



Trichoderma and *Glomus* Modulate Morphological and Physiological Traits of Vegetable Seedlings Under Heat Stress

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Abstract

Scorching field temperatures, intensified by climate change, pose a critical threat to crop establishment. This is particularly true for transplants, which having been raised in a controlled nursery, often lack the hardiness to survive the stressful transition to the open field. Beneficial soil microorganisms, such as *Trichoderma harzianum* and *Glomus* spp., have the potential to enhance plant tolerance to abiotic stress. This study evaluates their effects of increasing temperatures (25, 30, and 35 °C) on tomato (*Solanum lycopersicum*), cabbage (*Brassica oleracea*), cucumber (*Cucumis sativus*), and melon (*Cucumis melo*) seedlings. Seedlings were inoculated with *Trichoderma* or *Glomus*, alongside a non-inoculated control, and assessed for germination, chlorophyll, total phenolic content (TPC), photosynthesis, plant height, sturdiness index, shoot weight, and leaf area. Germination was highest in melon and cucumber at 30–35 °C, while tomato reached 88% germination at 30 °C. *Trichoderma* increased chlorophyll content (13.4 CCI) at 35 °C and TPC in cabbage (34.84 mg GAE g⁻¹ d.w.). In cucumber, *Glomus* enhanced photosynthesis (8.30 μmol CO₂ m⁻² s⁻¹), height (+68%), and sturdiness index (+71%). Melon at 30–35 °C showed greater shoot weight (5.28 g) and leaf area (123.5 cm²). Microbial effects were crop- and trait-specific, underscoring the need for targeted applications to optimize seedling production under rising temperatures.

Keywords *Solanum lycopersicum* · *Brassica oleracea* · *Cucumis sativus* · *Cucumis melo* · Abiotic stress · Heat stress · Seedling establishment · Beneficial soil microorganisms

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Introduction

Climate change presents one of the most critical challenges for global agriculture, as rising temperatures and unpredictable weather patterns threaten crop productivity and food security (IPCC, 2021; Masson-Delmotte, 2022). Sustainable agricultural practices, including ecological and microbiome-based approaches, have been emphasized as essential for mitigating these challenges (Pasupulla et al. 2021; Pisante et al. 2012).

Within this context, nursery seedling production plays a crucial role by supplying uniform, high-quality seedlings for commercial cultivation. Efficient management is crucial to ensure a consistent supply of young seedlings, particularly for high-value vegetables and flowers (Mohanta et al. 2020). However, the assumption that greenhouse cultivation fully protects plants from environmental stresses is misleading. Recent studies suggest that greenhouse environments, particularly under high seedling density and restricted root volumes, can exacerbate the negative effects of elevated

temperatures, rendering plants more susceptible to heat stress than those grown in open-field conditions (Mahajan et al. 2025; Mikó et al. 2025).

These challenges are particularly acute during late spring and summer, when temperatures frequently exceed the optimal range for seedling development, resulting in reduced both quality and overall production efficiency (Abdalla et al. 2020; Zhu et al. 2021).

Plants exhibit diverse responses to elevated temperatures, which alter the structure and function of cells, tissues, and organs (Wahid et al. 2012). Heat stress impairs the photosynthetic apparatus (Shao et al. 2007), compromises vigor and germination, reduces biomass accumulation, and exacerbates oxidative damage (Wahid et al. 2007; Hasanuzzaman et al. 2013). Similar findings have been reported in cereals such as rice, where high temperatures during sensitive stages severely limit photosynthetic activity and yield formation (Lu et al. 2025). Although genetic improvement is often proposed to enhance crop resilience, it is costly and time-consuming, making it impractical for short nursery cycles (Ab Rahman et al. 2018). Therefore, alternative strategies that can be rapidly implemented are needed, particularly those that exploit natural plant–microbe interactions to enhance seedling resilience under stress.

Harnessing these interactions provides a cost-effective and environmentally friendly approach to improving crop performance under adverse conditions. In greenhouse nurseries, where seedlings are especially exposed to heat stress, beneficial soil microorganisms (BSM) have emerged as promising tools to sustain production. Among them, *Trichoderma* spp. and arbuscular mycorrhizal fungi (*Glomus* spp.) are increasingly recognized for their ability to enhance plant tolerance to abiotic stressors, offering practical solutions for nursery growers. This evidence is further supported by recent reviews highlighting the role of BSM in mitigating temperature stress, with arbuscular mycorrhizal fungi shown to enhance thermotolerance across crops (Jian et al. 2024) and *Trichoderma* species increasingly recognized as versatile allies against abiotic stress under climate change scenarios (Senizza et al. 2023).

Extensive research has demonstrated that BSM inoculation can mitigate the adverse effects of salinity, drought, high temperature, nutrient deficiency, and alkalinity (Rodriguez et al. 2008; Bae et al. 2009; Contreras-Cornejo et al. 2009; Msimbira and Smith 2020; Kumar et al. 2022). More recent studies confirm these findings, demonstrating that AM fungi enhance osmolyte accumulation and stress-related protein expression in cucumber under heat stress (Liu et al. 2023), while *Trichoderma harzianum* protects plants against combined heat and drought by improving ROS scavenging (Geng et al. 2025). This ability is particularly valuable in commercial seedling production, where

maintaining optimal physiological quality from germination to transplanting is both critical and costly.

Heat stress has also been shown to severely compromise seedling establishment, emphasizing the importance of biological tools in mitigating its effects (Su et al. 2024; González-García et al. 2023). In this context, *Trichoderma* spp., traditionally employed for disease biocontrol, and arbuscular mycorrhizal fungi such as *Glomus* spp. are increasingly recognized for their ability to modulate plant responses to abiotic stress (Zaidi et al. 2014; Kashyap et al. 2017; Tripathi et al. 2021). Yet, only a few studies have focused on the early seedling stage, which is the most sensitive to environmental stress. Sofy et al. (2022) reported that the application of *Trichoderma* enhances salt stress tolerance in spinach plants. Under 150 mM NaCl, treated plants showed greater shoot and root length and an increased number of leaves compared to the control group. Mastouri et al. (2010) also examined the effect of *T. harzianum* T22 treatment in tomato seeds under different physiological and abiotic stresses, showing that *T. harzianum* T22 increased the germination rate under cold and heat stress but did not affect the percentage of germinated seeds. Similarly, *T. harzianum* and *Glomus mosseae* have been shown to enhance tomato yield and nutrient content under greenhouse conditions (Nzanza et al. 2012). More recent work has demonstrated that *T. harzianum*, combined with optimized light spectra, promotes photosynthetic carbon metabolism and vigorous growth in tomato seedlings (Wang et al. 2025).

Together, these findings suggest that both *Trichoderma* and *Glomus* can contribute to thermotolerance, but evidence for their role during the earliest phases of seedling establishment remains scarce. The growing commercial interest in microbial-based inputs further underscores the need for research in this area, as BSM inoculants are increasingly developed to improve nutrient uptake and crop productivity (Elliott et al. 2021). By elucidating the role of *Trichoderma* and *Glomus* in enhancing heat tolerance at the seedling stage, this study seeks to provide mechanistic insights and practical guidance for designing resilient nursery production systems in a warming climate.

The objective of this research is to evaluate the impact of *Trichoderma harzianum* and a *Glomus* mix (*G. intraradices* + *G. mosseae*) on the morphological and physiological responses of tomato (*Solanum lycopersicum*), cabbage (*Brassica oleracea*), cucumber (*Cucumis sativus*), and melon (*Cucumis melo*) seedlings exposed to heat stress. Understanding these interactions could lead to the development of more resilient nursery production systems, helping mitigate climate change-induced stress in early plant growth stages.

Materials and Methods

Experimental Location

The study was conducted at the University of Georgia (College of Agricultural and Environmental Sciences, Department of Horticulture, Controlled Environment Agriculture Crop Physiology and Production Laboratory) in Athens, Georgia, USA (33° 93' 11.36" N, 83° 36' 39.28" W).

Substrate Preparation

The substrate was a commercial growing mix (50%–60% sphagnum peat moss, softwood bark, perlite, dolomite limestone, and a wetting agent) with a pH of 5.65 and bulk density of 100–400 g/L (MM830-F3B; SunGro Horticulture, Canada). The substrate was autoclaved in aluminium trays (53 × 33 cm) for 1 h at 121 °C with a biological indicator for 2 days. After the sterilization process, when the substrate returned to room temperature, sowing was carried out. No additional fertilization was applied during the experimental cycle beyond the starter fertilizer charge already present in the substrate, to avoid interactions and isolate the role of BSM.

Treatments

The treatments for each horticultural crop consisted of nine combinations derived from three air temperatures (25, 30, and 35 °C) and three beneficial soil microorganisms (BSM) [not treated or control (C), *T. harzianum* (T), and *G. intraradices*+*G. mosseae* (G)], arranged in a 3 × 3 factorial design. The three temperature regimes (25, 30, and 35 °C) were selected to represent conditions typically encountered in nursery seedling production in a multitude of greenhouse environments, ranging from optimal to strongly stressful levels. This range was sufficient to capture relevant plant responses to heat stress without extending beyond the values normally observed in commercial practice. The morphological and physiological parameters assessed (chlorophyll content, photosynthetic rate, phenolic content,

plant height, sturdiness index, shoot biomass, and leaf area) are widely recognized as sensitive indicators of seedling vigor and stress adaptation, as also demonstrated in recent studies on heat-stressed seedlings (Sakpal et al. 2023; Moloi et al. 2025), thus providing a comprehensive evaluation of growth performance and stress physiology.

Plant Materials and Growth Conditions

During the initial growth cycle, tomato (cv. 'San Marzano') and cabbage ('Tiara F1' *Brassica oleracea* cv. 'Capitata') seeds were sown in 72-cell plug trays filled with sterilized substrate. After sowing, the seedling trays were transferred to growth chambers measuring 100 × 75 × 185 cm (height × depth × length) (PGR15 Conviron Controlled Environment Chamber, Winnipeg, MB, Canada). In the second growth cycle, cucumber (*Cucumis sativus* cv. 'Gateway F1') and melon (*Cucumis melo* 'Sarah choice F1') were sown in 36-cell plug trays.

The chamber temperature was maintained at 25, 30, and 35 °C, as indicated in Table 1. The growth chambers were equipped with a fixed light intensity of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the plant level, providing a 12-hour photoperiod. Relative humidity was maintained between 60% and 70% using humidifiers. The vapor pressure deficit (VPD) found in the three growth chambers ranged from 0.78 to 2.18 kPa, measured using a temperature/RH data logger (MX2301A; OnsetHOB0®, Bourne, MA, USA). Plants were irrigated manually as needed. Each treatment included four replicates of 18 plants, with further details provided in Sect. "Plant Materials and Growth Conditions".

Soil Microorganism Application

Microbial treatments included commercial mycorrhizal inoculum *T. harzianum* and *Glomus* mix and a non-inoculated control (C). *T. harzianum* Rifai strain KRL-AG2 powder containing 1.0×10^7 colony forming units per gram dry weight (RootShield® WP BioWorks, Fairport, NY, USA) was dissolved in 3.5 L of water (0.38 g/L). *G. mosseae* and *G. intraradices* were inoculated, adding 36.75 g of a commercial product in 3.5 L of water (10.5 g/L) (Dynomyco Groundwork BioAg, Moshav Mazor, Israel). These treatments were applied separately to ensure the individual effects of Trichoderma and Glomus could be assessed without interference.

Control plants (C) were treated with water only. Plants in the *Trichoderma* (T) treatment received inoculation with *T. harzianum*, while plants in the *Glomus* (G) treatment were inoculated with the Glomus mix. During the first cycle, 5 mL of the prepared inoculum was applied directly to each plant tray. At the start of the second cycle, microbial treatments

Table 1 Test specifications and characteristics for both cycles

Cultivation cycle	Species	Growth chamber	Day/Night temperature	Vapour pressure deficit
I (12/2023-01/2024)	<i>L. esculentum</i> and <i>B. oleracea</i>	1	25/20°C	0.78 kPa
		2	30/25°C	1.42 kPa
		3	35/30°C	2.18 kPa
II (01/2024-02/2024)	<i>C. sativus</i> and <i>C. melo</i>	1	25/20°C	0.62 kPa
		2	30/25°C	0.98 kPa
		3	35/30°C	1.87 kPa

included 1.94 g of RootShield and 378 g of Dynomyco dissolved in 3.5 L of water. Inoculum quantities were calculated based on the substrate volume per plant.

Inoculation was performed at two time points: 0 days after sowing (DAS) and 15 DAS. Control plants received the same volume of water, ensuring uniform application conditions across all treatments. Each treatment consisted of four replicates, with 18 plants in each replicate. This design enabled evaluation of the specific effects of *Trichoderma* and *Glomus* inoculation on seedling growth and physiological performance under controlled conditions.

Physiological Analysis

Leaf chlorophyll (Chl) content was first quantified non-destructively using the chlorophyll meter (CCM-200; Opti-Sciences, MA, USA). Anthocyanin (ANs) content was similarly monitored with the anthocyanin meter (ACM-200; Opti-Sciences MA, USA). The Net photosynthetic rate of the plants was measured one day before the harvest using the portable open infrared gas analyzer system (CIRAS-3; PP Systems, Amesbury, MA, USA). The second fully expanded leaf at the seedling stage was selected for measurement. The photosynthetic photon flux density (PPFD) provided by the leaf cuvette's light-emitting diode (LED) light source was fixed at $200 \mu\text{mol m}^{-2} \text{s}^{-1}$. The cuvette temperature was set to 25, 30, and 35 °C, respectively, for heat stress treatment. Additionally, a destructive spectrophotometric determination of chlorophyll a, chlorophyll b, carotenoids, and xanthophylls was performed following the method described by Wellburn and Lichtenthaler (1984). Freeze-dried samples (0.1 g) were ground and homogenized with 20 mL of 96% ethanol, shaken for 15 min, and stored at 4 °C for 24 h. The supernatant was then analyzed with a spectrophotometer (Perkin-Elmer UV/VIS Lambda), using the following equations:

- $\text{Ch-a} = 13.36A_{664} - 5.19 A_{649}$.
- $\text{Ch-b} = 27.43A_{649} - 8.12 A_{664}$.
- $C_x + c = (1000A_{470} - 2.13Ca - 97.63Cb)/209$.

Plant Growth Measurement

The number of germinated seedlings was recorded daily, and the germination percentage was calculated as the ratio of sprouted seeds to the total number of seeds sown on each day after sowing (DAS). To enhance visualization, blue LEDs (Pro 650e; LumiGrow, Emeryville, CA, USA) were activated to stimulate photosynthetic activity. A high-resolution camera (Chameleon[®] 3; FLIR, Wilsonville, OR, USA), equipped with a long-pass filter (SP700-R45×2; Midwest Optical Systems, Inc., Palatine, IL, USA), was

used to capture emitted light from plant material in the red/infrared spectrum (650–740 nm). This imaging technique allowed for non-invasive monitoring of seedling development across treatments.

When the seedlings reached the stage of 3–4 mature leaves, plants were cut at the collar level, weighed for fresh weight, and measured for plant height, fresh weight, stem diameter, and number of leaves (≥ 1 cm). In addition, the sturdiness index (SI) of individual plants was calculated as the ratio of plant height to stem collar diameter: $\text{SI} = \text{plant height} / \text{collar diameter}$. The total leaf area was determined using the leaf area meter (LI-3100 C; Lincoln, NE, USA). Afterward, the sampled plants were divided into subgroups; half of the samples were dried in a ventilated oven at 80 °C for 48 h, allowing the dry matter content of the tissues to be evaluated. The remaining samples were placed in a freezer at −20 °C and then freeze-dried for subsequent analysis. Roots were washed thoroughly in running water, dried, weighed, and then oven-dried for determination of dry matter. Total water content (TWC) was calculated as:

$$\text{TWC} = 100 \times (\text{fresh weight} - \text{dry weight}) / \text{fresh weight}$$

At the end of the second cycle, the dry mass of each part was weighed, and the Dickson Quality Index (DQI) (Dickson et al. 1960) was calculated with the following formula:

$$\text{DQI} = [(\text{stem thickness} / \text{plant height}) + (\text{root dry weight} / \text{shoot dry weight})] \times \text{total dry weight}$$

Analysis of Total Phenolic Content

For the determination of total phenolic content (TPC), freeze-dried samples (0.1 g) were extracted in 10 mL of methanol for 1 h on a shaker at 150 rpm and 22 °C. The extracts were then centrifuged for 15 min at 4500 rpm and 22 °C, filtered with filter paper, and aliquots were analyzed using the Folin–Ciocalteu method (Michiu et al. 2022).

The TPC was determined using the Folin–Ciocalteu method, with gallic acid (GA) as the calibration standard, and measured with a spectrophotometer (UV-1800; Shimadzu, Columbia, MD, USA). Specifically, 100 μL of leaf extract was placed in a 10 mL test tube, followed by adding 6 mL of distilled water and 0.5 mL of Folin–Ciocalteu reagent. The mixture was shaken for 10 s, and 4 min after adding the Folin–Ciocalteu reagent, 1.5 mL of a sodium carbonate solution (7.5% m/v) was added. The absorbance of the coloured reaction product was measured at 750 nm after two hours in the dark at room temperature. The TP content in the extracts was calculated using a standard calibration curve obtained with different concentrations of gallic acid stock solution (0.25 g GA/100 mL). The results have been

expressed as mg gallic acid equivalent (GAE) per gram of dry weight.

Determination of BSM Concentration in the Rhizosphere

At harvest, soil samples were collected from the rhizosphere of six plants from each treatment plot. The quantification of fungal Colony Forming Units (CFU) in the rhizosphere was conducted 30 days after sowing by an external laboratory. The quantification procedure involved full-length ITS amplicon sequencing using the PacBio Sequel II platform, with approximately 10,000 CCS reads per sample.

The UPGMA method, a hierarchical clustering technique based on average linkage, was employed to classify the samples according to their pairwise similarities. The procedure begins by identifying the two most similar samples, determined by the minimum distance between them. These samples are then clustered together, with a new node created at a midpoint equidistant between them. Subsequently, the distance between this newly formed cluster and all remaining samples is recalculated as the average of the distances between each sample in the cluster and the others. This analysis was conducted to confirm whether the inoculated microorganisms successfully established in the substrate, thereby ensuring that the observed seedling responses could be attributed to the presence of *Trichoderma* and *Glomus* in the rhizosphere.

Data Analysis

Treatments were arranged in the growth chambers using a 3 × 3 factorial experimental design with four replicates. A mixed linear model was performed using a statistical software (SAS version 9.4; SAS Institute, Cary, NC, USA) to

evaluate the effects of air temperature stress and endophytes inoculum on morpho-physiological parameters. The model was defined as:

$$Y_{ilmn} = \mu + b_i + p_l + (p \times c)l_m + e_{ilmn}$$

where y_{ilmn} represents the dependent variable (germination rate, plant height, collar diameter, SI, shoot weight, leaf count, leaf area index, shoot, and root dry matter); μ is the overall average of each dependent variable; b_i represents the fixed effect of the i th air temperature treatment ($i=25, 30$, and 35°C); p_l represents the fixed effect of the j th soil microorganism inoculation treatment ($j=\text{with control without inoculation and two treatments: } Trichoderma \text{ inoculation, and } Glomus \text{ inoculation}$); $(p \times c)l_m$ represents the first order interaction between the i th air temperature treatment and j th BSM inoculation treatment. Data were presented as least-squares means $\pm$ standard error (SE). Multiple comparison of least-squares means was performed using the Tukey HSD *post hoc* test. The threshold for significance was set when $P < 0.05$.

Results

Tomato

Plant Growth Measurement

Plant emergence differed under varying air temperature conditions from 4 to 6 DAS (Table 2). At 4 DAS, germination reached 37% at 30°C and 50% at 35°C , while no emergence was observed at 25°C ($P < 0.05$). By 5 DAS, germination was 46% higher at 30°C compared to 25°C , and by 6 DAS it was 13% higher at 30°C than at 35°C ($P < 0.05$).

Table 2 Germination rate of tomato seeds under different air temperature conditions ($25, 30$, and 35°C) and beneficial soil microorganisms (Control, *Glomus* and *Trichoderma*)

	Germination rate (%)			
	4 DAS	5 DAS	6 DAS	8 DAS
Air Temperature				
25°C	0 ± 0.052 b	54 ± 0.031 b	83 ± 0.027 ab	87 ± 0.035
30°C	37 ± 0.052 a	79 ± 0.031 a	88 ± 0.027 a	91 ± 0.035
35°C	50 ± 0.052 a	56 ± 0.031 b	78 ± 0.027 b	82 ± 0.035
Beneficial Soil Microorganisms				
Control	25 ± 0.052	58 ± 0.031 b	79 ± 0.027	86 ± 0.035
<i>Glomus</i>	34 ± 0.052	61 ± 0.031 ab	85 ± 0.027	85 ± 0.035
<i>Trichoderma</i>	28 ± 0.052	70 ± 0.031 a	85 ± 0.027	88 ± 0.035
Significances				
Air Temperature	***	***	*	ns
BSM	ns	*	ns	ns
Air Temperature x BSM	ns	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P < 0.05$) among treatments according to Tukey's HSD test. ns=not significant

At 8 DAS, however, germination rates converged across treatments (86–91%) and were not significantly affected by temperature ($P \geq 0.05$) (Fig. 1).

Physiological Analysis

Air temperature also influenced leaf chlorophyll content (Fig. 2). Plants grown at 35 °C showed the highest values (15.8 CCI, +23% compared to 25 °C; $P < 0.05$). Among BSM treatments, *Trichoderma* increased chlorophyll content by +5% compared to the control, whereas *Glomus*-treated plants showed an 8% reduction ($P < 0.05$). Leaf anthocyanin content was slightly lower in *Glomus*-treated plants (3.5 ACI) compared to the control (3.8 ACI) and *Trichoderma* (3.6 ACI), corresponding to a reduction of about 8% ($P < 0.05$).

Morphological traits also differed across treatments. Plant height was 5% lower in *Trichoderma*-treated plants (12.3 cm) compared to the control (13.0 cm) ($P < 0.05$). The interaction between temperature and BSM was significant for collar diameter ($P < 0.05$). At temperatures below 35 °C, plants treated with either *Glomus* or *Trichoderma* showed thicker collars (+12–15%) compared to the control.

Conversely, sturdiness index (SI) was higher in control plants (47) than in those treated with *Glomus* (44.4, –6%) or *Trichoderma* (42.3, –10%) (Table 3).

The shoot weight of tomato plants did not differ significantly across temperature or BSM treatments ($P > 0.05$, Table 4). However, air temperature significantly influenced leaf count ($P < 0.05$). Plants at 35 °C produced +17% more leaves (4.95) compared to 25 °C (4.22), while plants at 30 °C showed intermediate values (4.48). Leaf area (LA) was not significantly affected by temperature alone ($P > 0.05$), but the interaction between air temperature and BSM was significant ($P < 0.05$). Notably, *Glomus*-treated plants at 35 °C exhibited a 12% larger LA compared to the control under the same temperature. Shoot dry matter content decreased significantly at 35 °C (9.4%, –16% compared to 25 °C and 30 °C; $P < 0.05$), highlighting the negative impact of heat stress on biomass accumulation. In contrast, root dry matter remained stable across treatments ($P > 0.05$). Overall, these results suggest that while temperature was the primary driver of variation in tomato seedlings, *Glomus* inoculation under high heat stress (35 °C) partially mitigated reductions in leaf area, although it did not influence shoot biomass or dry matter.

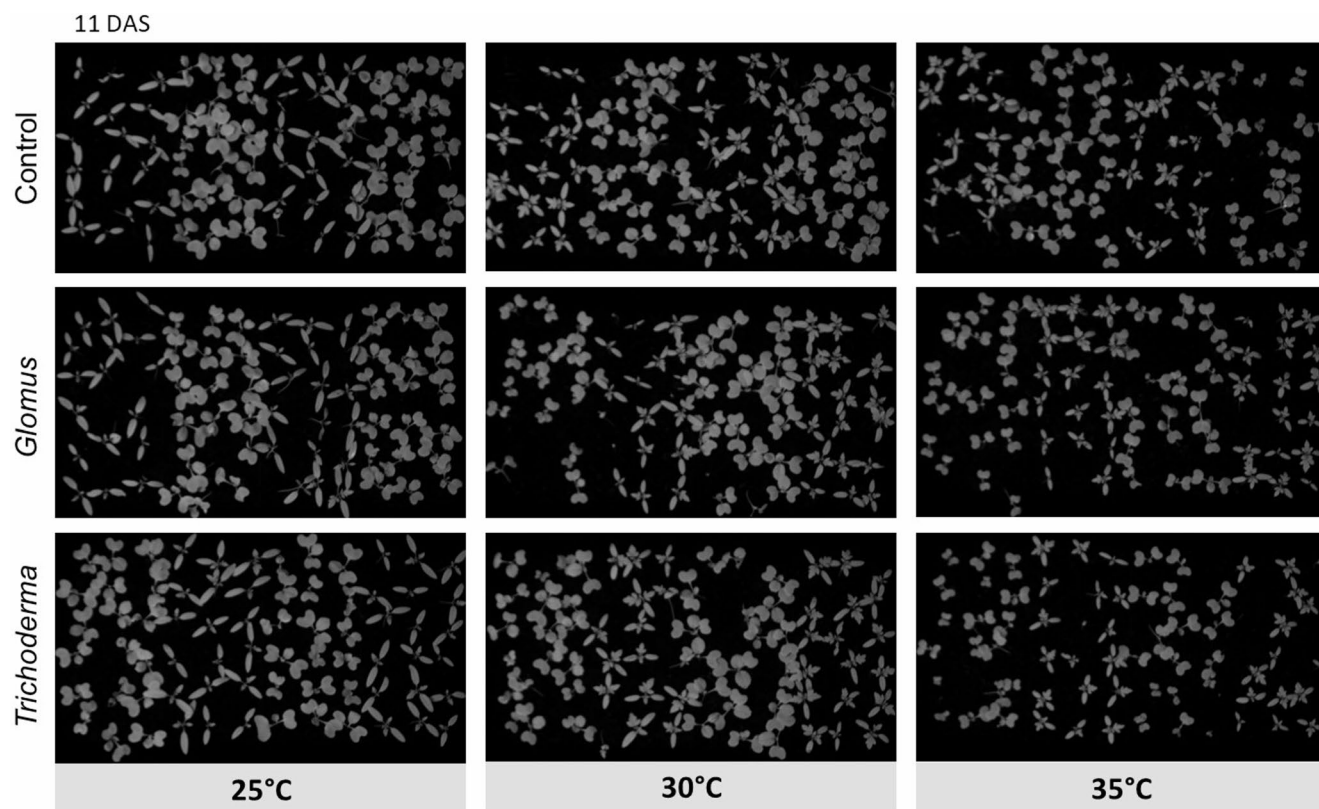


Fig. 1 Monitoring of tomato and cabbage seedling at 8 days after sowing (DAS) under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganism treatments (Control, *Glomus*,

and *Trichoderma*). Images were captured using a specialized germination monitoring camera

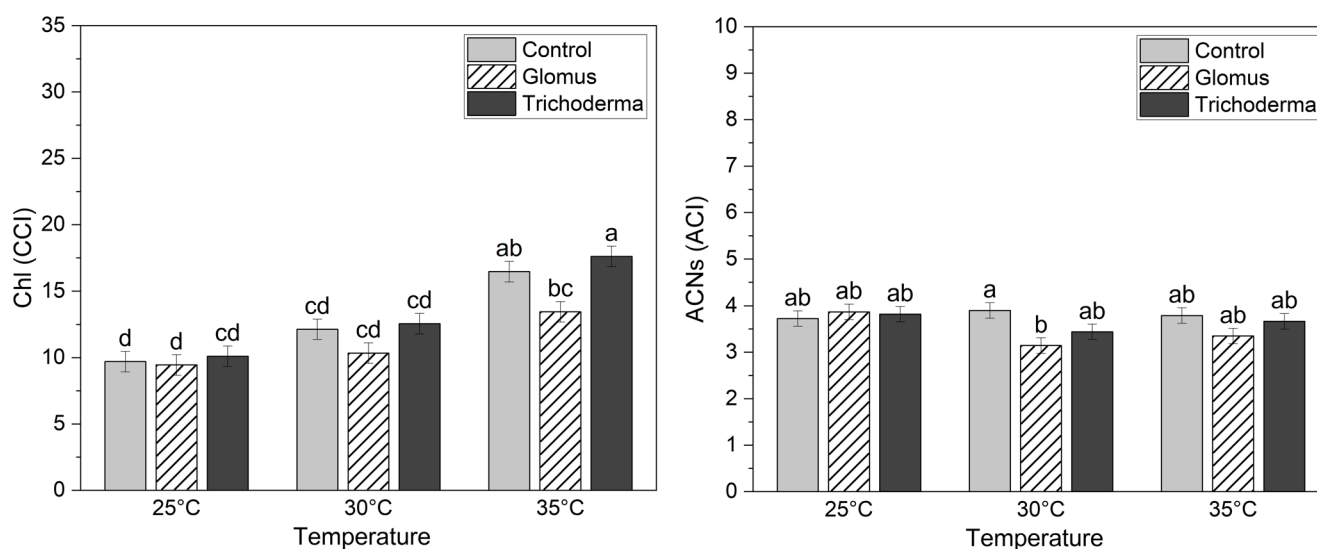


Fig. 2 Effect of air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus*, and *Trichoderma*) on tomato leaf chlorophyll (Chl) reported as chlorophyll content index (CCI), anthocyanin (ACNs) reported as anthocyanin content

index (ACI). Different letters indicate significant differences ($P < 0.05$) between treatments according to Tukey's HSD test. Bars indicate standard error

Table 3 Plant height, collar diameter, and sturdiness index (SI) of tomato seedlings under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus*, and *Trichoderma*)

	Plant height (cm)	Collar diameter (cm)	Sturdiness index
Air Temperature			
25 °C	12.8±0.175	0.29±0.004	45.1±0.605
30 °C	12.5±0.175	0.29±0.004	44.2±0.605
35 °C	12.6±0.175	0.29±0.004	44.5±0.608
Beneficial Soil Microorganisms			
Control	13.0±0.175 a	0.28±0.004	47.0±0.601 a
<i>Glomus</i>	12.7±0.175 ab	0.29±0.004	44.4±0.607 b
<i>Trichoderma</i>	12.3±0.175 b	0.30±0.004	42.3±0.611 b
Significances			
Air Temperature	ns	ns	ns
BSM	*	ns	***
Air Temperature x BSM	ns	*	ns

Means are followed by standard error, and different letters indicate significant differences ($P < 0.05$) between treatments according to Tukey's HSD test. ns=not significant

Phenols and Pigment Analysis

The air temperature and BSM treatment did not significantly affect the total phenolic content (TPC), chlorophyll a, xanthophyll, and carotenoid content in leaf tissue ($P > 0.05$) (S.M.2).

Cabbage

Plant Growth Measurement

Cabbage seedling emergence from 3 to 8 DAS was not significantly affected by air temperature or BSM treatments (S.M.2) ($P > 0.05$).

Physiological Analysis

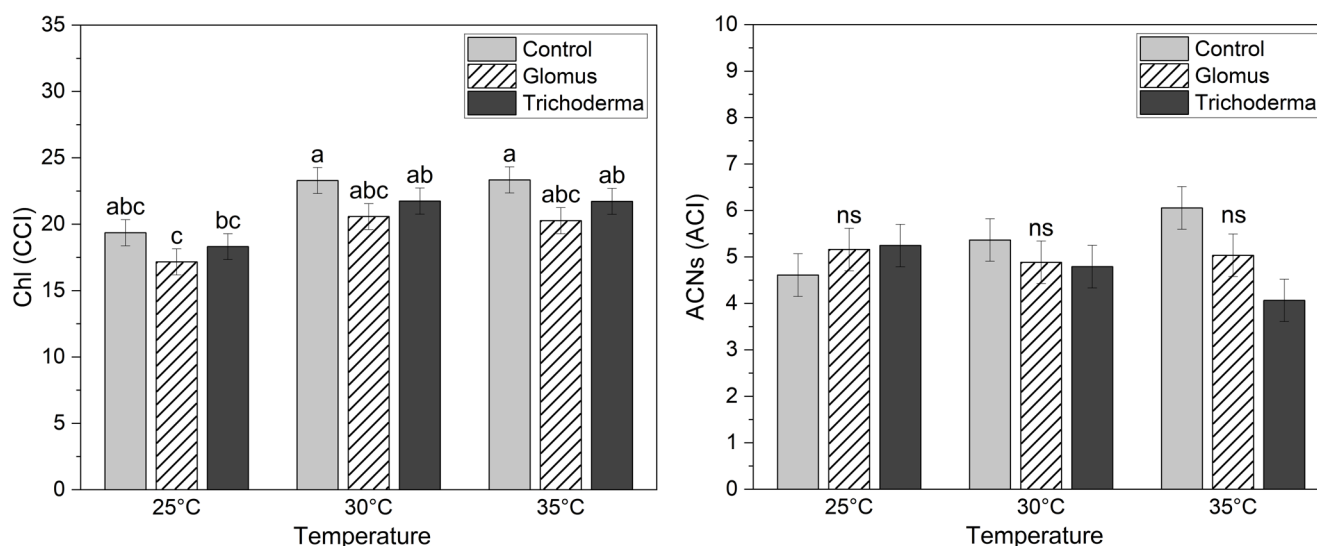
Leaf chlorophyll content increased significantly under higher air temperatures (Fig. 3). Plants grown at 30 and 35 °C showed 21.9 and 21.8 CCI, respectively, corresponding to an increase of about 19% compared to 25 °C (18.3 CCI) ($P < 0.05$). Control plants had slightly higher chlorophyll content (21.9 CCI) than *Glomus*-treated plants ($P < 0.05$). Anthocyanin content did not vary significantly among treatments ($P > 0.05$).

Plant height was significantly reduced at 35 °C (5.9 cm, –14% compared to 25 °C; $P < 0.05$). In contrast, seedlings at 25 °C and 30 °C reached 6.8 and 6.7 cm, respectively. Interaction effects between air temperature and BSM indicated that control and *Glomus*-treated plants at 25 °C, and control and *Trichoderma*-treated plants at 30 °C, had significantly greater height ($P < 0.05$). By contrast, control plants at 35 °C exhibited the lowest values ($P < 0.05$). Collar diameter was significantly higher at 25 °C (0.17 cm) than at 30 °C (0.15 cm) and 35 °C (0.13 cm, –24% vs. 25 °C) ($P < 0.05$). The sturdiness index (SI) increased under heat stress, with seedlings at 35 °C reaching 46.1 SI, compared

Table 4 Shoot weight, leaf count, leaf area meter (LA), shoot and root dry matter of tomato seedling under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus* and *Trichoderma*)

	Shoot weight (g)	Leaf count (true)	LA (cm ²)	Shoot dry matter (%)	Roots dry matter (%)
Air Temperature					
25 °C	1.51±0.063	4.22±0.081b	31.5±1.353	11.2±0.002 a	6.35±0.348
30 °C	1.59±0.063	4.48±0.081 b	33.1±1.353	11.3±0.002 a	6.94±0.348
35 °C	1.63±0.063	4.95±0.081 a	31.9±1.353	9.4±0.002 b	6.55±0.333
Beneficial Soil Microorganisms					
Control	1.51±0.063	4.47±0.081	29.9±1.353 b	10.4±0.002	6.65±0.333
<i>Glomus</i>	1.68±0.063	4.62±0.081	34.8±1.353 a	10.5±0.002	6.91±0.348
<i>Trichoderma</i>	1.54±0.063	4.57±0.081	31.8±1.353 ab	11.0±0.002	6.29±0.348
Significances					
Air Temperature	ns	***	ns	***	ns
BSM ¹	ns	ns	*	ns	ns
Air Temperature x BSM	ns	*	*	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

**Fig. 3** Effect of air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus*, and *Trichoderma*) on cabbage leaf chlorophyll (Chl) reported as Chlorophyll Content Index (CCI), anthocyanin (ACNs) reported as anthocyanin

content index (ACI). Different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant. Bars indicate standard error

to 41.0 at 25 °C (+12%) and 44.9 at 30 °C (+3%) ($P<0.05$) (Table 5).

Shoot weight was not significantly affected by either air temperature or BSM treatments ($P>0.05$, Table 6). However, air temperature strongly influenced leaf count, leaf area (LA), and shoot dry matter. Plants grown at 35 °C produced the highest number of leaves (4.87 leaves, +19% compared to 25 °C; $P<0.05$), but with reduced LA (28.5 cm², -17% vs. 25 °C) and shoot dry matter (10.2%, -28% vs. 25 °C) ($P<0.05$). By contrast, seedlings at 25 °C and 30 °C developed fewer leaves (4.0–4.3) but maintained larger LA (33–35 cm²) and higher shoot dry matter (13–14%). Root dry matter content was not significantly affected by treatments ($P>0.05$).

Phenols and Pigment Analysis

Total phenolic content (TPC) varied significantly across air temperature treatments (Table 7). The highest TPC was observed at 35 °C (35.72 mg GAE g⁻¹ d.w., +24% compared to 30 °C; $P<0.05$), while the lowest value was recorded at 30 °C (28.90 mg GAE g⁻¹ d.w.). Regarding BSM treatments, plants inoculated with *Trichoderma* showed the highest TPC (34.84 mg GAE g⁻¹ d.w., +15% compared to control), whereas control plants had the lowest (30.30 mg GAE g⁻¹ d.w.) ($P<0.05$). A significant interaction between air temperature and BSM confirmed that phenolic accumulation depended on both factors ($P<0.05$).

Chlorophyll a, chlorophyll b, xanthophylls, and carotenoids were strongly influenced by air temperature ($P<0.001$). At 35 °C, pigment concentrations reached the

Table 5 Plant height, collar diameter, and sturdiness index of cabbage seedlings under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (Control, *Glomus* and *Trichoderma*)

	Plant height (cm)	Collar diameter (cm)	Sturdiness index
Air Temperature			
25 °C	6.81±0.085 a	0.17±0.002 a	41.0±0.738 b
30 °C	6.68±0.085 a	0.15±0.002 b	44.9±0.747 a
35 °C	5.89±0.085 b	0.13±0.002 c	46.1±0.750 a
Beneficial Soil Microorganisms			
Control	6.45±0.085	0.16±0.002	42.7±0.741
<i>Glomus</i>	6.44±0.085	0.15±0.002	44.8±0.750
<i>Trichoderma</i>	6.49±0.085	0.15±0.002	44.5±0.743
Significances			
Air Temperature	***	***	***
BSM	ns	ns	ns
Air Temperature x BSM	*	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

highest levels (Chl a: 3998 mg g⁻¹ d.w.; Chl b: 1788 mg g⁻¹ d.w.; Xan-Car: 447.3 mg g⁻¹ d.w.) compared with 25 and 30 °C. In contrast, BSM treatments and their interaction with temperature did not significantly affect pigment contents ($P>0.05$).

Cucumber

Plant Growth Measurement

Cucumber plant emergence differed under air temperatures conditions from 3 to 10 DAS (Table 8). At 3 DAS, germination was absent at 25 °C, while it reached 51% at 30 °C and 85% at 35 °C ($P<0.05$). From 4 to 10 DAS, no significant

Table 6 Shoot weight, leaf count, leaf area meter (LA), shoot and root dry matter of cabbage seedling under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (Control, *Glomus* and *Trichoderma*)

	Shoot weight (g)	Leaf count	LA (cm ²)	Shoot dry matter (%)	Roots dry matter (%)
Air Temperature					
25 °C	1.42±0.047	4.08±0.088 b	34.5±1.193 a	14.2±0.005 a	7.25±0.362
30 °C	1.51±0.047	4.32±0.088 b	33.1±1.193 a	13.8±0.005 a	8.32±0.378
35 °C	1.38±0.047	4.87±0.088 a	28.5±1.193 b	10.2±0.005 b	7.83±0.378
Beneficial Soil Microorganisms					
Control	1.45±0.047	4.42±0.088	31.9±1.193	13.7±0.005	7.27±0.378
<i>Glomus</i>	1.40±0.047	4.38±0.088	31.5±1.193	12.1±0.005	7.66±0.362
<i>Trichoderma</i>	1.46±0.047	4.47±0.088	32.7±1.193	12.3±0.005	8.47±0.378
Significances					
Air Temperature	ns	***	***	***	ns
BSM	ns	ns	ns	*	ns
Air Temperature x BSM	ns	ns	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

Table 7 Cabbage total phenolic content, chlorophyll a and b, xanthophylls, and carotenoids under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (Control, *Glomus* and *Trichoderma*)

	TPC mg GAE eq g ⁻¹ d.w.	Chl a mg pigment g ⁻¹ d.w.	Chl b mg pigment g ⁻¹ d.w.	Xan_Car mg pigment g ⁻¹ d.w.
Air Temperature				
25 °C	32.24±1.142 ab	2641±309 b	1154±143 b	320.2±30.38 b
30 °C	28.90±1.142 b	2739±309 b	1214±143 b	362.1±30.38 ab
35 °C	35.72±1.142 a	3998±309 a	1788±143 a	447.3±30.38 a
Beneficial Soil Microorganisms				
Control	30.30±1.142 b	3420±309	1509±143	420.5±30.38
<i>Glomus</i>	31.72±1.142 ab	2959±309	1328±143	349.0±30.38
<i>Trichoderma</i>	34.84±1.142 a	3000±309	1318±143	360.0±30.38
Significances				
Air Temperature	**	***	***	***
BSM	*	ns	ns	ns
Air Temperature x BSM	*	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) between treatments according to Tukey's HSD test. ns=not significant

differences were observed among air temperature or BSM treatments ($P>0.05$).

Physiological Analysis

Air temperature significantly influenced leaf chlorophyll content (Fig. 4). Plants grown at 25 °C showed higher chlorophyll values (39.2 CCI) compared to 30 °C and 35 °C

Table 8 Germination rate of cucumber seeds under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (Control, *Glomus* and *Trichoderma*). DAS indicates days after sowing

	Germination rate (%)				
	3 DAS	4 DAS	6 DAS	7 DAS	10 DAS
Air Temperature					
25 °C	0±0.026 ^c	77±0.044	90±0.021	90±0.021	94±0.019
30 °C	51±0.026 ^b	85±0.044	92±0.021	92±0.021	92±0.019
35 °C	85±0.026 ^a	93±0.044	94±0.021	94±0.021	94±0.019
Beneficial Soil Microorganisms					
Control	45±0.026	88±0.044	91±0.021	91±0.021	92±0.019
<i>Glomus</i>	46±0.026	81±0.044	89±0.021	89±0.021	91±0.019
<i>Trichoderma</i>	45±0.026	88±0.044	95±0.021	95±0.021	96±0.019
Significances					
Air Temperature	***	ns	ns	ns	ns
BSM	ns	ns	ns	ns	ns
Air Temperature x BSM	ns	ns	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) between treatments according to Tukey's HSD test. ns=not significant

(26.9 and 26.5 CCI, respectively; $P<0.05$). BSM treatments did not significantly affect chlorophyll content ($P>0.05$).

Leaf anthocyanin content was higher under 35 °C (5.3 ACI, +15% compared to 25 °C; $P<0.05$). Net photosynthetic rate (PN) was significantly influenced by the interaction between air temperature and BSM ($P<0.05$). At 35 °C, *Glomus*-treated plants exhibited the highest PN (8.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) compared to *Trichoderma* (5.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and to control plants at 30 °C (4.2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

Cucumber plant height also varied significantly among temperature treatments (Table 9). Plants at 35 °C reached 12.8 cm, compared with 7.6 cm at 25 °C (+68%; $P<0.05$). Collar diameter decreased slightly at 35 °C compared to 30 °C ($P<0.05$). The sturdiness index (SI) increased progressively with temperature, reaching 33.9 at 35 °C versus 19.8 at 25 °C (+71%; $P<0.05$). Conversely, the Dickson Quality Index (DQI) was higher at 25 °C (0.07) and decreased at 35 °C (0.05; $P<0.01$).

As shown in Table 10, the shoot weight of cucumber plants varies significantly among the air temperature conditions, with the highest weights observed for plants grown at 30 and 35 °C (4.98 and 4.42 g, respectively). Therefore, air temperature conditions influenced the number of true leaves for plants under 30 and 35 °C (4.0 and 4.2 g, respectively) ($P<0.05$). The leaf area index (LA) was higher for plants

under 30 °C (149.4 LA) than 25 and 35 °C. The shoot dry matter was affected by the air temperature conditions and BSM treatment ($P<0.05$). The BSM treatment did not demonstrate a significant difference among the plants treated with BSM ($P>0.05$). Plants under 35 °C showed a lower dry matter content (6.5%) compared to 25 °C (8.6%) and 30 °C (7.5%) *Glomus*-treated plants exhibit a higher shoot dry matter (8.2%) compared to *Trichoderma*-treated plants (6.9%). Roots dry matter content was higher for *Glomus* and *Trichoderma*-treated plants (6.9 and 6.5%) ($P<0.05$).

Phenols and Pigment Analysis

Total phenolic content (TPC) did not differ significantly among air temperature or BSM treatments ($P>0.05$; Table 11). In contrast, chlorophyll content varied with temperature. The highest chlorophyll a levels were recorded at 35 °C (5381 mg pigment g^{-1} d.w.) and 25 °C (4371 mg pigment g^{-1} d.w.), both significantly higher than at 30 °C ($P<0.05$). Chlorophyll b content was also highest at 35 °C (2437 mg pigment g^{-1} d.w.) compared to 30 °C and 25 °C ($P<0.05$). Xanthophyll and carotenoid contents did not vary significantly among temperature treatments ($P>0.05$). Similarly, BSM treatments had no significant effect on any of the measured parameters ($P>0.05$).

Melon

Plant Growth Measurement

Plant emergence differed significantly under varying air temperature conditions from 3 to 7 DAS (Table 12). At 3 DAS, germination was lowest at 25 °C (0%), intermediate at 30 °C (8%), and highest at 35 °C (72%) ($P<0.05$). By 7 DAS, germination reached 85% at 25 °C compared to 97% at 30 and 35 °C ($P<0.05$). At 10 DAS, however, germination rates did not differ among treatments ($P>0.05$). BSM treatments had no significant effect on emergence ($P>0.05$).

Physiological Analysis

Air temperature significantly influenced leaf chlorophyll content (Fig. 5). Plants at 25 °C (14.72 CCI) and 35 °C (14.04 CCI) showed higher chlorophyll values than those at 30 °C ($P<0.05$). *Trichoderma*-treated plants under 35 °C exhibited the highest chlorophyll content (16.44 CCI) (+17% compared to control). Anthocyanin content also increased under 35 °C (3.41 ACI), about +13% higher than at 25 °C ($P<0.05$). The net photosynthesis rate (P_N) did not show a significant interaction between air temperature conditions and BSM treatment ($P>0.05$).

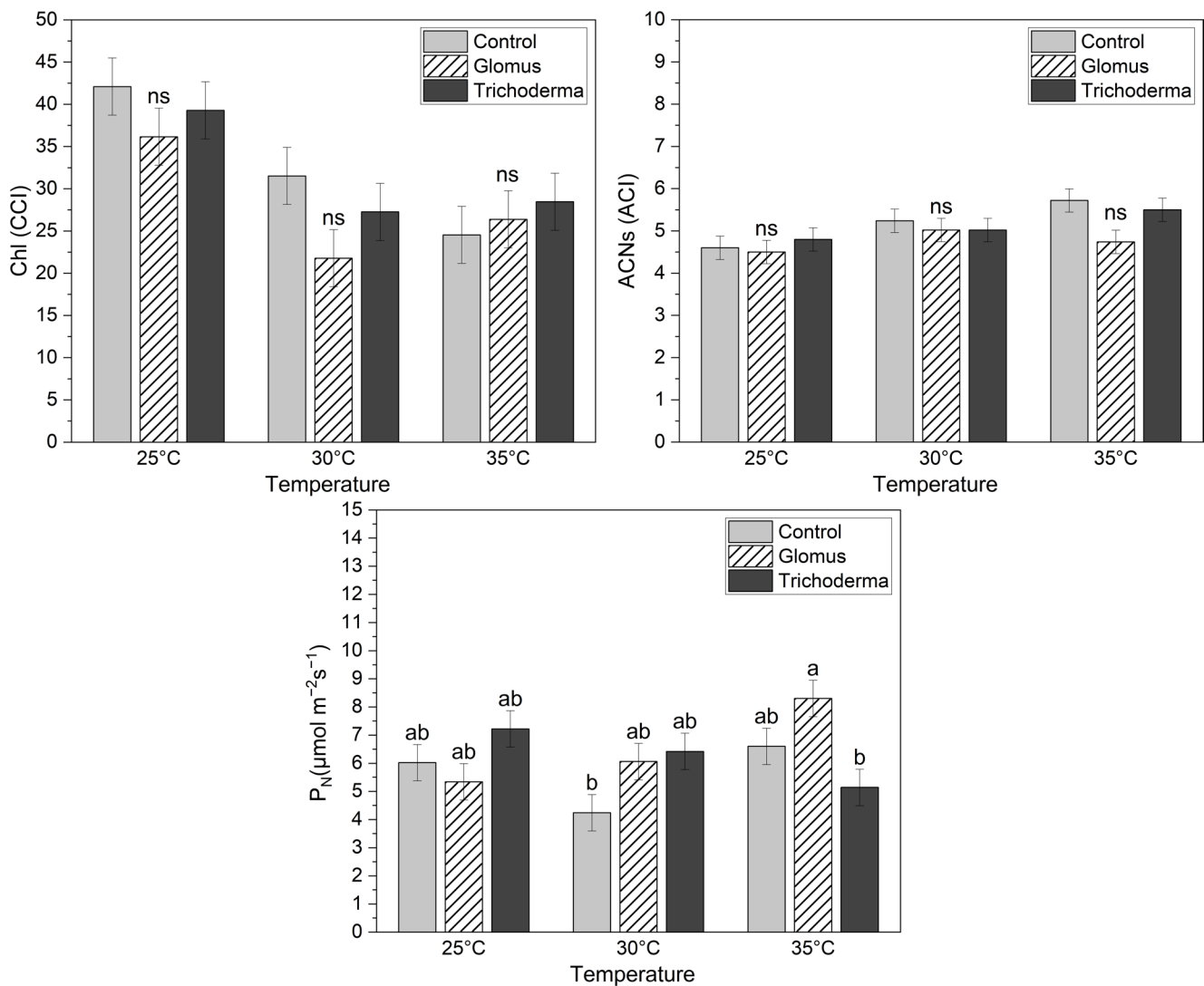


Fig. 4 Effect of air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus* and *Trichoderma*) on cucumber leaf chlorophyll (Chl) reported as Chlorophyll Content Index (CCI), Anthocyanin (ACNs) reported as Anthocyanin

Content Index (ACI) and net photosynthesis (P_N). Different letters indicate significant differences ($P < 0.05$) among treatments according to Tukey's HSD test. ns = not significant. Bars indicate standard error

Air temperature strongly affected plant morphology (Table 13). Plant height increased from 13.0 cm at 25 °C to 31.1 cm at 35 °C ($P < 0.05$). BSM also influenced height: *Trichoderma*-treated plants (25.5 cm) were significantly taller than *Glomus*-treated plants (22.6 cm). A significant interaction was observed, with *Trichoderma* at 30 °C and the control at 35 °C producing the tallest plants. Collar diameter decreased slightly at 35 °C (0.28 cm) compared to 25 °C (0.33 cm) ($P < 0.05$). The Sturdiness index increased markedly with temperature, from 40.0 at 25 °C to 113 at 35 °C (+182%, $P < 0.05$). Conversely, the DQI was highest at 25 °C (0.03) and decreased under 30–35 °C (0.02) ($P < 0.05$).

Shoot weight also responded to air temperature (Table 14). Plants grown at 30 °C (5.38 g) and 35 °C (5.17 g)

were significantly heavier than those at 25 °C (3.25 g), representing increases of +65% and +59%, respectively ($P < 0.05$). Leaf number rose sharply with temperature, from 2.9 leaves at 25 °C to 6.2 at 35 °C ($P < 0.05$). Leaf area (LA) also increased significantly at 30–35 °C compared to 25 °C. Root dry matter content was highest at 35 °C (8.81%), about +52% greater than at 25 °C (5.8%) ($P < 0.05$). BSM treatments had a limited influence, though *Trichoderma*-treated plants showed slightly higher leaf area and shoot weight compared to *Glomus*.

Phenols and Pigment Analysis

No significant differences were observed in TPC, xanthophylls, or carotenoid content among treatments ($P > 0.05$;

Table 9 Plant height, collar diameter, sturdiness index (SI), and Dickson quality index (DQI) of cucumber seedlings under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus* and *Trichoderma*)

	Plant height (cm)	Collar diameter (cm)	SI	DQI
Air Temperature				
25 °C	7.6±0.295 c	0.38±0.066 ab	19.8±0.780 c	0.07±0.004 a
30 °C	11.4±0.295 b	0.40±0.066 a	28.5±0.780 b	0.06±0.004 ab
35 °C	12.8±0.295 a	0.38±0.066 b	33.9±0.780 a	0.05±0.005 b
Beneficial Soil Microorganisms				
Control	10.3±0.295	0.38±0.066	27.1±0.780	0.05±0.003
<i>Glomus</i>	10.5±0.195	0.38±0.066	27.2±0.780	0.06±0.005
<i>Trichoderma</i>	11.0±0.195	0.40±0.066	27.9±0.780	0.06±0.005
Significances				
Air Temperature	***	*	***	**
BSM	ns	ns	ns	ns
Air Temperature x BSM	ns	*	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

Table 15). However, chlorophyll a and b contents peaked at 30 °C, with values of 5066 and 1912 mg pigment g⁻¹ d.w., respectively ($P<0.05$). This represented a +30% increase in Chl a and a +61% increase in Chl b compared to 25 °C. BSM treatments did not significantly affect any measured parameters, and no significant interactions with air temperature were detected ($P>0.05$).

Table 10 Shoot weight, leaf count, leaf area meter (LA), shoot and root dry matter of cucumber seedling under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control with tap water, *Glomus* and *Trichoderma*)

	Shoot weight (g)	Leaf count	LA (cm ²)	Shoot dry matter (%)	Roots dry matter (%)
Air Temperature					
25 °C	3.67±0.179 b	3.07±0.091 b	109±5.943 b	8.58±0.003 a	5.98±0.003
30 °C	4.98±0.179 a	4.04±0.091 a	149±5.943 a	7.47±0.003 b	6.39±0.003
35 °C	4.42±0.179 a	4.24±0.091 a	115±5.943 b	6.53±0.003 c	6.73±0.003
Beneficial Soil Microorganisms					
Control	4.25±0.179	3.80±0.091	125±5.943	7.56±0.003 ab	5.71±0.002 b
<i>Glomus</i>	4.25±0.179	3.64±0.091	121±5.943	8.16±0.003 a	6.86±0.003 a
<i>Trichoderma</i>	4.57±0.179	3.91±0.091	127±5.943	6.87±0.003 b	6.54±0.003 a
Significances					
Air Temperature	***	***	***	***	ns
BSM	ns	ns	ns	***	***
Air Temperature x BSM	ns	ns	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

Table 11 Cucumber total phenolic content (mg Gallic acid equivalent g⁻¹ dry weight), chlorophyll a and b, xanthophylls, and carotenoids (mg pigment g⁻¹ dry weight) under different air temperature conditions (25, 30, and 35 °C). Beneficial soil microorganisms (BSM) (Control, *Glomus*, and *Trichoderma*)

	TPC mg GAE eq g ⁻¹ d.w.	Chl a mg pigment g ⁻¹ d.w.	Chl b mg pigment g ⁻¹ d.w.	Xan_Car mg pigment g ⁻¹ d.w.
Air Temperature				
25 °C	56.84±3.566 b	4371±208.2 b	1605±141.5 b	688.9±22.75
30 °C	58.44±3.566 b	4505±208.2 b	1616±141.5 b	770.3±22.75
35 °C	64.74±3.566 a	5381±208.2 a	2437±141.5 a	758.8±22.75
Beneficial Soil Microorganisms				
Control	56.27±3.566	4677±208.2	1896±141.5	719.9±22.75
<i>Glomus</i>	62.58±3.566	4712±208.2	1846±141.5	739.1±22.75
<i>Trichoderma</i>	61.17±3.566	4867±208.2	1916±141.5	759.1±22.75
Significances				
Air Temperature	ns	**	**	ns
BSM	ns	ns	ns	ns
Air Temperature x BSM	ns	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) between treatments according to Tukey's HSD test. ns=not significant

Determination of BSM Concentration in the Rhizosphere

As shown in Fig. 6, the *Fungi Incertae sedis* group reached the highest relative abundance in the *Glomus* treatment at 25 °C (0.48) and in the *Trichoderma* treatment at 25 °C

Table 12 Germination rate of melon seeds under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus*, and *Trichoderma*)

	Germination rate (%)				
	3 DAS	4 DAS	6 DAS	7 DAS	10 DAS
Air Temperature					
25 °C	0±0.057 b	4±0.031 b	85±0.029 b	85±0.029 b	100±0.017
30 °C	8±0.062 b	95±0.034 a	97±0.031 a	97±0.031 a	97±0.019
35 °C	72±0.057 a	95±0.031 a	97±0.029 a	97±0.029 a	97±0.017
Beneficial Soil Microorganisms					
Control	36±0.062	60±0.031	89±0.029	89±0.029	95±0.017
<i>Glomus</i>	22±0.057	65±0.031	94±0.029	94±0.029	98±0.017
<i>Trichoderma</i>	22±0.057	69±0.034	97±0.031	97±0.031	100±0.019
	Significances				
Air Temperature	***	***	*	*	ns
BSM	ns	ns	ns	ns	ns
Air Temperature x BSM	ns	ns	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

(0.30). This group decreased sharply at higher temperatures, with abundances dropping to 0.05 in *Trichoderma* at 35 °C and 0.06 in the control at the same temperature. In contrast, the *Ascomycota Trichoderma* group showed the highest abundance in the *Trichoderma* treatment at 30 °C (0.52) and remained relatively high in the *Trichoderma* treatment at 35 °C, while being nearly absent or very low in the *Glomus* treatments across all temperatures and in the control at 25 °C and 30 °C. Overall, the relative abundance of general fungi was higher in *Glomus* treatments under both 30 °C and 35 °C conditions compared to the control and *Trichoderma* treatments.

In the dendrogram (Fig. 7), each branch represents a group of substrate samples, and the way branches join reflects their similarity. Samples that cluster together at a lower level are more similar to each other. The horizontal length of the branches indicates the degree of similarity, with shorter branches representing higher similarity. *Glomus* at 30 °C and 35 °C clustered closely, as indicated by the short branch connecting them. Similarly, *Trichoderma* at 30 °C and 35 °C, as well as the control at 30 °C and 35 °C, showed strong similarity. *Trichoderma* at 25 °C and the control at 25 °C also grouped together, suggesting comparable microbial communities under those conditions.

The red numbers on the branches represent bootstrap values, which indicate the confidence level of the clustering. A value of “1” corresponds to 100% confidence, meaning the clustering was consistently supported in all bootstrap resamplings. In contrast, a value of “0.444” (44.4% confidence) indicates weaker support for that particular cluster.

Discussion

The mechanisms underlying the interactions between plant species and beneficial soil microorganisms (BSM) during heat stress remain poorly understood (Mathur et al. 2021). This study provides insights into the physiological and morphological responses of tomato, cabbage, cucumber, and melon seedlings inoculated with fungal symbionts under heat-stress conditions.

Plant Growth Measurement

Trichoderma spp. are widely reported to promote seed germination and early seedling growth. For example, *T. harzianum* enhanced tomato seedling tolerance to abiotic stress (Mastouri et al. 2010) and improved cucumber root and shoot development (Yedidia et al. 2001; Lian et al. 2023). In melon (*Cucumis melo* cv. ‘Helios’), arbuscular mycorrhizal fungi (AMF) increased drought tolerance and fruit quality traits under deficit irrigation (Miceli et al. 2023).

In our trial, seedling emergence was not significantly affected by BSM treatments, likely due to the short nursery cycle (3–4 weeks), which limited the establishment of effective colonization (Smith and Read 2010). Similar conclusions have been drawn in cereals, where beneficial effects of stress priming became evident only after longer exposure or across generations (Ju et al. 2025; Suriyasak et al. 2025). Germination was faster at 30–35 °C across all four species, consistent with reports that moderate heat accelerates enzymatic activities (e.g., α -amylase) and hormonal changes (ABA/GA balance), thereby promoting early germination (Wahid et al. 2007; Hasanuzzaman et al. 2013). However, severe or prolonged heat reduces protein stability and membrane integrity, lowering final germination rates (Lu et al. 2025).

Consistent with this, Azarmi et al. (2011) found no significant differences in tomato germination between *Trichoderma*-treated and untreated seeds, while Mastouri et al. (2010) reported that *T. harzianum* T22 accelerated germination speed at 35 °C without altering final germination percentages.

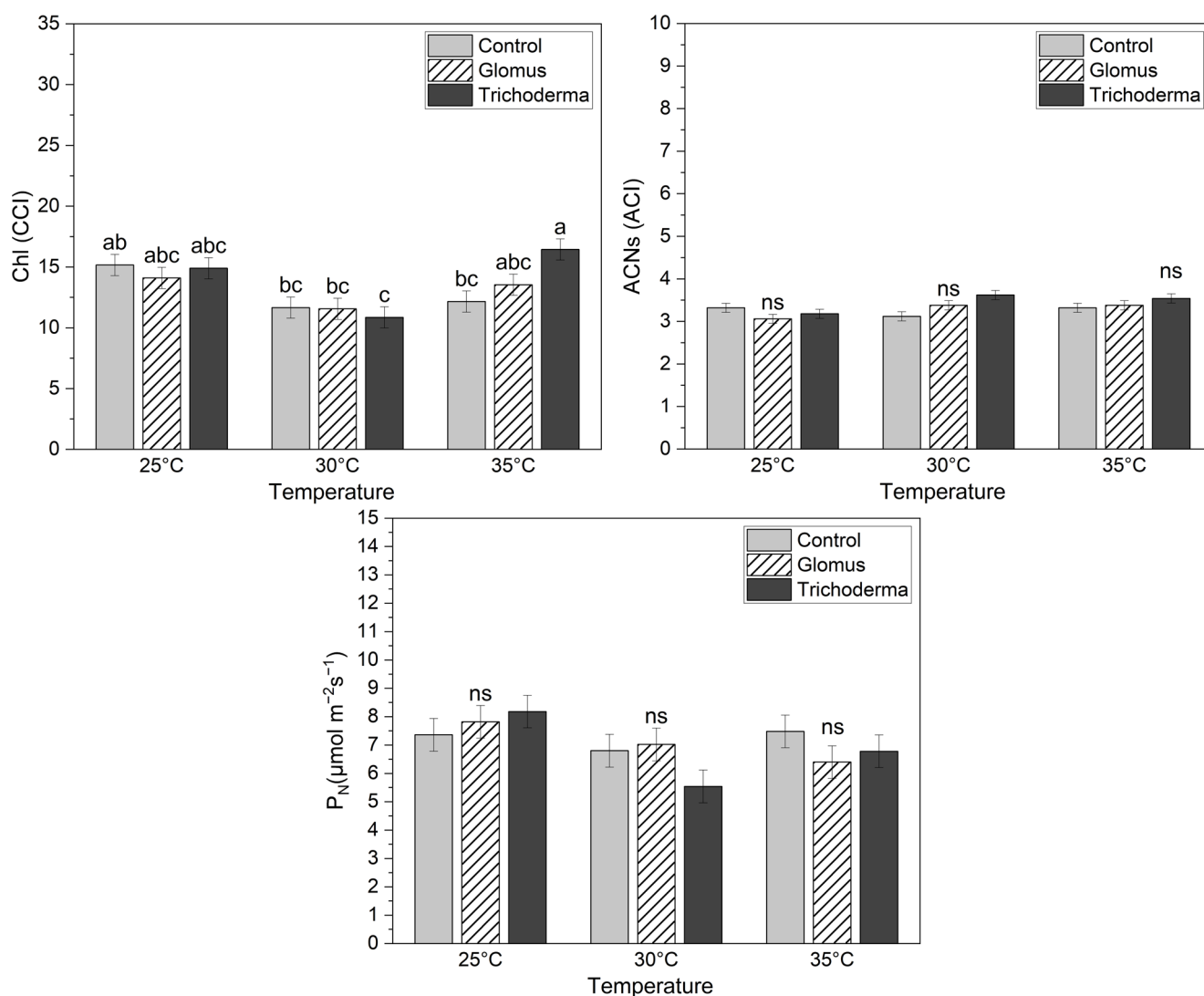


Fig. 5 Effect of air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control with tap water, *Glomus* and *Trichoderma*) on melon leaf chlorophyll (Chl) reported as Chlorophyll Content Index (CCI), Anthocyanin (ACNs) reported as Anthocy-

anin Content Index (ACI) and net photosynthesis (P_N). Different letters indicate significant differences ($P < 0.05$) among treatments according to Tukey's HSD test. ns = not significant. Bars indicate standard error

Physiological Analysis

High-temperature stress disrupts the photosynthetic apparatus by reducing PSII efficiency, impairing Rubisco activity, and enhancing ROS production, which destabilizes chloroplast membranes (Hasanuzzaman et al. 2013; Wahid et al. 2007). Anthocyanins act as antioxidants in these conditions (Zhang et al. 2019), yet their accumulation is highly species- and genotype-dependent (Ke et al. 2025). In our study, cucumber and melon showed increased anthocyanin levels at 35 °C, suggesting a species-specific response, as heat stress is generally known to suppress anthocyanin biosynthesis in many plants. By contrast, tomato and cabbage showed no significant response, confirming that induction is not universal across species or cultivars (Ke et al. 2025).

BSM are known to enhance host performance under stress (Kohler et al. 2007; Brotman et al. 2013). Liu et al. (2023) demonstrated that AMF increased chlorophyll content and induced heat shock proteins in cucumber, while Senizza et al. (2023) showed that *Trichoderma* mitigated combined heat and drought stress in *Arabidopsis thaliana*. In our case, however, no significant BSM effects emerged, probably due to strain-specific variability and the limited colonization period of the nursery phase. Morphologically, plant height increased in melon and cucumber at higher temperatures, decreased in cabbage, and was unaffected in tomato, partly consistent with Zhou et al. (2017), who found no significant height or leaf number changes in heat-stressed tomato cultivars.

Table 13 Plant height, collar diameter, sturdiness index (SI), and Dickson quality index (DQI) of melon seedlings under heat stress conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus* and *Trichoderma*)

	Plant height (cm)	Collar diameter (cm)	SI	DQI
Air Temperature				
25 °C	13.0±0.746 c	0.33±0.068 a	40.0±3.053 c	0.03±0.002 a
30 °C	28.0±0.746 b	0.31±0.068 a	91.9±3.053 b	0.02±0.002 b
35 °C	31.1±0.746 a	0.28±0.068 b	113.0±3.053 a	0.02±0.002 b
Beneficial Soil Microorganisms				
Control	24.0±0.746 ab	0.32±0.068	80.4±3.053	0.03±0.002
<i>Glomus</i>	22.6±0.746 b	0.30±0.068	78.5±3.053	0.03±0.002
<i>Trichoderma</i>	25.5±0.746 a	0.31±0.068	86.0±3.053	0.02±0.002
Significances				
Air Temperature	***	***	***	***
BSM	*	ns	ns	ns
Air Temperature x BSM	***	ns	*	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

Interestingly, seedlings of all species showed increased water content and reduced dry matter as temperature rose, a pattern contrary to typical stress-induced dehydration. The absence of BSM effects here suggests that their benefits may become more evident under nutrient deficiency or prolonged

Table 15 Melon total phenolic content (mg Gallic acid equivalent g⁻¹ dry weight), chlorophyll a and b, xanthophylls, and carotenoids (mg pigment g⁻¹ dry weight) under different air temperature conditions (25, 30, and 35 °C). Beneficial soil microorganisms (BSM) (Control, *Glomus*, and *Trichoderma*)

	TPC mg GAE eq g ⁻¹ d.w.	Chl a mg pigment g ⁻¹ d.w.	Chl b mg pigment g ⁻¹ d.w.	Xan_Car mg pigment g ⁻¹ d.w.
Air Temperature				
25 °C	84.05±4.165	3895±217.2 b	1185±107.5 b	630.9±23.15
30 °C	81.56±4.165	5066±217.2 a	1912±107.5 a	680.3±23.15
35 °C	71.17±4.165	3885±217.2 b	1328±107.5 b	653.4±23.15
Beneficial Soil Microorganisms				
Control	75.63±4.165	4258±217.2	1445±107.5	656.2±23.15
<i>Glomus</i>	81.31±4.165	4078±217.2	1415±107.5	623.9±23.15
<i>Trichoderma</i>	79.83±4.165	4510±217.2	1566±107.5	684.4±23.15
Significances				
Air Temperature	ns	**	***	ns
BSM	ns	ns	ns	ns
Air Temperature x BSM	ns	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

drought, rather than acute heat stress. Yeasmin et al. (2019), for example, found that *Glomus intraradices* alleviated heat stress in asparagus by improving biomass, underscoring the importance of host–microbe specificity.

Table 14 Shoot weight, leaf count, leaf area meter (LA), shoot and root dry matter of melon seedling under different air temperature conditions (25, 30, and 35 °C) and beneficial soil microorganisms (BSM) (Control, *Glomus* and *Trichoderma*)

	Shoot weight (g)	Leaf count	LA (cm ²)	Shoot dry matter (%)	Roots dry matter (%)
Air Temperature					
25 °C	3.25±0.205 b	2.87±0.138 c	70.8±5.608 b	6.91±0.002	5.80±0.006 b
30 °C	5.38±0.205 a	5.13±0.138 b	130±5.608 a	7.24±0.002	6.13±0.006 b
35 °C	5.17±0.205 a	6.22±0.138 a	117±5.608 a	6.90±0.002	8.81±0.006 a
Beneficial Soil Microorganisms					
Control	4.66±0.205 ab	4.76±0.138 ab	107±5.608 ab	7.04±0.002	7.73±0.006
<i>Glomus</i>	4.05±0.205 b	4.42±0.138 b	94.9±5.608 b	6.97±0.002	6.72±0.006
<i>Trichoderma</i>	5.09±0.205 a	5.04±0.138 a	115±5.608 a	7.05±0.002	6.29±0.006
Significances					
Air Temperature	***	***	***	ns	***
BSM	*	**	*	ns	ns
Air Temperature x BSM	ns	ns	ns	ns	ns

Means are followed by standard error, and different letters indicate significant differences ($P<0.05$) among treatments according to Tukey's HSD test. ns=not significant

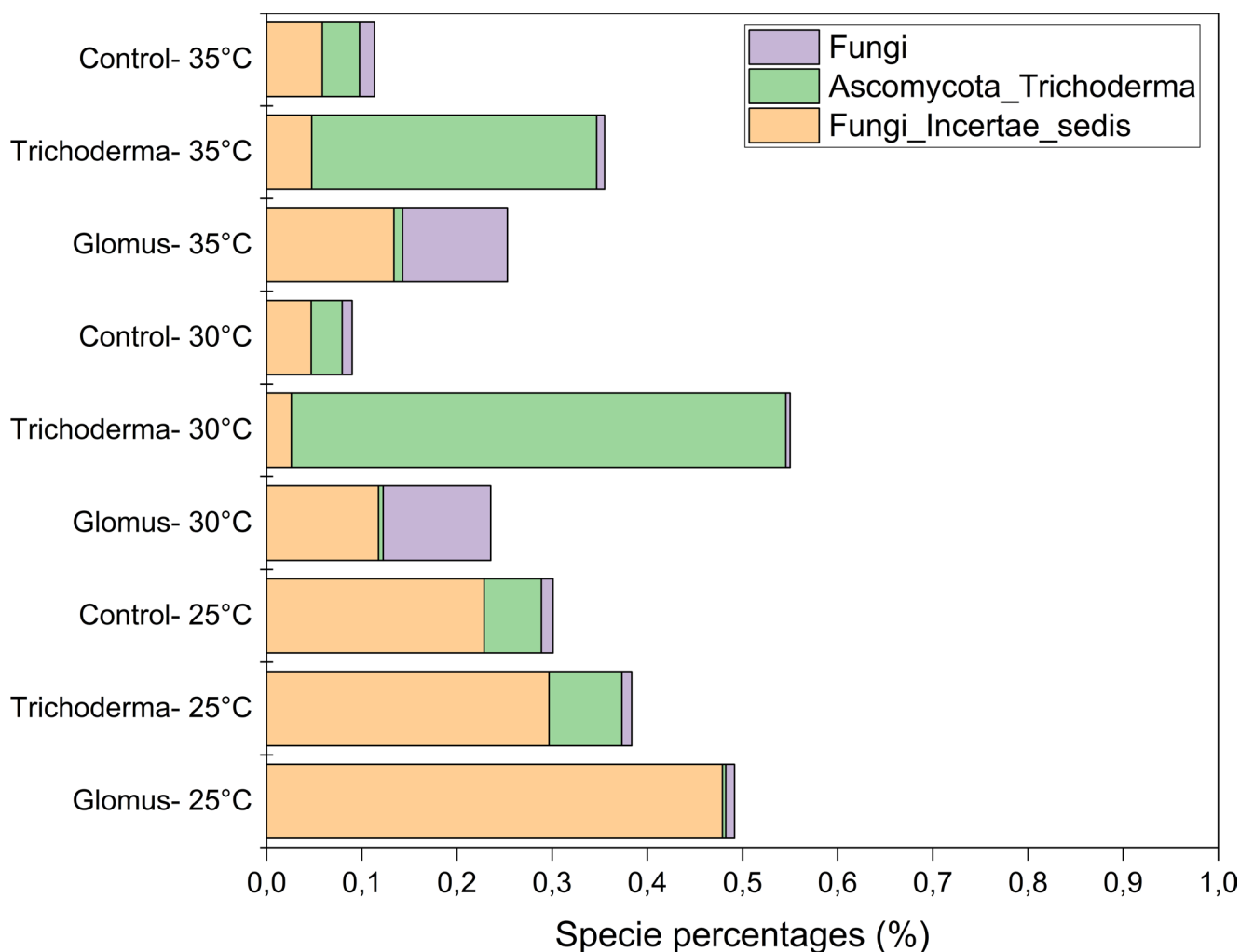


Fig. 6 The taxonomy distribution of all substrate sample expressed in species percentages (%)

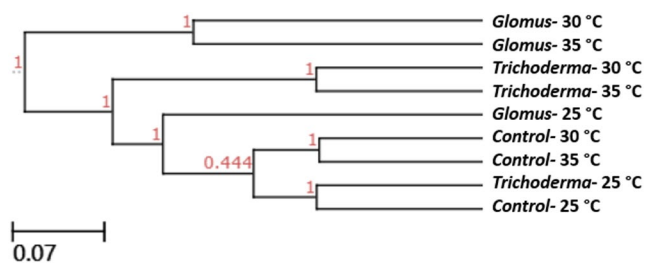


Fig. 7 UPGMA clustering tree based on weighted unifrac

Phenols and Pigment Analysis

Alhaithloul et al. (2021) reported that extreme heat reduced total phenolic content (TPC) in tomato seedlings from ≈ 131 to ≈ 67 mg GAE 100 g^{-1} FW. In contrast, our results showed no effect of temperature on tomato TPC, suggesting that phenolic metabolism may be less responsive to short-term heat or that stress duration was insufficient to trigger declines (Hasanuzzaman et al. 2013).

No significant effects of BSM inoculation on TPC or pigments were detected, consistent with the strong strain- and host-dependency of microbial impacts (Smith and Read, 2017). Contrasting reports exist: Jam et al. (2023) reported a 15.2% increase in SPAD chlorophyll values in peanut leaves after *Trichoderma* inoculation, whereas Yu et al. (2021) observed reduced chlorophyll levels with a different *T. asperellum* strain. Likewise, Zhang et al. (2018) demonstrated that *Glomus mosseae* enhanced chlorophyll and photosynthetic traits in ryegrass under cadmium stress. More recently, Liu et al. (2025) found that *Trichoderma viride* improved antioxidant defenses and photosynthetic efficiency in melon, highlighting that microbial contributions to pigment stability require strain–host compatibility and sufficient colonization.

Rhizosphere Analysis

The dendrogram analysis showed distinct clustering of treatments with Glomus and Trichoderma, reflecting their temperature-specific responses. AMF colonization is particularly sensitive to heat. Martin and Stutz (2004) reported reduced colonization of *Glomus intraradices* in pepper at 38 °C, while Mathur et al. (2021) found that heat stress in maize reduced AMF colonization by impairing spore viability and root signalling. Similarly, Jia et al. (2023) showed that temperatures rising from 29 to 32 °C reduced *G. mosseae* colonization in alfalfa under cadmium stress. Our findings are consistent, with the commercial Glomus mix showing lower colonization and reduced plant growth promotion at 30–35 °C compared to 25 °C.

For *Trichoderma*, Singh et al. (2014) reported optimal growth of *T. harzianum* at 25 °C, while Poosapati et al. (2014) showed that most *T. asperellum* and *T. harzianum* strains failed to germinate at 35 °C, with only a few isolates retaining partial thermotolerance. Similarly, Sala et al. (2020) noted that spore production in *T. harzianum* was optimal at 25 °C, consistent with the stronger colonization observed at lower temperatures in our study. These results underscore that both AMF and Trichoderma colonization efficiencies are constrained by heat, highlighting the need for selecting thermotolerant strains for nursery applications under rising temperatures.

Conclusions

As global temperatures continue to rise, understanding the mechanisms by which BSM influence heat stress tolerance in plants becomes increasingly critical. The results of the present study did not reveal significant differences among the BSM tested, suggesting that none of the examined symbionts were particularly effective in mitigating thermal stress. Maybe the short duration of a nursery cycle is sufficient to allow mycorrhizal associations to fully develop and express their potential benefits under heat stress conditions. Data analysis revealed that air temperature had a significant influence on the considered parameters, whereas the effects of BSM were non-significant. This suggests that, under the experimental conditions examined, temperature had a predominant effect over microbial inoculation. Nevertheless, the results of this study contribute to advancing the understanding of plant–endophyte interactions under heat stress and provide practical insights for crop management during the critical early phases of nursery production. Future research should focus on strain-specific thermotolerance and the selection of microbial inoculants that can maintain effectiveness across varying nursery temperature regimes.

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Data Availability All data generated or analyzed during this study are included in the manuscript. For further inquiries, please contact the corresponding author.

Declarations

Conflicts of interest The authors declare no conflicts of interest.

Consent for Publication All authors have read and approved the final version of the manuscript.

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