**BIOCHEMISTRY & PHYSIOLOGY - SHORT COMMUNICATION** 



# Auxin transport inhibition triggers pedicel expansion and alters abscission zone dynamics in tomato fruit

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#### Abstract

Auxin transport plays a key role in plant growth and organ abscission by regulating cell division and tissue differentiation. In this study, we investigated the effects of 2,3,5-triiodobenzoic acid (TIBA), an auxin transport inhibitor, on tomato pedicel development, with a focus on the abscission zone. Using the model tomato 'Micro-Tom', TIBA treatment led to marked pedicel thickening due to increased periclinal cell division in cortical and procambial tissues. Histological analysis also revealed localized programmed cell death in the distal abscission zone, indicating a disruption of auxin gradients and possible activation of ethylene signaling pathways. These results show that auxin transport inhibition promotes both hyperplastic growth and cell separation processes, underscoring the complex hormonal crosstalk controlling abscission. TIBA's effects on pedicel anatomy suggest potential applications in delaying fruit drop and extending harvest windows, although further research is needed to evaluate impacts on tomato fruit quality and plant performance, in commercial varieties.

Keywords Auxin transport · TIBA · Abscission zone · Programmed cell death · Tomato pedicel · Ethylene

# 1 Introduction

Abscission in tomato is a critical process for fruit detachment and harvest timing, tightly regulated by the interplay between auxin and ethylene. While auxin typically inhibits abscission by maintaining cell wall integrity and suppressing programmed cell death (PCD) in the abscission zone (AZ), exogenous auxin application can paradoxically trigger abscission under certain conditions (Saniewsky et al. 2017; Botton and Ruperti 2019). This duality highlights the complexity of hormonal interactions during abscission (Chersicola et al. 2017). The auxin transport inhibitor

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TIBA (2,3,5-triiodobenzoic acid) disrupts polar auxin transport (PAT), causing localized auxin accumulation, which can alter tissue-specific responses and accelerate abscission through meristematic reactivation and PCD (Wulf et al. 2019; Zou et al. 2019). However, the specific effects of TIBA on pedicel morphology and AZ development in tomato remain poorly understood.

TIBA's disruption of auxin flow has been shown to induce cell proliferation in meristematic regions, leading to tissue thickening, while interfering with the normal PCD process, especially within the AZ (Kühn et al. 2016; Kućko et al. 2020). Recent studies, including those by Tanbarger and Tadeo (2025), have demonstrated that TIBA triggers distinct cellular reprogramming in tomato, including enhanced periclinal division and localized necrosis. These findings suggest that TIBA's effects are both spatially and developmentally nuanced, particularly in regions like the AZ, where auxin and ethylene signaling converge to regulate abscission (Breitel et al. 2016).

The miniature tomato 'Micro-Tom' serves as an ideal model for studying these effects due to its compact size, rapid growth and development cycle, and fully sequenced genome, which facilitate high-throughput studies and precise histological analyses (Marti et al. 2006). Importantly,

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'Micro-Tom' tomato retains physiological responses found in larger, commercial tomato cultivars, including hormone sensitivity and the formation of abscission zones (Campos et al. 2010). Its compact architecture allows for detailed cellular-level analysis of the pedicel, making it particularly suitable for investigating the impact of TIBA on pedicel morphology and abscission. By correlating auxin transport inhibition with meristematic reactivation and PCD, we seek to elucidate how these processes interact to influence pedicel development And fruit retention. The objective of this study was to investigate the effects of TIBA on tomato pedicel growth, focusing on morphological changes, abscission zone architecture, and tissue thickening.

## 2 Material and methods

## 2.1 Plant material, growth conditions, and treatments

This study utilized 'Micro-Tom' tomato due to its compact size and rapid growth cycle, while maintaining the key physiological and morphological features from commercial tomato varieties. The experiments took place in a controlled greenhouse environment, with average midday solar radiation of 1000  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>, nighttime temperature at 18.3 °C, daytime temperature at 28.2 °C, and relative humidity of 77% at night and 52% during the day.

Seeds were sown in trays filled with a 1:1 mixture of peat-based substrate (Plantmax HT, Eucatex, Brazil) and expanded vermiculite. After 30 days, seedlings were transplanted into 430 mL pots containing the same substrate, supplemented with 1 g L<sup>-1</sup> of NPK fertilizer (10:10:10) and 4 g L<sup>-1</sup> of dolomitic limestone. At the onset of flowering, plants were manually pollinated.

Seven days post-pollination, all the pollinated flowers, which were developing into fruit, were sprayed with 8 ml of 2,3,5-triiodobenzoic acid (TIBA) solution at 20 mg L<sup>-1</sup> (40  $\mu$ M Sigma Aldrich 98%; Sigma-Aldrich, Saint Louis, MO, USA) added to 0.1% of Tween 20 (Sigma-Aldrich, Saint Louis, MO, USA) per plant, while control plants received an equivalent volume of water (added 0.1% tween). The experiment followed a complete block design with four biological replications per treatment.

#### 2.2 Histological analysis and quantification

Pedicel samples were collected from three fruits per plant in both TIBA-treated and control groups, seven days post-treatment. The samples were immediately fixed under vacuum in a modified Karnovsky solution (2% glutaraldehyde, 2% paraformaldehyde, 0.001 M of CaCl<sub>2</sub> in 0.05 M cacodylate buffer, pH 7.2), then refrigerated for 72 h.

Following fixation, samples were dehydrated through an ascending ethanol series (10% to 100% v/v) and gradually infiltrated with increasing ratios of ethanol and embedding medium (3:1, 1:1, 1:3). Samples were then embedded in HistoResin (Leica, Heidelberg, Germany), with polymerization at room temperature for 48 h, as recommended by the manufacturer. Cross-sections of 5  $\mu$ m thickness were obtained using a manual rotary microtome (Leica RM2235, Heidelberg, Germany) and stained with Periodic Acid-Schiff (PAS) reagent (Feder and O'Brien 1968).

The stained slides were mounted with entellan (Merck, Rahway, USA), and sections were examined using an upright microscope equipped with a Premiere MA88-300 camera (Zeiss Jenamed, Jena, Germany). High-resolution digital images were captured for subsequent analysis.

Programmed cell death was assessed by evaluating cell collapse, cytoplasmic clearance, and nuclear fragmentation in the AZ region. Cell collapse was defined as the loss of turgor and structural integrity, cytoplasmic clearance as the presence of empty or vacuolated cytoplasm, and nuclear fragmentation as condensed or discontinuous nuclear staining.

Quantitative measurements were performed on the pedicel and histological sections expansion using ImageJ software (version 1.46r; National Institutes of Health, Bethesda, MD, USA) (Schneider et al. 2012).

#### 2.3 Statistical analysis

All quantitative data were analyzed using RStudio (version 2025.05.0+496; RStudio Team 2025), a graphical interface for the R statistical computing environment (R Core Team 2025). Statistical significance between control and TIBA-treated groups was assessed using Student's T-test. Normality of the data was evaluated using the Shapiro–Wilk test. Results are reported as mean  $\pm$  standard deviation (SD), with exact *n*-values provided in the figure legends. A *p*-value < 0.05 was considered statistically significant.

## **3** Results and discussion

Application of TIBA (2,3,5-triiodobenzoic acid), a known auxin transport inhibitor, led to a marked increase in radial expansion of tomato pedicels by 7 days post-anthesis (DPA). In TIBA-treated pedicels, histological analysis revealed a significant increase in the number of cortical and medullary cell layers, which corresponded to enhanced cell division. Compared to controls (Fig. 1b–c), treated pedicels exhibited significantly greater thickness, especially in the cortical and procambial regions (Fig. 1d–f).

Histological sections revealed that treated pedicels exhibited significantly greater thickness than controls,



Fig. 1 Tomato fruit pedicel: control and after 7 days of TIBA treatment. **a** Detailed view of pedicel, showing proximal, distal, and abscission zone (AZ) regions. **b**-**c** Control plant with normal pedicel. **d**-**f** TIBA-treated pedicels (black arrows), with **d** expanded pedicel detail. **g** Pedicel diameter comparison between control and TIBA-treated plants. **c**, **f** Histological sections under light microscopy. Figure 1a: Created in BioRender. Riboldi, L. (2024) https://BioRender.com/g59n016

particularly in the cortical and procambial regions (Fig. 1c, f). This expansion was associated with enhanced periclinal cell divisions, as indicated by an approximate 25% increase in the number of cortical cell layers (p < 0.01), alongside a significant increase in total cross-sectional area (Fig. 1g). These data support the hypothesis that inhibition of polar auxin transport leads to local auxin accumulation, thereby promoting cell proliferation and tissue expansion.

Our findings are consistent with recent studies that show auxin accumulation, either through exogenous application or polar transport disruption, can stimulate secondary growth and tissue thickening via activation of perivascular cell division (Wulf et al. 2019; Dong et al. 2021). In the present study, TIBA-induced ectopic proliferation was particularly evident near the vascular bundles, suggesting altered auxin gradients may override positional cues maintaining radial patterning (Fig. 1f–g). The prominence of periclinal divisions in cortical and procambial tissues aligns with previous observations that these regions are highly responsive to auxin-regulated transcriptional networks involved in cell cycle activation (Breitel et al. 2016; Brunoud et al. 2012; Yu et al. 2023).

Interestingly, this hyperplastic response occurred concurrently with localized programmed cell death (PCD) within the distal pith region, particularly at the fruit-pedicel junction (Fig. 1f). Although PCD in the AZ is well documented in the context of abscission, its induction via auxin transport inhibition points to a finely tuned auxin-ethylene crosstalk that modulates developmental cell death (Chersicola et al. 2017; Meir et al. 2019).

This dual effect of TIBA, inducing both tissue expansion and PCD, highlights the complex morphogenetic role of auxin transport in pedicel development (Kacprzyk et al. 2024). Auxin gradients are known to maintain AZ cell identity and quiescence by suppressing ethylene sensitivity (Li et al. 2022; Shi et al. 2022). Disruption of basipetal auxin flow destabilizes this equilibrium, predisposing AZ cells to ethylene-induced senescence and eventual abscission. Although we did not directly measure ethylene signaling, our results are consistent with models where auxin transport inhibition leads to increased ethylene response and activation of PCD pathways (Botton and Ruperti 2019; Xu et al. 2019).

Further supporting this interpretation, we observed that in TIBA-treated pedicels, the most pronounced cellular proliferation occurred in the cortical and medullary parenchyma, regions where auxin transport is critical for maintaining differentiation states (Fig. 2a–c). These proliferative changes mimic secondary meristematic activity, suggesting partial reprogramming of pedicel tissues (Mazzoni-Putman et al. 2021; Vanneste et al. 2025). Similar reactivation of division competence in differentiated cells has been reported during adventitious root formation and stress-induced organogenesis, often in response to auxin redistribution (Zhang et al. 2022). TIBA-treated samples exhibited hallmark features of PCD-cytoplasmic shrinkage, nuclear condensation, and cell wall collapse-restricted to a narrow band corresponding to the anatomically AZ. These features were infrequent or absent in control pedicels, which maintained normal tissue integrity (Figs. 2d and h).

In contrast, control pedicels showed predominantly anticlinal divisions and retained a well-defined AZ structure with localized PCD on the distal side (Fig. 2e–g), reinforcing the notion that normal auxin flux is essential for tissue compartmentalization and abscission zone stability. The presence of abnormal cell proliferation alongside cell death in TIBA-treated samples suggests that auxin gradients orchestrate not only growth but also spatial segregation of developmental fates (Kacprzyk et al. 2024). Recent work has shown that localized auxin minima can act as developmental triggers for boundary formation and cell differentiation (Weijers and Wagner 2016), further supporting the idea that auxin transport inhibition can induce both proliferative and degenerative processes depending on local tissue conditions.

The observed phenotypes further highlight the suitability of the 'Micro-Tom' tomato as a model for high-resolution histological analyses. Its compact architecture, rapid lifecycle, and documented hormonal responsiveness (Campos et al. 2010) made it an ideal system for dissecting auxinmediated developmental processes. However, caution should be exercised in extrapolating these results to commercial cultivars, which may exhibit different hormone sensitivity and abscission dynamics.

Our data contributes to growing evidence that auxin transport inhibitors like TIBA affect not only hormone distribution but also trigger complex downstream effects, including mechanical stress, altered vasculature, and cell wall remodeling. Recent transcriptomic studies have shown that inhibition of auxin transport leads to broad transcriptional reprogramming, including upregulation of cell cycle, stress response, and senescence-related genes (Wang et al. 2023). These molecular changes likely underpin the cellular phenotypes observed in our study.

Overall, these results support a model in which TIBAinduced disruption of auxin transport gradients triggers dual morphogenetic programs in tomato pedicels: ectopic cell division in perivascular tissues and PCD in the AZ. This duality may reflect context-specific auxin-ethylene interactions that regulate fruit retention and organ abscission. Although our study did not quantify ethylene levels, the patterns observed suggest enhanced ethylene sensitivity in distal pedicel regions. Future work should include hormone quantification and transcriptome analyses to clarify the molecular basis of these effects and assess whether similar responses occur in other cultivars.



**Fig. 2** Pedicel thickening induced by TIBA treatment after 7 days. **a–h** Longitudinal light microscopy sections of tomato pedicels at the abscission zone (AZ), distal side (DS), and proximal side (PS). **a–d** TIBA-treated pedicels: **a** General view of the AZ, cortical, and medullary parenchyma; **b** Procambial region with periclinal divisions (arrows); **c** AZ with meristematic centers and cell cords (arrows); **d** Medullary region showing periclinal divisions (arrows) and in detail programmed cell death (PCD, asterisks). **e–h** Control pedicels: **e** General view of the AZ, DS, and PS; **f** Procambial region with fewer periclinal divisions (white arrows); **g** Lack of meristematic centers in the AZ; **h** Distal medullary parenchyma without meristematic activity or PCD. Abbreviations: AZ=abscission zone; co=cortex; DS=distal side; pc=procambium; pi=pith; PS=proximal side; vs=vascular system

In order to better contextualize our findings, we propose a conceptual model that illustrates the dual effects of auxin transport inhibition on pedicel development and abscission regulation (Fig. 3). Disruption of polar auxin flow by TIBA triggers a cascade of hormonal responses, notably involving cytokinin and ethylene signaling (Breitel et al. 2016). Elevated cytokinin activity, either directly or through reduced auxin antagonism, promotes meristematic reactivation and periclinal cell divisions in cortical and medullary regions, ultimately leading to pedicel expansion (Su et al. 2011; Pacifici et al. 2015). Simultaneously, local auxin accumulation and disrupted gradient maintenance trigger cellular stress responses, which may further enhance tissue remodeling and alter cell fate programs (Vanneste et al. 2025).

In parallel, auxin depletion in the distal pedicel region increases tissue sensitivity to ethylene, a known inducer of programmed cell death (PCD) and abscission zone activation (Botton and Ruperti 2019; Shi et al. 2022). This hormonal shift facilitates the initiation of cell wall degradation and nuclear condensation characteristic of PCD in the AZ. The model posits that these processes are interconnected: while cytokinin-mediated proliferation contributes to pedicel thickening and possibly delays abscission mechanically, enhanced ethylene signaling promotes PCD and tissue separation. This dual regulatory effect underscores how auxin transport inhibition can tip the developmental balance between fruit retention and organ abscission, depending on tissue context and hormonal crosstalk.

The agricultural implications of our findings lie in the potential to modulate fruit abscission and retention by targeting auxin transport pathways. However, the trade-offs between tissue overgrowth, stress responses, and potential impacts on vascular integrity must be carefully evaluated. While TIBA application may delay abscission, excessive cell proliferation could impair pedicel function or reduce fruit quality. Therefore, targeted manipulation of auxin transport, possibly through tissue-specific or inducible systems, may offer more precise strategies for crop management.



Fig. 3 Diagram illustrating the effects of auxin transport inhibition induced by 2,3,5-triiodobenzoic acid (TIBA) in pollinated tomato plants. Created in BioRender. Riboldi, L. (2024) https://BioRender.com/f84j784

Building on these findings, this study demonstrates that the inhibition of polar auxin transport by TIBA promotes significant radial expansion in tomato pedicels through increased periclinal cell division in the cortical and procambial regions. Simultaneously, TIBA induces localized programmed cell death in the distal abscission zone, suggesting that auxin depletion disrupts tissue identity and activates separation processes. These results support a model in which auxin gradients coordinate both proliferative and degenerative pathways in pedicel development.

The dual effects observed, hyperplasia and cell death, highlight the central role of auxin transport in maintaining pedicel structure and delaying abscission. Our findings provide anatomical evidence for auxin-ethylene interaction during abscission regulation and establish a basis for future studies targeting hormonal modulation to control fruit retention and harvest timing.

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Author contributions All authors contributed to the study's conception and design. Material preparation, data collection, and analysis were conducted by Lucas Baiochi Riboldi. Mônica Lanzoni Rossi and Erika Mendes Graner prepared the samples and performed microscopic analyses. Marcílio de Almeida, Paulo Roberto de Camargo e Castro, and Sérgio Tonetto de Freitas oversaw the project design. The initial draft of the manuscript was written by Lucas Baiochi Riboldi, with all authors providing feedback on earlier versions. All authors reviewed and approved the final manuscript.

#### Declarations

**Conflict of interest** The authors declare that they have no conflicts of interest related to this work submitted for publication.

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