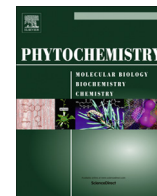




Contents lists available at ScienceDirect

Phytochemistry

journal homepage: www.elsevier.com/locate/phytochem

Fruits from ripening impaired, chlorophyll degraded and jasmonate insensitive tomato mutants have altered tocopherol content and composition

Juliana Almeida^a, Ramón Asís^b, Virginia Noel Molineri^b, Ivan Sestari^c, Bruno Silvestre Lira^a, Fernando Carrari^d, Lázaro Eustáquio Pereira Peres^e, Magdalena Rossi^{a,*}

^a Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

^b CIBICI, Facultad de Ciencias Químicas, Universidad Nacional de Córdoba, Córdoba, Argentina

^c Universidade Federal de Santa Catarina, Campus Curitibanos, Curitibanos, SC, Brazil

^d Instituto de Biotecnología, Instituto Nacional de Tecnología Agropecuaria and Consejo Nacional de Investigaciones Científicas y Técnicas, Hurlingham, Buenos Aires, Argentina

^e Departamento de Ciências Biológicas, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba, SP, Brazil

ARTICLE INFO

Article history:

Received 2 August 2014

Received in revised form 20 October 2014

Available online xxx

Keywords:

Tomato mutants
Solanum lycopersicum
 Solanaceae
 Atocopherol
 Carotenoids
 Chlorophyll
 Jasmonic acid
 Ripening
 Antioxidant capacity

ABSTRACT

Since isoprenoids are precursors in chlorophyll, carotenoid and tocopherol pathways, the study of their metabolism is of fundamental importance in understanding the regulatory cross-talk that contributes to the nutritional quality of tomato fruits. By means of an integrated analysis of metabolite and gene expression profiles, isoprenoid metabolism was dissected in ripening-impaired (*ripening inhibitor* and *non-ripening*), senescence-related (*lutescent1* and *green flesh*) and jasmonate insensitive (*jasmonic acid insensitive 1-1*) tomato mutants, all in the Micro-Tom genetic background. It was found that the more upstream the location of the mutated gene, the more extensive the effect on the transcriptional profiles of the isoprenoid-related genes. Although there was a distinct effect in the analyzed mutations on chlorophyll, carotenoid and tocopherol metabolism, a metabolic adjustment was apparent such the antioxidant capacity mostly remained constant. Transcriptional profiles from fruits of ripening and senescence-related tomato mutants suggested that maintenance of the *de novo* phytol diphosphate synthesis might, in later ripening stages, compensate for the lack of chlorophyll-derived phytol used in tocopherol production. Interestingly, an impairment in jasmonate perception led to higher total tocopherol levels in ripe fruits, accompanied by an increase in antioxidant capacity, highlighting the contribution of tocopherols to this nutritionally important trait.

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1. Introduction

Fruit ripening involves a series of coordinated biochemical and physiological processes resulting in organoleptic changes in texture, aroma and color (Seymour et al., 1993). One of the most important and visible changes in tomato (*Solanum lycopersicum* L.), a climacteric fruit, involves de-greening and accumulation of carotenoids; a phenomenon that is associated with a chloroplast-to-chromoplast transition (Egea et al., 2011). Tomato is one of

the most consumed fruits worldwide and is a major source of many dietary nutrients, such as minerals, antioxidants and vitamins; all of which contribute to the prevention of chronic diseases (Seybold et al., 2004; Perez-Fons et al., 2014). In particular tocopherols, which belong to the vitamin E (VTE) family, are potent lipid soluble antioxidant molecules that reduce free-radical damage to membrane lipids by scavenging peroxy radicals (Brigelius-Flohé et al., 2002; Niki and Traber, 2012). Tocopherols can also act as scavengers of singlet oxygen (¹O₂) and, in plants, this function is related to protection of the photosynthetic apparatus from oxygen toxicity (Trebst, 2003; Krieger-Liszskay and Trebst, 2006).

Tocopherols are isoprenoid-derived compounds that are synthesized from the condensation of a chromanol ring and a prenyl side-chain from the shikimate (SK) and 2-C-methyl-D-erythritol 4-phosphate (MEP) pathways, respectively (Dellapenna and

* Corresponding author at: Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 277, 05508-900 São Paulo, Brasil. Tel.: +55 11 3091 7556; fax: +55 11 3091 7547.

E-mail addresses: juliana.almeida.silva@usp.br (J. Almeida), rasis@fcq.unc.edu.ar (R. Asís), vicky_412@hotmail.com (V.N. Molineri), ivan.sestari@ufsc.br (I. Sestari), bslira.bsl@gmail.com (B.S. Lira), carrari.fernando@inta.gob.ar (F. Carrari), lazaro.peres@usp.br (L.E.P. Peres), mmrossi@usp.br (M. Rossi).

Pogson, 2006). The MEP pathway also provides precursors for other plastid isoprenoids, such as chlorophylls (Chls) and carotenoids, the latter of which can be divided into two classes based on their chemical structures: linear or cyclized hydrocarbons, termed carotenes, and xanthophylls that are oxygenated derivatives of carotenes. The xanthophylls lutein, violaxanthin and neoxanthin are components of the light harvesting complex (LHC) and act both as antenna pigments and as protective molecules, by reducing the production of reactive oxygen species (ROS). β -Carotene is a component of the photosynthetic reaction center (Dall'Osto et al., 2006) and during tomato fruit ripening, it accumulates together with the primary ripening-related pigment lycopene (Bramley, 2002).













A recent study focusing on the transcriptional regulation of tocopherol biosynthesis in tomato (cv. M82) (Quadra et al., 2013) showed that expression of genes encoding enzymes of the tocopherol-core, MEP and SK pathways are controlled both temporally and spatially, and that the supply of the prenyl donor, phytyl diphosphate, appears to be a limiting step in VTE accumulation at later fruit stages. In *Arabidopsis thaliana*, it has been shown that phytyl diphosphate for tocopherol biosynthesis can also originate from the activity of phytol kinase (VTE5), which functions in phytol recycling after Chl degradation (Ischebeck et al., 2006; Valentin et al., 2006). The strong correlation between the expression of VTE5 and the VTE biosynthetic genes, and the content of Chls and VTE in tomato leaves and fruits supports the contribution of phytol

recycling enzymes to tocopherol biosynthesis in this species as well (Quadra et al., 2013).

This metabolic cross-talk suggests that changes in carotenoid biosynthesis and Chl metabolism might affect tocopherol content, but a better understanding of the accumulation of these metabolites depends on deciphering the complexity of the isoprenoid metabolic network and its branching (Vranová et al., 2012). To this end, senescence and ripening-related tomato mutants represent potentially excellent models, since they provide a means to study metabolic fluxes between these pathways (Table 1). *Non-ripening* (*nor*) and *ripening inhibitor* (*rin*) are tomato mutants with impaired fruit ripening, which fail to undergo typical ripening-related *de novo* carotenoid biosynthesis and Chl degradation (Giovannoni, 2004). Another mutant, *green flesh* (*gf*) is deficient in the STAY-GREEN1 (SGR1) protein involved in destabilization of the Chl-apoprotein complexes and recruitment of the Chl catabolic enzymes, which are a prerequisite for Chl catabolism; thus the fruit retains Chls even at the ripe stage (Barry et al., 2008; Park et al., 2007; Hörtensteiner, 2009). In contrast, the *lutescent* (*l*) mutant displays premature leaf senescence and its fruits lack Chl (Barry et al., 2012).

The ethylene and cytokinin signaling pathways are well-defined and mediate senescence and de-greening, while other hormones, such as jasmonic acid (JA), have also been demonstrated to affect these processes (Lim et al., 2007). Altered patterns of senescence and de-greening have been reported in JA-insensitive or JA-defi-

Table 1
Solanum lycopersicum L. (cv. Micro-Tom) genotypes used in this study.

Genotype	Mature green fruit	Ripe fruit	Mutant gene function/phenotype	Tomato locus ^a	Reference
Micro-Tom (MT) <i>dwarf</i> (<i>d</i>) and <i>self-pruning</i> (<i>sp</i>) (control genotype)			<i>D</i> is a brassinosteroid biosynthesis enzyme encoding gene. The mutant allele reduces all organ sizes, except the fruits. <i>SP</i> regulates vegetative to reproductive switching of sympodial meristems. The mutant shows a determinate growth habit	Solyc02g089160 Solyc06g074350	Meissner et al. (1997), Martí et al. (2006), Bishop et al. (1999)
MT- <i>non ripening</i> (MT- <i>nor</i>)			<i>NOR</i> is a NAC transcription factor. Mutant fruits do not ripe due to an alteration of the program that triggers climacteric ethylene biosynthesis	Solyc10g006880	Giovannoni et al. (1995)
MT- <i>ripening inhibitor</i> (MT- <i>rin</i>)			<i>RIN</i> is a MADS-box transcription factor. Mutants show an altered fruit ripening program, which fails to trigger climacteric respiration and ripening related ethylene biosynthesis	Solyc05g012020	Vrebalov et al. (2002)
MT- <i>green flesh</i> (MT- <i>gf</i>)			<i>gf</i> plants harbor a mutant allele of the STAY-GREEN1 protein encoding gene. The plants are deficient in chlorophyll degradation and present brownish fruits with green seed placental tissues	Solyc08g080090	Barry et al. (2008)
MT- <i>lutescent 1</i> (MT- <i>l</i>)			<i>L</i> is locus with unknown function. Mutant plants present non-pigmented ovaries and yellowish leaves	?	Jen (1974)
MT- <i>jasmonic acid insensitive 1-1</i> (MT- <i>jai</i>)			<i>JAI</i> is an F-box protein. Mutant plants are insensitive to JA and show delayed senescence of petals and styles, as well as glabrous ovaries	Solyc05g052620	Li et al. (2004)

^a Sol Genomics Network (<http://solgenomics.net/>).

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