



Involvement of reactive oxygen species and auxin in serotonin-induced inhibition of primary root elongation

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ABSTRACT

The well-known neurotransmitter 5-hydroxytryptamine (serotonin) not only regulates sleep and mood in humans and animals but may also play important roles in modulating growth, development, and defense responses, such as seed germination, flowering, and abiotic stress tolerance, in plants. Serotonin inhibits primary root (PR) growth; however, the physiological and molecular mechanisms underlying serotonin-mediated PR growth inhibition remain largely unclear. Here, we investigate the effects of serotonin on root growth and development in *Arabidopsis*. Serotonin inhibits PR elongation by affecting both the meristem and elongation zones. In the meristem zone, serotonin represses both meristem cell division potential and stem cell niche activity. Serotonin induces H₂O₂ overaccumulation in the elongation zone and reduces O₂⁻ accumulation in the meristem zone by a *UPB1* pathway, thereby disrupting reactive oxygen species (ROS) equilibrium in root tips, thus resulting in PR growth inhibition. Serotonin also regulates auxin distribution in root tips by decreasing auxin-related gene expression and repressing auxin transport through modulation of *AUX1* and *PIN2* abundances in root tips. Taken together, our data indicate that high concentrations of serotonin result in stress responses in plants by inhibiting PR elongation through the regulation of H₂O₂ and O₂⁻ distribution in PR tips and through an auxin pathway via the repression of auxin biosynthesis and transport.

1. Introduction

Serotonin (5-hydroxytryptamine) is a well-known neurotransmitter, hormone, and mitogenic factor that mediates a series of physiological activities in humans and animals (Kang et al., 2009; Ramakrishna et al., 2012). Since the first report of the phyto-serotonin in cowhage (*Mucuna pruriens*) fruit (Bowden et al., 1954), serotonin has been found in at least 40 plant species (Kang et al., 2009; Pelagio-Flores et al., 2011, 2016). Similar to melatonin, serotonin may play an important role in modulating plant growth, development, morphogenesis, and defense responses (Murch et al., 2009; Kang et al., 2007; Zhang et al., 2013; Pelagio-Flores et al., 2016; Erland et al., 2017). Significant increases in *de novo* shoot formation have been shown to be correlated with increased endogenous serotonin levels (Murch et al., 2009). Both pathogenic infection and senescence induce serotonin accumulation in plants; however, the physiological roles of serotonin in delaying senescence

and improving pathogen tolerance are different (Kang et al., 2009). Serotonin was found to accumulate in senescence-induced tissues of vascular parenchyma cells, and the senescence-retarding activity of serotonin is associated with its high antioxidant activity. Nutrient recycling from senescing leaves to sink tissues was maintained during senescence, while pathogenic infection-induced serotonin accumulation was found to function in the strengthening of the cell wall (Kang et al., 2009).

A sequence of two enzymatic reactions regulates serotonin biosynthesis in plants. The first reaction is the catalytic turnover of tryptophan to tryptamine by tryptophan decarboxylase (TDC), and the second reaction catalytically converts tryptamine into serotonin by tryptamine 5-hydroxylase (T5H). The *T5H* gene is constitutively expressed, whereas *TDC* gene expression is significantly induced by senescence signals; as a result, *TDC* is the bottleneck for serotonin biosynthesis in rice (Kang et al., 2007). The serotonin level is very low in

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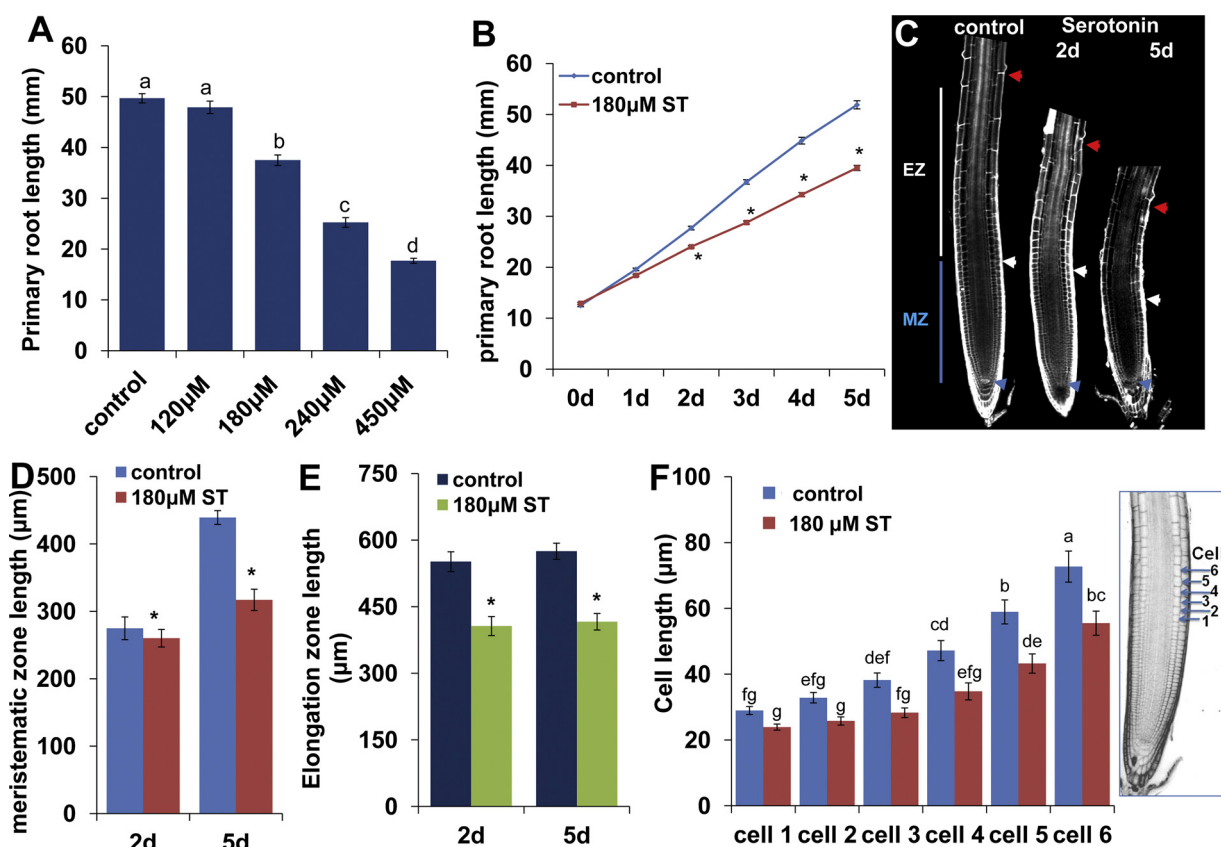


Fig. 1. Serotonin inhibits PR growth by reducing the length of the meristem and elongation zones. (A) Five-day-old seedlings were transferred to 1/4 MS medium containing 0–450 μM serotonin for 5 d. The PR elongation was determined. (B–F) Five-day-old seedlings were transferred to 1/4 MS medium containing 180 μM serotonin for 1–5 d. (B) The length of PRs, (C, D) the length of the meristem zone, (E) the length of the elongation zone, and (F) the cell length of six consecutive cells in the transition zone were determined. ST, serotonin. Error bars represent the SE. Asterisks indicate a significant difference from the control (Student's *t* test, $P < 0.05$). Different letters indicate that values were significantly different at $P < 0.05$ according to Tukey's test.

young leaves and seeds; however, nutrient deficiency, leaf detachment, and senescence markedly induce the accumulation of serotonin in plants. Overexpression of two rice *TDC* genes, *OsTDC-1* and *OsTDC-3*, resulted in increased serotonin levels (peaking at approximately $3,500 \mu\text{g g}^{-1}$ FW) and repressed growth and fertility in transgenic rice and *Arabidopsis* plants (Kanjanaphachao et al. 2012). However, the physiology and molecular mechanisms underlying serotonin-mediated growth inhibition in plants remain largely unclear. Although *Arabidopsis* has no known functional *TDC* and *T5H* ortholog, many studies have indicated that *Arabidopsis* exhibits T5H activity that produces serotonin to regulate plant growth (Kanjanaphachao et al. 2012).

Primary root (PR) growth is tightly regulated by the differential accumulation of reactive oxygen species (ROS) in root tips (Tsukagoshi et al., 2010; Silva-Navas et al., 2016). The *UPBEAT1* (*UPB1*) transcription factor regulates the distribution of H_2O_2 and O_2^- in elongation and meristem zones of roots by repressing the gene expression of peroxidases in roots independent of the auxin pathway (Tsukagoshi et al., 2010). Recently, Pelagio-Flores et al. (2016) found that serotonin regulates ROS distribution in roots by jasmonic acid/ethylene signaling pathways. However, how serotonin induces ROS accumulation and the elevated ROS levels regulate PR growth in serotonin-treated seedlings requires further investigation.

In addition to the ROS pathway, auxin plays a vital role in modulating root system development (Mähönen et al., 2014; Silva-Navas et al., 2016). Maintaining a steep auxin gradient in the meristem zone and maximal auxin accumulation in the quiescent center (QC) is critical for normal meristem cell activity and root growth (Liu et al., 2016). *PLETHORA* (*PLT*) controls meristem cell activity and root development in a dose-dependent manner (Sabatini et al., 1999; Liu et al., 2016;

Silva-Navas et al., 2016). Auxin modulates root stem cell niche activity by affecting PLTs accumulation in root tips (Aida et al., 2004; Mähönen et al., 2014; Silva-Navas et al., 2016).

Plasma membrane-localized auxin carriers, including the auxin influx carriers AUXIN1/LIKE AUX1 (AUX1/LAX) and auxin efflux carriers PIN-FORMEDs (PINs), also play important roles in establishing and maintaining auxin gradients in root tips (De Smet et al., 2007). Different auxin carriers can regulate a common physiological process (Liu et al., 2016). For example, PIN4 is required for root exudate methyl 3-(4-hydroxyphenyl) propionate (MHPP)-mediated root system architecture (RSA) remodeling (Liu et al., 2016). AUX1 and PIN2 are involved in alkaline stress adaptation (Li et al., 2015). Serotonin, derived from the common substrate L-tryptophan with auxin, may act as a competitive inhibitor of auxin-regulated gene expression (Pelagio-Flores et al., 2011). However, the exact role for serotonin-mediated root development by the auxin pathway remains to be elucidated.

In this study, we investigated the involvement of ROS and auxin in serotonin-regulated root system development in *Arabidopsis*. Our results indicate that serotonin disrupts ROS distribution in root tips; serotonin also affects auxin distribution in root tips by decreasing auxin biosynthesis and repressing AUX1 and PIN2 abundances. Potential mechanisms involved in this process are discussed.

2. Materials and methods

2.1. Plant materials and growth conditions

Seeds of the wild-type *col-0* and transgenic and mutant *Arabidopsis* lines were sterilized with 50 % bleach for 5 min, washed five times with

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