roles. **Molecular Plant**, Oxford, v. 6, n. 2, p. 275–286, 2013.
- JIANG, C.; BELFIELD, E.J.; CAO, Y.; SMITH, J.A. C.; HARBERD, N.P. An Arabidopsis soil-salinity-tolerance mutation confers ethylene-mediated enhancement of sodium/potassium homeostasis. **The Plant Cell**, Rockville, v. 25, n. 9, p. 3535–3552, 2013.
- JIANG, K.; LIBERATORE, K.L.; PARK, S.J.; ALVAREZ, J.P.; LIPPMAN, Z.B. Tomato yield heterosis is triggered by a dosage sensitivity of the florigen pathway that fine-tunes shoot architecture. **PLoS Genetics**, San Francisco, v. 9, n. 12, p. 1-13, 2013. Disponível em: <<http://www.ncbi.nlm.nih.gov/pubmed/24385931>>. Acesso em: 15 jan. 2016.
- JONES, M.G. Gibberellins and the *procera* mutant of tomato. **Planta**, New York, v. 172, n. 2, p. 280–284, 1987.
- JUNG, J.-H.; PARK, C.-M. Auxin modulation of salt stress signaling in Arabidopsis seed germination. **Plant Signaling & Behavior**, Georgetown, v. 6, n. 8, p. 1198–1200, 2011.
- KAPULNIK, Y.; RESNICK, N.; MAYZLISH-GATI, E.; KAPLAN, Y.; WININGER, S.; HERSHENHORN, J.; KOLTAI, H. Strigolactones interact with ethylene and auxin in regulating root-hair elongation in Arabidopsis. **Journal of Experimental Botany**, Oxford, v. 62, n. 8, p. 2915–2924, 2011.
- KELLY, M.O.; BRADFORD, K.J. Insensitivity of the *diageotropica* tomato mutant to auxin. **Plant Physiology**, Lancaster, v. 82, n. 3, p. 713–717, 1986.
- KHAN, M.I.R.; SYEED, S.; NAZAR, R.; ANJUM, N.A. An Insight into the Role of Salicylic Acid and Jasmonic Acid in Salt Stress Tolerance. In: KHAN, A.N.; NAZAR, R.; IQBAL, N.; ANJUM, A.N. (Ed.). **Phytohormones and Abiotic Stress Tolerance in Plants**. Berlin: Springer Berlin Heidelberg, 2012. chap. 12, p. 277–300.
- KIM, Y.S.; SAKURABA, Y.; HAN, S.H.; YOO, S.C.; PAEK, N.C. Mutation of the arabidopsis NAC016 transcription factor delays leaf senescence. **Plant and Cell Physiology**, Tokyo, v. 54, n. 10, p. 1660–1672, 2013.
- KING, K.E.; MORITZ, T.; HARBERD, N.P. Gibberellins are not required for normal stem growth in *Arabidopsis thaliana* in the absence of GAI and RGA. **Genetics**, Bethesda, v. 159, n. 2, p. 767–76, 2001.
- KOREN, D.; RESNICK, N.; MAYZLISH GATI, E.; BELAUSOV, E.; WEININGER, S.; KAPULNIK, Y.; KOLTAI, H. Strigolactone signaling in the endodermis is sufficient to

restore root responses and involves SHORT HYPOCOTYL 2 (SHY2) activity. **The New Phytologist**, London, v. 198, n. 3, p. 866–874, 2013.

KOUDOUNAS, K.; MANIOUDAKI, M.E.; KOURTI, A.; BANILAS, G.; HATZOPOULOS, P. Transcriptional profiling unravels potential metabolic activities of the olive leaf non-glandular trichome. **Frontiers in Plant Science**, Lausanne, v. 6, n. 8, p. 1–10, 2015.

KRIEGER U.; LIPPMAN Z. B.; ZAMIR D. The flowering gene *SINGLE FLOWER TRUSS* drives heterosis for yield in tomato. **Nature Genetics**, New York, v. 42, n. 5, p. 459–463, 2010.

KRIEGER-LISZKAY, A.; FUFEZAN, C.; TREBST, A. Singlet oxygen production in photosystem II and related protection mechanism. **Photosynthesis Research**, Dordrecht, v. 98, n. 1–3, p. 551–564, 9 out. 2008.

LEVENE H. Robust tests for equality of variances. In: OLKIN I. **Contributions to probability and statistics: essays in honor of Harold Hotelling**. Palo Alto: Stanford University Press, 1960. p. 278–292.

LEVITT, J. **Responses of Plants to Environmental Stresses**. New York: Academic Press, 1972. 698 p.

LI, B.; LI, Q.; XIONG, L.; KRONZUCKER, H.J.; KRÄMER, U.; SHI, W. Arabidopsis plastid *AMOS1/EGY1* integrates abscisic acid signaling to regulate global gene expression response to ammonium stress. **Plant Physiology**, Lancaster, v.160, n. 4, p. 2040–2051, 2012.

LI, K.; WANG, Y.; HAN, C.; ZHANG, W.; JIA, H.; LI, X. GA signaling and CO/FT regulatory module mediate salt-induced late flowering in *Arabidopsis thaliana*. **Plant Growth Regulation**, Dordrecht, v. 56, n. 3, p. 195–206, 2007.

LIFSCHITZ, E.; AYRE, B.G.; ESHED, Y. Florigen and anti-florigen: a systemic mechanism for coordinating growth and termination in flowering plants. **Frontiers in Plant Science**, Lausanne, v. 5, n. 165, p. 465, 2014.

LIFSCHITZ, E.; EVIATAR, T.; ROZMAN, A.; SHALIT, A.; GOLDSHMIDT, A.; AMSELLEM, Z.; ALVAREZ, J.P.; ESHED, Y. The tomato *FT* ortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli. **Proceedings of the National Academy of Sciences of the United States of America**, Washington, v. 103, n. 16, p. 6398–6403, 2006.

LIU, M.; GOMES, B.L.; MILA, I.; PURGATTO, E.; PERES, L.E.P.; FRASSE, P.; MAZA, E.; ZOUINE, M.; ROUSTAN, J.-P.; BOUZAYEN, M.; PIRRELLO, J. Comprehensive profiling of ethylene response factor expression identifies ripening-associated *ERF* genes and their link to key regulators of fruit ripening in tomato. **Plant Physiology**, Lancaster, v. 170, n. 3, p. 1732–1744, 2016.

LIVNE, S.; LOR, V.S.; NIR, I.; ELIAZ, N.; AHARONI, A.; OLSZEWSKI, N.E.; ESHED, Y.; WEISS, D. Uncovering DELLA-independent gibberellin responses by characterizing new tomato *procera* mutants. **The Plant Cell**, Rockville, v. 27, n. 6, p. 1579–1594, 2015.

LOMBARDI-CRESTANA, S.; AZEVEDO, M.S.; E SILVA, G.F.F.; PINO, L.E.; APPEZZATO-DA-GLORIA, B.; FIGUEIRA, A.; NOGUEIRA, F.T.S.; PERES, L.E.P. The tomato (*Solanum lycopersicum* cv. Micro-Tom) natural genetic variation *Rgl1* and the DELLA Mutant *procera* control the competence necessary to form adventitious roots and shoots. **Journal of Experimental Botany**, Oxford, v. 63, n. 15, p. 5689–5703, 2012.

LUO, M.H.; YUAN, S.; CHEN, Y.E.; LIU, W.J.; DU, J.B.; LEI, T.; WANG, M.B.; LIN, H.H. Effects of salicylic acid on the photosystem 2 of barley seedlings under osmotic stress. **Biologia Plantarum**, Praha, v. 53, n. 4, p. 663–669, 2009.

LUO, Z.; ZHANG, J.; LI, J.; YANG, C.; WANG, T.; OUYANG, B.; LI, H.; GIOVANNONI, J.; YE, Z. A STAY-GREEN protein SISGR1 regulates lycopene and β -carotene accumulation by interacting directly with *SIPSY1* during ripening processes in tomato. **New Phytologist**, Oxford, v. 198, n. 2, p. 442–452, 2013.

MAGGIO, A.; BARBIERI, G.; RAIMONDI, G.; PASCALE, S. de. Contrasting effects of GA₃ treatments on tomato plants exposed to increasing salinity. **Journal of Plant Growth Regulation**, New York v. 29, n. 1, p. 63–72, 2010.

MAGGIO, A.; RAIMONDI, G.; MARTINO, A.; PASCALE, S. de. Salt stress response in tomato beyond the salinity tolerance threshold. **Environmental and Experimental Botany**, Oxford, v. 59, n. 3, p. 276–282, 2007.

MAGOME, H.; YAMAGUCHI, S.; HANADA, A.; KAMIYA, Y.; ODA, K. The DDF1 transcriptional activator upregulates expression of a gibberellin-deactivating gene, *GA2ox7*, under high-salinity stress in Arabidopsis. **The Plant Journal**, Oxford, v. 56, n. 4, p. 613–626, 2008.

MATEO, A.; FUNCK, D.; MÜHLENBOCK, P.; KULAR, B.; MULLINEAUX, P.M.; KARPINSKI, S. Controlled levels of salicylic acid are required for optimal photosynthesis and redox homeostasis. **Journal of Experimental Botany**, Oxford, v. 57, n. 8, p. 1795–1807, 2006.

MAYMON, I.; GREENBOIM-WAINBERG, Y.; SAGIV, S.; KIEBER, J.J.; MOSHELION, M.; OLSZEWSKI, N.; WEISS, D. Cytosolic activity of SPINDLY implies the existence of a DELLA-independent gibberellin-response pathway. **Plant Journal**, Malden, v. 58, n. 6, p. 979–988, 2009.

McCOURT, R.M.; DELWICHE, C.F.; KAROL, K.G. Charophyte algae and land plant origins. **Trends Ecology & Evolution**, Barking, v. 19, n. 12, p. 661–666, 2004.

MIMOUNI, H.; WASTI, S.; MANAA, A.; GHARBI, E.; CHALH, A.; VANDOORNE, B.; LUTTS, S.; AHMED, H. B. Does Salicylic Acid (SA) improve tolerance to salt stress in plants? A study of SA effects on tomato plant growth, water dynamics, photosynthesis, and biochemical parameters. **OMICS: A Journal of Integrative Biology**, Larchmont, v. 20, n. 3, p. 180–190, 2016.

MOLINERO-ROSALES, N.; LATORRE, A.; JAMILENA, M.; LOZANO, R. *Single flower truss* regulates the transition and maintenance of flowering in tomato. **Planta**, New York, v. 218, p. 427–434, 2004.

- MONTEIRO, C.C.; CARVALHO, R.F.; GRATÃO, P.L.; CARVALHO, G.; TEZOTTO, T.; MEDICI, L.O.; PERES, L.E.P.; AZEVEDO, R.A. Biochemical responses of the ethylene-insensitive never ripe tomato mutant subjected to cadmium and sodium stresses. **Environmental and Experimental Botany**, Oxford, v. 71, n. 2, p. 306–320, 2011.
- MUNNS, R.; JAMES, R.A.; XU, B.; ATHMAN, A.; CONN, S. J.; JORDANS, C.; BYRT, C. S.; HARE, R.A.; TYERMAN, S.D.; TESTER, M.; PLETT, D.; GILLIHAM, M. Wheat grain yield on saline soils is improved by an ancestral Na⁺ transporter gene. **Nature Biotechnology**, New York, v. 30, n. 4, p. 360–364, 2012.
- MUNNS, R.; TESTER, M. Mechanisms of salinity tolerance. **Annual Review of Plant Biology**, Palo Alto, v. 59, n. 1, p. 651–681, 2008.
- MWANAMWENGE, J.; LOSS, S.; SIDDIQUE, K.H.; COCKS, P. Effect of water stress during floral initiation, flowering and podding on the growth and yield of Faba bean (*Vicia faba* L.). **European Journal of Agronomy**, Amsterdam, v. 11, n. 1, p. 1–11, 1999.
- NEILL, S.J.; HORGAN, R. Abscisic acid production and water relations in wilted tomato mutants subjected to water deficiency. **Journal of Experimental Botany**, Oxford, v. 36, n. 8, p. 1222–1231, 1985.
- OGAWA, D.; ABE, K.; MIYAO, A.; KOJIMA, M.; SAKAKIBARA, H.; MIZUTANI, M.; MORITA, H.; TODA, Y.; HOBO, T.; SATO, Y.; HATTORI, T.; HIROCHIKA, H.; TAKEDA, S. *RSSI* regulates the cell cycle and maintains meristematic activity under stress conditions in rice. **Nature Communications**, London, v. 2, p. 278, 2011.
- OH, K.; IVANCHENKO, M.G.; WHITE, T.J.; LOMAX, T.L. The *diageotropica* gene of tomato encodes a cyclophilin: A novel player in auxin signaling. **Planta**, New York, v. 224, n. 1, p. 133–144, 2006.
- PAN, Y.-J.; LIU, L.; LIN, Y.-C.; ZU, Y.-G.; LI, L.-P.; TANG, Z.-H. Ethylene antagonizes salt-induced growth retardation and cell death process via transcriptional controlling of ethylene-, BAG- and senescence-associated genes in *Arabidopsis*. **Frontiers in Plant Science**, Lausanne, v. 7, p. 1–10, 2016.
- PARK, S.-Y.; YU, J.-W.; PARK, J.-S.; LI, J.; YOO, S.-C.; LEE, N.-Y.; LEE, S.-K.; JEONG, S.-W.; SEO, H. S.; KOH, H.-J.; JEON, J.-S.; PARK, Y.-I.; PAEK, N.-C. The Senescence-Induced Staygreen Protein Regulates Chlorophyll Degradation. **The Plant Cell**, Rockville, v. 19, n. 5, p. 1649–1664, 2007.
- PENG, J.; LI, Z.; WEN, X.; LI, W.; SHI, H.; YANG, L.; ZHU, H.; GUO, H. Salt-induced stabilization of EIN3/EIL1 confers salinity tolerance by deterring ROS accumulation in *Arabidopsis*. **PLoS Genetics**, San Francisco, v. 10, n. 10, p. e1004664, Oct. 2014. Disponível em: <<http://www.ncbi.nlm.nih.gov/pubmed/25330213>>. Acesso em: 05 maio 2016.
- PÉREZ-ALFOCEA, F.; ALBACETE, A.; GHANEM, M.E.; DODD, I.C. Hormonal regulation of source–sink relations to maintain crop productivity under salinity: a case study of root-to-shoot signalling in tomato. **Functional Plant Biology**, Victoria, v. 37, n. 7, p. 592–603, 2010.

- PHILIPPAR, K.; FUCHS, I.; LUTHEN, H.; HOTH, S.; BAUER, C.S.; HAGA, K.; THIEL, G.; LJUNG, K.; SANDBERG, G.; BOTTGER, M.; BECKER, D.; HEDRICH, R. Auxin-induced K⁺ channel expression represents an essential step in coleoptile growth and gravitropism. **Proceedings of the National Academy of Sciences of the United States of America**, Washington, v. 96, n. 21, p. 12186–12191, 1999.
- PHILIPPAR, K.; IVASHIKINA, N.; ACHE, P.; CHRISTIAN, M.; LÜTHEN, H.; PALME, K.; HEDRICH, R. Auxin activates *KAT1* and *KAT2*, two K⁺-channel genes expressed in seedlings of *Arabidopsis thaliana*. **The Plant Journal**, Malden, v. 37, n. 6, p. 815–827, 2004.
- PINO, L.E.; LOMBARDI-CRESTANA, S.; AZEVEDO, M.S.; SCOTTON, D.C.; BORGIO, L.; QUECINI, V.; FIGUEIRA, A.; PERES, L.E.P. The *Rgl* allele as a valuable tool for genetic transformation of the tomato ‘Micro-Tom’ model system. **Plant Methods**, London, v. 6, n. 23, p.1-23, 2010.
- POTTERS, G.; PASTERNAK, T.P.; GUISEZ, Y.; JANSEN, M. A. K. Different stresses, similar morphogenic responses: Integrating a plethora of pathways. **Plant, Cell and Environment**, New York, v. 32, n. 2, p. 158–169, 2009.
- QUADRANA, L.; ALMEIDA, J.; OTAIZA, S.N.; DUFFY, T.; SILVA, J.V.C.; GODOY, F.; ASÍS, R.; BERMUDEZ, L.; FERNIE, A.F.; CARRARI, F.; ROSSI, M. Transcriptional regulation of tocopherol biosynthesis in tomato. **Plant Molecular Biology**, Dordrecht, v. 81, n. 3, p. 309–325, 2013.
- RAIOLA, R.; TENORE, G.C.; BARONE, A.; FRUSCIANTE, L.; RIGANO, M.M. Vitamin E content and composition in tomato fruits: beneficial roles and bio-fortification. **International Journal of Molecular Sciences**, Basel, v. 16, n. 2, p. 29250–29264, 2015.
- RAO, M.V.; DAVIS, K.R. Ozone-induced cell death occurs via two distinct mechanisms in *Arabidopsis*: the role of salicylic acid. **The Plant Journal**, Oxford, v. 17, n. 6, p. 603–614, 1999.
- RASMUSSEN, A.; MASON, M.G.; DE CUYPER, C.; BREWER, P.B.; HEROLD, S.; AGUSTI, J.; GEELLEN, D.; GREB, T.; GOORMACHTIG, S.; BEECKMAN, T.; BEVERIDGE, C. A. Strigolactones suppress adventitious rooting in *Arabidopsis* and pea. **Plant Physiology**, Lancaster, v. 158, n. 4, p. 1976–1987, 2012.
- 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, n. 3, p. 241–250, 1999.
- REEVES, A.F. Tomato Trichomes and Mutations Affecting Their Development. **American Journal of Botany**, Baltimore, v. 64, n. 2, p. 186–189, 1977.
- RUIZ-LOZANO, J.M.; AROCA, R.; ZAMARREÑO, Á.M.; MOLINA, S.; ANDREO-JIMÉNEZ, B.; PORCEL, R.; GARCÍA-MINA, J.M.; RUYTER-SPIRA, C.; LÓPEZ-RÁEZ, J.A. Arbuscular mycorrhizal symbiosis induces strigolactone biosynthesis under drought and

improves drought tolerance in lettuce and tomato. **Plant, Cell and Environment**, New York, v. 39, n. 2, p. 441–452, 2016.

RUSH, D.W.; EPSTEIN, E. Genotypic Responses to Salinity: Differences between Salt-sensitive and Salt-tolerant Genotypes of the Tomato. **Plant Physiology**, Lancaster, v. 57, n. 2, p. 162–6, 1976.

RUYTER-SPIRA, C.; KOHLEN, W.; CHARNIKHOVA, T.; ZEIJL, A. van; BEZOUWEN, L. van; DE RUIJTER, N.; CARDOSO, C.; LOPEZ-RAEZ, J.A.; MATUSOVA, R.; BOURS, R.; VERSTAPPEN, F.; BOUWMEESTER, H. Physiological effects of the synthetic strigolactone analog GR24 on root system architecture in Arabidopsis: another belowground role for strigolactones? **Plant Physiology**, Lancaster, v. 155, n. 2, p. 721–734, 2011.

RYAN, P.R.; LIAO, M.; DELHAIZE, E.; REBETZKE, G.J.; WELIGAMA, C.; SPIELMEYER, W.; JAMES, R.A. Early vigour improves phosphate uptake in wheat. **Journal of Experimental Botany**, Oxford, v. 66, n. 22, p. 7089–7100, 2015.

RYU, H.; CHO, Y.-G. Plant hormones in salt stress tolerance. **Journal of Plant Biology**, Seoul, v. 58, n. 3, p. 147–155, 2015.

SAS INSTITUTE. **SAS/STAT® 9.2: user's guide**. Cary, 2008.

SELTMANN, M. A; HUSSELS, W.; BERGER, S. Jasmonates during senescence. **Plant Signaling & Behavior**, Georgetown, v. 5, n. 11, p. 1493–1496, 2010.

SHABALA, S.; CUIN, T.A. Potassium transport and plant salt tolerance. **Physiologia Plantarum**, Copenhagen, v. 133, n. 4, p. 651–669, 2008.

SHAHBAZ, M.; ASHRAF, M.; AL-QURAINY, F.; HARRIS, P.J.C. Salt tolerance in selected vegetable crops. **Critical Reviews in Plant Sciences**, Boca Raton, v. 31, n. 4, p. 303–320, 2012.

SHALIT, A.; ROZMAN, A.; GOLDSCHMIDT, A.; ALVAREZ, J.P.; BOWMAN, J.L.; ESHED, Y.; LIFSCHITZ, E. The flowering hormone florigen functions as a general systemic regulator of growth and termination. **Proceedings of the National Academy of Sciences of the United States of America**, Washington, v. 106, n. 20, p. 8392–8397, 2009.

SHAN, C.; MEI, Z.; DUAN, J.; CHEN, H.; FENG, H.; CAI, W. *OsGA2ox5*, a gibberellin metabolism enzyme, is involved in plant growth, the root gravity response and salt stress. **PLoS One**, San Francisco, v. 9, n. 1, p. 1–10, 2014. Disponível em: <<http://www.ncbi.nlm.nih.gov/pubmed/24475234>>. Acesso em: 22 maio 2016.

SHAN, X.; WANG, J.; CHUA, L.; JIANG, D.; PENG, W.; XIE, D. The role of Arabidopsis Rubisco activase in jasmonate-induced leaf senescence. **Plant Physiology**, Lancaster, v. 155, n. 2, p. 751–764, 2011.

SHAPIRO, S.S.; WILK, M.B. An analysis of variance test for normality (complete samples). **Biometrika**, London, v. 52, n. 3/4, p. 591–611, 1965.

SHARP, R.E.; LENOBLE, M.E.; ELSE, M.A.; THORNE, E.T.; GHERARDI, F. Endogenous ABA maintains shoot growth in tomato independently of effects on plant water balance: evidence for an interaction with ethylene. **Journal of Experimental Botany**, Oxford, v. 51, n. 350, p. 1575–1584, 2000.

SHI, Q.; BAO, Z.; ZHU, Z.; YING, Q.; QIAN, Q. Effects of different treatments of salicylic acid on heat tolerance, chlorophyll fluorescence, and antioxidant enzyme activity in seedlings of *Cucumis sativa* L. **Plant Growth Regulation**, Dordrecht, v. 48, n. 2, p.127–135, 2006.

SHINOHARA, N.; TAYLOR, C.; LEYSER, O. Strigolactone can promote or inhibit shoot branching by triggering rapid depletion of the auxin efflux protein pin1 from the plasma membrane. **PLoS Biology**, San Francisco, v. 11, n. 1, p. e1001474, 2013. Disponível em: <<http://dx.plos.org/10.1371/journal.pbio.1001474>>. Acesso em: 30 maio 2016.

SKŁODOWSKA, M.; GAPIŃSKA, M.; GAJEWSKA, E.; GABARA, B. Tocopherol content and enzymatic antioxidant activities in chloroplasts from NaCl-stressed tomato plants. **Acta Physiologiae Plantarum**, Warszawa, v. 31, n. 2, p. 393–400, 2009.

SNIR, A.; NADEL, D.; GROMAN-YAROSLAVSKI, I.; MELAMED, Y.; STERNBERG, M.; BAR-YOSEF, O.; WEISS, E. The origin of cultivation and proto-weeds, long before neolithic farming. **PLoS One**, San Francisco, v. 10, n. 7, p. 1–12, 2015. Disponível em: <<http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0131422>>. Acesso em: 13 fev. 2016.

SPOLEN, W.G.; LENOBLE, M.E.; SAMUELS, T.D.; BERNSTEIN, N.; SHARP, R.E. Abscisic acid accumulation maintains maize primary root elongation at low water potentials by restricting ethylene production. **Plant Physiology**, Lancaster, v. 122, n. 3, p. 967–976, 2000.

SPOONER, D.M.; PERALTA, I.E.; KNAPP, S. Comparison of AFLPs with Other Markers for Phylogenetic Inference in Wild Tomatoes [*Solanum* L. Section *Lycopersicon* (Mill.) Wettst.]. **Taxon**, Utrecht, v. 54, n. 1, p. 43–61, 2005.

STAM, P.; ZEVEN, A.C. The theoretical proportion of the donor genome in near-isogenic lines of self-fertilizers bred by backcrossing. **Euphytica**, Dordrecht, v. 30, n. 2, p. 227–238, 1981.

STASWICK, P.E.; TIRYAKI, I. The oxylipin signal jasmonic acid is activated by an enzyme that conjugates it to isoleucine in Arabidopsis. **The Plant Cell**, Rockville, v. 16, n. 8, p. 2117–2127, 2004

STEVENS, M.A.; RICK, C.M. Genetics and breeding. In: ATHERTON, J.; RUDICH, J. (Ed.). **The tomato crop: a scientific basis for improvement**. London: Chapman & Hall, 1986. p. 35–100.

SUN, X.; FU, T.; CHEN, N.; GUO, J.; MA, J.; ZOU, M.; LU, C.; ZHANG, L. The stromal chloroplast Deg7 protease participates in the repair of photosystem II after photoinhibition in Arabidopsis. **Plant Physiology**, Lancaster, v. 152, n. 3, p. 1263–1273, 2010.

- SZYMKOWIAK, E.J.; SUSSEX, I.M. The internal meristem layer (L3) determines floral meristem size and carpel number in tomato periclinal chimeras. **The Plant Cell**, Rockville, v. 4, n. 9, p. 1089–1100, 1992.
- TANG, X.; MU, X.; SHAO, H.; WANG, H.; BRESTIC, M. Global plant-responding mechanisms to salt stress: physiological and molecular levels and implications in biotechnology. **Critical Reviews in Biotechnology**, Boca Raton, v. 35, n. 4, p. 425–437, 2015.
- TANKSLEY, S.D.; GANAL, M.W.; PRINCE, J.P.; VICENTE, M.C.; BONIERBALE, M.W.; BROUN, P.; FULTON, T.M.; GIOVANNONI, J.J.; GRANDILLO, S.; MARTIN, G.B. High density molecular linkage maps of the tomato and potato genomes. **Genetics**, Bethesda, v. 132, n. 4, p. 1141–1160, 1992.
- TAO, J.-J.; CHEN, H.-W.; MA, B.; ZHANG, W.-K.; CHEN, S.-Y.; ZHANG, J.-S. The role of ethylene in plants under salinity stress. **Frontiers in Plant Science**, Lauseanne, v. 6, p. 1059, 2015.
- THARA, V.K.; TANG, X.; GU, Y. Q.; MARTIN, G.B.; ZHOU, J.M. *Pseudomonas syringae* pv tomato induces the expression of tomato *EREBP*-like genes *Pti4* and *Pti5* independent of ethylene, salicylate and jasmonate. **The Plant Journal**, Malden, v. 20, n. 4, p. 475–483, 1999.
- THOMAS, H.; OUGHAM, H. The stay-green trait. **Journal of Experimental Botany**, Oxford, v. 65, n. 14, p. 3889–3900, 2014.
- TUINEN, A. van; PETERS, A.H.L.J.; KENDRICK, R.E.; ZEEVAART, J.A.D.; KOORNNEEF, M. Characterisation of the *procera* mutant of tomato and the interaction of gibberellins with end-of-day far-red light treatments. **Physiologia Plantarum**, Copenhagen, v. 106, n. 1, p. 121–128, 1999.
- TUTEJA, N.; SOPORY, S.K. Chemical signaling under abiotic stress environment in plants. **Plant Signaling & Behavior**, Georgetown, v. 3, n. 8, p. 525–536, 2008.
- UMEHARA, M.; HANADA, A.; YOSHIDA, S.; AKIYAMA, K.; ARITE, T.; TAKEDA-KAMIYA, N.; MAGOME, H.; KAMIYA, Y.; SHIRASU, K.; YONEYAMA, K.; KYOZUKA, J.; YAMAGUCHI, S. Inhibition of shoot branching by new terpenoid plant hormones. **Nature**, London, v. 455, n. 7210, p. 195–200, 2008.
- URANO, D.; COLANERI, A.; JONES, A.M. $G\alpha$ modulates salt-induced cellular senescence and cell division in rice and maize. **Journal of Experimental Botany**, Oxford, v. 65, n. 22, p. 6553–6561, 2014.
- URANO, K.; KURIHARA, Y.; SEKI, M.; SHINOZAKI, K. “Omics” analyses of regulatory networks in plant abiotic stress responses. **Current Opinion in Plant Biology**, London, v. 13, n. 2, p. 132–138, 2010.
- VALENTIN, H.E.; LINCOLN, K.; MOSHIRI, F.; JENSEN, P.K.; QI, Q.; VENKATESH, T. V.; KARUNANANDAA, B.; BASZIS, S.; NORRIS, S.; SAVIDGE, B.; GRUYS, K.J.; LAST, R. The Arabidopsis vitamin E pathway *gene 5-1* mutant reveals a critical role for

phytyl kinase in seed tocopherol biosynthesis. **The Plant Cell**, Rockville, v. 18, n. 1, p. 212–224, 2006.

VARGAS, I.; GALLEGOS, H. Sumer: where engineering was born. **Journal of Professional Issues in Engineering**, Utah, v. 116, n. 1, p. 83–92, 1990.

VENDEMIATTI, E.; ZSÖGÖN, A.; SILVA, G.F.F.; JESUS, F.A.; CUTRI, L.; TANAKA, F.; NOGUEIRA, F.T.S.; PERES, L.E.P. Loss of type-IV glandular trichomes in tomato (*Solanum lycopersicum*) is a heterochronic trait reversible by the promotion of juvenile phase of vegetative development. **New Phytologist**, London, 2016. In press.

VERSLUES, P.E.; AGARWAL, M.; KATIYAR-AGARWAL, S.; ZHU, J.; ZHU, J.-K. Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. **The Plant Journal**, Oxford, v. 45, n. 4, p. 523–539, 2006.

VICENTE, M.H.; ZSÖGÖN, A.; SÁ, A.F.L.; RIBEIRO, R.; PERES, L.E.P. Semi-determinate growth habit adjusts the vegetative-to-reproductive balance and increases productivity and water-use efficiency in tomato (*Solanum lycopersicum*). **Journal of Plant Physiology**, Stuttgart, v. 177, n. 1, p. 11–19, 2015.

VICENTE, M.H. **Regulação do balanço vegetativo-reprodutivo pelo crescimento semi-determinado em tomateiro (*Solanum lycopersicum* L. cv. Micro-Tom) e seu impacto na produtividade e eficiência no uso da água**. 2013. 87 p. Dissertação (Mestrado em Fisiologia e Bioquímica de Plantas) – Escola Superior de Agricultura “Luiz de Queiroz”, Universidade de São Paulo, Piracicaba, 2013. Disponível em: <http://www.teses.usp.br/teses/disponiveis/11/11144/tde-10092013-161029/publico/Mateus_Henrique_Vicente.pdf>. Acesso em: 20 maio 2016.

VOGEL, J.T.; WALTER, M.H.; GIAVALISCO, P.; LYTOVCHENKO, A.; KOHLEN, W.; CHARNIKHOVA, T.; SIMKIN, A.J.; GOULET, C.; STRACK, D.; BOUWMEESTER, H.J.; FERNIE, A.R.; KLEE, H.J. *SlCCD7* controls strigolactone biosynthesis, shoot branching and mycorrhiza-induced apocarotenoid formation in tomato. **The Plant Journal**, Malden, v. 61, n. 2, p. 300–311, 2010.

WADA, K.C.; TAKENO, K. Stress-induced flowering. **Plant Signaling & Behavior**, Georgetown, v. 5, n. 8, p. 944–947, 2010.

WAHID, A.; PERVEEN, M.; GELANI, S.; BASRA, S.M.A. Pretreatment of seed with H₂O₂ improves salt tolerance of wheat seedlings by alleviation of oxidative damage and expression of stress proteins. **Journal of Plant Physiology**, Stuttgart, v. 164, n. 3, p. 283–294, 2007.

WANG, H.; JONES, B.; LI, Z.; FRASSE, P.; DELALANDE, C.; REGAD, F.; CHAABOUNI, S.; LATCHÉ, A.; PECH, J.-C.; BOUZAYEN, M. The tomato *Aux/IAA* transcription factor *IAA9* is involved in fruit development and leaf morphogenesis. **The Plant Cell**, Rockville, v. 17, n. 10, p. 2676–2692, 2005.

WANG, Y.; MOPPER, S.; HASENSTEIN, K.H. Effects of salinity on endogenous ABA, IAA, JA, and SA in *Iris hexagona*. **Journal of Chemical Ecology**, New York, v. 27, n. 2, p. 327–342, 2001.

- WANG, Y.; SHEN, W.; CHAN, Z.; WU, Y. Endogenous Cytokinin Overproduction Modulates ROS Homeostasis and Decreases Salt Stress Resistance in *Arabidopsis Thaliana*. **Frontiers in Plant Science**, Lausanne, v. 6, n. November, p. 1004, 2015.
- WASTI, S.; MIMOUNI, H.; SMITI, S.; ZID, E.; AHMED, H.B. Enhanced salt tolerance of tomatoes by exogenous salicylic acid applied through rooting medium. **OMICS: A Journal of Integrative Biology**, Larchmonte, v. 16, n. 4, p. 200–207, 2012.
- WEES, S.C.M. van; GLAZEBROOK, J. Loss of non-host resistance of *Arabidopsis NahG* to *Pseudomonas syringae* pv. *phaseolicola* is due to degradation products of salicylic acid. **The Plant Journal**, Malden, v. 33, n. 4, p. 733–742, 2003.
- WEISS, D.; ORI, N. Mechanisms of cross talk between gibberellin and other hormones. **Plant Physiology**, Lancaster, v. 144, n. 3, p. 1240–1246, 2007.
- WOLTERS, H.; JÜRGENS, G. Survival of the flexible: hormonal growth control and adaptation in plant development. **Nature Reviews Genetics**, London, v. 10, n. 5, p. 305–317, 2009.
- XU, M.Y.; ZHANG, L.; LI, W.W.; HU, X.L.; WANG, M.B.; FAN, Y.L.; ZHANG, C.Y.; WANG, L. Stress-induced early flowering is mediated by *miR169* in *Arabidopsis thaliana*. **Journal of Experimental Botany**, Oxford, v. 65, p. 89–101, 2013.
- YAMAGUCHI, T.; HAMAMOTO, S.; UOZUMI, N. Sodium transport system in plant cells. **Frontiers in Plant Science**, Lausanne, v. 4, n. 17, p. 1–7, 2013.
- YANG, C.; MA, B.; HE, S.-J.; XIONG, Q.; DUAN, K.-X.; YIN, C.-C.; CHEN, H.; LU, X.; CHEN, S.-Y.; ZHANG, J.-S. *MAOHUZI6/ethylene insensitive3-like1* and *ethylene insensitive3-like2* regulate ethylene response of roots and coleoptiles and negatively affect salt tolerance in rice. **Plant Physiology**, Lancaster, v. 169, n. 1, p. 148–165, 2015.
- YANG, Q.; CHEN, Z.-Z.; ZHOU, X.-F.; YIN, H.-B.; LI, X.; XIN, X.-F.; HONG, X.-H.; ZHU, J.-K.; GONG, Z. Overexpression of *SOS (Salt Overly Sensitive)* genes increases salt tolerance in transgenic *Arabidopsis*. **Molecular Plant**, v. 2, n. 1, p. 22–31, 2009.
- YANG, Y.; MA, C.; XU, Y.; WEI, Q.; IMTIAZ, M.; LAN, H.; GAO, S.; CHENG, L.; WANG, M.; FEI, Z.; HONG, B.; GAO, J. A zinc finger protein regulates flowering time and abiotic stress tolerance in chrysanthemum by modulating gibberellin biosynthesis. **The Plant Cell**, Rockville, v. 26, n. 5, p. 2038–2054, 2014.
- YEN, H.C.; LEE, S.; TANKSLEY, S.D.; LANAHAN, M.B.; KLEE, H.J.; GIOVANNONI, J.J. The tomato *Never-ripe* locus regulates ethylene-inducible gene expression and is linked to a homolog of the *Arabidopsis ETR1* gene. **Plant Physiology**, Lancaster, v. 107, n. 4, p. 1343–1353, 1995.
- YUAN, S.; LIN, H.-H. Role of salicylic acid in plant abiotic stress. **Zeitschrift für Naturforschung. Teil C: Biochemie, Biophysik, Biologie, Virologie**, Tübingen, v. 63, n. 5/6, p. 313–320, 2008.

ZHANG, H.X.; BLUMWALD, E. Transgenic salt-tolerant tomato plants accumulate salt in foliage but not in fruit. **Nature Biotechnology**, New York, v. 19, n. 8, p. 765–768, 2001.

ZHANG, H.X.; HODSON, J.N.; WILLIAMS, J.P.; BLUMWALD, E. Engineering salt-tolerant *Brassica* plants: characterization of yield and seed oil quality in transgenic plants with increased vacuolar sodium accumulation. **Proceedings of the National Academy of Sciences of the United States of America**, Washington, v. 98, n. 22, p. 12832–12836, 2001.

ZHANG, J.; JIA, W.; YANG, J.; ISMAIL, A.M. Role of ABA in integrating plant responses to drought and salt stresses. **Field Crops Research**, Amsterdam, v. 97, n. 1, p. 111–119, 2006

ZHANG, X.; ZOU, Z.; GONG, P.; ZHANG, J.; ZIAF, K.; LI, H.; XIAO, F.; YE, Z. Over-expression of *microRNA169* confers enhanced drought tolerance to tomato. **Biotechnology Letters**, Dordrecht, v. 33, n. 2, p. 403–409, 2011.

ZHU, J.K. Plant salt tolerance. **Trends in Plant Science**, Kidlington, v. 6, n. 2, p. 66–71, 2001.

ZHU, J.-K. Salt and drought stress signal transduction in plants. **Annual Review of Plant Biology**, Palo Alto, v. 53, n. 1, p. 247–273, 2002.