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Effects of Exogenous Salicylic Acid (SA), 6-Benzylaminopurine (6-BA), or Abscisic Acid (ABA) on the Physiology of *Rosa hybrida* 'Carolla' under High-Temperature Stress

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Abstract: The study of the regulatory mechanism of exogenous plant growth regulators (PGRs) on the relevant physiological indicators is essential to maintain the normal growth of *Rosa hybrida* under high-temperature conditions. The photosynthetic and physiological characteristics of the ornamental cut rose *Rosa hybrida* 'Carolla' under high temperature were studied by spraying leaves with various concentrations of exogenous salicylic acid (SA; 0.5, 1.0, 1.5, or 2.0 mmol·L^{-1}), 6-benzylaminopurine (6-BA; 10, 20, 30, or 50 µmol·L^{-1}), abscisic acid (ABA; 10, 20, 30, or 50 mg·L^{-1}), or distilled water (control). The results indicated that a foliar spray of either SA, 6-BA, or ABA could mitigate the impact of high temperatures. Compared to the control, the application of SA, 6-BA, or ABA increased the net CO_2 assimilation rate (A_n), transpiration rate (E), stomatal conductance (G_s), and water use efficiency (WUE) of 'Carolla', while decreasing the leaf relative electrical conductivity (REC) and malondialdehyde (MDA) content. The applications of SA, 6-BA, or ABA increased the activities of the antioxidant enzymes superoxide dismutase (SOD), peroxidase (POD), and ascorbate peroxidase (APX) and altered the proline (Pro), soluble protein, and soluble sugar contents. The results showed that foliar sprays of SA, 6-BA, or ABA could enhance the heat tolerance of 'Carolla' by promoting photosynthesis, cell membrane structural stability, antioxidant enzyme activity, and osmoregulation in plants under high-temperature stress. The experiment showed that 1.5 mmol·L^{-1} SA, 20 µmol·L^{-1} 6-BA, or 75 µmol·L^{-1} ABA could alleviate the damage caused by high temperatures, with 20 µmol·L^{-1} 6-BA having the best effect.

Keywords: plant growth regulators; exogenous hormones; heat stress; physiological characteristics; cut rose; antioxidant capacity

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1. Introduction

Cut roses (*Rosa hybrida* L.) are an ornamental cash crop valued for their flowers' beauty, colour, and fragrance and for their long flowering period. However, growing marketable roses is complex, influenced by not only nutritional status but also other external environmental conditions such as temperatures. High temperatures, such as when the ambient temperature is consistently higher than 30 °C in the summer, cause the roses to enter a semi-dormant state [1]. As global warming continues to disrupt climate patterns and cause frequent high temperatures in the summer, the production of roses faces the serious challenge of unpredictable high temperatures.

High temperature is one of the major abiotic stresses, affecting all aspects of plant growth and development [2,3]. High temperatures reduce leaf surface area, decrease

leaf water content, increase premature leaf decay, increase leaf temperature, decrease leaf antioxidant enzyme activity, lead to increased malondialdehyde (MDA) content, and cause oxidative stress that disrupts cell membrane permeability and increases electrolyte leakage, causing membrane injury in wheat grain [4], rice [5], tobacco [6], and *Brassica napus* [7]. High temperatures cause changes in the structural organization of chloroplasts and thylakoids, resulting in the inhibition of photosynthesis [8]. Heat damage in plants causes cellular aging and, in severe cases, death [9].

In roses, high temperatures turn the leaves yellow and wrinkled, increase the stem base and plant height, and weaken both the growth potential and the disease resistance [10]. The floral organs are the most sensitive to high temperatures [11]. High temperature hinders flower bud differentiation, causing floral buds to shift to leaf buds, decreasing the number of blooms, shortening the flowering period, and aborting flowers [12]. Other studies have shown that high temperature promotes the formation of foliage flowers [13] and leads to an increased incidence of bent peduncles [14]. High temperature also affects rose physiology, reducing chlorophyll content, stomatal conductance, and intercellular CO_2 concentration, and causing a decrease in photosynthetic rate [15]. In China rose cultivars Slater and Old Blush, high temperature decreased SOD and POD activities, increased MDA content, and increased the relative conductivity, causing cell membrane damage, decreasing proline and soluble sugar contents, and increasing water loss [16]. High temperature limits plant growth and development, which impacts not only the ornamental value of the produced roses but also the yield and economic value. As a result, reducing the stress injury caused by high temperatures on the rose crop is a pressing issue for producers.

The spraying of exogenous substances is a simple and efficient method for affecting plant culture, and its use to improve plant resistance to stress has been attracting more attention. Plant growth regulators play intrinsic roles in the plant responses to stress. Salicylic acid (SA) regulates plant stress resistance [17,18] and cellular antioxidant mechanisms to enhance plant tolerance to biotic and abiotic stresses [19]. Most abiotic stresses increase the in-plant concentration of SA, suggesting that SA is involved in stress signaling [20]. Grapes (*Vitis vinifera* L.) show a dramatic increase in SA levels at the onset of thermal acclimation, and exogenous SA induces similar levels of heat tolerance to thermal acclimation [21]. Inhibitors of SA synthesis demonstrate a direct role of SA synthesis in heat acclimation, which not only reduces the endogenous SA content but also reduces the level of heat tolerance [22]. Cytokinins have important roles in alleviating biotic and abiotic stresses [23]. Brief heat treatment of the roots of bean seedlings results in a sixfold decrease in CK content and a fourfold increase in ABA levels in xylem exudates [24]. Abscisic acid (ABA) plays a key role in the regulation of plant responses to high temperature stress [25]. Osmotic stress leads to a rapid increase of endogenous ABA in roots and shoots. Plants rapidly accumulate ABA when subjected to abiotic stress, which then activates multiple stress responses [26]. Foliar spraying of these growth regulators alleviates the stress caused by high temperatures. SA application slows the rate of chlorophyll degradation, increases the activities of the antioxidant enzymes SOD, POD, and APX, and suppresses MDA content and relative conductivity in miniature roses [27]. The use of the synthetic cytokinin 6-benzylaminopurine (6-BA) significantly increases the antioxidant enzyme activity and decreases the MDA content and relative conductivity in the leaves of sweet pepper seedlings. Application of ABA reduces the MDA content of chickpea under high-temperature stress [28], enhances the antioxidant capacity of muscadine grapes [29] and blueberries [30], and induces tolerance to stress by increasing the contents of MDA and Pro in sugarcane leaves [31].

High temperatures seriously threaten the growth and development of roses, and the application of exogenous plant growth regulators (PGRs) may alleviate this damage. However, the mechanisms via which exogenous PGRs regulate the physiological indices of roses under high-temperature stress are poorly understood, and studies on the effect of the cytokinin 6-BA on high-temperature resistance have rarely been reported. Our data show that spraying exogenous SA, 6-BA, or ABA alleviates the damage of roses under high

temperatures, and that 6-BA is the most effective treatment. Treatment with 6-BA allows the rose plants to maintain normal growth and development under high-temperature stress.

2. Materials and Methods

2.1. Plant Material and Experimental Design

The experiment was conducted in controlled environment chambers (Thermoline TPG-6000-TH) at Henan Agricultural University. Two year old soil-grown plants of *Rosa hybrida* 'Carolla' were pruned uniformly before treatment. The day/night temperatures during the experiment were 35/20 °C, and the relative humidity (RH) was maintained at approximately 70–80%. Light irradiance was up to 850 μmol·m^{-2}·s^{-1} under a 12/12 h light/dark cycle. The nutrient solution was composed of $Ca(NO_3)_2 \cdot 4H_2O$, KNO_3, EDTA-Fe, $Mg(NO_3)_2 \cdot 6H_2O$, $(NH4)_2PO_4$, $MnSO_4 \cdot 5H_2O$, $ZnSO_4 \cdot 7H_2O$, H_3BO_3, $CuSO_4 \cdot 5H_2O$, and $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$ provided at 1.841, 2.323, 64.5, 204.8, 575, 12.05, 8.63, 9.27, 1.25, and 0.88 mg·L^{-1}, and H_2SO_4 provided at 281 μL·L^{-1}, respectively (EC 1.0 dS·m^{-1}, pH 6.0 ± 0.2). Pest and disease control was applied as required.

One week after bud break, the first salicylic acid (SA), 6-benzyl amino purine (6-BA), and abscisic acid (ABA) sprays were carried out on plant leaves. For each treatment, around 30 plants were used. The foliar applications were conducted at 10 day intervals. Treatments included a control (CK) with no SA, 6-BA, or ABA: low, 0.5 mmol·L^{-1} SA, 10 μmol·L^{-1} 6-BA, or 37.5 μmol·L^{-1} ABA; medium, 1.0 mmol·L^{-1} SA, 20 μmol·L^{-1} 6-BA, or 75 μmol·L^{-1} ABA; high, 1.5 mmol·L^{-1} SA, 30 μmol·L^{-1} 6-BA, or 112.5 μmol·L^{-1} ABA; highest, 2.0 mmol·L^{-1} SA, 50 μmol·L^{-1} 6-BA, or 187.5 μmol·L^{-1} ABA. CK plants were sprayed with distilled water. These sprays were applied in the morning hours (6:00 to 9:00 a.m.).

2.2. Determination of Physiological and Biochemical Traits

2.2.1. Determination of Chlorophyll (Chl) Content

Chl was measured according to [32]. Leaf samples (0.1 g) were homogenized with 1 mL of 80% (*v*/*v*) cold acetone under dark conditions and macerated at 4 °C for 24 h. After centrifuging at 12,000× *g* for 10 min, the reaction solution was read at 645 nm and 663 nm using a fluorescence plate reader (Infinite 200 PRO, Tecan, Grödlg, Austria). The amount of Chl was determined according to the following formula:

$$\text{Chl content (mg·g}^{-1}\text{ FW)} = (20.29 \times A645 + 8.05 \times A663) \times (Vt/W),$$

where Vt is the final volume of the extraction solution (mL), and W is the weight of the sample (g).

2.2.2. Determination of Photosynthetic Indices

The photosynthetic indices, including A_n, E, and G_s, were measured at 10:00 a.m. The parameters of the portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE, USA) were set according to [33]. The CO_2 concentration in the LI-6400 leaf chamber (Ca) was set at 400 μmol CO_2·mol^{-1} air, the leaf temperature was set at 25 °C, and the RH of the incoming air was set at 65–70%. The flow rate was set to 500 μmol·s^{-1}, and photosynthetic photon flux density (PPFD) was 1800 μmol·m^{-2}·s^{-1}. The water use efficiency was calculated as follows: WUE (μmol·mmol^{-1}) = net photosynthetic rate/transpiration rate [34].

2.2.3. Determination of Relative Electrical Conductivity (REC) and Malondialdehyde (MDA) Content

The relative electrical conductivity (REC) was determined according to [35]. The leaves of plants of comparable size (trying to ensure the integrity of the leaves, with fewer stem nodes) were taken. The leaves were washed with tap water and then rinsed with distilled water three times, the surface water was blotted out with filter paper, the leaves were cut into long strips of suitable length (avoiding the main veins), and the fresh samples were quickly weighed into 10 portions of 0.1 g each and placed in graduated test tubes with

10 mL of deionized water. The samples (ten pieces) were bathed for 30 min at 25 °C before the initial electrical conductivity (C_0) was read using a Delta 326 conductivity meter (Leici Inc., Shanghai, China). Samples were also read after bathing for 5 min at 100 °C and after cooling for the final electrical conductivity (C_1). The REC was calculated as follows: relative electrical conductivity (%) = $(C_1 - C_0)/C_0 \times 100$.

The MDA activity was determined according to [36]. The samples (0.25 g) were homogenized with 5 mL of 5% (w/v) trichloroacetic (TCA) and then centrifuged at 10,000× g at 4 °C for 15 min. Supernatant (2 mL) was mixed with 2 mL of 0.67% (w/v) thiobarbituric acid (TBA) and allowed to react for 30 min in boiling water. After cooling, reactions were read at 450, 532, and 600 nm. The MDA activity was calculated as follows: MDA ($mmol \cdot g^{-1}$) = 6.45 × (A532 − A600) − 0.56 × A450.

2.2.4. Determination of Enzymatic Activity

The antioxidant enzyme activity was measured according to [37]. For crude enzyme extraction, samples (0.25 g) were homogenized with 9 mL of phosphate-buffered saline (PBS, 50 mM, pH 7.8). After centrifuging at 10,000× g for 15 min at 4 °C, the supernatant was utilized to determine SOD, POD, and APX activity.

The reaction solution of SOD consisted of 0.05 mL of enzyme extract, PBS (50 mM, pH 7.8), methionine (Met, 130 mM), nitro blue tetrazolium (NBT, 750 μM), ethylenediaminetetraacetic acid disodium salt (EDTA-Na_2, 100 μM), and 20 μM riboflavin. The reactions were incubated at a lux illuminance of 4000 lux for 20 min. The reactions were read at 560 nm with PBS (50 mM, pH 7.8) as the blank reference. SOD activity was calculated as follows:

$$\text{SOD } (U \cdot g^{-1} \text{ FW}) = Vt \times (A_{CK} - A_E)/(0.5 \times A_{CK} \times W \times V_s),$$

where A_{CK} is the reading of the blank reference, A_E is the reading of the sample, and V_s is the determination volume of the reaction mixture solution in mL.

The reaction for POD consisted of 1 mL of enzyme extract, PBS (50 mM, pH 6.0), 0.2% (v/v) guaiacol, and 30% (v/v) H_2O_2. The reactions were read at 470 nm every minute. Reactions were repeated three times, and PBS (50 mM, pH 6.0) was the blank reference. The POD activity was calculated as follows:

$$\text{POD } (U \cdot g^{-1} \text{ FW}) = (A470 \times Vt)/(0.01 \times t \times W \times V_s),$$

where t is the reaction time in min.

The reaction mixture of APX included 0.1 mL of enzyme extract, PBS (50 mM, pH 7.0), ascorbic acid (ASA, 15 mM), and H_2O_2 (0.3 mM). The reactions were read at 290 nm with PBS (50 mM, pH 7.0) as the blank reference. The APX activity was calculated as follows:

$$\text{APX } (U \cdot g^{-1} \text{ FW}) = (A290 \times Vt)/(0.01 \times t \times W \times V_s).$$

2.2.5. Determination of Osmotic Substance Contents

Proline was extracted with sulfosalicylic acid according to [38]. Samples (0.25 g) were extracted with 3% sulfosalicylic acid (w/v) for 5 min in boiling water. The reaction mixture including 2 mL of extracted supernatant, acid-ninhydrin reagent, and glacial acetic acid was boiled for 30 min. After cooling, 5 mL of toluene was added, and the mixture was read at 520 nm. The proline content was calculated according to a proline standard curve and expressed as μg proline per g ($\mu g \cdot g^{-1}$).

Soluble sugar content was determined according to [39]. After drying at 105 °C for 1 h and then at 70 °C for 24 h, the samples (0.05 g) were homogenized in 4 mL of 80% ethanol, then bathed for 40 min at 80 °C, and centrifuged at 12,000× g for 1 min. The residue was repeatedly extracted with 4 mL of 80% ethanol, and then combined with the other supernatants. The supernatant was destained with 0.01 g of active carbon at 80 °C for 30 min. The reaction to determine the soluble sugar content included 1 mL of supernatant, 1.2 mL of H_2O, 0.005 g of anthrone, and 3.8 mL of concentrated sulfuric acid. The reactions

were read at 625 nm, and the result was calculated according to the glucose solution standard curve, described as mg·g^{-1} dry weight (DW).

Soluble protein was extracted with Coomassie brilliant blue [39]. Samples (0.50 g) homogenized in 5 mL PBS (50 mM, pH 7.8) were centrifuged at 10,000× *g* at 4 °C for 15 min. Supernatant (0.1 mL), 0.9 mL of H_2O, and 5 mL of Coomassie brilliant blue were mixed and read at 595 nm. The soluble protein content was calculated according to a bovine serum albumin (BSA) standard curve, described as mg·g^{-1} fresh weight (FW).

2.2.6. Statistical Analysis

Statistical Analysis System (version 9.3, SAS Institute Inc., Cary, NC, USA) was used to perform statistical analyses using ANOVA, and Sigma Plot (Systat Software, Inc., Chicago, IL, USA) was used for making graphs. The values are described as means ± SD; different letters denote significant differences ($p < 0.05$) according to Duncan's multiple range tests.

3. Results

3.1. Effects of Different Concentrations of SA, 6-BA, or ABA on Chl Content of Rosa hybrida 'Carolla' under High-Temperatures Stress

Chloroplasts are one of the main sites for intracellular ROS production, and the oxidative degradation of chlorophyll is accelerated at high temperatures due to the massive accumulation of ROS. Chlorophyll is the material basis for photosynthesis in plants, and its content largely reflects the strength of photosynthesis in leaves.

Spraying SA, 6-BA, or ABA significantly increases the Chl content of rose leaves under high-temperature stress compared to the control (Figure 1). With increasing concentrations, the chlorophyll content increased and then decreased. The most effective treatments were moderate SA (1.5 mmol·L^{-1} SA), moderate 6-BA (20 μmol·L^{-1} 6-BA), and moderate ABA (75 μmol·L^{-1} ABA), which generated 1.615-, 2.120-, and 1.450-fold increased Chl content over the control, respectively. After spraying 20 μmol·L^{-1} 6-BA, the Chl content reached 1.75 mg·g^{-1} FW, which was the highest level of chlorophyll under high-temperature stress. This suggests that exogenous PGRs can increase the content of the photosynthetic pigment under high temperatures.

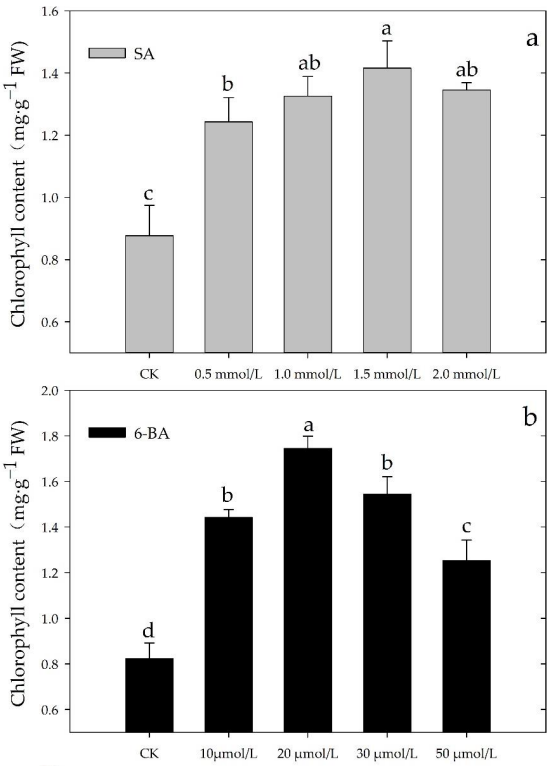

Figure 1. *Cont.*

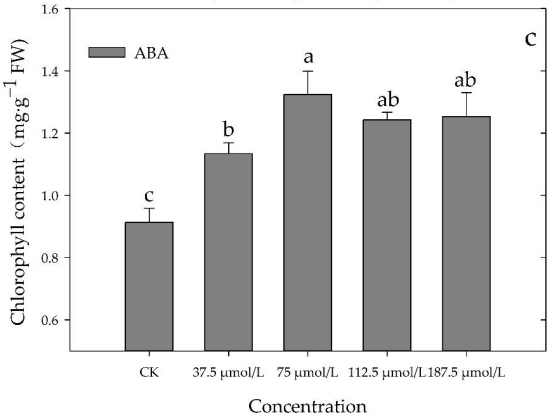

Figure 1. Effects of different concentrations of SA (**a**), 6-BA (**b**), or ABA (**c**) on chlorophyll content (Chl) of *Rosa hybrida* 'Carolla'. CK: distilled water. Vertical bars mean standard errors (n = 10). The values are described as means ± SD; different letters denote significant differences ($p < 0.05$) according to Duncan's multiple range tests.

3.2. Effects of Different Concentrations of SA, 6-BA, or ABA on A_n and WUE of Rosa hybrida 'Carolla' under High-Temperature Stress

Under high-temperature stress, plants maintain their survival by consuming large amounts of carbon, and the increase in net photosynthetic rate (A_n) helps to promote the accumulation of carbon. Increasing concentrations of the different PGR treatments increased and then decreased the A_n under high temperature stress (Figure 2a). Water use efficiency (WUE) increased after SA treatment, reaching 14.597 μmol·mmol^{-1} with the high 2.0 mmol·L^{-1} SA treatment, which was 1.507 times higher than the control (Figure 2b). Compared to the SA and ABA treatments, the moderate 6-BA concentration, 75 μmol·L^{-1}, resulted in the best A_n and WUE under high temperature stress, with the A_n reaching 14.660 μmol CO_2·m^2·s^{-1}, 2.507 times higher than the control, and the WUE reaching 15.007 μmol·mmol^{-1}, 1.487 times higher than the control.

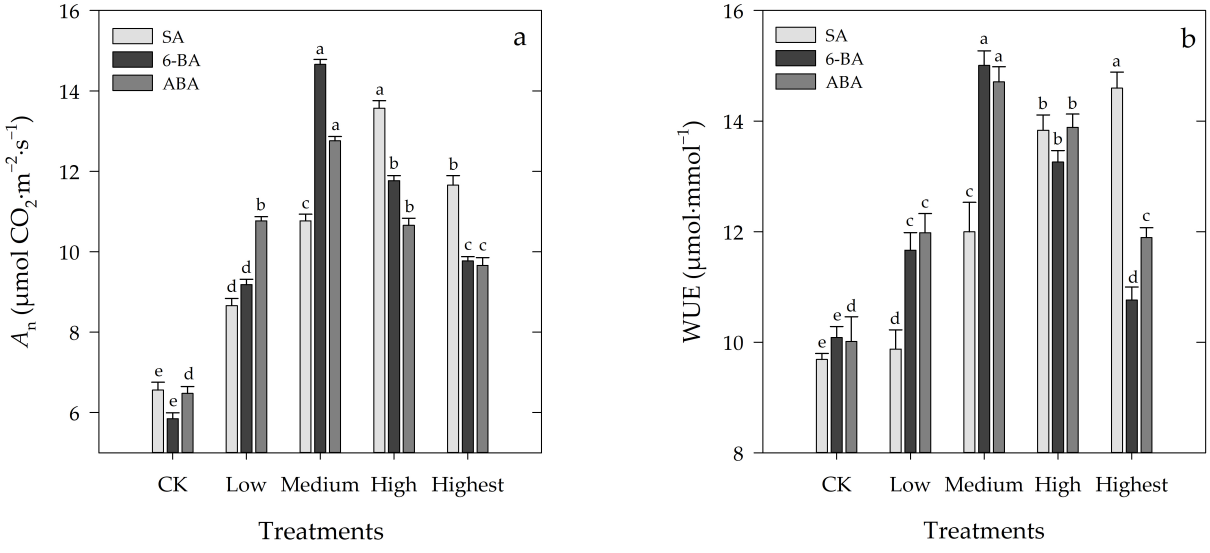

Figure 2. Effects of different concentrations of SA, 6-BA, or ABA on the net CO_2 assimilation rate net (A_n, (**a**)) and water use efficiency (WUE, (**b**)) of *Rosa hybrida* 'Carolla'. CK: distilled water. Low: 0.5 mmol·L^{-1} SA, 10 μmol·L^{-1} 6-BA, 37.5 μmol·L^{-1} ABA; medium: 1.0 mmol·L^{-1} SA, 20 μmol·L^{-1} 6-BA, 75 μmol·L^{-1} ABA; high: 1.5 mmol·L^{-1} SA, 30 μmol·L^{-1} 6-BA, 112.5 μmol·L^{-1} ABA; highest: 2.0 mmol·L^{-1} SA, 50 μmol·L^{-1} 6-BA, 187.5 μmol·L^{-1} ABA; Vertical bars denote standard errors (n = 10). The values are described as the means ± SD; different letters denote significant differences ($p < 0.05$) according to Duncan's multiple range tests.

3.3. Effects of Different Concentrations of SA, 6-BA, or ABA on E and Gs of Rosa hybrida 'Carolla' under High-Temperature Stress

High temperatures can influence the respiration and transpiration of a plant through the degree of stomatal opening. When the level of heat stress is within the plant's tolerance range, the plant will increase its evapo-transpiration capacity to prevent leaf damage from high temperatures. The transpiration rate under the lowest ABA treatments (37.5 μmol·L^{-1} ABA) was 1.591 times higher than the control, at 2.666 mol H_2O·m^2·s^{-1}, and then gradually decreased with increasing concentrations (Figure 3a). Under high-temperature stress, a moderate SA treatment (1.5 mmol·L^{-1}) produced the best transpiration rate and stomatal conductance, with the transpiration rate reaching 2.877 mol H_2O·m^2·s^{-1}, 1.890 times higher than the control, and stomatal conductance reaching 0.981 mol H_2O·m^2·s^{-1}, 1.449 times higher than the control (Figure 3b).

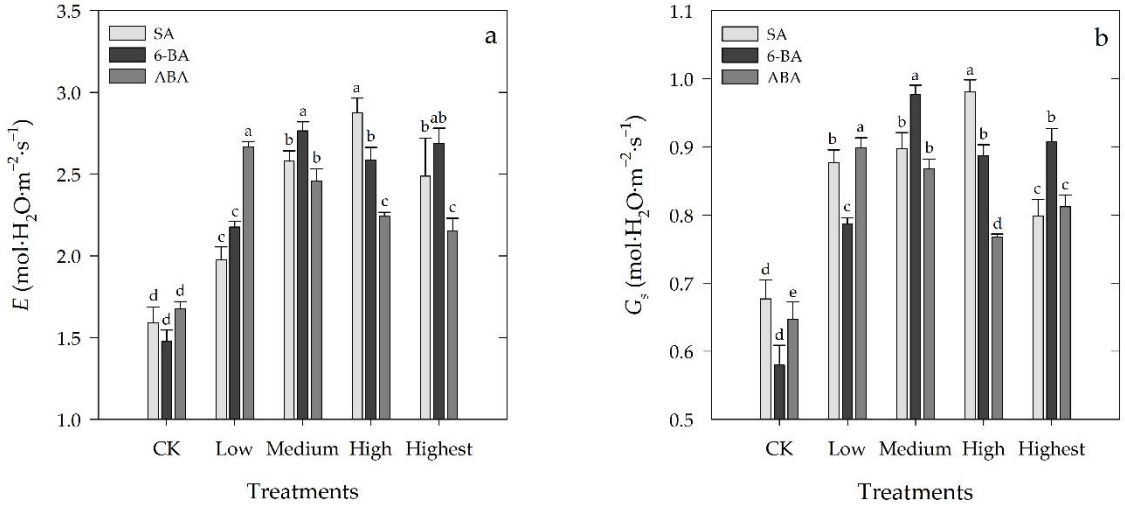

Figure 3. Effects of different concentrations of SA, 6-BA or ABA on the transpiration rate (E, (**a**)) and stomatal conductance (G_s, (**b**)) of *Rosa hybrida* 'Carolla'. CK: distilled water. Low: 0.5 mmol·L^{-1} SA, 10 μmol·L^{-1} 6-BA, 37.5 μmol·L^{-1} ABA; medium: 1.0 mmol·L^{-1} SA, 20 μmol·L^{-1} 6-BA, 75 μmol·L^{-1} ABA; high: 1.5 mmol·L^{-1} SA, 30 μmol·L^{-1} 6-BA, 112.5 μmol·L^{-1} ABA; highest: 2.0 mmol·L^{-1} SA, 50 μmol·L^{-1} 6-BA, 187.5 μmol·L^{-1} ABA; Vertical bars denote standard errors (n = 10). The values are described as the means ± SD; different letters denote significant differences ($p < 0.05$), according to Duncan's multiple range tests.

3.4. Effects of Different Concentrations of SA, 6-BA, or ABA on MDA and REC of Rosa hybrida 'Carolla' under High-Temperature Stress

Under high-temperature stress, the membranes of plants are damaged, and the cell membrane loses selective and active absorption, while its permeability increases, causing electrolyte leakage and increasing the conductivity of tissue leachate. Therefore, measuring the REC of leaves is used as a physiological indicator to judge the degree of cell membrane damage by high temperature. High-temperature stress disrupts the cell membrane system of plants, causing peroxidation of the plasma membrane, and MDA is the final breakdown product of the oxidation reaction. The amount of MDA content is a common indicator of the degree of damage to the membrane system.

Under high-temperature stress, the MDA content reached 16.586 mmol·g^{-1}, and the REC was 68.364% under the control treatment (Figure 4). Different concentrations of PGRs showed decreasing then increasing trends, with moderate levels of any of the PGRs yielding the best effects. The most suitable concentrations were 1.5 mmol·L^{-1} SA, 20 μmol·L^{-1} 6-BA, or 112.5 μmol·L^{-1} ABA. The overall best alleviation came from the 20 μmol·L^{-1} 6-BA treatment, which decreased the MDA content to 9.245 mmol·g^{-1} and the REC to 55.477%.

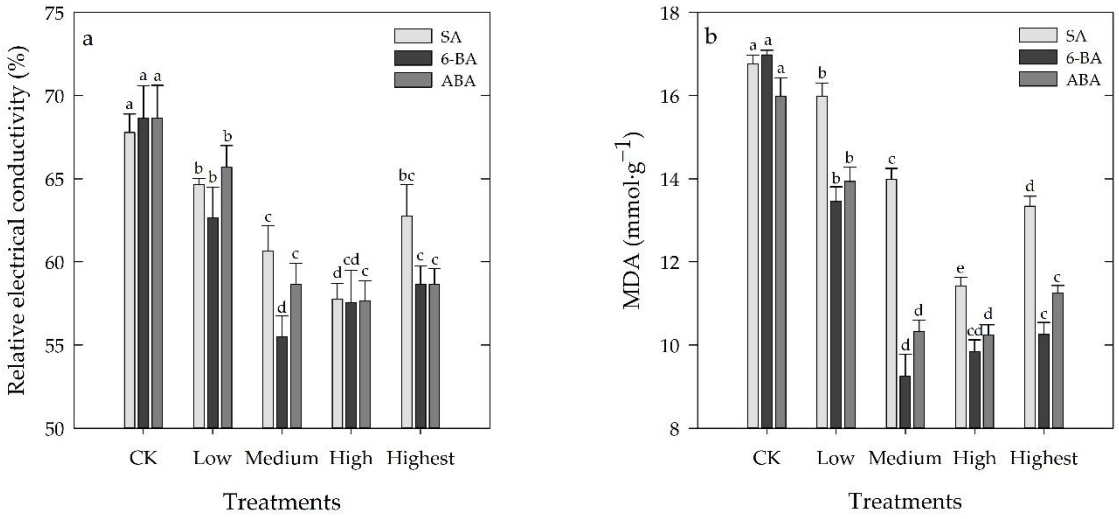

Figure 4. Effects of different concentrations of SA, 6-BA, or ABA on the relative electrical conductivity (REC, (**a**)) and MDA content (**b**) of *Rosa hybrida* 'Carolla'. CK: distilled water. Low, 0.5 mmol·L^{-1} SA, 10 µmol·L^{-1} 6-BA, 37.5 µmol·L^{-1} ABA; medium: 1.0 mmol·L^{-1} SA, 20 µmol·L^{-1} 6-BA, 75 µmol·L^{-1} ABA; high: 1.5 mmol·L^{-1} SA, 30 µmol·L^{-1} 6-BA, 112.5 µmol·L^{-1} ABA; highest: 2.0 mmol·L^{-1} SA, 50 µmol·L^{-1} 6-BA, 187.5 µmol·L^{-1} ABA; Vertical bars denote standard errors (n = 10). The values are described as the means ± SD; different letters denote significant differences ($p < 0.05$) according to Duncan's multiple range tests.

3.5. Effects of Different Concentrations of SA, 6-BA, or ABA on Antioxidant Enzyme Activity of Rosa hybrida 'Carolla' under High-Temperature Stress

Reactive oxygen species (ROS) in plant tissues accumulate dramatically under stress and can affect normal cell development when reaching high concentrations. Antioxidant enzymes in plants can scavenge harmful substances such as ROS to a certain extent, thus reducing the damage to plant cells. The activities of three antioxidant enzymes, SOD, POD, and APX, reacted differentially to the different concentrations of the three PRGs under high temperature stress. The 20 µmol·L^{-1} 6-BA treatment increased SOD, POD, and APX activities the most, reaching 55.245, 194.245, and 121.770 U·g^{-1} FW, respectively, up 35.150%, 466.18%, and 34.155% from the control (Figure 5).

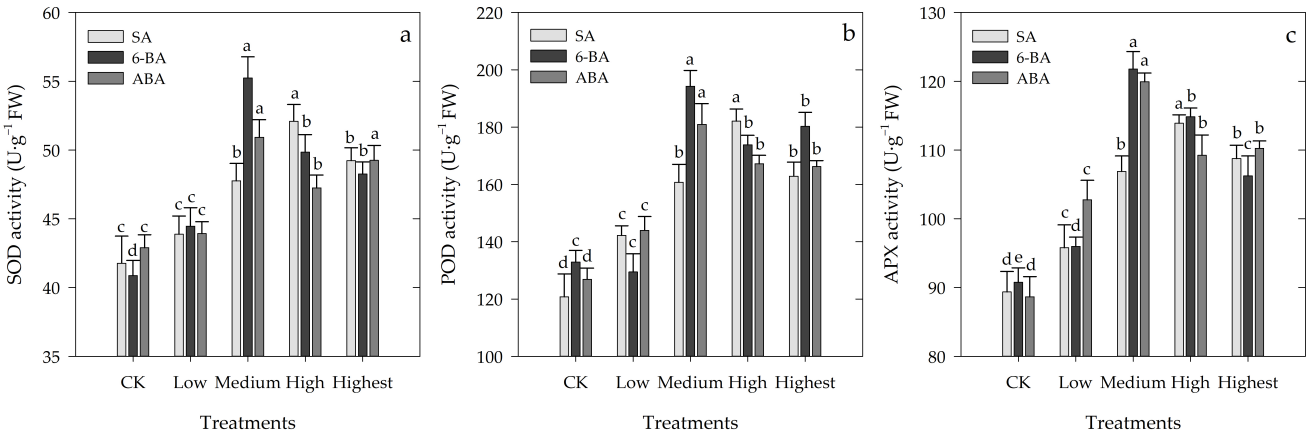

Figure 5. Effects of different concentrations of SA, 6-BA or ABA on activities of the antioxidant enzymes SOD (**a**), POD (**b**) and APX (**c**) of *Rosa hybrida* 'Carolla'. CK: distilled water. Low, 0.5 mmol·L^{-1} SA, 10 µmol·L^{-1} 6-BA, 37.5 µmol·L^{-1} ABA; medium: 1.0 mmol·L^{-1} SA, 20 µmol·L^{-1} 6-BA, 75 µmol·L^{-1} ABA; high: 1.5 mmol·L^{-1} SA, 30 µmol·L^{-1} 6-BA, 112.5 µmol·L^{-1} ABA; highest:

2.0 mmol·L^{-1} SA, 50 µmol·L^{-1} 6-BA, 187.5 µmol·L^{-1} ABA; Vertical bars denote standard errors (n = 10). The values are described as the means ± SD; different letters denote significant differences ($p < 0.05$) according to Duncan's multiple range tests.

3.6. Effects of Different Concentrations of SA, 6-BA, or ABA on Osmoregulatory Substances of Rosa hybrida 'Carolla' under High-Temperature Stress

Under high-temperature stress, the plant body maintains itself by losing water, which reduces the soil water potential in the plant growth environment and can affect its normal water uptake and transport [40], while the increase in the content of osmoregulatory substances reduces the water potential of plant cells and, thus, enhances the water uptake of plants. The 20 µmol·L^{-1} 6-BA treatment significantly increased the contents of proline, soluble sugar, and soluble protein. Under this 6-BA treatment, proline reached 1.598 µg·g^{-1}, 2.287 times that of the control, soluble sugar content reached 2.169 mg·g^{-1} DW, 2.562 times that of the control, and soluble protein content reached 2.745 mg·g^{-1} FW, 1.427 times that of the control (Figure 6).

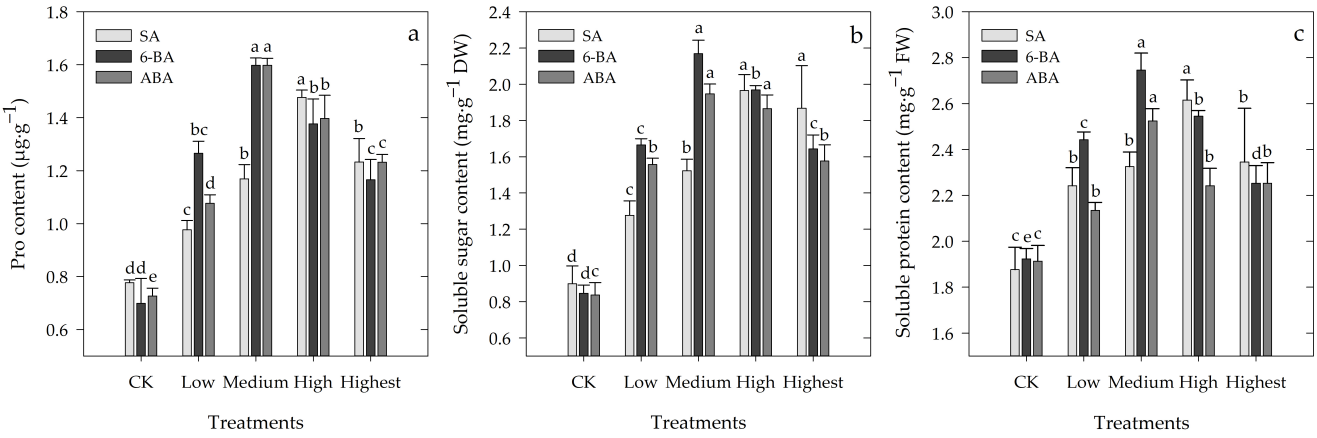

Figure 6. Effects of different concentrations of SA, 6-BA or ABA on the contents of the osmoregulatory substances proline (**a**), soluble sugars (**b**) and soluble proteins (**c**) of *Rosa hybrida* 'Carolla'. CK: distilled water. Low, 0.5 mmol·L^{-1} SA, 10 µmol·L^{-1} 6-BA, 37.5 µmol·L^{-1} ABA; medium: 1.0 mmol·L^{-1} SA, 20 µmol·L^{-1} 6-BA, 75 µmol·L^{-1} ABA; high: 1.5 mmol·L^{-1} SA, 30 µmol·L^{-1} 6-BA, 112.5 µmol·L^{-1} ABA; highest: 2.0 mmol·L^{-1} SA, 50 µmol·L^{-1} 6-BA, 187.5 µmol·L^{-1} ABA; Vertical bars denote standard errors (n = 10). The values are described as the means ± SD; different letters denote significant differences ($p < 0.05$) according to Duncan's multiple range tests.

4. Discussion

With global warming, high-temperature stress has become a more commonly devastating adverse stress for plants. Exogenous application of plant growth regulators (PGRs) can regulate the growth and development of plants under high-temperature stress. The PGRs SA and ABA are known to affect photosynthesis and other physiology of plants under high-temperature stress. SA is involved in the signaling process that enhances the tolerance to high temperatures [41]. ABA can regulate plant stress resistance in various ways, such as increasing the content of osmotic substances, enhancing the activity of intracellular enzymes, and regulating the expression of relevant drought resistance genes [42]. Cytokinins can modulate plant responses to abiotic stressors [23,43]. Spraying exogenous SA [44,45] or ABA [28,29] enhances photosynthesis, improves leaf water status and antioxidant enzyme activity, and alleviates plant damage caused by high temperature, which is similar to the results of this study.

Photosynthesis is the main way plants obtain the energy needed for growth and development, and the chlorophyll content directly affects the strength of photosynthesis. Chlorophyll biosynthesis requires a series of enzymatic reactions, and either too high or too low temperatures will inhibit the enzymatic reactions. High-temperature stress not only

reduces the rate of chlorophyll synthesis but also accelerates the degradation of chlorophyll due to the massive accumulation of reactive oxygen species at high temperatures. Chlorophyll content is significantly enhanced after spraying exogenous hormones, which may be because chlorophyll synthesis is promoted by spraying exogenous hormones under high-temperature conditions, e.g., 6-BA treatment of wheat leaves could promote the synthesis of chlorophyll precursor D-aminolevulinic acid [46]. Exogenous SA and ABA could alleviate the decreasing chlorophyll content under high-temperature stress [47]. ABA significantly increased the chlorophyll content in the legume *Medicago sativa* L. under high-temperature stress [48]. SA significantly increased the chlorophyll and carotenoid contents of *Artemisia annua* L. (0–1.00 mmol·L^{-1} SA) [49], but a high concentration of SA reduced the chlorophyll and carotenoid contents in *Helianthus annuus* L. [50]. In miniature rose, spray application of 1.5 or 2.0 mmol·L^{-1} SA slowed the rate of chlorophyll degradation in high-temperature stressed leaves [27]. In this study, 1.5 mmol·L^{-1} SA was found to significantly increase the chlorophyll content of the hybrid rose 'Carolla' seedlings; however, the chlorophyll content starts to decrease with increasing concentration, similar to the results reported above. In addition, 6-BA also decreased the chlorophyll content in the 'Carolla' seedlings at high concentrations. High-temperature stress reduces An, and the reduced carbon assimilation rate is associated with an effect on the activity of 1,5-diphosphate ribulose carboxylase (RuBPcase), a key enzyme for CO_2 assimilation in the dark reaction of photosynthesis [51]. However, spraying 6-BA could increase the activity of photosynthesis-related enzymes such as RuBPcase [52]. In addition, it is also closely related to light energy delivery. The net CO_2 assimilation rate also increases significantly after exogenous hormone spraying, which may be because exogenous hormone spraying under high-temperature conditions increases the light energy being used for delivery, further leading to an increase in carbon assimilation rate.

Stomatal conductance is regulated by a variety of environmental signals. The stomatal opening allows CO_2 diffusion into the leaf pulp and also allows water vapor to be emitted from the interior of the plant into the atmosphere, and stomatal closure helps to separate inside and adverse conditions outside the plant, primarily controlling transpiration rates [53]. Stomatal movement is the fastest response to ABA signals, and it has been demonstrated that external application of ABA can significantly increase the net photosynthetic response rate, stomatal conductance, and transpiration rate of plant leaves by altering the degree of stomatal opening [54,55]. In the present study, external application of ABA significantly also increased stomatal opening, which is consistent with this study. However, in other abiotic stresses, concerning stomatal regulation, ABA is used to resist external stresses by inducing stomatal closure [53]. We hypothesized that, under high-temperature conditions, PGRs would first induce stomatal opening to reduce the temperature by increasing transpiration water loss, thereby first alleviating the damage of high temperature on leaves. In addition, we concluded that the different effects of external ABA application on plant stomatal opening and closing are closely related to both the concentration and the time of external ABA application. In the present study, the effect of ABA-induced stomatal closure was weakened because of the longer duration of external ABA treatment on leaves, thus promoting stomatal opening, as confirmed by the results of some studies [56,57]. Exogenous PGRs increase stomatal conductance by inducing leaf stomatal opening, which increases the transpiration rate of leaves. However, exogenous PGRs also increase the water use efficiency of the plant. This series of changes may be due to a complex regulatory network in the plant that regulates the water uptake of the plant.

Oxidative stress is accompanied by the presence of other abiotic stressors such as high temperatures, and certain compounds may directly cause oxidative stress, and SA is an effective preventive medication against these compounds [20]. SA was shown to be the major signaling molecule necessary for stimulatory ozone-induced expression of GSH-based defense genes [58]. Glutathione levels are reported to be lower in plants subjected to oxidative stress, and glutathione *S*-transferase is inhibited by SA in a noncompetitive manner in vitro, suggesting that SA may regulate glutathione synthesis [59]. It is generally believed

that higher activity of protective enzymes indicates a stronger heat resistance of plants [60]. The activity of the antioxidant enzyme SOD is closely related to plant heat tolerance [21]. APX plays an important role in plant resistance to oxidative stress [61]. Spraying 6-BA under high-temperature stress significantly increases the activities of the above three enzymes. For this promoting effect of 6-BA, it may be that 6-BA is involved in the synthesis process of antioxidant enzymes and stimulates the expression of some key enzymes in the synthesis process, and it was reported that 6-BA can promote the ab initio synthesis of SOD under low-temperature adversity [62]. Spraying ABA alleviated oxidative stress in *Arabidopsis* under high-temperature stress [63]. Spraying SA significantly increased the activity of SOD in Kentucky Bluegrass [64]. Lipoxygenase (LOX) is an important enzyme that catalyzes the first step in the formation of oxylipin from polyunsaturated fatty acids, and the regulation of its activity and transcriptional expression has become an important part of the regulation of oxylipin synthesis, which is widely involved in the response of plants to a variety of stresses [65]. It was reported that O_2^- and H_2O_2 accumulation is lower, and stress response gene expression is significantly upregulated in LOX gene overexpression plants, suggesting that LOX may be positively regulating the stress response to adversity by regulating ROS accumulation and stress response gene expression [66]. Studies have shown that oxylipin, such as the phytohormone jasmonic acid (JA), is synthesized by LOX through the Allene oxide synthase (AOS) pathway and plays an important role in plant adversity stress [67]. In this study, we found that the external application of PGRs under high temperatures improved the antioxidant enzyme activity of plants, maintained the normal physiological metabolic function of plant leaves, enhanced the antioxidant protection system, and overall improved the heat resistance of plants. In addition, we found that the levels of SOD and APX activities were consistent with the dynamic balance of ROS, indicating that there is a synergistic effect between SOD and APX in 'Carolla' rose. The trends of SOD, POD, and APX activities showed a significant negative correlation with MDA content, indicating that exogenous PGR treatment alleviates high temperature injury precisely by increasing the activities of the antioxidant enzymes SOD, POD, and APX, which reduces MDA content and, thus, protects the cell membranes to enhance heat tolerance of roses. We also found that the effects of exogenous hormones on MDA content and leaf REC were correlated. Exogenous PGRs affect the excessive accumulation of ROS and alleviate cell membrane damage, thus increasing the selective permeability of cell membrane, and reducing the relative electrical conductivity of leaves. This indicates that exogenous PGRs help to reduce the damage to the cellular biomembrane of cells by high-temperature stress and enable the rose seedlings to better adapt to the high-temperature environment.

When plants are exposed to high temperatures, they actively accumulate organic or inorganic substances to reduce the cellular osmotic potential and maintain the structural stability of cell membranes to counteract the harmful effects of heat stress on plants. At present, the main osmoregulatory substances in plants are free proline, soluble protein, and soluble sugar. Proline content can, to a certain extent, reflect the ability of a plant to adapt to high temperatures [68]. Pro detoxifies excess ROS, regulates cellular osmotic balance, protects biofilms, and stabilizes enzymes/proteins [69]. Upregulation of Pro biosynthetic enzymes (such as pyrroline-5-carboxylate reductase and γ-glutamate kinase) and downregulation of Pro oxidase activity are the reasons for the elevated Pro levels [70]. SA (0.5 mM) significantly induces the activity of Pro biosynthetic enzymes (such as pyrrolidine 5-carboxylate reductase and γ-glutamate kinase) under stress, which is involved in the increase in Pro metabolism under abiotic stress [71,72]. Soluble proteins have an osmoregulatory effect and prevent cytoplasmic dehydration. Studies have shown that exogenous hormones increase the contents of soluble proteins under high-temperature stress [73–75], which is consistent with the present study. It has been reported that plants produce certain proteins in response to biotic and abiotic stresses, some of which are produced by plant hormones such as SA [76]. SA plays an effective role in regulating plastid extracellular proteins associated with adversity [77], inducing the synthesis of defense-type proteins such as protein kinase and Rubisco [78]. In addition, SA increases amino acids and

partial proteins of tissues under the stress of adversity [79] and induces the accumulation of solutes in leaves [80]. Soluble sugar plays an important role in the protection of various enzymes in cells and the stability of membrane systems [81]. It was shown that SA inhibits sucrose uptake in a concentration-dependent manner (10–200 μM) [82] and that the content of polysaccharides and soluble sugars is increased with 100 μmol·L^{-1} [83], 0.5 mM, and 1.0 mM SA [84]. Studies in *Arabidopsis* found that cytokinin regulates the expression of sucrase and mobilizes the transport of hexose [85]. Cytokinins increase fruit sugar content mainly by altering the distribution of carbohydrates among reservoir sources [86]. SA treatment significantly increases the protein and proline contents and reduces the effects of heat stress in *Cicer arietinum* [87]. ABA treatment provides partial protection from heat stress in chickpeas by upregulating osmoprotectants [28]. This study illustrated that spraying exogenous PGRs can alleviate stress caused by heat by regulating the osmotic balance of cells, which mitigates the damage caused by high temperatures to plants.

This study summarized the effects of exogenous SA, 6-BA, or ABA on the tolerance of different plants under high-temperature stress (Table 1). The appropriate concentration of exogenous PGRs to enhance the heat tolerance of plants varies from plant to plant. Interestingly, previous studies have shown that other factors such as exogenous calcium [6,88], jasmonates [89,90], and brassinosteroids (BRs) [91,92] can also regulate the effects of abiotic stressors such as high temperature on plant growth and development. Since the effects of PGRs on plant function are dose-dependent, too high concentrations can be detrimental to plant stress tolerance. Furthermore, the effect of the addition of exogenous PGRs on endogenous hormones in 'Carolla' under high-temperature stress was not elucidated in this study. It is known that plant tolerance to adversity stresses such as high temperature is a highly complex regulatory network involving the combined participation of multiple endogenous hormones. Therefore, in subsequent studies, it will be important to consider the changes between hormones within the plant and the transcriptional expression of heat resistance-related molecules regulated downstream of the hormones to provide new ideas for maintaining plant health under high temperatures.

Table 1. Enhanced temperature resistance upon exogenous PGR application in different plants.

Plant Name	Applied PGRs Concentration	Parameters Studied	Response *	Reference
Mustard (*Sinapis alba* L.)	100 μM SA 45 °C	H_2O_2 content and catalase activity	–	[93]
Kentucky bluegrass (*Poa pratensis* L.)	0.25 mmol/100 mL SA 46 °C	O_2^- generating rate and H_2O_2 SOD and CAT activity	– +	[64]
Cicer arietinum L.	100 μM SA	Catalase (CAT) activities Peroxidase (POX), ascorbate peroxidase (APOX)	– +	[87]
Winter wheat (*Triticum aestivum cv.*)	0.01 mM SA 10/5 and 5/3 °C	Ice nucleation activity	+	[77]
Cucumber (*Cucumis sativa* L.)	1 mM SA 40 °C	Electrolyte leakage, H_2O_2, and thiobarbituric acid-reactive substances (TBARS) Fv/Fm, the photosystem II electron transport (ΦPS II), SOD, CAT, GPX, APX, and GR activity	– +	[45]
Solanum tuberosum L.	10^{-5} M SA 42 °C	Catalase activity H_2O_2 content	– +	[94]
Pea (*Pisum sativun* L.)	150 μM SA 45 °C	MDA content, leaf injury, and the synthesis of heat-shock proteins (HSP 70 and Hsp 17.6)	–	[22]
Grapevine (*Vitis vinifera* L.)	100 μmol/L SA 38 °C	CAT activity Heat killing time, POD, APX, SOD activity, H_2O_2, GR, AsA, and GSH	– +	[95]
Platycodon grandiflorum	1.5 mmol/L SA 35/25 °C (day/night)	Relative conductivity SOD, CAT activity, proline, soluble protein, chlorophyll, carotenoid, leaf photosynthesis, ASA, and GSH content	– +	[73]
Phalaenopsis 'Red Sky'	80 μmol/L SA 40 °C	CAT, the relative electrical conductivity, and MDA content SOD, POD activity, proline, and soluble protein	– +	[74]

Table 1. *Cont.*

Plant Name	Applied PGRs Concentration	Parameters Studied	Response *	Reference
Miniature rose 'Golden Coast'	2.0 mmol/L SA	The degradation rate of chlorophyll, MDA content, and relative conductivity	−	[27]
	36 °C	Free proline (Pro) content, superoxide dismutase (SOD) activity, peroxidase (POD) activity, ascorbate peroxidase (APX) activity	+	
Sweet pepper (*Capsicum annum* L.)	10 μmol/L 6-BA	O_2^- production rate, MDA content, and relative electric conductivity	−	[62]
	40 °C/30 °C (day/night)	SOD, POD, APX activity, chlorophyll content, and chlorophyll fluorescence parameters	+	
Sweet pepper cultivar 'P13201'	10 μmol/L 6-BA	O_2^- production rate, MDA content, and relative conductivity	−	[96]
	40 °C/30 °C (day/night)	SOD, POD, APX activity, non-photochemical fluorescence quenching (NPQ), the actual photochemical yield of PSII (yield), actual photochemical efficiency of PSII (ΦPSII) chlorophyll *a*, chlorophyll *b*, and total chlorophyll	+	
Chickpea (*Cicer arietinum* L.)	2.5 μM ABA	Electrolyte leakage, 2,3,5-triphenyl tetrazolium chloride (TTC), malondialdehyde, and hydrogen peroxide	−	[28]
	40/35 °C	Shoot length, survival rate, endogenous ABA, proline, glycine betaine, trehalose, and chlorophyll	+	
Reed (*Phragmites communis Trin.*)	10 μM ABA	H_2O_2 and MDA content	−	[25]
	45 °C	Superoxide dismutase, catalase, ascorbate peroxidase, and peroxidase	+	
Sugarcane varieties GT 28 and YL 6	100 μM ABA 0 °C	MDA and GA3 content	−	[31]
		Proline, ABA, and the ratio of ABA/GA3	+	
Lucerne (alfalfa, *Medicago sativa* L.)	0.1 mM ABA 38 °C	Electrolyte leakage, stomatal conductance	−	[48]
		Leaf water potential	+	
Paeonia ostii 'Fengdan'	40 mg/L ABA	Leakage rate of electrolyte and MDA content	−	[75]
	40 °C	SOD activity, soluble protein, chlorophyll, proline, and soluble sugar	+	
Rhododendron lapponicum	10 mg/L ABA 37 °C/25 °C (day/night)	The degradation rate of chlorophyll	−	[97]
		SOD, POD, and CAT activity	+	

* "−" indicates inhibition; "+" indicates facilitation.

5. Conclusions

Our results showed that exogenous applications of the plant growth regulators SA, 6-BA, and ABA maintain the growth and development of 'Carolla' rose seedlings under high-temperature stress by regulating photosynthetic properties, such as chlorophyll content, net photosynthetic rate, transpiration rate, water utilization, cell membrane stability in leaves, antioxidant enzyme activity, and osmoregulatory substance content. This experiment showed that individual applications of 1.5 mmol·L^{-1} SA, 20 μmol·L^{-1} 6-BA, or 75 μmol·L^{-1} ABA could effectively reduce the damage of high-temperature stress on *Rosa hybrida* 'Carolla'. The 20 μmol·L^{-1} 6-BA treatment had the best mitigation effect. This study provides the data needed to use outside factors to regulate the growth and development of *Rosa hybrida* under high temperatures in an effort to support its normal growth and development.

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