Scientia Horticulturae 214 (2017) 107–113

Contents lists available at ScienceDirect

Scientia Horticulturae

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

Serotonin content in fresh and processed tomatoes and its accumulation during fruit development

Shohei Hano[a,1], Tomoki Shibuya[a,1], Nozomi Imoto[a], Ayaka Ito[a], Shunsuke Imanishi[b], Hisashi Aso[a], Yoshinori Kanayama[a,*]

[a] Graduate School of Agricultural Science, Tohoku University, 468-1 Aramaki Aza-Aoba, Aoba-ku, Sendai 980-0845, Japan
[b] NARO Institute of Vegetable and Floriculture Science, Ano, Tsu 514-2392, Japan

ARTICLE INFO

Article history:
Received 22 August 2016
Received in revised form 9 November 2016
Accepted 11 November 2016
Available online 26 November 2016

Keywords:
Fruit
Serotonin
Solanum lycopersicum
Tomato
Tryptophan decarboxylase

ABSTRACT

Serotonin is an aromatic amine neurotransmitter in the central nervous system; however, approximately 98% of serotonin is synthesized and stored in the peripheral system. We analyzed tomatoes (*Solanum lycopersicum*), which are relatively rich in serotonin, because serotonin has been found to have anti-obesity effects in the peripheral system. Serotonin content was very low in processed tomato products, whereas fresh tomatoes were much richer in serotonin. Serotonin content increased in all fruit tissues during tomato fruit development, reaching maximum levels at the ripe stage. Differences in serotonin content were relatively small among fruit tissues at the ripe stage. During storage, serotonin content did not decrease at either room temperature or at the lower temperature (4° C). Sequence and expression analyses were performed for tryptophan decarboxylase (TDC) and tryptamine 5-hydroxylase (T5H) genes, which could be related to the serotonin biosynthesis pathway from tryptophan. As a result, expression of *SlTDC1*, one of the tomato putative TDC family genes, and *SlT5H*, the tomato putative T5H homolog, likely corresponds to an increase in serotonin content during fruit development. The results suggest that fresh tomatoes are a promising source of serotonin, and *SlTDC1* and *SlT5H* might be involved in physiological mechanisms of serotonin accumulation.

1. Introduction

Serotonin is an aromatic amine neurotransmitter that controls several physiological functions, such as mood, sleep, and anxiety in animals and humans (Veenstra-VanderWeele et al., 2000). However, approximately 98% of serotonin is synthesized and stored in the peripheral system. Although serotonin in the peripheral system also has some functions, the functions are not yet fully understood (Watanabe et al., 2011). Recently, it has been found that in mice, serotonin enhances lipid metabolism by stimulating the excretion of bile in the peripheral system (Watanabe et al., 2010, 2011, 2016). Serotonin intake via food cannot cross the blood-brain barrier, and thus acts in the peripheral system. Xiao et al. (1998) reported that intake of banana, which is relatively rich in serotonin, increases the blood serotonin level. Therefore, considering the anti-obesity effects of serotonin, it is important in horticultural science to focus on vegetables and fruits as sources of serotonin and to investigate serotonin content, synthesis, and accumulation.

Serotonin content in tomato (*Solanum lycopersicum*) appears to be relatively high among vegetables (Feldman and Lee, 1985). In addition, tomatoes are rich in lycopene, which has an antioxidant activity (Hu et al., 2013), and 13-oxo-9,11-octadecadienoic acid in tomato juice regulates lipid metabolism (Kim et al., 2012). Tomatoes are the most abundantly produced fruit globally (FAOSTAT, http://faostat.fao.org). Therefore, in a health-oriented modern society, providing new information regarding a functional ingredient, such as serotonin, in tomatoes may result in increasing the value of tomatoes due to health benefits, thereby further increasing tomato consumption. In animals, serotonin is synthesized by tryptophan hydroxylase, which catalyzes the hydroxylation of tryptophan to produce 5-hydroxytryptophan, followed by aromatic amino acid decarboxylase to form serotonin, with tryptophan hydroxylase acting as a rate limiting enzyme (Veenstra-VanderWeele et al., 2000). In plants (such as rice and pepper), it is reported that serotonin is synthesized by tryptophan decarboxylase (TDC), which catalyzes

Abbreviations: DAF, days after flowering; PLP, pyridoxal phosphate; SSC, soluble solids content; TDC, tryptophan decarboxylase; TYDC, tyrosine decarboxylase; T5H, tryptamine 5-shydroxylase.

* Corresponding author at: Graduate School of Agricultural Science, Tohoku University, 468-1 Aramaki Aza-Aoba, Aoba-ku, Sendai 980-0845, Japan.
E-mail address: yoshinori.kanayama.a7@tohoku.ac.jp (Y. Kanayama).

[1] These authors equally contributed to the paper.

http://dx.doi.org/10.1016/j.scienta.2016.11.009
0304-4238/

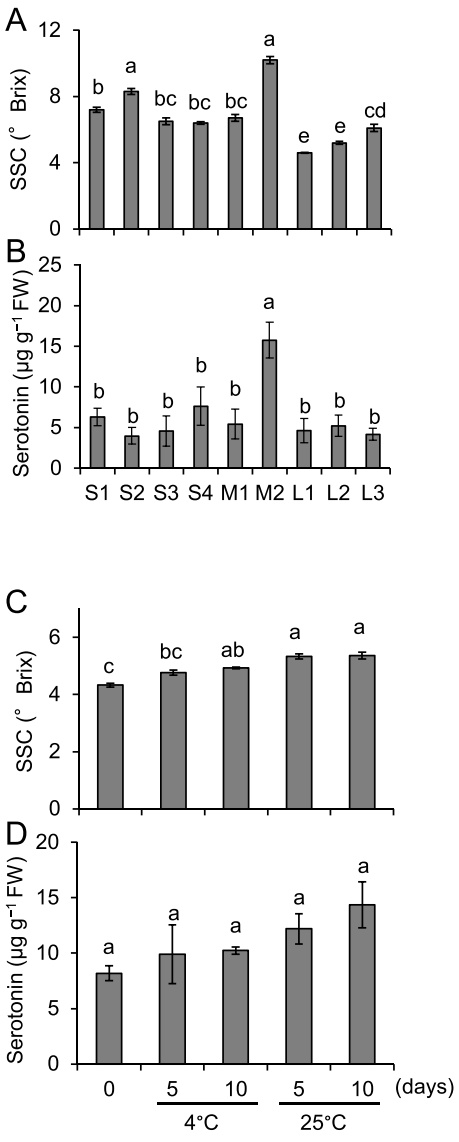

Fig. 1. Serotonin content in fresh tomatoes. The nine cultivars or brands of tomatoes purchased and used for the analysis were cherry tomatoes (S1, S2, S3, S4), middle-sized tomatoes (M1, M2), and large-sized tomatoes (L1, L2 L3). SSC was measured for reference (A), as well as serotonin content (B). SSC for reference (C) and serotonin content (D) in fresh fruit were also measured for five and ten days at 4 ° C or 25 ° C, after the harvest at breaker stage. Pericarp tissues were used for the analysis and each value was determined in three independent biological replicates. Values indicate means ± standard error (n = 3). Values with the same letter were not significantly different at $P < 0.05$ according to Tukey's test.

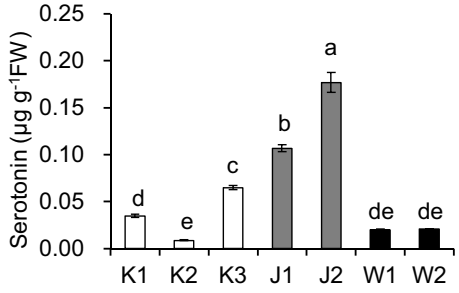

Fig. 2. Serotonin content in processed tomatoes. Tomato ketchup (K1, K2, K3), tomato juice (J1, J2), and canned whole tomatoes (W1, W2) were used for the analysis, and two or three items in each type of processed tomato were from different companies. Each value was determined in three independent extractions. Values indicate means ± standard error (n = 3). Values with the same letter were not significantly different at $P < 0.05$ according to Tukey's test.

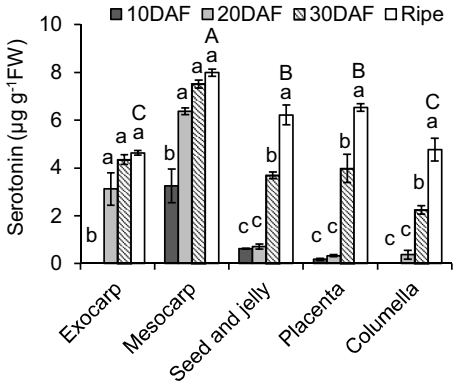

Fig. 3. Serotonin content in various fruit tissues. Exocarp, mesocarp, seed and jelly, placenta, and columella tissues were sampled at ten days after flowering (DAF), 20 DAF, 30 DAF, and the ripe stage, and analyzed. Each value was determined in three independent biological replicates and indicate a mean ± standard error (n = 3). Different lowercase letters indicate significant differences among fruit developmental stages in each tissue and different uppercase letters indicate significant differences among tissues at the ripe stage at $P < 0.05$ according to Tukey's test.

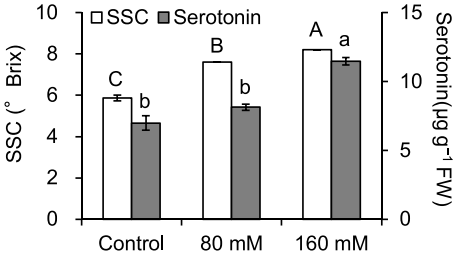

Fig. 4. Effect of salt stress on soluble solids and serotonin content in fruit. Plants were supplied with 80 mM or 160 mM NaCl and fruit was harvested at the ripe stage. Pericarp tissues were used for the analysis and each value was determined in three independent biological replicates. Values indicate means ± standard error (n = 3). Values with the same letter were not significantly different at $P < 0.05$ according to Tukey's test. The SSC data in control and 80 mM is the same as that in Ikeda et al. (2016).

the decarboxylation of tryptophan to form tryptamine, following which catalysis by tryptamine 5-hydroxylase (T5H) forms serotonin (Kang et al., 2009a; Park et al., 2009). In rice leaves, senescence increases TDC gene expression and serotonin content, and the overexpression of the TDC gene increases serotonin content and delays senescence (Kang et al., 2009a). Tryptamine synthesized by TDC is converted to serotonin by T5H, a cytochrome P450 enzyme (Fujiwara et al., 2010). Upon pathogen infection in pepper fruit, the expression of the TDC gene and serotonin content are increased to induce responses to infection (Park et al., 2009). Despite these previous findings, very few studies have focused on serotonin accumulation and the expression of serotonin synthesis-related genes during fruit development.

In this study, to evaluate tomato fruit as a promising source of serotonin, we measured serotonin content in both fresh and processed tomatoes, and compared serotonin content in various fruit tissues. We also investigated serotonin synthesis-related genes to understand the determining factors of serotonin accumulation during fruit development.

2. Materials and methods

2.1. Determination of serotonin content in fresh and processed tomatoes

Fresh fruits of cherry tomatoes, middle-, and large-sized tomatoes were purchased from local markets, and their pericarp tissues