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RETRACTED: Individual and Interactive Ecophysiological Effect of Temperature, Watering Regime and Abscisic Acid on the Growth and Development of Tomato Seedlings

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Abstract: Climate change is a major concern to people all over the world. Most studies have considered singular or dual effects of climate change implications on plant growth and development; however, the combination of multiple factors has received little attention. We therefore studied the single and combined effects of two environmental stress factors (high temperature and water stresses) and abscisic acid on tomato seedlings (*Solanum lycoperscum* L.). Plants were grown in controlled environment growth chambers under two temperatures (22/18 °C or 28/24 °C; 16 h light/8 h dark), two watering regimes (well-watered or water-stressed), and two abscisic acid treatments (0 and 100 µL of 1mM abscisic acid solution, every other day). Plants were placed under experimental conditions for a total of 33 days, including a 13-day period of initial growth and hardening. Morphological, biochemical, and physiological parameters were measured to assess the growth and development of plants in response to the three factors. ANOVA and Scheffé's multiple-comparison procedures were used to establish significant differences among treatments and among the three factors being manipulated. All three factors decreased plant height and growth rate. Dry mass accumulation was negatively affected by high temperatures. Transpiration, stomatal conductance, and gas exchange parameters were negatively affected by all three factors; additionally, net carbon dioxide assimilation was reduced by water stress and abscisic acid application. Non-photochemical quenching was decreased in plants grown under higher temperature and in abscisic acid-treated plants. Though it was not significant, abscisic acid appears to mitigate the negative effect of higher temperature and water stress on the nitrogen balance index and total chlorophyll content.

Keywords: abscisic acid; biomass; tomato; *Solanum lycoperscum* L.; climate change; growth and development; global warming; temperature; water stress

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Citation: Al-Deeb, T.; Abo Gamar, M.; Khaleel, S.; Al-Ghzawi, A.L.; Al Khateeb, W.; Jawarneh, M.; Jahmani, M.Y.; Al-Zoubi, O.; Habeeb, T. RETRACTED: Individual and Interactive Ecophysiological Effect of Temperature, Watering Regime and Abscisic Acid on the Growth and Development of Tomato Seedlings. *Agronomy* **2023**, *13*, 930. https://doi.org/10.3390/agronomy13030930

Academic Editor: Guangsheng Zhou

Received: 11 February 2023
Revised: 5 March 2023
Accepted: 10 March 2023
Published: 21 March 2023
Retracted: 22 January 2025

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1. Introduction

The issue of global warming and climate change is at the forefront of many minds in communities worldwide, both scientific and non-scientific. Due to the release of compounds known as greenhouse gases into Earth's atmosphere, the temperature of the globe is rising at an alarming rate [1]. This increase in temperature is causing drastic changes to agricultural areas, as well as natural ecosystems [2–4]. Due to the stressors brought by global warming, plants must adapt in order to mitigate negative effects [5]. The decrease in the ozone layer coupled with increase in greenhouse gases release will lead to temperature rising and a higher intensity of water stress [6]. Humans, according to the Intergovernmental Panel on Climate Change (IPCC), have made a major contribution to the warming of the earth; through activities such as, fossil fuel burning and greenhouse gases release. Even

This paper has been retracted. A retraction notice was published on 22 January 2025 in *Agronomy* **2025**, *15*, 266. https://doi.org/10.3390/agronomy15020266

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with protocols in place to slow down the release of greenhouse gases, the effects of global warming will be seen for many years to come [7].

High temperature is a major climate change factor and can irreversibly harm plant growth and development [8]. Heat stress happened when temperature exceeded the optimum temperature of the plant [9]. Overall, heat stress reduces plant biomass by decreasing photosynthesis, and increasing stomatal conductance and transpiration [10]. Previous studies reported that photosynthesis rate is decreased at high temperatures in different ways, such as Rubisco deactivation [11], increasing mitochondrial respiration [12] and reducing the activity of photosystem II [13]. In addition, higher temperatures have been shown to damage the thylakoid membrane, and thus, to decrease the ATP production and increase the permeability of the thylakoid membrane to H^+ ions [14]. Heat stressed *Quercus velutina* and *Quercus alba* [15] and *Quercus rubra* and *Pinus taeda* [16] seedlings showed significant reduction in growth and photosynthetic rate. Higher temperature reduces dry mass accumulation and lowers the ratio of shoot to root mass [17]. In potato (*Solanum tuberosum* L.) seedlings, the increase in temperature led to reduce chlorophyll concentration, and photosystem II and enzyme activities [18]. Gametophyte damage and failure of fertilization occurred in faba bean plants grown under high temperature [19].

Water stress is the main threat and the most harmful stress factor among the abiotic stress factors on plant seedlings [20]. Plants exposed to water stress are affected by a range of visible symptoms, such as a decrease in the stem elongation and leaf expansion [21,22]. Moreover, water stress decreases stomatal conductance [23]. Reductions in the rate of carbon uptake, total dry mass, plant height, stem diameter, leaf gas exchange and increased oxidative damage have been found in plant seedlings grown under water stress [24]. In drought-stressed cotton leaves, the rate of photosynthesis was reduced to 66% in comparison to non-stressed leaves [25]. Different faba bean genotypes responded differently to different water regimes [26]. Drought stress led to significant reduction in leaves number and size, shoot dry weight and seed production in faba bean plants [27].

Hormone levels within plants are affected by a variety of stressors, from the minute to the extreme. Abscisic acid is an important stress and development hormone present in plants, and responds to both heat and water stress [28]. It is present in most major plant organs and is involved in stomatal closure, leaf abscission, reduction of reactive oxygen species, seed dormancy, and seedling development [28–30]. Crop sustainability with regards to climate change and global warming is a topic of great concern for people all over the globe. Earlier studies have looked at temperature [31,32] or watering regime [33–35] or abscisic acid [28,29,36] some have examined a combination of two of them [9,37–39]. To date, however, no studies have been found to examine the interactive effects of temperature, watering regime, and abscisic acid applications on tomato seedlings.

In this study, we used tomato (*Solanum lycopersicum* L.) as an experimental plant. The purpose of this study was to determine the collective effects of temperature, watering regime, and exogenous abscisic acid applications on tomato plants. Results of this study should provide further information about plant stress responses as well as potential alleviation of stress factors due to abscisic acid applications, and help us to predict the effects of this hormone on crops in future climates.

2. Materials and Methods

2.1. Plant Material and Growth Conditions

Seeds from tomato plants were placed into Petri dishes containing blue germination blotters. Each Petri dish was given 10 mL of distilled water to begin germination; afterwards, water was given as needed. Controlled environment growth chambers (Model PGR15, Conviron, Controlled Environments Ltd., Winnipeg, MB, Canada) were used to incubate petri dishes under 22°/18 °C (16 h light/8 h dark) and photosynthetic photon flux density (PPFD) of 600 photon m^{-2} s^{-1} (daily monitored), and the radicle growth was daily monitored. Once exhibiting radicles 2 mm in length, seeds were moved to new Petri dishes. The germination process, in total, lasted roughly 7 days. A mixture of Perlite, Vermiculite,

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and peat moss (1:1:2, by volume) was used to transplant seedling, after the majority of seeds from each Petri dish had grown to an adequate length and exhibited cotyledons. After being placed into the soil mixture, approximately 30 pellets of nutricote-controlled NPK fertilizer (14-14-14, Type 100, Chissor-Asahi® Fertiliser Co. Ltd., Tokyo, Japan) were added to each pot. Seedlings were watered using a fine-spray. Watering was gradually increased in spray size as the plants grew larger and hardier. Seedlings were grown in the lower temperature growth chamber for a period of 5 days until established and having produced their first foliage leaves. At the emergence of the first foliage leaves, all seedlings were measured for height, placed under one of the eight treatments by random selection, and labeled. Light in the growth chambers was provided by incandescent lamps (Philips 40 W/120 W; Huixquilucan, Estado de México, Mexico) and fluorescent bulbs (Sylvania Pentron FP39/841/HO/ECO; Wilmington, MA, USA). The light output was measured by a sensor in the growth chamber.

Tomato plants were randomly assigned to lower (22 °C day/18 °C night) or higher (28 °C day/24 °C night) temperature growth chambers, each 16 h light/8 h dark. Under each temperature regime, half of the plants were watered to field capacity (well-watered) and half were watered at the leaf wilting point (water-stressed). Abscisic acid applications (G) were given to half of the plants under each watering regime, while the other plants received distilled water treatments (100 µL of distilled water); these solutions were applied to the apical meristem of each plant every second day. In total, eight different experimental treatments were used:

(1) Lower temperature, well-watered, with no abscisic acid application.
(2) Lower temperature, well-watered, with abscisic acid application.
(3) Lower temperature, water-stressed, with no abscisic acid application.
(4) Lower temperature, water-stressed, with abscisic acid application.
(5) Higher temperature, well-watered, with no abscisic acid application.
(6) Higher temperature, well-watered, with abscisic acid application.
(7) Higher temperature, water-stressed, with no abscisic acid application.
(8) Higher temperature, water-stressed, with abscisic acid application.

Under their respective treatment, plants were grown for 21 days in one of the two Conviron growth chambers (Model PGR15, Conviron, Controlled Environments Ltd., Winnipeg, MB, Canada). Each chamber held four trays of plants; the first with experimental treatments 1 through 4 (the lower temperature treatments), and the second with experimental treatments 5 through 8 (the elevated temperature treatments). Trays were rotated within the chamber every second day, prior to their distilled water/abscisic acid applications, in order to decrease the variation in growth due to placement within the chambers. The experiment was replicated three times in order to show reproducibility.

2.2. Plant Growth

After 21 days of growth, stem height was measured from the soil surface to apical meristem of each surviving plant using a ruler. Stem diameter was also measured on each plant using a Digimatic caliper (Mitutoyo Corp. Kanagawa, Japan) placed at the midway point between soil and the apical meristem. The three plants showing average growth, per condition, were harvested and dried at 60 °C for 72 h in a forced air Fisher Isotemp® Premium oven (Model 750F, Fisher Scientific, Nepean, ON, Canada) in order to determine the leaf mass, stem mass, root mass, and leaf area. An average-sized leaf from each plant was removed and weighed on an analytical balance (Model ED224s, Sartorius Extend, Sartorius Mechatronics, Goettingen, Germany) before and after drying in order to determine the leaf moisture content. Leaf area of each plant was determined using a ΔT area meter (Delta-T Devices, Cambridge, UK). The leaves, stems, and roots of each plant were weighed separately on the same analytical balance in order to determine the dry mass accumulation of each plant. Growth indices were measured using the dry matter data; measurements included specific leaf mass (g m^{-2}), leaf mass ratio, leaf area ratio (cm^2 g^{-1}), and shoot-root mass ratio [40].

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2.3. Measurement of Gas Exchange

Net CO_2 assimilation ($A_{N,}$ μmol CO_2 m^{-2} s^{-1}), transpiration (E, mmol H_2O m^{-2} s^{-1}) and stomatal conductance (g_s, mmol m^{-2} s^{-1}) were measured from at least three leaves in each experimental condition between the hours of 10:00 and 13:00. They were measured using a LI-COR portable photosynthesis system (Model LI-6400XT LI-COR Inc., Lincoln, NE, USA). Before measurements were taken, the infrared gas analyzer was calibrated to an ambient CO_2 level of 400 μmol mol^{-1}, a flow rate of 500 mL s^{-1}, and a light intensity of 600 photon m^{-2} s^{-1}. The measurements taken with the photosynthesis system enabled the determination of water use efficiency (WUE, μmol CO_2 $mmol^{-1}$ H_2O) of each of the leaves measured by dividing net CO_2 assimilation by stomatal conductance [41].

2.4. Measurement of Chlorophyll Fluorescence

Chlorophyll fluorescence was measured using the Fluorpen FP 100 portable fluorometer (Photon Systems Instruments, Drasov, Czech Republic). Measurements were taken from the abaxial leaf surface and used to determine the effective and maximum quantum yield of three leaves per treatment. Under light-adapted conditions, the effective quantum yield ($\Delta F/F_m'$) was measured to assess photosystem II (PSII) efficiency through the evaluation of photosynthetic electron transport. Leaves were then dark-adapted for 30 minutes within the fluorometer clamp. Dark-adapted leaves were measured for maximum quantum yield of PSII (F_v/F_m), non-photochemical quenching (qNP), and photochemical quenching (qP) in order to assess the overall efficiency of PSII.

2.5. Analysis of Photosynthetic Pigments

Four disk punches (each approximately 0.275 cm^2) from three leaves per treatment were soaked in 5 mL of dimethyl sulfoxide (VWR International Inc., Mississauga, Ontario, Canada) contained in 12 mL vials in order to establish concentrations of chlorophyll *a*, chlorophyll *b*, carotenoids, total chlorophyll, and chlorophyll *a*/*b*. The disks and dimethyl sulfoxide were placed in a room-temperature dark container for 24 h; after which, 1 mL of each solution was placed into a cuvette and measured for absorbance at 664 nm, 648 nm, and 470 nm using a UV–visible spectrophotometer (Ultraspec 3100 *pro*, Biochrom Ltd., Cambridge, UK). Concentrations of chlorophyll *a*, chlorophyll *b*, carotenoids, total chlorophyll, and chlorophyll *a*/*b* were calculated from the absorbencies measured [42].

2.6. Measurement of Water Potential

Measurement of water potential was carried out in the Dew Point PotentiaMeter (Model WP4C, Decagon Devices Inc., Pullman, WA, USA). Three leaves and three volumes of soil from each of the three trials were measured for water potential (MPa) after calibration using a 0.01 M solution of potassium hydroxide (KOH). Each water potential reading took 25–45 minutes to establish equilibrium, and the water potential was recorded from each sample in order to establish differences between plants grown with and without abscisic acid application.

2.7. Measurement of NBI, Chlorophyll, and Flavonoids

Nitrogen balance index (NBI), chlorophyll, flavonoids, and anthocyanins measurements were taken from at least three leaves from separate plants in each treatment. Each measurement of optical absorbance was recorded for the values of the four components, which were taken using the Dualex Scientific® (Dualex Scientific, Force-A, Orsay Cedex, France). NBI refers to the amount of nitrogen coming into the plant system, less the amount leaving the system. It is determined using the ratio of chlorophyll to flavonoids, which are both measured by assessing light transmission to and from the leaf. An increase in leaf chlorophyll content shows a greater amount of photosynthetic processes taking place, while the flavonoid presence is indicative of antioxidant stress response within the plant.

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2.8. Data Analysis

The effects of temperature, water stress, abscisic acid, and their interactions on the growth and development of tomato plants were determined using a general linear model (GLM) procedure. A three-way analysis of variance from this output was used to determine the differences between lower (22/18 °C) or higher (28/24 °C) temperature regime at a well-watered (watered to field capacity) or water-stressed (watered at leaf wilting point) state with a hormone application of no abscisic acid (100 µL of distilled water) or abscisic acid (100 µL of 1 mM abscisic acid solution) every other day [43]. Then, a one-way ANOVA procedure was used to establish significant differences among each of the eight experimental treatments as well as among the three factors being manipulated, using Scheffé's multiple comparison procedure at the 5% confidence level (SAS software). For most of the parameters three trials were used, excluding chlorophyll fluorescence and leaf moisture; the equipment for chlorophyll fluorescence failed during the second trial, and leaf moisture was overlooked in the first trial. Data are reported as the mean ± standard error.

3. Results

3.1. Plant Growth and Development

Overall, the height of tomato plants was significantly affected by temperature, watering regime, abscisic acid, and the interaction between temperature and abscisic acid application (Table 1). Plants grown under higher temperatures were shorter than plants grown under lower temperatures (Table 2). Water-stressed plants were shorter than well-watered plants (Table 2). As well, plants grown with an abscisic acid application were shorter than those grown without it (Table 2). As per the temperature (T) × abscisic acid (A) interaction, plants that were grown under lower temperatures with no abscisic acid were tallest, and plants grown under higher temperatures with abscisic acid were shortest. Plants treated with abscisic acid were generally shorter than plants which were not treated with abscisic acid; however, it was only significant in plants grown under lower temperature and well-watered, as well as plants grown under lower temperature and water-stressed conditions (Figure 1A).

Table 1. Analysis of variance for the effects of temperature, watering regime, abscisic acid, and their interactions on stem height, stem diameter, leaf area, and leaf number of tomato plants.

Source	Stem Height			Stem Diameter			Leaf Area			Leaf Number		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Temperature (T)	1	19.1	18.85 ****	1	5.1	3.10	1	1304.8	0.19	1	18.9	4.56 *
Watering regime (W)	1	5.0	4.95 *	1	23.9	14.57 ***	1	45,850.4	6.78 *	1	5.0	1.21
Abscisic acid (A)	1	60.9	60.17 ****	1	43.4	26.43 ****	1	13,969.7	2.07	1	3.0	0.00
T × W	1	0.1	0.04	1	1.0	0.55	1	4074.9	0.60	1	0.0	0.41
T × A	1	15.1	14.90 ***	1	0.4	0.23	1	1911.5	0.28	1	1.7	0.97
W × A	1	0.1	0.10	1	0.2	0.12	1	347.4	0.05	1	4.0	0.97
T × W × A	1	0.1	0.07	1	1.2	0.72	1	384.4	0.06	1	3.1	0.76
Error	228	1.0	-	228	1.6	-	63	6760.1	-	63	4.1	-

Note: * $p < 0.05$; *** $p < 0.001$; **** $p < 0.0001$. Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

The stem diameter was significantly influenced by watering regime and abscisic acid (Table 1). Well-watered plants had thicker stems than water-stressed plants; similarly, plants without abscisic acid application also exhibited thicker stems than plants with abscisic acid applications (Table 2). Although not significant, plants grown under higher temperatures, regardless of watering regime or abscisic acid application, had a general trend toward thinner stems (Figure 1B).

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Table 2. Effects of temperature, watering regime and abscisic acid on stem height, stem diameter, leaf area, and leaf number of tomato plants.

Parameter	Temperature		Watering Regime		Abscisic Acid	
	Lower	Higher	Well-Watered	Water Stressed	(−) ABA	(+) ABA
Stem height (cm)	2.07 ± 0.13A	1.60 ± 0.07B	2.01 ± 0.11A	1.66 ± 0.11B	2.31 ± 0.13A	1.33 ± 0.06B
Stem diameter (mm)	4.72 ± 0.13A	4.51 ± 0.13A	4.95 ± 0.14A	4.28 ± 0.11B	5.03 ± 0.12 A	4.17 ± 0.12B
Leaf area (plant^{-1})	125.88 ± 11.94A	134.84 ± 16.03A	156.45 ± 15.90A	105.12 ± 10.8B	144.59 ± 13.55A	125.21 ± 14.34A
Leaf number (plant^{-1})	7.43 ± 0.34A	6.42 ± 0.33B	7.17 ± 0.36A	3.67 ± 0.33A	7.14 ± 0.30A	6.8 ± 0.38A

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled-environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 236 (stem height and diameter) and 71 (leaf area and number) samples from three experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple-comparison procedure.

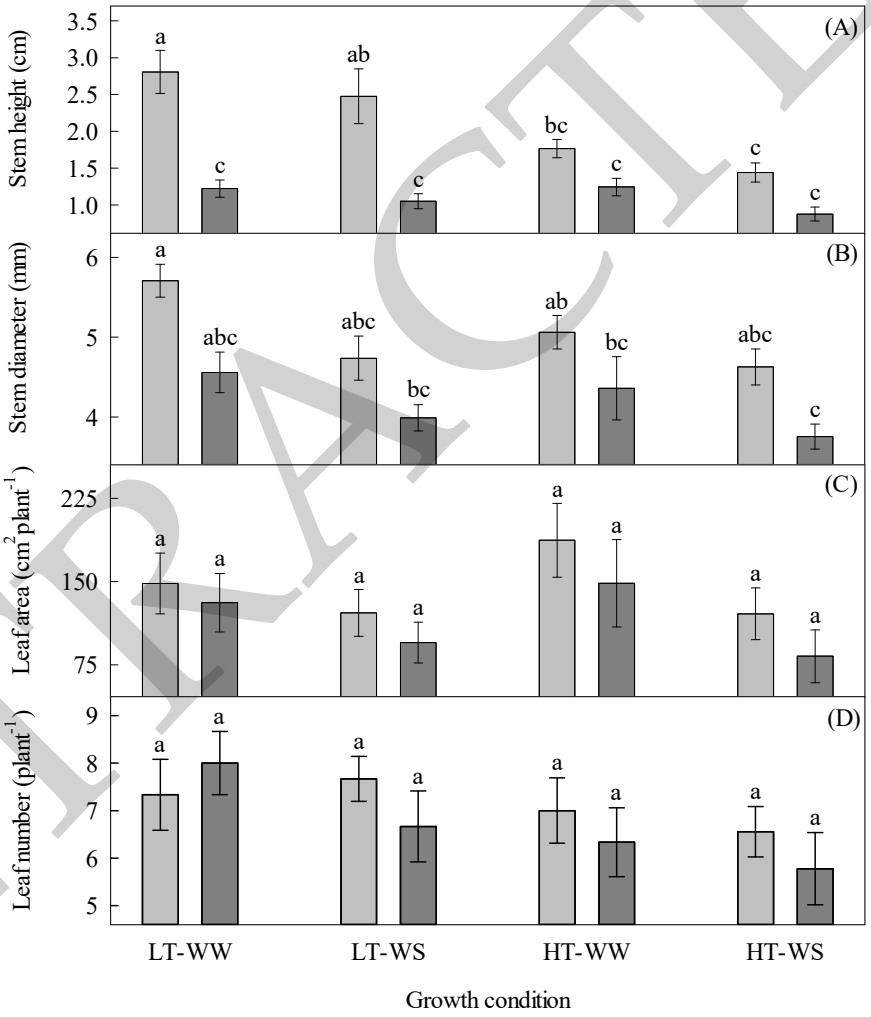


Figure 1. Growth of 33-day-old tomato plants grown under eight experimental conditions including two temperature regimes, two watering regimes, and two abscisic acid concentration applications after 12 days of initial germination and growth in growth chambers with lower temperature, watering to field capacity, and without abscisic acid application. (**A**) Stem height, (**B**) stem diameter, (**C**) leaf area, and (**D**) leaf number. LT, lower temperature; HT, higher temperature; WW, well-watered; WS, water-stressed; light gray, no abscisic acid; dark gray, abscisic acid. Data are the means ± SE of 236 (stem height and diameter) and 71 (leaf area and number) samples from three experiments. Bars with different letters above them are significantly different, according to Scheffé's multiple comparison procedure at the 5% confidence level.

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The watering regime was the only significant factor with respect to leaf area (Table 1). Well-watered plants exhibited larger leaves, while water-stressed plants showed smaller leaves (Table 2). Plants grown with abscisic acid also tended to have smaller leaves, though it was not significant (Figure 1C).

The leaf number was significantly influenced only by temperature (Table 1). Overall, plants grown under higher temperatures had a lower leaf number than plants grown under lower temperatures (Table 2).

3.2. Growth Rate

Overall, the growth rate of tomato plants was significantly affected by temperature, watering regime, abscisic acid application, and the interaction between temperature and abscisic acid application (Table 3). Plants grown under lower temperatures had a faster growth rate than plants grown under higher temperatures (Table 4). In the same way, well-watered plants or plants not treated with abscisic acid also exhibited a faster growth rate than water-stressed plants or plants treated with abscisic acid, respectively (Table 4).

Table 3. Analysis of variance for the effects of temperature, watering regime, abscisic acid, and their interactions on growth rate of tomato plants.

Source	Growth Rate		
	df	**MS**	**F**
Temperature (T)	1	0.0	17.69 ****
Watering regime (W)	1	0.0	5.10 *
Abscisic acid (A)	1	0.1	59.92 ****
T × W	1	0.0	0.13
T × A	1	0.0	13.18 ***
W × A	1	0.0	0.05
T × W × A	1	0.0	0.14
Error	228	0.0	-

Note: * $p < 0.05$; *** $p < 0.001$; **** $p < 0.0001$. Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperatures, well-watered or water-stressed regime, and the abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

Table 4. Effects of temperature, watering regime and abscisic acid on growth rate of tomato plants.

Parameter	Temperature		Watering Regime		Abscisic Acid	
	Lower	**Higher**	**Well-Watered**	**Water-Stressed**	**(−) ABA**	**(+) ABA**
Growth rate (cm d^{-1})	0.09 ± 0.006A	0.07 ± 0.003B	0.09 ± 0.005A	0.07 ± 0.005B	0.10 ± 0.006A	0.05 ± 0.003B

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 236 samples from three experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple-comparison procedure.

With regards to the temperature (T) × abscisic acid (A) interaction, lower temperature plants that had no abscisic acid application had the fastest growth rate, while plants under higher temperatures that were given abscisic acid applications had the slowest growth rate. In the case of the temperature (T) × watering status (W) × abscisic acid (A) interaction, abscisic treatment significantly reduced the growth rate of plants grown under lower temperature regardless of the watering status (Figure 2).

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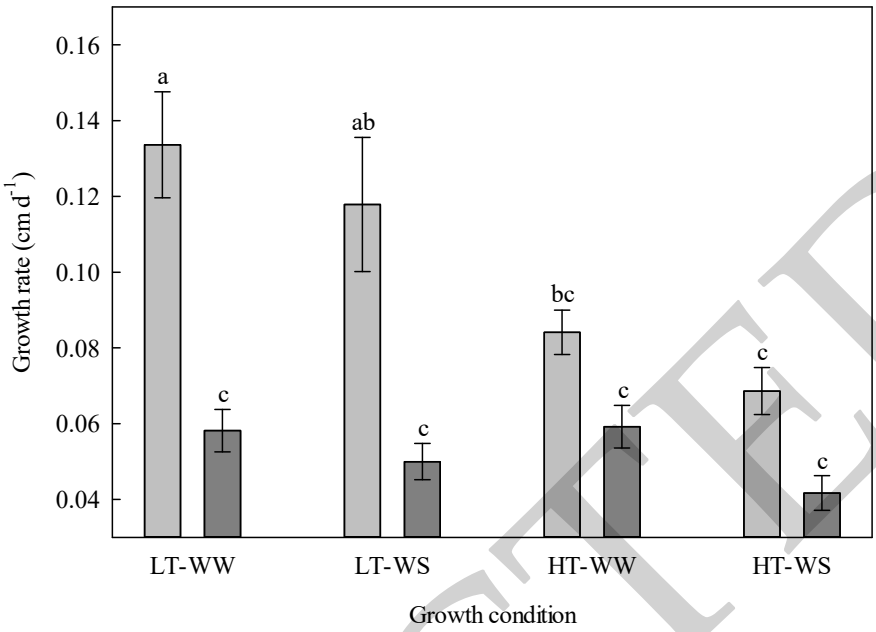


Figure 2. Growth rate of 33-day-old tomato plants grown under eight experimental conditions including two temperature regimes, two watering regimes, and two abscisic acid concentration applications after 12 days of initial germination and growth in growth chambers with lower temperature, watering to field capacity, and without abscisic acid application. LT, lower temperature; HT, higher temperature; WW, well-watered; WS, water stressed; light gray, no abscisic acid; dark gray, abscisic acid. Data are the means ± SE of 236 samples from three experiments. Bars with different letters above them are significantly different, according to Scheffé's multiple comparison procedure at the 5% confidence level.

3.3. Dry Mass Accumulation

Overall, the leaf mass, stem mass, root mass, and total mass were all significantly influenced by watering regime (Table 5). In all cases, well-watered plants had a higher mass than water-stressed plants (Table 6). As well, the leaf mass was significantly reduced by abscisic acid application (Table 5); higher masses were obtained from plants grown without abscisic acid (Table 6).

Table 5. Analysis of variance for the effects of temperature, watering regime, abscisic acid, and their interactions on dry mass accumulation of tomato plants.

Source		Leaf Mass		Stem Mass		Root Mass		Total Mass	
	df	MS	F	MS	F	MS	F	MS	F
Temperature (T)	1	249,850.0	1.01	1486.5	0.89	9755.5	0.53	405,992.4	0.96
Watering regime (W)	1	2,085,836.9	8.47 **	8934.7	5.37 *	145,050.6	7.81 **	3,684,945.8	8.69 **
Abscisic acid (A)	1	1,076,900.1	4.37 *	5772.5	3.47	11,514.1	0.62	1,490,885.6	3.52
T × W	1	258,843.6	1.05	2078.9	1.25	44,307.1	2.38	585,002.5	1.38
T × A	1	0.8	0.00	938.4	0.56	2062.8	0.11	5919.3	0.01
W × A	1	49,314.3	0.20	191.4	0.11	507.4	0.03	66,784.3	0.16
T × W × A	1	19,593.2	0.08	149.9	0.09	4932.7	0.27	3306.1	0.01
Error	63	246,196.0	-	1664.5	-	18,581.7	-	424,047.2	-

Note: * $p < 0.05$; ** $p < 0.01$. Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

On the basis of one-way ANOVA, there were no significant differences in plant biomass among treatments. However, the leaf mass, stem mass, and total mass showed lower masses in plants that had abscisic acid treatment.

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Table 6. Effects of temperature, watering regime, and abscisic acid on dry mass accumulation of tomato plants.

Parameters	Temperature		Watering Regime		Abscisic Acid	
	Lower	Higher	Well-Watered	Water-Stressed	(−) ABA	(+) ABA
Leaf mass (mg)	975.7 ± 89.4A	857.8 ± 87.1A	1077.9 ± 91.5A	749.2 ± 75.8B	1052.4 ± 88.9A	783.2 ± 82.7B
Stem mass (mg)	71.3 ± 7.9A	61.9 ± 6.3A	76.7 ± 7.1A	56.0 ± 6.8B	76.8 ± 7.8A	56.5 ± 6.0A
Root mass (mg)	236.5 ± 18.9A	212.9 ± 27.6A	266.4 ± 26.5A	181.5 ± 17.9B	241.1 ± 20.4A	208.4 ± 26.4A
Total mass (mg)	1283.4 ± 111.9A	1132.6 ± 118.7A	1421.1 ± 121.5A	986.7 ± 96.6B	1370.4 ± 112.8A	1048.1 ± 112.9A

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 71 samples from three experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple-comparison procedure.

3.4. Growth Indices

Specific leaf mass (SLM) was not significantly affected by any factors or their interactions (Table 7). The leaf mass ratio (LMR) was significantly affected by the interaction between temperature and abscisic acid application, though by no other factors or interactions (Table 7). The highest LMR was seen in plants grown under higher temperatures with no abscisic application, while the lowest was seen in plants grown under higher temperatures with abscisic application. Plants grown in lower temperatures did not fluctuate as drastically under differing abscisic acid levels.

Table 7. Analysis of variance for the effects of temperature, watering regime, abscisic acid, and their interactions on growth indices of tomato plants.

Source	SLM			LMR		LAR		S:R	
	df	MS	F	MS	F	MS	F	MS	F
Temperature (T)	1	325.7	0.15	0.0	0.24	11081.7	2.79	42.3	5.85 *
Watering regime (W)	1	6795.0	3.07	0.0	0.06	15154.2	3.82	19.4	2.68
Abscisic acid (A)	1	395.8	0.18	0.0	2.90	876.1	0.22	3.1	0.43
T × W	1	4035.4	1.82	0.0	0.45	3755.8	0.95	49.4	6.83*
T × A	1	432.7	0.20	0.0	4.81 *	226.4	0.06	32.3	4.46 *
W × A	1	856.5	0.39	0.0	1.46	2348.7	0.59	47.2	6.52 *
T × W × A	1	146.9	0.07	0.0	1.42	5485.2	1.38	12.7	1.75
Error	63	2213.1	-	0.0	-	3969.3	-	7.2	-

Note: * $p < 0.05$. Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled-environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

The leaf area ratio (LAR) was not significantly affected by any factors or their interactions (Table 7).

Temperature and the interactions between temperature and watering regime, temperature and abscisic acid, and watering regime and abscisic acid significantly affected shoot to root ratio (S:R). Plants grown under lower temperatures experienced a greater S:R than plants grown under higher temperatures (Table 8). With respect to the interaction between temperature (T) × watering regime (W), the highest S:R was found in plants grown under lower temperatures that were well-watered, while the lowest S:R was found in plants grown under higher temperatures that were well-watered. The temperature (T) × abscisic acid (A) interaction showed the greatest S:R in plants grown under lower temperatures with abscisic acid application, while the lowest S:R was found in plants under higher temperatures and abscisic acid application. The interaction between watering regime (W) × abscisic acid (A) showed the highest S:R in well-watered plants grown with abscisic acid application and the lowest S:R in water-stressed plants grown with abscisic acid application. In general, growth indices in the case of temperature (T) × watering status (W) × abscisic acid (A) interaction, were not significant different between treatments (Figure 3). However, the only

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exception was S:R mass ratio, which was significantly higher in ABA-treated plants grown under lower temperature, well-watered than the others ABA-treated plants grown under higher temperature, regardless of watering status (Figure 3D).

Table 8. Effects of temperature, watering regime, and abscisic acid on growth indices of tomato plants.

Parameter	Temperature		Watering Regime		Abscisic Acid	
	Lower	Higher	Well-Watered	Water-Stressed	(−) ABA	(+) ABA
SLM (g m^{-2})	86.38 ± 10.41A	82.86 ± 4.22A	94.24 ± 9.53A	75.22 ± 5.43A	82.64 ± 6.10A	86.60 ± 9.38A
LMR	0.75 ± 0.01A	0.76 ± 0.01A	0.75 ± 0.01A	0.75 ± 0.01A	0.76 ± 0.01A	0.74 ± 0.01A
LAR (cm^2 g^{-1})	125.38 ± 14.15A	100.01 ± 5.62A	97.48 ± 8.06A	127.14 ± 12.49A	116.03 ± 11.54A	108.90 ± 10.09A
S:R mass ratio	5.35 ± 0.64A	3.90 ± 0.30B	5.09± 0.67A	4.15 ± 0.29A	4.47 ± 0.35A	4.77 ± 0.64A

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 71 samples from three experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple-comparison procedure.

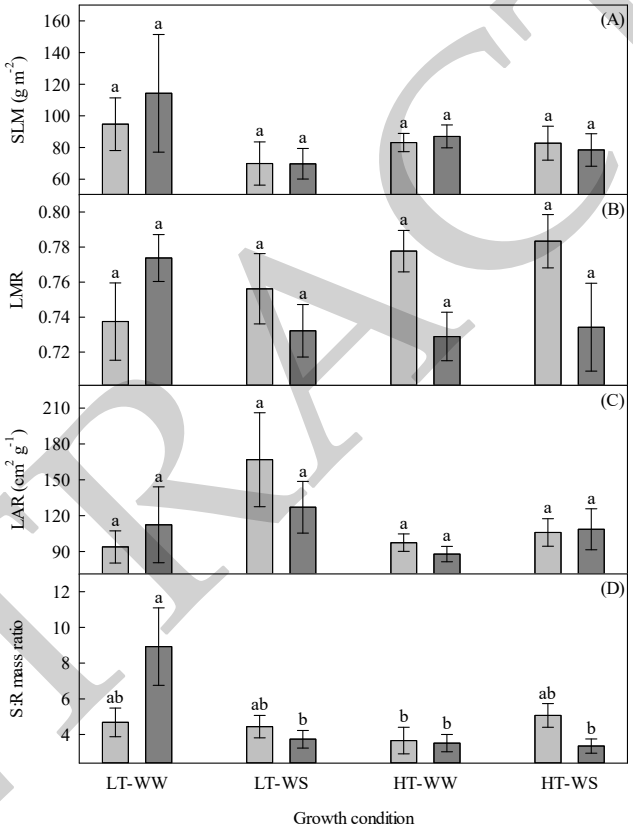


Figure 3. Growth indices of 33-day-old tomato plants grown under eight experimental conditions including two temperature regimes, two watering regimes, and two abscisic acid concentration applications after 12 days of initial germination and growth in growth chambers with lower temperature, watering to field capacity, and without abscisic acid application. (**A**) Specific leaf mass (SLM), (**B**) leaf mass ratio (LMR), (**C**) leaf area ratio (LAR), and (**D**) shoot to root ratio (S:R). LT, lower temperature; HT, higher temperature; WW, well-watered; WS, water stressed; light gray, no abscisic acid; dark gray, abscisic acid. Data are the means ± SE of 71 samples from three experiments. Bars with different letters above them are significantly different according to Scheffé's multiple comparison procedure at the 5% confidence level.

3.5. Gas Exchange

Net CO_2 assimilation was significantly affected by watering regime and abscisic acid application (Table 9). Well-watered plants or plants that were not treated with abscisic acid

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had a higher rate of net CO_2 assimilation than water-stressed plants or plants that were treated with abscisic acid, respectively (Table 10).

Table 9. Analysis of variance for the effects of temperature, watering regime, abscisic acid, and their interactions on the gas exchange of tomato plants.

Source		Net CO_2 Assimilation		Transpiration		Stomatal Conductance		Water Use Efficiency	
	df	MS	F	MS	F	MS	F	MS	F
Temperature (T)	1	152.4	3.56	54.9	5.64 *	0.3	5.60 *	2.6	2.21
Watering regime (W)	1	350.8	8.21 **	77.1	7.93 **	0.4	6.88 *	0.0	0.02
Abscisic acid (A)	1	432.3	10.11 **	130.2	13.40 ***	0.3	6.30 *	2.5	2.15
T × W	1	6.9	0.16	12.3	1.26	0.0	0.79	0.0	0.00
T × A	1	0.4	0.01	19.4	2.00	0.2	4.02 *	0.6	0.52
W × A	1	43.0	1.01	36.7	3.77	0.2	3.38	1.9	1.61
T × W × A	1	16.0	0.37	8.5	0.87	0.1	1.41	0.2	0.17
Error	80	42.8	-	9.7	-	0.1	-	1.2	-

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

Table 10. Effects of temperature, watering regime, and abscisic acid on gas exchange of tomato plants.

Parameter	Temperature		Watering Regime		Abscisic Acid	
	Lower	Higher	Well-Watered	Water-Stressed	(−) ABA	(+) ABA
A_N (µmol CO_2 m^{-2} s^{-1})	10.80 ± 1.04A	8.19 ± 1.08A	11.48 ± 1.05A	7.51 ± 1.02B	11.70 ± 1.06A	7.29 ± 0.98B
E (mmol H_2O m^{-2} s^{-1})	5.19 ± 0.49A	3.61 ± 0.57B	5.33 ± 0.55A	3.46 ± 0.49B	5.61 ± 0.50A	3.18 ± 0.52B
g_s (mmol m^{-2} s^{-1})	0.31 ± 0.04A	0.20 ± 0.04B	0.32 ± 0.04A	0.19 ± 0.03B	0.32 ± 0.04A	0.20 ± 0.04B
WUE (µmol CO_2 mmol H_2O^{-1})	2.34 ± 0.15A	2.68 ± 0.17A	2.53 ± 0.14A	2.50 ± 0.18A	2.34 ± 0.16A	2.68 ± 0.17A

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 88 samples from three experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple-comparison procedure.

Temperature, watering regime, and abscisic acid were all having significant effect on transpiration rate (Table 9). Plants grown under lower temperatures, well-watered, or without abscisic acid application had higher transpiration rates than plants grown under higher temperatures, water-stressed, or with abscisic acid application, respectively (Table 10). Stomatal conductance was affected significantly by temperature, watering regime, abscisic acid application and the interaction between temperature and abscisic acid (Table 9). Plants grown under lower temperatures that were well-watered or without abscisic application had higher stomatal conductance than plants grown under higher temperatures that were water-stressed or with abscisic acid application, respectively (Table 10). Lower temperature plants grown without abscisic acid application had the highest stomatal conductance while higher temperature plants grown with abscisic acid application had the lowest stomatal conductance in regard to the significant interaction between temperature (T) × abscisic acid (A).

Water use efficiency (WUE) was not affected significantly by any factors or their interactions (Table 9).

In the case of temperature (T) × watering status (W) × abscisic acid (A) interaction, though they were not significant, net CO_2 assimilation, transpiration rate, and stomatal

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conductance were all lower in case on plants grown at higher temperature compared with plants grown under lower temperatures and in abscisic acid-treated plants compared with the untreated ones (Figure 4).

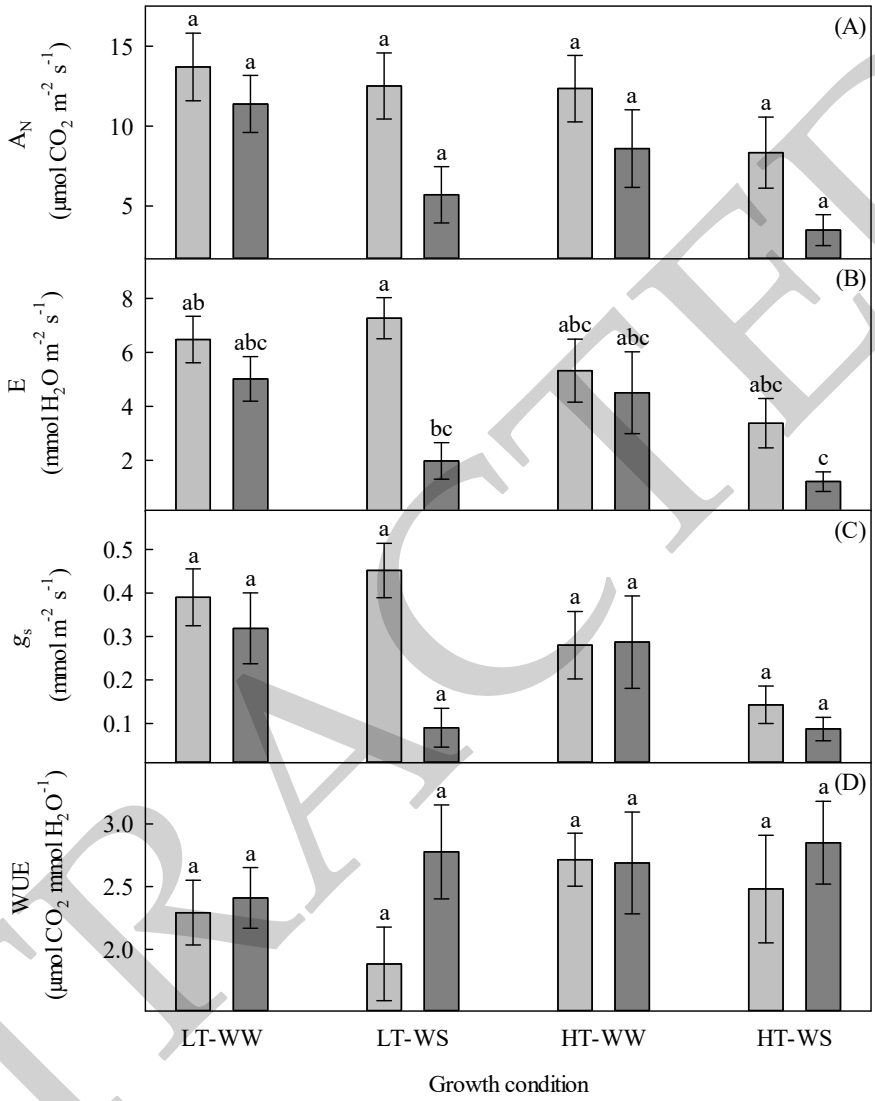


Figure 4. Gas exchange of 33-day-old tomato plants grown under eight experimental conditions including two temperature regimes, two watering regimes, and two abscisic acid concentration applications after 12 days of initial germination and growth in growth chambers with lower temperature, watering to field capacity, and without abscisic acid application. (**A**) Net CO_2 assimilation (AN), (**B**) transpiration (E), (**C**) stomatal conductance (gs), and (**D**) water use efficiency (WUE). LT, lower temperature; HT, higher temperature; WW, well-watered; WS, water stressed; light gray, no abscisic acid; dark gray, abscisic acid. Data are the means ± SE of 88 samples from three experiments. Bars with different letters above them are significantly different according to Scheffé's multiple comparison procedure at the 5% confidence level.

3.6. Chlorophyll Fluorescence

Non-photochemical quenching was the only chlorophyll fluorescence parameter significantly affected by any factor. Temperature and abscisic acid had significant effects on non-photochemical quenching (Table 11). Plants under lower temperatures or without abscisic application experienced a higher amount of non-photochemical quenching than plants under higher temperatures or with abscisic acid application, respectively (Table 12). In the case of temperature (T) × watering status (W) × abscisic acid (A) interaction, there was no significant effect on chlorophyll fluorescence (Figure 5).

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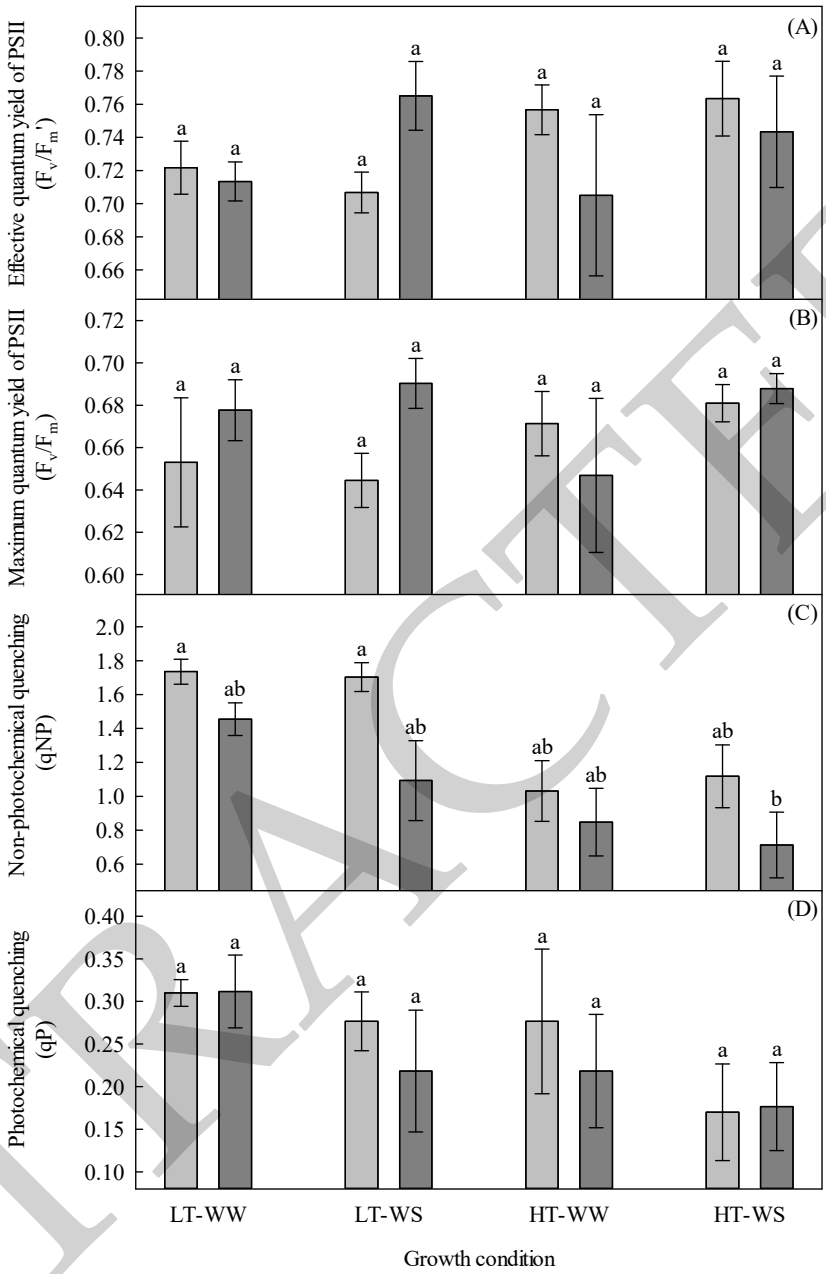


Figure 5. Chlorophyll fluorescence of 33-day-old tomato plants grown under eight experimental conditions including two temperature regimes, two watering regimes, and two abscisic acid concentration applications after 12 days of initial germination and growth in growth chambers with lower temperature, watering to field capacity, and without abscisic acid application. (**A**) Effective quantum yield of PSII ($\Delta F/F_m'$), (**B**) maximum quantum yield of PSII (F_v/F_m), (**C**) non-photochemical quenching (qNP), and (**D**) photochemical quenching (qP). LT, lower temperature; HT, higher temperature; WW, well-watered; WS, water stressed; light gray, no abscisic acid; dark gray, abscisic acid. Data are the means ± SE of 48 samples from two experiments. Bars with different letters above them are significantly different according to Scheffé's multiple comparison procedure at the 5% confidence level.

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Table 11. Analysis of variance for effects of temperature, watering regime, abscisic acid, and their interactions on effective quantum yield of PSII ($\Delta F/F_m'$), maximum quantum yield of PSII (F_v/F_m), non-photochemical quenching (qNP), and photochemical quenching (qP) of tomato plants.

Source	$\Delta F/F_m'$			F_v/F_m		qNP		qP	
	df	MS	F	MS	F	MS	F	MS	F
Temperature (T)	1	0.0	0.73	0.0	0.15	3.9	23.44 ****	0.1	2.92
Watering regime (W)	1	0.0	1.28	0.0	0.96	0.2	0.88	0.1	2.92
Abscisic acid (A)	1	0.0	0.09	0.0	0.89	1.6	9.90 **	0.0	0.45
T × W	1	0.0	0.01	0.0	0.69	0.1	0.54	0.0	0.02
T × A	1	0.0	2.84	0.0	2.49	0.1	0.41	0.0	0.00
W × A	1	0.0	1.86	0.0	0.88	0.2	1.38	0.0	0.00
T × W × A	1	0.0	0.24	0.0	0.03	0.0	0.05	0.0	0.60
Error	40	0.0	-	0.0	-	0.2	-	0.0	-

Note: ** $p < 0.01$; **** $p < 0.001$. Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

Table 12. Effects of temperature, watering regime, and abscisic acid on chlorophyll fluorescence of tomato plants.

Parameter	Temperature		Watering Regime		Abscisic Acid	
	Lower	Higher	Well-Watered	Water-Stressed	(−) ABA	(+) ABA
$\Delta F/F_m'$	0.73 ± 0.01A	0.74 ± 0.02A	0.72 ± 0.01A	0.75 ± 0.01A	0.74 ± 0.01A	0.73 ± 0.02A
F_v/F_m	0.67 ± 0.01A	0.67 ± 0.01A	0.66 ± 0.01A	0.68 ± 0.01A	0.66 ± 0.01A	0.68 ± 0.01A
qNP	1.50 ± 0.08A	0.93 ± 0.09B	1.27 ± 0.10A	1.16 ± 0.11A	1.40 ± 0.09A	1.03 ± 0.11B
qP	0.28 ± 0.02A	0.21 ± 0.03A	0.28 ± 0.03A	0.21 ± 0.03A	0.26 ± 0.03A	0.23 ± 0.03A

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 48 samples from two experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple-comparison procedure.

3.7. Photosynthetic Pigments

Photosynthetic pigments were not significantly affected by any factors or their interactions (Tables 13 and 14).

Table 13. Analysis of variance for effects of temperature, watering regime, abscisic acid, and their interactions on photosynthetic pigments of tomato plants.

Source	Chlorophyll *a*			Chlorophyll *b*		Carotenoids		Total Chl		Chl *a*/*b*	
	df	MS	F	MS	F	MS	F	MS	F	MS	F
Temperature (T)	1	15.6	0.62	1.8	2.46	5.0	2.84	28.1	0.91	0.1	0.05
Watering regime (W)	1	1.2	0.05	0.2	0.24	0.6	0.33	2.3	0.08	0.0	0.00
Abscisic acid (A)	1	1.1	0.05	0.1	0.07	0.1	0.05	1.7	0.05	0.0	0.00
T × W	1	7.5	0.30	1.8	2.44	0.0	0.00	16.7	0.54	0.2	0.20
T × A	1	0.4	0.02	0.5	0.71	0.2	0.08	0.0	0.00	0.4	0.39
W × A	1	4.6	0.18	0.3	0.47	0.7	0.41	7.5	0.24	0.0	0.03
T × W × A	1	2.2	0.09	0.2	0.33	0.1	0.05	3.9	0.13	0.0	0.02
Error	59	25.2	-	0.7	-	1.8	-	30.8	-	1.0	-

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

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Table 14. Effects of temperature, watering regime, and abscisic acid on photosynthetic pigments of tomato plants.

Parameter	Temperature		Watering Regime		Abscisic Acid	
	Lower	Higher	Well-Watered	Water-Stressed	(−) ABA	(+) ABA
Chl *a* ($\mu g\ cm^{-2}$)	13.12 ± 0.77A	14.14 ± 0.89A	13.48 ± 0.89A	13.75 ± 0.78A	13.78 ± 0.88A	13.47 ± 0.79A
Chl *b* ($\mu g\ cm^{-2}$)	4.04 ± 0.14A	4.38 ± 0.15A	4.15 ± 4.26A	4.26 ± 0.16A	4.25 ± 0.16A	4.16 ± 0.13A
Carotenoids ($\mu g\ cm^{-2}$)	2.67 ± 0.21A	3.25 ± 0.23A	2.85 ± 0.24A	3.06 ± 0.22A	3.01 ± 0.24A	2.91 ± 0.22A
Total Chl ($\mu g\ cm^{-2}$)	17.16 ± 0.85A	18.52 ± 0.99A	17.63 ± 0.97A	18.02 ± 0.89A	18.02 ± 0.99A	17.63 ± 0.86A
Chl *a*/*b*	3.28 ± 0.17A	3.23 ± 0.16A	3.25 ± 0.19A	3.25 ± 0.15A	3.24 ± 0.16A	3.26 ± 0.17A

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 67 samples from three experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple-comparison procedure.

3.8. Water Potential and Leaf Moisture

Watering regime significantly affected soil water potential and leaf water potential (Table 15). Plants that were well-watered had a higher soil, as well as leaf water, potential than those that were water-stressed (Table 16). No other factor or combination of factors played a significant role in leaf or soil water potential or leaf moisture (Table 15, Figure 6).

Table 15. Analysis of variance for the effects of temperature, watering regime, abscisic acid, and their interactions on water potential and moisture of tomato plants.

Source	Soil Water Potential			Leaf Water Potential			Leaf Moisture %		
	df	MS	F	df	MS	F	df	MS	F
Temperature (T)	1	0.4	0.45	1	2.3	1.90	1	20.0	0.06
Watering regime (W)	1	2.7	2.99 *	1	24.2	19.79 ****	1	70.9	0.21
Abscisic acid (A)	1	1.1	1.18	1	2.2	1.83	1	803.0	2.43
T × W	1	0.9	1.04	1	1.1	0.91	1	55.7	0.17
T × A	1	1.4	1.51	1	2.5	2.07	1	435.3	1.32
W × A	1	1.6	1.79	1	0.7	0.54	1	26.1	0.08
T × W × A	1	1.3	1.44	1	0.3	0.22	1	173.1	0.52
Error	64	0.9	-	64	1.2	-	40	330.0	-

Note: * $p < 0.05$; **** $p < 0.0001$. Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

Table 16. Effects of temperature, watering regime, and abscisic acid on water potential and moisture of tomato plants.

Parameter	Temperature		Watering Regime		Abscisic Acid	
	Lower	Higher	Well-Watered	Water-Stressed	(−) ABA	(+) ABA
Soil water potential (MPa)	−0.36 ± 0.07A	−0.51 ± 0.22A	−0.24 ± 0.03A	−0.63 ± 0.22 B	−0.32 ± 0.07A	−0.56 ± 0.22A
Leaf water potential (MPa)	−1.70 ± 0.16A	−2.06 ± 0.25A	−1.30 ± 0.08A	−2.46 ± 0.25B	−1.71 ± 0.17A	−2.06 ± 0.24A
Leaf moisture (%)	68.94 ± 3.81A	70.23 ± 3.50A	70.80 ± 4.17A	68.37 ± 3.04A	73.68 ± 1.78A	65.50 ± 4.71A

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperature, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 72 samples (leaf and soil water potential) from three experiments and 48 samples (leaf moisture) from two experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple-comparison procedure.

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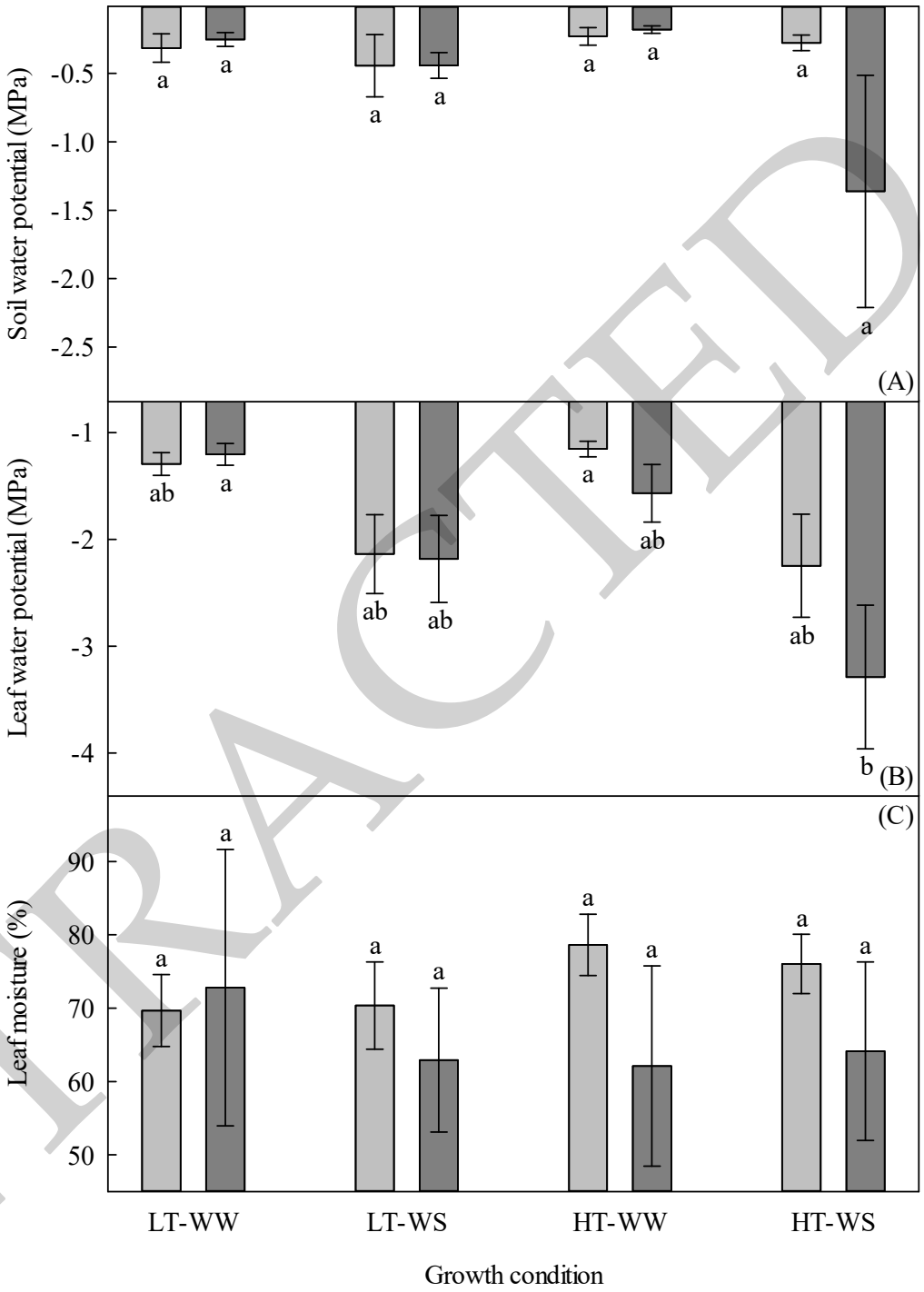


Figure 6. Water potential and leaf moisture of 33-day-old tomato plants grown under eight experimental conditions, including two temperature regimes, two watering regimes, and two abscisic acid concentration applications after 12 days of initial germination and growth in growth chambers with lower temperature, watering to field capacity, and without abscisic acid application. (**A**) Soil water potential, (**B**) leaf water potential, and (**C**) leaf moisture. LT, lower temperature; HT, higher temperature; WW, well-watered; WS, water stressed; light gray, no abscisic acid; dark gray, abscisic acid. Data are the means ± SE of 72 samples (leaf and soil water potential) from three experiments and 48 samples (leaf moisture) from two experiments. Bars with different letters above or below them are significantly different according to Scheffé's multiple comparison procedure at the 5% confidence level.

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3.9. Nitrogen Balance Index, Chlorophyll and Flavonoids

The temperature significantly affected the nitrogen balance index of plants (Table 17). Plants grown under higher temperatures had a higher nitrogen balance index than plants grown under lower temperatures (Table 18).

Table 17. Analysis of variance for the effects of temperature, watering regime, abscisic acid, and their interactions on the nitrogen balance index, chlorophyll, and flavonoids of tomato plants.

Source	Nitrogen Balance Index			Chlorophyll			Flavonoids		
	df	MS	F	df	MS	F	df	MS	F
Temperature (T)	1	1458.8	22.61 ****	1	185.8	2.72	1	0.3	7.79 **
Watering regime (W)	1	0.7	0.01	1	13.2	0.19	1	0.0	0.08
Abscisic acid (A)	1	196.7	3.05	1	452.8	6.63 *	1	0.0	0.10
T × W	1	72.1	1.12	1	425.7	6.23 *	1	0.1	1.14
T × A	1	2.3	0.03	1	39.9	0.58	1	0.0	0.01
W × A	1	37.9	0.59	1	8.0	0.12	1	0.0	0.22
T × W × A	1	25.0	0.39	1	19.8	0.29	1	0.0	0.21
Error	83	64.5	-	96	68.3	-	83	0.0	-

Note: * $p < 0.05$; ** $p < 0.01$; **** $p < 0.0001$. Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperatures, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days.

Table 18. Effects of temperature, watering regime and abscisic acid on nitrogen balance index, chlorophyll and flavonoids of tomato plants.

Parameter	Temperature		Watering Regime		Abscisic Acid	
	Lower	Higher	Well-Watered	Water-Stressed	(−) ABA	(+) ABA
Nitrogen balance index	30.64 ± 0.97B	38.85 ± 1.44A	34.39 ± 1.28A	34.29 ± 1.39A	32.82 ± 1.50A	35.83 ± 1.11A
Chlorophyll (µg cm^{-2})	32.56 ± 1.16A	35.23 ± 1.22A	34.25 ± 1.14A	33.54 ± 1.26A	31.81 ± 1.16B	35.98 ± 1.18A
Flavonoids (µg cm^{-2})	1.10 ± 0.03A	0.98 ± 0.03B	1.04 ± 0.03A	1.06 ± 0.03A	1.05 ± 0.03A	1.04 ± 0.03A

Note: Plants were grown under lower (22/18 °C) or higher (28/24 °C) temperatures, well-watered or water-stressed regime, and abscisic application of 0 or 100 µL of 1 mM solution every other day. Plants were grown in controlled environment growth chambers for 21 days, following an initial germination period of 7 days and growth period of 5 days. Data are the means ± SE of 91 (nitrogen balance index and flavonoids) and 104 (chlorophyll) samples from three experiments. Means (±SE) followed by different upper-case letters within rows and factors are significantly different ($p < 0.05$), according to Scheffé's multiple comparison procedure.

Chlorophyll was affected significantly by abscisic acid and the interaction between temperature and watering regime (Table 17). Plants treated with abscisic acid had a higher amount of total chlorophyll than those grown without abscisic acid (Table 18). In regard to the interaction between temperature (T) × watering regime (W), the highest amount of total chlorophyll was exhibited by plants grown in higher temperatures that were well-watered, while the lowest amount of total chlorophyll was shown by plants grown in lower temperatures that were water-stressed.

Flavonoids were significantly affected by temperature only (Table 17). An increase in temperature significantly decreased the amount of flavonoids within the plant (Table 18). Though not significant, the presence of abscisic acid appears to elevate both the nitrogen balance index and chlorophyll within plants (Figure 7A,B).

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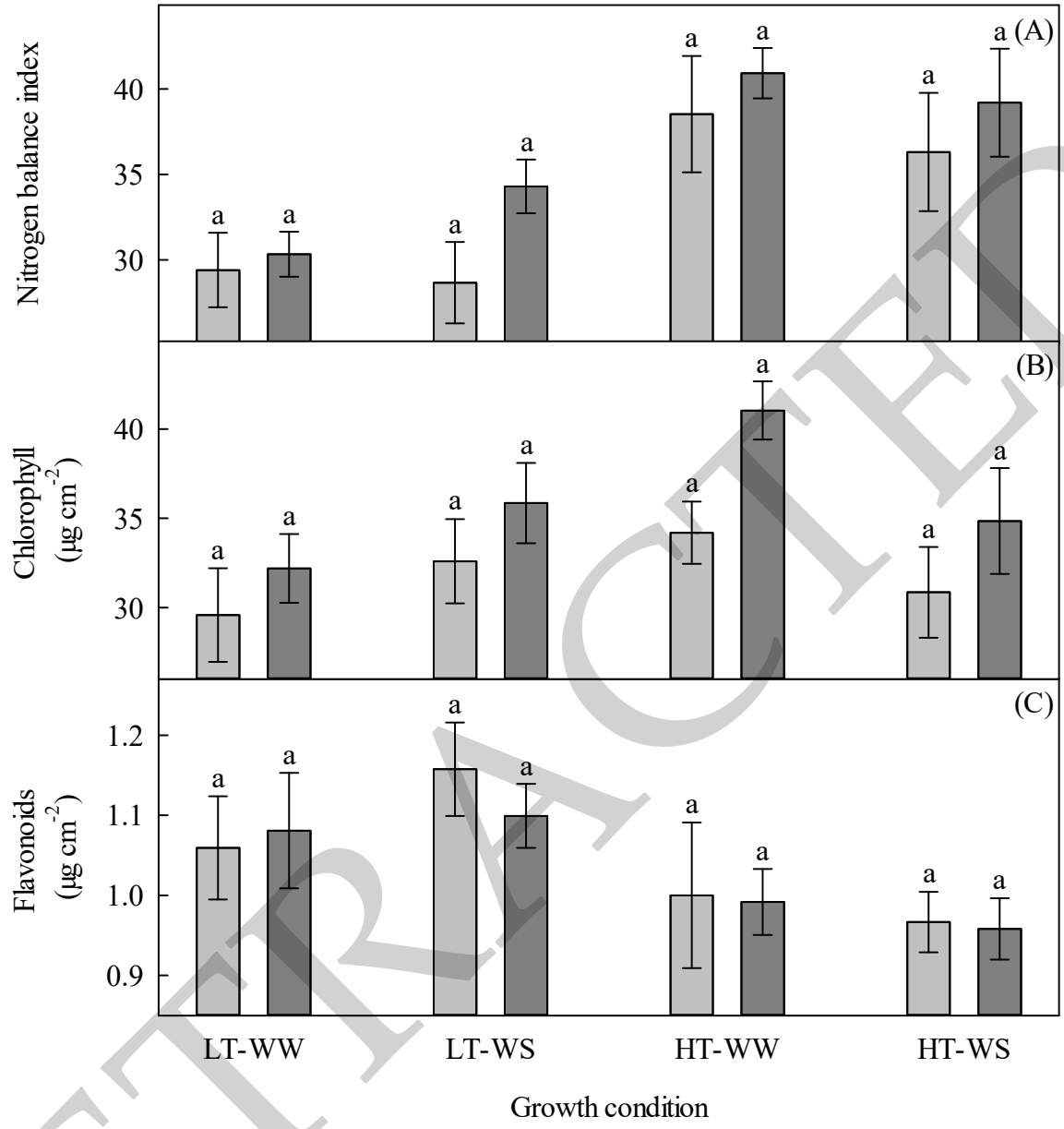


Figure 7. Nitrogen balance index, chlorophyll, and flavonoids of 33-day-old tomato plants grown under eight experimental conditions, including two temperature regimes, two watering regimes, and two abscisic acid concentration applications after 12 days of initial germination and growth in growth chambers with lower temperature, watering to field capacity, and without abscisic acid application. (**A**) Nitrogen balance index, (**B**) chlorophyll, and (**C**) flavonoids. LT, lower temperature; HT, higher temperature; WW, well-watered; WS, water-stressed; light gray, no abscisic acid; dark gray, abscisic acid. Data are the means ± SE of 91 (nitrogen balance index and flavonoids) and 104 (chlorophyll) samples from three experiments. Bars with different letters above them are significantly different according to Scheffé's multiple comparison procedure at the 5% confidence level.

4. Discussion

4.1. Effects of Temperature

In this study, we investigated the single and interactive effects of two components of climate change, temperature and water stress, and a natural plant hormone, abscisic acid, on the growth, development, and morphology of tomato plants. Plants grown under higher temperatures exhibited shorter stems and a lower leaf number than those grown under lower temperatures (Table 2). Plants in previous studies have been shown to have

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a smaller stem height and leaf area, though they usually maintain the leaf number [44]. Contrary to previous studies, no significant effect on the leaf area in regard to temperature change was found. As well, a slower growth rate was seen in plants grown under higher temperatures (Table 4). This coincides with the results of past research showing declines in the photosynthetic process [45].

Higher temperatures had no significant effect on the dry mass accumulation or on the SLM, LMR, or LAR of plants. This is unusual, as when temperatures increase, a reduced biomass is expected [17] and has been shown in a number of studies [4,31]. However, S:R was decreased under higher temperatures (Table 8), which shows that slight mass changes may be taking place.

Both the transpiration and stomatal conductance rates were negatively affected by higher temperatures, whereas the net CO_2 assimilation and water use efficiency (WUE) were not significantly affected (Table 10). Bunce [46] reported that a high temperature significantly decreases stomatal conductance in winter wheat and barley. On the contrary, it was shown that transpiration and stomatal conductance usually increase, up to a point, as the temperature increases [16,47,48]. It is possible that the higher temperatures caused the plant to undergo a stress response to heat and close its stomata, thereby limiting the amount of transpiration and thus reducing stomatal conductance to prevent water loss.

The temperature significantly decreased non-photochemical quenching (qNP) but did not affect the effective or maximum quantum yield ($\Delta F/F_m'$ and Fv/F_m, respectively) or photochemical quenching (qP) (Table 12). Similar results were reported by Gerganova et al. [49], who found that high temperatures significantly reduced qNP in tomato plants. Our results disagree with the past research on temperature and canola [40], as the research has noted an increase in qNP as a mechanism induced by high temperatures in order to protect the photoreaction center of PSII [50]. Photosynthetic pigments, carotenoids, water potential, and leaf moisture were not significantly affected by the temperature (Tables 14 and 16). As well, the chlorophyll levels, as measured by Dualex Scientific, were not affected by the temperature (Table 18). The nitrogen balance index (NBI) significantly increased with exposure to higher temperatures, which is in agreement with Munyon et al. [51], who reported that the nitrogen balance index increased significantly with increasing the temperature in cereal rye, crimson clover, triticale, and winter wheat. These results suggest that plants grown under higher temperatures may use more carbon to synthesize polyphenols than chlorophyll [52]. On the other hand, our results indicated that the flavonoid levels decreased in plants grown under higher temperatures, which is consistent with [18], who found that high temperatures downregulated the expression of genes required in the flavonoid biosynthesis pathway in *Arabidopsis* seedlings. High temperatures induce expression of the repressors of anthocyanin biosynthesis and downregulate the expression of the anthocyanin biosynthetic genes [18,53].

4.2. Effects of Watering Regime

In our study, the presence of water stress significantly reduced the stem height, stem diameter, leaf area, growth rate, and dry mass accumulation of leaves, stem, root, and the total plant (Tables 2, 4 and 6). These results are consistent with other findings related to the effects of water stress on tomatoes [54]. No growth indices were found to be significantly affected by water stress (Table 8). This is inconsistent with earlier studies, particularly in regard to S:R, which has been shown to decrease under water shortage [48]. Though it was expected that an increase in the number of leaves dropped from the plant would occur under drought conditions, as was found in an earlier study [33], our results did not support this.

We also found that the net CO_2 assimilation, transpiration rate, and stomatal conductance were all reduced due to water stress, though WUE was not (Table 10). These significant effects are in accordance with stomatal closure, which has been shown to occur in water-stressed plants, including canola [9,55]. As well, no aspects of chlorophyll fluores-

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cence were significantly affected (Table 12). This is unusual, as a rise in qNP usually occurs in response to water deficits in order to protect the photosystem [50].

Photosynthetic pigments were not affected significantly by water stress conditions (Table 14), nor leaf moisture (Table 16). However, a significant reduction of the soil water potential and leaf water potential was found in accordance with the water stress (Table 16). Our results are in agreement with Osakabe et al. [56], who reported that the leaf water potential decreased during water stress, which reduced the expression of photosynthesis-related genes and so decreased CO_2 assimilation. The NBI, total chlorophyll, and flavonoids were all decreased by water stress (Table 18); however, they were not significant. Our results are contrary to results seen in other studies, especially with regards to flavonoids [41,55].

4.3. Effects of Abscisic Acid (ABA)

In the current study, ABA had significantly negative effects on the stem height, stem diameter, and growth rate (Tables 2 and 4), all of which coincide with past studies on ABA treatment effects [28,38,44].

The leaf area and number were decreased by abscisic acid application (Table 2); however, they were not significant. It was found that ABA treatment decreased the total number of leaves per plant while increasing the leaf area [57].

Abscisic acid-treated plants exhibited a lower leaf mass, along with lower CO_2 assimilation rate, lower rate of transpiration, and lower stomatal conductance (Tables 6 and 10). Similarly, Gomez-Cadenas et al. [58] reported that ABA treatment decreased CO_2 assimilation, as well as stomatal conductance in citrus plants. Furthermore, Saradadev et al. [59] found that ABA-treated plants had a lower stomatal conductance and transpiration rate than the untreated ones. Stomatal closure induced by ABA treatment might explain the reduction in transpiration, as well as CO_2 assimilation in ABA-treated plants [60].

Shoot, root, and total dry mass accumulation, as well as all growth indices and WUE, were not significantly affected by ABA application. The only chlorophyll fluorescence parameter affected significantly by ABA treatment was qNP, which was reduced by ABA treatment (Table 12). Photosynthetic pigments, water potential, leaf moisture, NBI, and flavonoids were not significantly affected by ABA treatments (Tables 14, 16 and 18). However, ABA treatment had no impact on the chlorophyll content in vivo [61].

4.4. Interactive Effects of Temperature, Watering Regime, and Abscisic Acid

It is important to study the effects of the factors associated with climate change, along with those factors that may alleviate stress on plants.

The interactive effects of the temperature and watering regime have been studied thoroughly, as they are two of the main stress factors associated with climate change [16,40,47,48,62]. Some research has also been done on the interaction between the factors of climate change and abscisic acid [28,30,63]. Interactions between temperature, watering regime, and abscisic acid are important in shaping our knowledge of how abscisic acid will interact with climatic factors.

In the current study, seven two-way interactions were observed (see Tables 1, 3, 7, 9 and 17). The parameters of the experiment were significantly affected by T × W in two cases (see Tables 7 and 17); by T × A in four cases (see Tables 1, 3, 7 and 9); and by W × A in one case (see Table 7).

Lower temperatures with no abscisic acid application produced the tallest plants with the highest rates of growth and stomatal conductance, while higher temperatures with abscisic acid application produced the shortest plants with the lowest rates of growth and stomatal conductance. The leaf mass ratio (LMR) was the greatest under higher temperatures with no abscisic application and lowest under higher temperatures with abscisic acid application. The total chlorophyll was the greatest in plants grown under higher temperatures that were well-watered and lowest in plants grown under lower temperatures that were water-stressed.

Two parameters were significantly affected by the T × W × A interaction; a reduced growth rate was shown in ABA-treated plants grown under lower temperatures, regardless

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of watering status, compared with ABA-untreated plants grown at low temperatures (Figure 2). Furthermore, the S:R mass ratio was the highest in ABA-treated plants grown at lower temperatures and well water conditions (Figure 3D).

The rest of the parameters were not significantly affected by the T × W × A interaction, which might be explained by the involvement of abscisic acid in the mitigation of some negative effects of temperature and water stress. With global climate change an inevitability, exogenous abscisic acid application to plants under climate change conditions deserves further investigation.

5. Conclusions

In conclusion, temperature and watering regimes have a substantial influence on the growth, development, physiology, and biochemistry of plant species, including tomatoes. Plant height was negatively affected by heat stress, water stress, and abscisic acid, as expected. Dry mass accumulation was negatively affected only by higher temperatures but was not positively affected by any other factor. Stomatal conductance and the transpiration rate were depressed by each stressor, as well as abscisic acid, and CO_2 assimilation was also reduced by water stress and the application of abscisic acid. These gas exchange parameters all exhibited the expected reactions to the stress factors and abscisic acid individually. Though there was some increase of qNP, no significant effects occurred on any other mechanism of chlorophyll fluorescence. This shows that, while measures may take place to protect photosystem II, the photosystem itself did not go through depression or excitation.

Overall, it appears that abscisic acid mitigated some of the parameters measured, though it did not have as much of an alleviation effect as previously thought. This study showed that abscisic acid may be a potential mitigating factor in plant responses to future climates, though research should be continued in order to provide a more broad and in-depth account of its effects on global climate change factors.

Author Contributions: T.A.-D. and M.A.G. conceived and designed the experiments, analyzed the data, and wrote the manuscript. S.K., A.L.A.-G., W.A.K., M.J. and M.Y.J. helped in the measurements of the gas exchange, chlorophyll fluorescence, photosynthetic pigments, and water potential. O.A.-Z. and T.H. helped in the nitrogen balance index; chlorophyll, flavonoids, and anthocyanins measurements and data analysis. All authors edited and provided a critical review of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by the Deanship of Scientific research/Al al-Bayt University and the Deanship of Scientific research/Yarmouk University (Grant's Number: 21/2020).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The datasets supporting the results of this article are freely available upon reasonable request from T.A.-D. and M.A.G.

Conflicts of Interest: The authors declare no conflict of interest.

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