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A plant physiological approach to reduce greenhouse energy consumption

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Abstract: The economic and environmental pressures associated with greenhouse heating for warm-season vegetable transplant production have prompted a search for biologically driven, cost-effective alternatives. This study investigates the potential of exogenously applied salicylic acid (SA), a phenolic phytohormone known for its stress-mitigating properties, to reduce energy consumption by enhancing seedling cold tolerance. Tomato seedlings (*Solanum lycopersicum* cv. Rutgers) were subjected to three concentrations of foliar-applied SA (0, 75, and 150 mg/L) and grown under two temperature regimes 16°C and 25°C, in growth chambers. Transplant morphological parameters, including shoot and root biomass, stem thickness, leaf development, and root system architecture, were analyzed over a 49-day growth cycle. At 16°C, application of 75 mg/L SA significantly enhanced seedling vigor, with shoot fresh weight, stem diameter, and leaf area comparable to those grown at standard commercial conditions of 25°C without SA. SA-treated seedlings exhibited enhanced root biomass and surface area, indicating improved cold tolerance. Importantly, energy modeling indicated that reducing the heating setpoint from 25°C to 16°C could lower heating energy requirements by approximately 45%, a savings enabled by the physiological benefits of SA. These findings underscore the dual role of SA as both a growth regulator and an abiotic stress mitigator, suggesting that targeted SA application could transform transplant production by reducing reliance on costly supplemental heating. This represents a novel integration of plant physiological intervention into sustainable energy management practices in horticulture.

1. Introduction

The growing demand for high-quality, affordable fresh produce has emphasized the need for more efficient production management strategies. One of the most critical sectors supporting this demand is the greenhouse transplant production industry, which supplies seedlings for both protected and open-field cultivation systems (Javanmardi and

Moradiani, 2017). Temperature is a primary factor that affects plant development rate (Hatfield and Prueger, 2015). Plants are considered cold-sensitive if they die or suffer severe damage at temperatures between 0 and 15°C, while cold-tolerant plants are still able to grow near the freezing point (Janda *et al.*, 2007).

For warm-season vegetable crops, primarily fruit-bearing species, field transplanting typically occurs after the last spring frost. Consequently, transplant production often begins when ambient temperatures remain well below the optimal range for these crops. During colder seasons, especially on winter nights, maintaining optimal internal greenhouse temperatures with supplemental heating is essential to ensure high-quality, healthy seedling growth and development.

To achieve a high-quality crop, greenhouses are heated when the average daily temperature falls below a specific threshold, depending on the crop species (Nishad and Krupa, 2022). This requirement significantly increases heating costs, especially in light of rising global energy prices. Greenhouse heating is one of the most energy-intensive aspects of protected cultivation, especially in colder climates. Energy expenses can account for 30-80% of total production costs, varying by location (Esen and Yuksel, 2013; Sun *et al.*, 2022). The annual natural gas consumption as the main energy source for greenhouse heating typically falls between 25 and 40 m^3 per square meter, with an average cost of approximately 7.8 US$ per square meter (de Zwart *et al.*, 2019; Stanghellini *et al.*, 2024). These high energy demands have forced the industry to adopt innovative technologies such as passive solar heating (Xu *et al.*, 2022), solar thermal collectors (Prieto *et al.*, 2023), geothermal systems (Luo *et al.*, 2023), heat pumps (Asgari *et al.*, 2025), and phase change materials (Zhu *et al.*, 2023), all of which offer more eco-friendly and cost-effective alternatives for maintaining optimal temperatures in greenhouse transplant production.

Salicylic acid (SA), a phenolic phytohormone, has emerged as a multifaceted regulator in plant biology, mediating both biotic and abiotic stress responses while influencing key developmental processes (Thilakarathne *et al.*, 2025). Its role in cold stress tolerance and growth regulation has been extensively documented by Saleem *et al.* (2021), underscoring its critical function in plant resilience and performance across diverse environments (Safari and Majidi, 2025).

Cold stress severely impairs plant metabolic functions, leading to membrane damage, destabilization of photosystem II, and oxidative stress due to the accumulation of reactive oxygen species (ROS) (Feng *et al.*, 2025). SA mitigates the effects of cold stress through a complex regulatory network (Hayat *et al.*, 2013; Saleem *et al.*, 2021). In tomatoes, SA enhances cold tolerance by preserving membrane integrity under chilling conditions (Aghdam *et al.*, 2014).

Beyond stress mitigation, SA exerts a significant influence on plant morphogenesis, including regulating seed germination, vegetative growth, root architecture, flowering, and fruit development through its interplay with other hormones, such as auxin and abscisic acid (Rivas-San Vicente and Plasencia, 2011; Li *et al.*, 2022). In tomatoes, SA application, either as a foliar spray or seed priming, has been shown to enhance seedling vigor, root and shoot biomass, and nutrient uptake under both optimal and stressful conditions (Javanmardi and Akbari, 2016). These growth-promoting effects are particularly evident under suboptimal temperatures or water-limited conditions, suggesting that SA plays a dual role as both a developmental regulator and a stress mitigator.

Tomato (*Solanum lycopersicum* L.) is one of the world's most important vegetable crops, with approximately 5.3 million hectares cultivated and an average annual production of about 190 million metric tons for fresh and processed markets (FAOSTAT, 2026). High-quality tomato transplants are essential across all production systems, as uniform and vigorous seedlings improve establishment, enable more predictable harvest timing, and support higher, more consistent yields (Leskovar, 2020).

Energy conservation in controlled horticultural systems has gained global attention following the Kyoto Protocol, which established binding commitments to reduce greenhouse gas (GHG) emissions (Protocol, 1997). Greenhouses, in particular, are energy-intensive facilities, with heating alone accounting for over 50% of total energy consumption (Djevic and Dimitrijevic, 2009; Zhang *et al.*, 2022). As such, implementing energy-saving strategies has become essential not only to reduce operational costs but also to meet climate mitigation goals without compromising crop productivity. While many studies have explored structural improvements and operational optimization (Zhang *et al.*, 2022), to the best of our knowledge, none have used plant physiology-based approaches, such as hormonal signaling, to reduce energy input requirements during transplant production without affecting quality or economic performance.

Given the background on heating requirements, SA, its effects on plant growth and development, and its role in mitigating cold stress, we hypothesized that SA application during transplant production could reduce greenhouse heating requirements by increasing seedling tolerance to low temperatures. The main goal of this study was to evaluate SA as a low-cost, plant physiology-based strategy to reduce greenhouse energy use while maintaining transplant quality, thereby improving the economic and environmental sustainability of late-season greenhouse transplant production systems.

2. Materials and Methods

Plant material and experimental design

Tomato seeds (*Solanum lycopersicum* cv. Rutgers) (BURPEE®, PA, USA) were used for this experiment. Seeds were sown in 72-cell plug trays, each cell containing 75 mL of PRO-MIX® BX growing media. For the first few days after seed sowing and until seed emergence, the trays were kept in a growth chamber at 25 ± 2°C and 70 ± 5% relative humidity in the dark. Starting cotyledon expansion, the light was then applied using Philips®, 20-watt, 2ft fluorescent Plant and Aquarium Grow Light Bulbs. Light intensity was set to an average instantaneous photosynthetic photon flux (PPF) of approximately 400 µmol/m²/s at the plant surface inside the chamber (16/8 h light/dark periods), as reported by Javanmardi *et al.* (2013). The temperature was maintained at 25 ± 2°C until the first true leaves appeared (one week). On day 14, after seed sowing, all plants were foliar sprayed with SA solutions (0, 75, and 150 mg/L) in a manner that allowed the solution to drip from the leaves. The second SA application was performed on day 28 after sowing. The seedlings were then divided into two groups, each containing treated seedlings with SA solutions (0, 75, and 150 mg/L). The first group was maintained in a growth chamber at 16 ± 2°C, 70 ± 5% relative humidity, and 16/8 h light/dark conditions. The second group was maintained in another identical growth chamber, but at 25 ± 2°C, 70 ± 5% relative humidity, and 16/8 h light/dark conditions (considered as a greenhouse condition for commercial transplant production). These conditions were kept for 3 weeks until the end of the experiment. The third SA application was performed on day 42 after sowing.

Measurements

All transplants were harvested for measurements on day 49 after sowing. Shoot length (cm), leaf number, leaf area (cm^2) using Petiole2® leaf area meter app, stem thickness at 2 cm above the substrate surface (mm) using digital caliper, shoot fresh weight (g), root characteristics including root fresh weight (g), root length, root surface area, root average diameter, root volume, root tips no. (using EPSON PERFECTION V750 Pro, STD 4800 Scanner, Calibrated for image analysis with WinRHIZO™) were determined. Recommended chemical fertilization for tomato transplant production was applied during the experiment, as described by Javanmardi and Moradiani (2017).

To estimate the greenhouse heat requirement (Q) for a specific temperature setup, the standard formula (Eq.1) for greenhouse heating load was used (Wang and Zhang, 2021):

$$Q = U \times A \times \Delta T \times t \qquad (1)$$

where Q is the required heating energy in Watt-hours (Wh), U is the thermal transmittance of the greenhouse coverings (W/m²·K), A is the greenhouse exposed surface area to the outside (m²), ΔT is the difference between the desired indoor temperature and the outdoor air temperature ($T_{in} - T_{out}$) in °C, and t is the duration (hours).

Statistical analysis

The experiment was arranged in a completely randomized design (CRD), with six treatments (three SA concentrations at two temperatures). Each treatment consisted of 9 plants as replicates. The data were checked for normality and homoscedasticity before ANOVA. One-way analyses of variance for data analyses and the Least Significant Differences (LSD) test for mean comparison were performed using JMP® 13.0.0 (SAS Institute, Inc., Cary, NC) statistical software.

3. Results and Discussions

Analysis of variance (ANOVA) indicated that salicylic acid (SA) exerted a significant effect on tomato seedling growth, markedly enhancing shoot traits, including shoot growth and length, leaf number, leaf area, stem thickness, and shoot fresh weight, across both low- and high-temperature regimes, demonstrating a consistent promotion of above-ground development. SA also significantly improved several root architectural and biomass parameters, such as root fresh weight, length, surface area, volume, and fork number; however, root average diameter and the number of root tips were not significantly affected, indicating that SA selectively influences root traits at this stage of seedling development (Table 1).

Shoot characteristics: Influence of SA at 16°C and 25°C

Shoot length. At 25°C, shoot length increased significantly with SA, particularly at 75 mg/L (18.22 cm), which was superior to both the control (16.55 cm) and the 150 mg/L treatment (16.27 cm). This suggests that SA promotes elongation more effectively under higher temperatures, likely by enhancing cell division and expansion. However, at 16°C, shoot length remained statistically unchanged across SA treatments, indicating that shoot elongation under cold stress is relatively insensitive to SA (Table 2).

In the transplant industry, the shorter, well-rooted, and compact seedlings are often favored over tall, leggy ones. They are sturdier, easier to handle, and less prone to damage during transport or transplanting, helping reduce transplant shock and improve field establishment (Huber *et al.*, 2021). Research by Kozai (2005) and Kubota *et al.* (2008) highlights that high-quality transplants are uniform, compact, and possess strong biomass traits that not only support healthy growth but also align well with automation systems. Unlike stretched seedlings, which are more vulnerable to stress, compact seedlings are more resilient and dependable from the greenhouse to the field. It has been stated that exogenous SA application often causes dwarf plant phenotypes, which is interpreted as being an SA-induced shift of plant resources from growth to

Table 1 - ANOVA for tomato seedlings' shoot and root characteristics, treated with salicylic acid (SA) and grown in the growth chambers at 16°C and 25°C

Source	DF	Shoot length	Leaf No.	Leaf area	Stem thickness	Shoot FW	Root FW	Root length	Root surface area	Root average diameter	Root volume	Root tips no.
Treatment	5	132.92 **	4.96 **	7171.09 **	1.66 **	14.47 **	2.29 **	25690.80	34336.10	2.32 NS	724.09 **	1729056 NS
Error	48	0.559	0.27	428.72	0.18	0.40	0.06	4219.2	5856.5	1.34	153.53	725068
Total	53											

Mean values followed by ** show statistical significance ($p \leq 0.01$).

Table 2 - Mean comparison of tomato seedlings' shoot characteristics, treated with salicylic acid (SA) and grown in the growth chambers at 16°C and 25°C

Treatments	SA (mg/L)	Shoot length (cm)	Leaf No.	Leaf area (cm^2)	Stem thickness (mm)	Shoot FW (g)
Low temperature (16°C)	0	10.22±0.25 c	5.22±0.15 d	75.26±4.54 c	4.53±0.17 b	3.41±0.28 c
	75	10.31±0.35 c	6.00±0.17 bc	107.96±6.36 b	5.16±0.06 a	4.51±0.18 b
	150	9.81±0.20 c	5.33±0.24 d	85.24±5.38 c	4.52±0.14 b	3.73±0.25 c
High temperature (25°C)	0	16.55±0.19 b	6.33±0.17 b	120.33±9.97 b	5.16±0.20 a	4.57±0.14 b
	75	18.22±0.22 a	7.22±0.15 a	154.49±7.57 a	5.23±0.11 a	6.99±0.15 a
	150	16.27±0.23 b	5.67±0.17 cd	118.61±5.93 b	4.22±0.15 b	5.08±0.23 b

Values represent mean ± Std Err.
In each column, the same letters show no significant differences using the Least Significant Difference (LSD) test.

defense (Bagautdinova *et al.*, 2022).

Leaf number

SA positively influenced leaf production at both temperatures, although the response was temperature-dependent. At a low temperature of 16°C, 75 mg/L SA significantly improved leaf number (6.00) compared to the control (5.22). The same impact was observed at 25°C, where 75 mg/L SA yielded the highest leaf number (7.22), exceeding that of the control (6.33). However, the difference between 75 mg/L SA at 16°C and control plants under 25°C was not significant (Table 2). The results indicate that although SA more effectively stimulates the initiation of leaf formation under optimal temperature conditions, the application of 75 mg/L SA at lower temperatures can also result in the production of transplants with a similar number of leaves compared to those grown under optimal conditions without SA. This aligns with SA's role in modulating hormonal pathways involved in leaf primordia formation, even under low temperatures.

Several studies underscore the beneficial role of SA in maintaining or even enhancing leaf development in tomatoes under chilling stress. SA was found to preserve leaf number and shoot elongation under cold stress by stabilizing PSII (Photosystem II) via HSP21 (Heat Shock Protein 21) and promoting the accumulation of antioxidants, as well as activating ethylene-regulated transcription factors that promote photoprotection and ascorbate production (Saleem *et al.*, 2021). Gharib and Hegazi (2010) observed that SA pretreatment at 10^{-4} M significantly increased the number of leaves and shoot length in bean seedlings under chilling (15°C), suggesting similar benefits in tomatoes, particularly at early growth stages. Similar results were observed in tomato seedlings, where SA priming improved leaf area and leaf number under low-temperature stress, in part by boosting antioxidant enzyme activity and stabilizing the hormonal balance (GA_3/ABA ratio) (Galviz *et al.*, 2021). The increase in the number of leaves can be attributed to several biochemical and molecular actions of SA: 1) enhanced cell division and expansion, particularly in the shoot apical meristem, contributing to increased leaf primordia initiation (Li *et al.*, 2022), 2) modulation of phytohormones through elevating auxin (IAA) and gibberellin (GA_3) levels while reducing abscisic acid (ABA), which create a hormonal environment conducive to leaf proliferation (Gharib and Hegazi, 2010), 3) antioxidant defense activation, by enhancing enzymes like SOD, CAT, and APX, SA reduces oxidative damage under chilling, allowing normal meristem activity and leaf initiation to continue (Saleem *et al.*, 2021), and 4) interaction with ethylene pathway, through regulation of SlEIL transcription factors, SA maintains photosystem activity and cellular redox homeostasis, indirectly supporting sustained leaf development (Saleem *et al.*, 2021).

Leaf area

Leaf area, a key indicator of photosynthetic potential, responded well to SA at both temperatures. At 16°C, the control showed reduced expansion (75.26 cm²), while 75 mg/L SA boosted it to 107.96 cm², a 43% increase. At 25°C, the largest leaf area (154.49 cm²) was again achieved with 75 mg/L SA (Table 2). The consistent effectiveness of 75 mg/L at both temperatures suggests this dose optimally activates pathways related to cell expansion and chloroplast development. However, the difference between 75 mg/L SA at 16°C and control plants under 25°C was not significant (Table 2). The results indicate that although SA more effectively stimulates the leaf expansion under optimal temperature conditions, the application of 75 mg/L SA at lower temperatures can also result in the production of transplants with a similar leaf area compared to those grown under optimal conditions without SA.

SA plays a central role in sustaining or enhancing leaf area in tomatoes under stress conditions through a range of mechanisms involving hormonal signaling, antioxidant defense, and cellular metabolism. Although chilling stress reduces leaf expansion in tomato plants by inhibiting cell division and elongation, the exogenous application of SA has been shown to ameliorate these effects. Saleem *et al.* (2021) found significantly higher leaf area retention in SA-treated tomato plants exposed to cold compared to untreated controls. This was linked to SA-induced upregulation of protective heat shock proteins (HSP21) and enhanced ascorbate production, which maintained photosystem II integrity and protected chloroplast structures essential for cell expansion (Saleem *et al.*, 2021). Further supporting this, Gharib and Hegazi (2010) showed that SA pretreatment (10^{-4} M) improved leaf area in common bean (*Phaseolus vulgaris*) under 15°C stress by modulating phytohormones such as gibberellic acid and indoleacetic acid, suggesting a similar effect could be expected in tomato due to comparable physiological stress responses.

Optimal concentrations of exogenous SA stimulate root and shoot elongation, enhance leaf area, and improve photosynthetic efficiency, whereas above-optimal levels can inhibit growth, likely due to the induction of oxidative stress (Chakma *et al.*, 2021; Bagautdinova *et al.*, 2022).
The improvement in leaf area under SA treatment is closely linked to enhanced antioxidant enzyme activity (e.g., superoxide dismutase, catalase), osmoprotectant accumulation (e.g., proline, soluble sugars), and hormonal balance that favors cell expansion. Moreover, SA appears to mediate these effects via complex crosstalk with auxins and gibberellins, thereby promoting sustained mitotic activity in leaf meristem regions even under stress (Li *et al.*, 2022).

Stem thickness

Stem diameter increased significantly with SA, particularly at 75 mg/L, under both conditions. Under the low temperature of 16°C, SA improved stem robustness from 4.53 mm (control) to 5.16 mm. Interestingly, no further increase was observed at 25°C since the 0, 75, and even 150 mg/L SA treatments showed similar values (~5.16-5.23 mm), suggesting a threshold of responsiveness under non-stress conditions. The difference between 75 mg/L SA at 16°C, control plants, and 75 mg/L SA under 25°C was not significant (Table 2). The results indicate that the application of 75 mg/L SA at lower temperatures can result in the production of transplants with a similar stem thickness compared to those grown under optimal conditions without SA.

A greater stem diameter of seedlings exhibits superior transplant resilience and higher yield potential. A robust stem facilitates the development of a well-structured vascular system, ensuring efficient transport of water, nutrients, and photoassimilates to expanding tissues (Chakma *et al.*, 2021). In stress environments, such as under drought or salinity, stem diameter often serves as a reliable morphological marker for plant health and stress adaptation. A thicker stem enhances the plant's ability to support larger leaf areas and fruit loads while reducing the risk of lodging or breakage during handling and environmental extremes. It has been demonstrated that foliar application of SA at 150 mg/L significantly increased stem diameter in grape tomato seedlings under moderate drought conditions (Chakma *et al.*, 2021), accompanied by improvements in root biomass, water-use efficiency, and yield. Similarly, 1.0 mM SA preserved stem thickness in eggplants exposed to salinity stress, suggesting its relevance for tomatoes under similar conditions (Sousa *et al.*, 2024). In peppers, SA-enhanced stem girth has been linked to improved hormonal balance, turgor maintenance, and reduced electrolyte leakage under deficit irrigation, suggesting that SA-mediated mechanisms promoting stem growth may be applicable broadly across solanaceous crops (Ghahremani *et al.*, 2023).

It has been demonstrated that the foliar application of 150 mg/L SA (~1.08 mM) significantly increased stem diameter compared to untreated controls under moderate drought stress (75% FC) (Chakma *et al.*, 2021). Ghahremani *et al.* (2023) demonstrated that foliar spraying of pepper plants with 1.5 mM SA under deficit irrigation significantly enhanced stem diameter compared to untreated plants. The increase in stem thickness was associated with improved water-use efficiency, reduced electrolyte leakage, and higher chlorophyll content. These physiological improvements help maintain cell turgor and vascular integrity, leading to sturdier stems under water stress.

Sousa *et al.* (2024) showed that 1.0 mM SA maintained the stem diameter of eggplant seedlings near control values (non-saline, untreated), at moderate salinity (2.5 dS m^{-1}). The increase was attributed to SA-enhanced antioxidant activity, osmolyte accumulation, and maintenance of relative water content, all of which support vascular growth under stress.

Shoot fresh weight

SA at 75 mg/L concentration increased shoot FW compared to 0 and 150 mg/L SA, irrespective of the ambient temperature. The increase was 32 and 53 percent higher compared to the 0 mg/L SA, at 16 and 25°C, respectively. Notably, the difference between 75 mg/L SA at 16°C and control plants under 25°C was not significant (Table 2). The results indicate that although 75 mg/L SA effectively increased shoot fresh weight under optimal temperature conditions, the application of 75 mg/L SA at lower temperatures can also result in the production of transplants with a similar shoot fresh weight compared to those grown under optimal conditions without SA. This aligns with SA's role in modulating hormonal pathways involved in biomass production, even under low temperatures.

The elevated biomass at 75 mg/L SA may reflect enhanced resource assimilation and partitioning toward shoot tissues, driven by SA-induced metabolic upregulation. In a study by Chakma *et al.* (2021), foliar application of SA at 150 mg/L under moderate drought conditions significantly increased shoot fresh weight in grape tomato seedlings compared to untreated controls. Similarly, Abd-Elkader *et al.* (2022) investigated the effects of acetylsalicylic acid (ASA) at 178 mM on tomato plants under low-temperature stress. They revealed that ASA application, especially when combined with potassium silicate, significantly enhanced shoot fresh weight and other agronomic traits, suggesting a synergistic effect in mitigating chilling injury.

Ghahremani *et al.* (2023) showed that 1.5 mM SA significantly improved shoot fresh weight compared to untreated sweet pepper plants under drought stress. They attributed the increase in biomass to enhanced water-use efficiency and reduced oxidative damage, highlighting SA's role in stress amelioration. Additionally, Mohammadi *et al.* (2023) reported that the combined application of gypsum and SA under salinity stress conditions resulted in a notable increase in shoot fresh weight in pepper plants. This combination treatment improved physiological traits and stress tolerance, emphasizing the potential of SA in integrated stress management strategies. In eggplant, Sousa *et al.* (2024) demonstrated that the exogenous application of SA at concentrations ranging from 0 to 1.5 mM under saline irrigation conditions effectively maintained shoot fresh weight by enhancing antioxidant activity and osmolyte accumulation. Furthermore, a study by Zhang *et al.* (2023) indicated that SA application improved shoot fresh weight in eggplant seedlings subjected to low-temperature stress. The treatment enhanced photosynthetic efficiency and reduced electrolyte leakage, contributing to better growth performance under chilling conditions.

Root characteristics: Influence of SA at 16°C and 25°C

Root fresh weight. At 16°C, 75 mg/L SA increased root fresh weight (FW) from 0.71 g to 1.11 g (a 56% increase), underscoring its stimulatory role even under cold-induced growth suppression. However, SA at 150 mg/L level reduced this benefit. At 25°C, 75 mg/L SA nearly doubled the root fresh weight compared to the control (2.06 g vs. 0.98 g), while 150 mg/L SA still performed well (1.47 g) (Table 3). The difference between root fresh weight produced under low temperature and 75 mg/L SA was not significant when compared with 0 mg/L SA at 25°C. These findings suggest a dose-dependent enhancement in root biomass, peaking at 75 mg/L SA under both temperature regimes.

Bagautdinova *et al.* (2022) cited several reports that SA promotes fresh and dry weights (through increased adventitious rooting) in a dose-dependent manner, where low concentrations enhance root formation, while higher levels (above 100-800 µM) inhibit it.

Root length. Root elongation was particularly stimulated by 75 mg/L SA at 16°C (401.22 cm), significantly higher than the control (251.01 cm). This was substantially higher than the root length produced under optimal temperatures of 25°C and 0 mg/L SA (Table 3). At 25°C, the effect was less pronounced, with 150 mg/L SA yielding the longest roots (352.22 cm), while 75 mg/L SA showed a

Table 3 - Mean comparison of tomato seedlings' root characteristics, treated with salicylic acid (SA) and grown in the growth chambers at 16°C and 25°C

Treatments	SA (mg/L)	Root FW (g)	Root length (cm)	Root surface area (cm^2)	Root volume (cm^3)
Low temperature (16°C)	0	0.71±0.07 e	251.01±42.91 c	209.46±23.55 cd	12.37±1.57 c
	75	1.11±0.09 c	401.22±23.39 a	274.06±9.98 bc	15.28±1.20 c
	150	0.81±0.06 de	298.07±16.12 bc	277.10±20.59 bc	22.85±2.75 bc
High temperature (25°C)	0	0.98±0.05 cd	219.25±10.21 c	149.08±10.43 d	18.36±1.53 c
	75	2.06±0.12 a	309.65±25.18 bc	386.57±67.57 a	41.38±12.89 a
	150	1.47±0.09 b	352.22±27.16 ab	365.60±71.83 a	33.08±11.90 ab

Values represent mean ± Std Err.
In each column, the same letters show no significant differences using the Least Significant Difference (LSD) test.

moderate enhancement. This suggests that while SA enhances root elongation under cold stress, higher doses may be required under warm conditions to sustain meristem activity.

Bagautdinova *et al.* (2022) cited several reports on the concentration-dependent effect of SA on the radicle/primary root length in dicots, where low SA concentrations stimulated and higher ones retarded root growth.

Root surface area. SA treatments significantly improved surface area at both temperatures, most notably at 25°C, where 75 and 150 mg/L SA increased root surface area to 386.57 and 365.60 cm^2, respectively, compared to 149.08 cm^2 in the control. The effect was also notable at 16°C, where SA boosted surface area by 30-32% relative to the untreated seedlings. This expanded root interface likely improves water and nutrient uptake capacity, contributing to overall seedling vigor.

Root volume. Data in Table 3 show that SA treatment significantly enhanced root volume, particularly at 25 °C, where 75 mg/L SA more than doubled the root volume (41.38 cm^3 vs. 18.36 cm^3 in the control). This substantial increase likely reflects enhanced lateral root proliferation and thickening. At 16 °C, SA had a moderate effect, with 150 mg/L SA increasing root volume from 12.37 to 22.85 cm^3, though the variation was less pronounced than at the higher temperature. Although root volume tended to increase with higher SA concentrations at both 16 °C and 25°C, the volume produced with 75 mg/L SA at 16°C was statistically similar to that produced at 25°C without SA.

In tomatoes, SA was shown to stabilize membranes, enhance antioxidant activity (via enzymes such as SOD, CAT, and APX), and aid in maintaining photosynthetic capacity, thereby indirectly supporting better root function and growth under chilling conditions (Galviz *et al.*, 2021). Seed treatment or exogenous application of SA enhanced early root elongation under cold by reducing reactive oxygen species (ROS) damage and modulating stress-responsive gene expression (Saleem *et al.*, 2021). In eggplant, SA at 1.0 mM mitigated the inhibitory effects of salt-induced osmotic stress, which shares physiological mechanisms with cold-induced water stress. This treatment helped maintain relative water content and reduced electrolyte leakage, indirectly sustaining root growth and overall seedling vigor (Sousa *et al.*, 2024).

SA, through interaction with auxin, shapes root architecture, enhancing or inhibiting elongation depending on concentration, developmental conditions, and stress, while also bolstering antioxidant enzyme activity and protecting roots from oxidative stress (Bagautdinova *et al.*, 2022). Additionally, SA signaling, via NPR1, MAPKs, and ROS-Ca^{2+} pathways, enhances stress perception and adaptive responses, promoting root resilience and growth (Saleem *et al.*, 2021). These integrative roles highlight SA's dynamic influence on root development under various environmental scenarios.

Energy savings from greenhouse temperature setpoint reduction after salicylic acid application

We investigated the role of SA as a plant physiology-based approach to reduce energy inputs during transplant development at lower temperatures without compromising seedling quality. Remarkably, transplants treated with 75 mg/L SA and maintained at 16°C developed morphological traits statistically comparable to those grown at 25°C without SA. Traits such as stem length, stem diameter, leaf number, leaf area, shoot and root fresh weights, and root volume did not differ significantly ($p>0.05$) between these two groups. This suggests that exogenous SA application can counterbalance the physiological slowdown typically induced by suboptimal temperatures. Thus, SA-mediated temperature compensation presents a promising strategy for lowering greenhouse heating requirements without compromising transplant quality.

To explore the real-world implications of these findings, we modeled potential energy savings associated with reducing the greenhouse setpoint temperature from 25°C to 16°C. This scenario is especially relevant during winter transplant production, where seedlings are typically started indoors 3-12 weeks (depending on crop species) before the last expected frost date. In many temperate regions, outdoor temperatures during this period can fall well below the optimal 18-25°C range for seedling development, necessitating supplemental heating.

One common approach to winter greenhouse heating is to maintain the air temperature at a crop-specific target level. We used the standard formula for greenhouse heating load (Eq. 1) to estimate the heat (Q) required to achieve a specific temperature in a greenhouse. Assuming an average outdoor winter temperature of 5°C, the temperature differentials were 20°C and 11°C for the 25°C and 16°C setpoints, respectively. We compared two scenarios of inside greenhouse temperature under otherwise identical conditions.

The relative energy savings can thus be estimated as:

$$\frac{Q_{25}-Q_{16}}{Q_{25}} = A$$

While all other variables in Eq.1 are constant (U, A, and t), the relative energy savings can thus be estimated based on the ΔT temperatures as:

$$\frac{(25-5)-(16-5)}{(25-5)} = 0.45 = 45\%$$

This indicates that reducing the heating setpoint from 25°C to 16°C has the potential to reduce heating energy demand by approximately 45%, assuming insulation, greenhouse design, and heating duration remain constant. It is essential to note that while some cool-season crops or vegetative seedlings may tolerate lower air temperatures with minimal developmental penalties, fruiting warm-season vegetables, such as tomatoes, are more thermosensitive (Galviz *et al.*, 2021).

Our findings demonstrate that while suboptimal temperatures can hinder plant growth and development, the strategic application of SA effectively mitigates these limitations. Our finding is consistent with other empirical studies, which report reductions of 30–50% in heating energy when dynamic setpoint strategies are employed (Chakma *et al.*, 2021; Zhang *et al.*, 2022).

By integrating SA treatments with reduced heating setpoints, growers can maintain plant quality and profitability while capitalizing on the energy-saving benefits of lower air temperatures. This approach offers a practical, climate-resilient pathway to more energy-efficient greenhouse operations.

4. Conclusions

This study reveals that exogenous application of SA, particularly at 75 mg/L, significantly enhances the morphological and physiological performance of tomato seedlings under suboptimal temperature conditions (16°C), achieving traits comparable to those grown under optimal standard greenhouse temperatures (25°C). SA improved shoot and root biomass, stem robustness, and leaf area while maintaining membrane integrity, hallmarks of improved cold tolerance.

From an energy efficiency perspective, these physiological improvements enabled a potential reduction in greenhouse heating setpoints by 9°C, which modeling indicated could lead to a 45% decrease in heating energy demand. This biologically driven strategy not only mitigates the adverse effects of cold stress but also offers a cost-effective, low-input alternative to conventional thermal energy inputs during critical transplant growth stages.

Incorporating SA treatments into commercial transplant production thus represents a promising avenue for reconciling high-quality seedling development with sustainable greenhouse operations. Future work should focus on applying SA to other crops and scaling this approach under variable greenhouse environments to validate its broader applicability and economic benefits.

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