GSC Advanced Research and Reviews

eISSN: 2582-4597 CODEN (USA): GARRC2

Cross Ref DOI: 10.30574/gscarr

Journal homepage: https://gsconlinepress.com/journals/gscarr/

(RESEARCH ARTICLE)

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Invertase of the cell wall controls the growth of both the apical and vegetative organs of the tomato

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GSC Advanced Research and Reviews, 2024, 21(02), 578–585

Publication history: Received on 18 October 2024; revised on 26 November 2024; accepted on 28 November 2024

Article DOI: https://doi.org/10.30574/gscarr.2024.21.2.0470

Abstract

Researchers have intensively studied how external factors like temperature, humidity, soil structure, and fertilizer affect tomato plant growth. However, little is known about how internal factors, particularly cell wall invertase, affect plant growth. This study aims to determine how the activity of the cell wall invertase enzyme regulates the apical and vegetative growth of plants. The study utilized four tomato plants, consisting of two transgenic and two wild-type plants. The transgenic plants in one set exhibit lower levels of the cell wall invertase, known as TLINA. Another set of transgenic plants, known as TINHI, exhibited higher levels of the cell wall invertase. We named both wild types of plants, WLINA and WINHI, respectively, and used them as the control plant. The study's results revealed that the transgenic plants (TLINA) ceased their apical shoot growth, leading to the growth of an axial shoot to take the place of the apical shoot. t. Also, the TLINA plants grew lower than wild-type plants. Interestingly, the vegetative organs of TINHI plants grew higher than both wild types and TLINA plants. This evidence suggested that cell wall invertase regulates the apical and vegetative organs of plants.

Keywords: Invertase; Transgenic; Tomato; Apical; Vegetative

1. Introduction

The tomato is a crop plant that is growing worldwide due to its benefits for human life, such as being a vitamin source [1] and being a fresh and healthy drink [2]. Despite natural growth in all types of soils and climates, cultivated tomato plants' growth or development is dependent on various factors, both external and internal. The growth of plants is influenced by various external factors such as temperature [3]–[5], humidity [6], soil [4], [5], fertilizer [7], [8]. Internal factors, such as enzymes [9], [10], hormones [11]–[13], sugars [14]–[16], genes [1], [4], [5]'

Several researchers have studied tomato plants to understand how external factors affect plant growth. For instance, several studies reported that differences in day and night temperature affected the growth of young tomato plants [17]. Researchers have studied factors related to climate, such as humidity [6], [18] and high pressure [11], [19], [20]. Types and structures of soil used in planting influence growth and productivity [21]. Sibomana et al. [22] also studied the impact of drought or water on plant growth. Studies have also reported on the use of bacteria and mycorrhiza to enhance tomato plant growth. Pseudomonas putida and Trichoderma atroviride stimulated growth and improved fruit yield [23]. On the other hand, mycorrhiza infected tomato roots improved plant growth [24]. Researchers used exogenous hormones [25] and sugars [26] to enhance both vegetative and reproductive growth. Also, the use of red light at night affected flowering [27], [28].

In addition to external factors, internal factors also influence crop growth and yield. For instance, studies of endogenous ABA modulated the flowering of tomato plants [29]. Recent studies have reported on the impact of invertase on the cell metabolism, growth, and development of various plants. In tomato, a silencing effect of CWIN (cell wall invertase)

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expression, *Lin5* (*Lycopersicum* invertase), diminished pollen viability, pollen tube elongation, and seed number [30]. Le Roy [31] found a strong correlation between the activity of invertase within cell walls and fruit carbohydrate levels, similar to the Lin5 gene. Interestingly, silencing the CWIN inhibitory protein may increase the cell wall invertase activity. Thus, tomato plants experience an increase in seed weight and fruit hexose content [32].

The cell wall invertase activity is critical in degrading sucrose, a disaccharide, into two monosaccharides, glucose and fructose. There are three types of enzymes based on where they work best, how well they dissolve, and the pH at which they work best. These are CWIN (cell wall invertase), CIN (cytoplasmic invertase), and VIN (vacuolar invertase). CWIN and VIN are invertase enzymes that are located successively in the cell wall and vacuole. Those have similar biochemical properties in that they both hydrolyze effectively sucrose at pH 4.5–5.5 and hydrolyzed disaccharides from the fructose residues, called β-fructo-furanosides [33]. In contrast, CIN works optimally in neutral pH; 7.0–7.8. The invertase hydrolyzes sucrose in the cytosol compartment, and it is not β-fructo-furanoside invertase [34]. VIN and CIN are soluble invertases, which means they have an acidic isoelectric point (pI). CWIN, on the other hand, is an insoluble invertase, which means it has a basic isoelectric point (pI) [35].

Endogenous inhibitors may contribute to the differences in invertase activities [36]. Invertase inhibitors consist of two forms that are CWIN inhibitors and vacuolar inhibitors [37]. Researchers have identified cDNA-coding CWIN inhibitors in tobacco [38], Arabidopsis [39], and maize [39]. Nicotiana tabacum's NtCIF amino acid sequence is a CWIN inhibitor. It is similar to some amino acid sequences found in the genomes of other plant species, like Arabidopsis's CWIN genes [39]–[41]. Also, protein translated from the *Nt-INVINH1* gene plays a role in inhibiting CWIN activities in the tobacco plants [42], [43]. Meanwhile, Jin et al. [32] reported that INVINH1 inhibits CWIN activity in addition to regulating vegetative and reproductive organ growths.

Cell wall invertase plays a crucial role in the metabolism, growth, and supply of sugars, and it has been extensively studied. For example, the enzyme regulates a reproductive organ like a flower, fruit, or seed [44]. The enzyme's mechanism of action is to supply hexoses to anthers and ovary development. Hexose transporters mediate the retrieval of hexoses released from CWIN activity into recipient cells [38], [45].

The observations mentioned above demonstrate that cell wall invertase plays a significant role in hydrolyzing sucrose in pollen, seeds, and fruit. However, no study has yet reported on the role of cell wall invertase activity in the vegetative organ growth of plants, particularly tomato plants. As a result, this study reveals evidence of the cell wall invertase activities having an effect on the vegetative organ growth of tomato plants.

2. Material and methods

This study used four tomato plant types, including two transgenic and two wild types. One kind of transgenic plant doesn't have the LIN5 gene, which is a cell wall invertase type (CWIN) [30]. This type of plant is called TINHI. TLINA was another type of transgenic plant that had the INVINH1 gene [32] turned off, which stops the cell wall invertase enzyme from working. For both will-type plants, those were WINHI and WLINA.

We planted seeds from the fourth type of plants in each pot, which contained a mixture of soil, sand, and goat manure in a ratio of 2:1:1. We selected and transferred the seedlings to another pot after ten days. We placed and grew the plants in the Universitas Tadulako greenhouse, maintaining temperatures between 25 and 35 °C. We usually watered the plants twice in the morning and afternoon. We performed fertilization and sprayed insecticides or fungicides on a monthly basis. We observed the phenotypes of both sets of plants at 25 and 35 °C. The observed phenotypic plants included seed germination, stem growth, and leaf growth. The obtained data were then analyzed using ANOVA by the JMP Statistical Program.

3. Results

Germinating seeds required two weeks. The seed originated from wild and transgenic (TINHI) plants that germinated normally. The plants have two green cotyledons. A week after planting, the plants have three leaves. Each leaf edge accounted for more than half of the leaf width. Leaf blades were thinner. The stems contain normal shoots. Numerous hairs covered the surface of the stem. The proximal part of the stem surface was brown, and the distal part was green. The stem seems round. Figure 1 partially depicts the phenotypic plants decoded above.

Similar observation: transgenic plants with the silenced *LIN5* gene (TLINA) have two green cotyledon leaves. Interestingly, the shoots of the TLINA plants grew abnormally and did not possess primordial leaves, resulting in leaf

absence (Figure 1). Numerous hairs covered the surface of the stem (Figure 1). The surface of the stems was almost all brown, which was different from the wild type and TINHI plants (Figure 1).

The cell wall invertase activity continues to influence the growth of the vegetative organ in plants aged beyond two weeks after planting for both transgenic (TINHI) and wild types (WINHI and WLINA), resulting in normal growth. On the other hand, the silenced invertase activity led to an abnormal growth, as shown in transgenic plants (TLINA) that still had no leaves (data not shown). Interestingly, measurements of the plant leaves at the second week after planting revealed, as depicted in Figure 2, that temperature influenced the invertase enzyme's activity. The results showed that the leaflets of transgenic plants (TINHI) grew wider at room temperature (25 oC) than they did at 35 oC. The heating temperature reduces the growth of leaves.

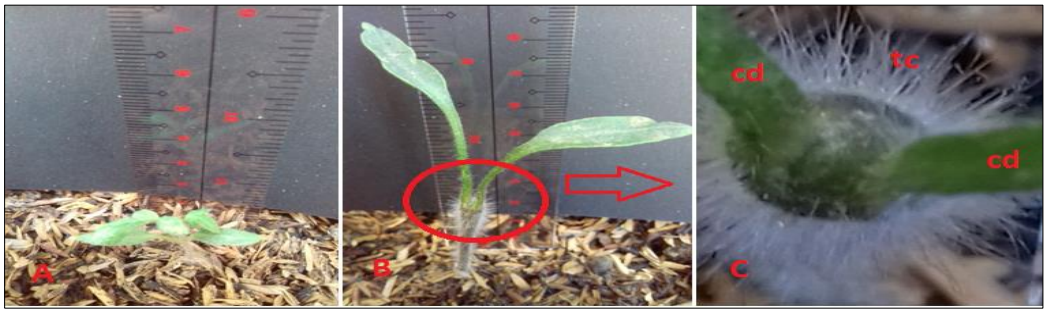

Figure 1 Comparison of transgenic TINHI and TLINA plant growth. Transgenic TINHI plants grew normally (A), while transgenic TLINA shoot growth was abnormal (B). Abnormal shoot growth was characterized by the absence of primordial leaf (C). Cd.cotiledone. Tc.trichome

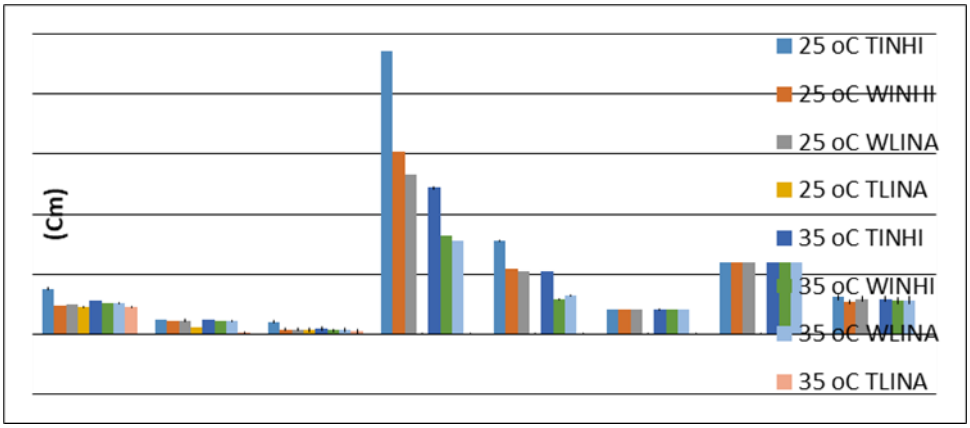

Figure 2 Measurement of the vegetative organ of transgenic (TINHI), transgenic (TLINA), wild type (WINHI), and wild type (WLINA) plants grown at 25 °C and 35 °C. The leaf and leaflet growth of transgenic plants TINHI was the fastest compared to other plants, both at normal and high temperatures. Heat temperature (35 °C) reduced the growth of leaves and leaflets compared to normal conditions (25 °C)

The cell wall invertase is silenced, which stimulates axial shoot growth. Plants aged 5 weeks after planting demonstrate this phenomenon, with the transgenic plants (WLINA) growing to produce leaves from axial buds (Figure 3). Consequently, the transgenic plants (TLINA) developed a sympodial stem, where the terminal shoot's initial growth preceded the axial shoot's growth. The stems of the transgenic plants TINHI, WINHI, and WLINA, which form from the growth of terminal shoots since the germinating embryo and are known as monopodial stems, differ from this outcome. Due to these conditional growths, the TLINA plants experience less growth than the WLINA, WINHI, and TINHI plants (Figures 4 and 5).

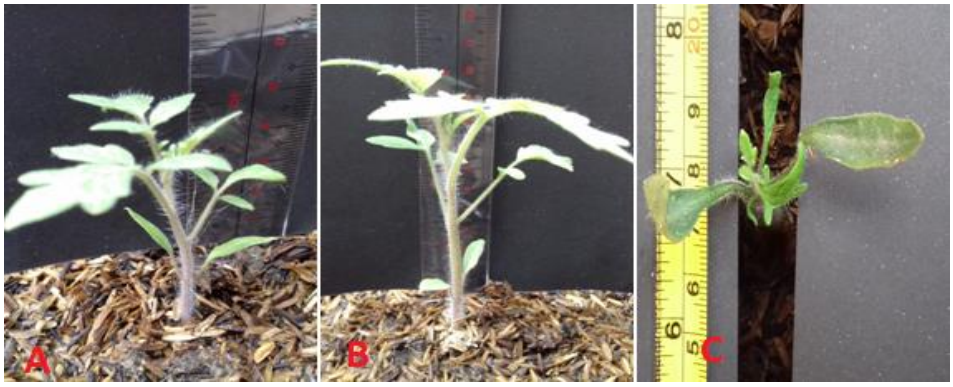

Figure 3 Transgenic TINHI (A) and wild type WINHI (B) plants show normal growth, but transgenic TLINA (C) grows abnormally to form leaves derived from an axial bud

Figure 4 Growth of transgenic plant TINHI (A), wild-type plant WLINA (B), and transgenic plant TLINA (C). TLINA transgenic plants grew shorter than other types of plants

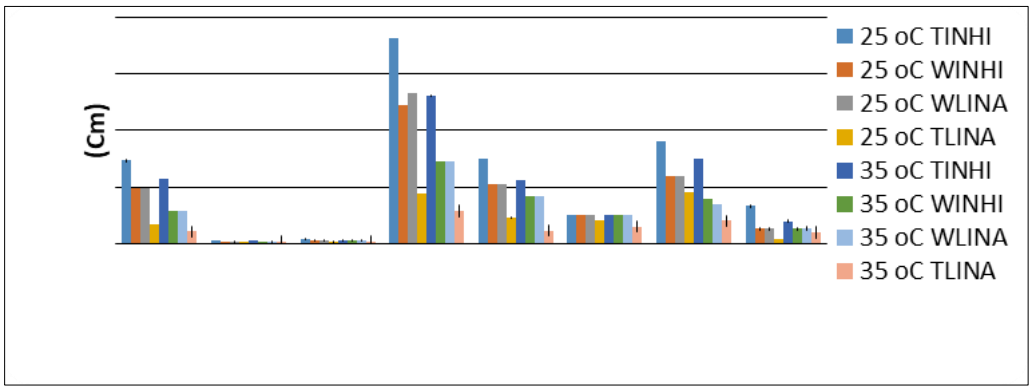

Figure 5 The vegetative organ of transgenic (TINHI), transgenic (TLINA), wild (WINHI), and wild (WLINA) plants grown at 25 °C and 35 °C was measured. We measured the growth of stems, the circumference of leaves, the number of leaflets, and the length of the petiole. At both normal and high temperatures, the transgenic plants (TINHI) grew faster than other plants. Heat temperature (35 °C) reduced the growth of the stem, leaf, and leaflet compared to normal conditions (25 °C)

4. Discussion

The results of the study revealed that the transgenic (TINHI) and wild-type (WINHI and WLINA) plants grew normally. However, transgenic plants (TLINA) grew abnormally (Figure 1). TLINA is a transgenic plant had silenced-cell wall invertase resulting in reducing the enzyme activity [30]. This finding indicates that cell wall invertase causes the shoot's abnormal growth. As such, the cell wall invertase enzyme plays an important role in growing the shoot. Also, the invertase plays a part in determining the height and width of the stems and leaves (Figures 4 and 5). The vegetative organs of TINHI-transgenic plants were bigger than those of wild-type plants. However, the silencing of the invertase reduced the stem and leaf growth (Figures 4 and 5). Thus, cell wall invertase regulates vegetative organ growth. The results support previous studies revealing that the cell wall invertase regulates reproductive organs. Jin et al. [32] had reported that the up-regulated cell wall invertase increased the size, number, and weight of tomato fruits. On the other hand, Zanor et al. [30] observed that the down-regulated cell wall invertase reduced fruit size, altered flower and fruit morphology, and reduced pollen germination.

Interestingly, the vegetative organs of the plants grown at normal temperature (25 ^{o}C) were higher than those at heat temperature (35 ^{o}C) (Figure 5). This result suggests that the increased temperature reduces invertase activity. Some workers have previously documented the impact of elevated temperatures. Pressman et al. (2002) reported that heat stress (32 ^{o}C) reduced the number of pollen grains per flower and the viability of the tomato pollen. Moreover, Rivero et al. [16] also reported that high temperatures reduced biomass on tomatoes and watermelon. However, this research provides evidence that the increased temperature reduces cell wall invertase, thereby reducing vegetative organ growth in tomato plants' stem and leaf.

Based on the results, we suggest that the heating temperature reduces invertase activity, which in turn reduces the hydrolysis of sucrose into two hexoses: glucose and fructose. As a result, the supply of sugar into cells for growing and developing vegetative organs was inhibited. The argument is based on studies reporting that sugar, including sucrose and glucose, as well as fructose, play a crucial role in sugar metabolism, growth and development, and gene expression regulation [34], [46]. Symplastic and apoplastic transports carry sucrose into the cytoplasm. Plasmodesmata facilitate the symplastic transport, while cell wall invertase hydrolyzes the sucrose transporter (SUT) into glucose and fructose in the apoplastic way [47], [48]. Furthermore, glucose and fructose are substances used for respiration, sucrose synthesis using sucrose synthase (SUS), and gene expression regulation [47], [48]. Therefore, an increase in temperature inhibits the growth of vegetative organs by reducing the activity of cell wall invertase, which hydrolyzes sucrose sugar into glucose and fructose sugar for organ metabolism and growth.

5. Conclusion

The inhibition of apical shoot growth in transgenic plants (TLINA) resulted in the development of an axial shoot that assumed the role of the apical shoot. Moreover, the TLINA plants had substandard levels of development in comparison to the wild-type plants. Significantly, the vegetative organs of TINHI plants showed superior development in comparison to both wild types and TLINA plants. These findings suggest that cell wall invertase regulates the growth of apical and vegetative organs in plants.

Compliance with ethical standards

Acknowledgments

We are grateful to Universitas Tadulako for its support of the research, as well as the Biology Education Laboratory for its provision of the requisite facilities.

Disclosure of conflict of interest

No conflict of interest to be disclosed.

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