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Mitigation of High Solar Irradiance and Heat Stress in Kiwifruit during Summer via the Use of Alleviating Products with Different Modes of Action—Part 1 Effects on Leaf Physiology and Biochemistry

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Abstract: Kiwifruit is a significant fruit crop species for many countries around the world. Due to climate change, it undergoes significant heat stress during the summer months in the Mediterranean area. Heat stress, along with high irradiance, generally imposes significant reductions in leaf photosynthetic activity and changes in leaf antioxidant status. In order to ameliorate these impacts, three alleviating commercial products (the osmoprotectant glycine betaine—commercial product BlueStim SP, the antioxidant mixture of tocopherol and phenolic compounds—commercial product Sun Protect, and reflectance calcium carbonate—commercial product Pureshade) were tested. In a fully mature kiwifruit orchard ('Hayward' cultivar), the prementioned products were foliarly applied during the summer months, and three assessments took place (in early and late August and late September) to assess their effects on photosynthetic activity, leaf carbohydrate concentration, the leaf sclerophylly indexes, leaf phenolic compound concentration, and antioxidant capacity. The three products induced various effects on leaf physiology and biochemistry, alleviating stress impact to some extent. Glycine betaine proved to be more efficient in alleviating the negative effects on the photosynthetic machinery, while leaf relative water content and, therefore, succulence remained at high levels. The reflectance calcium carbonate product resulted in lower leaf temperatures during the August measurements and in relatively high leaf carbohydrate concentrations. The discriminant analysis, which took place regarding all the measured parameters per assessment, resulted in distinct differences among the treatments, revealing the different modes of action and the effects of the products used. The alleviating products ameliorated the effects of heat and high irradiance stress in the kiwifruit leaves in terms of photosynthetic activity and hydration status, with glycine betaine being more effective than the others, especially under unfavorable conditions in mid-summer.

Keywords: antioxidant capacity; carbohydrates; chlorophyll fluorescence; phenolic compounds; photosynthesis

1. Introduction

Climate change, climate crisis, and global warming are all expressions of the same phenomenon observed during the last decades, with extreme weather conditions occurring in various places in the world. The outcome is the same, whatever term is used, and it is mostly attributed to the gradual increase of the earth's temperature over the last century due to the increase in carbon dioxide and methane concentrations in the atmosphere [1].

Some of the phenomena often observed nowadays due to global warming includes high summer temperatures and either mild or even extremely cold winters, depending

on the area [2]. While man has the means to endure the stress induced by extreme conditions, at least to some extent, plants are not able to respond equally effectively. The agricultural sector is vulnerable to high air temperatures [2,3], which significantly impair the physiological activities of the plants [4]. Annual crops may be able to avoid severe stress conditions, but perennials are not able to do so, as they are sessile organisms not able to move to favorable conditions and are, therefore, subjected to both winter and summer extreme conditions [5,6].

Heat stress (HS) is considered to be an increase in temperature over a threshold, which is specific to each plant species; for a period, it is able to provoke permanent injury in terms of growth and development [7]. Heat stress, as a result of high air temperature and high irradiance along with mild or severe drought stress, leads to an array of physiological, anatomical, molecular, and physiological alterations to plants, inhibiting growth and productivity [4,7,8]. One of the immediate effects is a reduction in photosynthetic activity and the relative water content of the leaves [2,9]. Following the closure of stomata to prevent excessive water loss, the production of reactive oxygen species (ROS) is inevitable, causing more or less oxidative stress [4,10]. Heat stress is thought to induce the synthesis of secondary metabolites, such as phenolic compounds [4,11], and overpower their oxidation by enhancing the activity of phenylalanine ammonia-lyase (PAL), one of the major enzymes in their biosynthetic pathway [7,11]. Indicators of HS are the damages observed in various plant tissues, such as sunburn in the leaves, stems, and branches, accelerated leaf senescence, and abscission, growth inhibition, poor fruit setting, high fruit drop, and reduced fruit quality [8,12]. Plants have evolved to cope with mild stress by activating a defense arsenal based on enzymatic and nonenzymatic antioxidants, such as phenolic compounds, tocopherols, ascorbic acid, etc., as well as by accumulating various compounds acting as osmolytes (sugar alcohols, proline, glycine betaine, etc.) [7].

Kiwifruit (*Actinidia* spp.) is a fruit species originating from southern China. It is fully acclimatized to the wet and warm conditions prevailing in the area [13], characterized by high air humidity, abundant rainfall (reaching 1200–1800 mm year⁻¹), frost-free growing seasons, and moderate light intensity [14], as its photosynthetic mechanism is saturated under 800–960 μmol (photon) m⁻² s⁻¹ PPFD (photosynthetic photon flux density) [15,16]. However, due to its high economic value, kiwifruit has been cultivated for many decades in the Mediterranean basin, where the summer season is dry and hot, with the solar irradiation exceeding 1800–2000 μmol (photon) m⁻² s⁻¹ PPFD during a typical summer day [15]. Under these conditions of excess radiation and high temperatures, kiwifruit leaves experience a reduced photosynthetic rate and photoinhibition, resulting in reduced growth rate, fruit quality, productivity, and storability [15,17–21].

The present research aimed to assess the efficacy of various foliarly applied products with different modes of action (i.e., an osmolyte—glycine betaine (GB), reflectance—calcium carbonate, and an antioxidant—tocopherol, among others) against heat and high solar irradiance stress in kiwifruit grown in an area in Greece, which is characterized by high summer temperatures.

2. Materials and Methods

2.1. Test Site Location—Plant Material

The trial took place in Agrinio county, Western Greece, in a 5-hectare kiwifruit orchard planted with the cultivar ‘Hayward’ during the years 2018 and 2019. During that initial year, the preliminary measurements were taken (data not presented), while in 2019, data on the overall kiwifruit vine appearance and many physiological and biochemical parameters were assessed and presented. The plants were 15 years old, trained as a pergola, planted at distances of 2.0 × 4 m, and had a trunk height of 1.8 m. Each plot comprised four vines and a total of 16 vines were used per treatment (four replications per treatment).

The cultural practices and inputs (water, fertilizers, and phytosanitary products) were the same for all the vines of the orchard. The soil was characterized as loam, with a pH value of 7.25, a CaCO₃ concentration of 3.05% w/w, an organic matter of 1.76% w/w, and

an electrical conductivity of 0.310 mS cm^{-1} (based on soil analysis results provided by the farmer).

2.2. Treatments and Measurements

Four treatments were foliarly applied during the two-year experimentation period. The first comprised the control, where no alleviation treatment was applied; the second one was a spray application of the osmoprotectant glycine betaine (as BlueStim 50% SP, distributed in Greece by Hellafarm, S.A.) at a dose rate of $600 \text{ g } 100 \text{ L}^{-1}$; the third one was a spray application of calcium carbonate (as Pureshade (calcium carbonate 62.5% *w/w*) distributed in Greece by Hellafarm, S.A.) at a dose rate of $3 \text{ L } 100 \text{ L}^{-1}$ (acting as reflective limestone based particle barrier), and the fourth one was a spray application of the antioxidant commercial product SunProtect (a mixture of UV absorbing compounds such as α -tocopherol (also an antioxidant), phenolic acids (ferulic acid) and boron) [22,23] at a dose rate of $120 \text{ mL } 100 \text{ L}^{-1}$. All products were applied thrice on 04/07, 07/08, and 21/08. An adjuvant was added to the tank mix of all products at a dose rate of $10 \text{ mL } 100 \text{ L}^{-1}$.

The photosynthetic capacity of the plants was measured with a portable photosynthesis system (Li-COR 6400) (Li-Cor, Lincoln, NE, USA) from 08.00 to 11.30 a.m., approximately. The portable photosynthesis system was adjusted to operate at 400 ppm CO_2 , the PAR was adjusted to $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (provided by LED arrays), the chamber temperature was adjusted to $25 \text{ }^\circ\text{C}$, and the flow rate was adjusted to 450 mL min^{-1} . Four leaves per plant were assessed, and three consecutive measurements were taken per leaf (eight leaves per plot, i.e., 32 leaves per treatment). At the same time, the chlorophyll content of the leaves was estimated using a Minolta SPAD 502 m (Konica Minolta, Inc. Tokyo, Japan), along with leaf temperature via the use of a hand-held IR thermometer (Axiomet, UK) for at least 20 fully expanded sun-oriented (at the time of measurement) leaves per plot. In all cases, fully mature and healthy leaves from the upper canopy level were selected for the measurements. Chlorophyll fluorescence measurements were also performed using a portable fluorimeter (OS 30p OPTI-Sciences) after 20 min dark adaptation of the leaves using suitable clips.

During the same period (early and late August and late September) three leaf sampling events took place to assess the effects of the alleviating products on the critical physiological and biochemical constituents of the leaves, which were used as stress indexes. Fully expanded and mature leaves were selected each time, which were placed in a cooler box filled with ice gel packs, and were then transferred to the laboratory for further analysis. For the analyses where dry leaf tissue was used, the leaves were lyophilized and then ground into a fine powder with a mill.

2.3. Leaf Sclerophylly Indexes

Leaf sclerophylly indexes were determined after measuring the fresh (FW), dry (DW), and turgor weight (TW) of the leaf and its area (LA) (using Image J software v. 1.53, University of Wisconsin, Madison, WI, USA). Sclerophylly indexes were measured based on the following equations: relative water content ($\text{RWC} = (\text{FW} - \text{DW})/(\text{TW} - \text{DW}) \times 100$; %), specific leaf area based on dry weight measurement ($\text{SLA} = \text{LA}/\text{DW}$; $\text{mm}^2 \text{ mg}^{-1}$), leaf tissue density ($\text{LTD} = \text{DW}/\text{FW}$; g kg^{-1}), water content at saturation ($\text{WCS} = (\text{TW} - \text{DW})/\text{DW}$; $\text{g H}_2\text{O g}^{-1} \text{ DW}$), water saturation deficit ($\text{WSD} = (\text{TW} - \text{FW})/(\text{TW} - \text{DW}) \times 100$; %), actual water content ($\text{WC} = (\text{FW} - \text{DW}) \times 100/\text{FW}$; %), and succulence ($\text{SUC} = (\text{FW} - \text{DW})/\text{LA}$; $\text{mg H}_2\text{O mm}^{-2}$). At least sixteen leaves were used per treatment each time.

2.4. Phenolic Compound Concentration and Antioxidant Capacity Determination

Approximately 0.5 g of dry leaf powder was weighed and extracted with 2.5 mL of 100% methanol (HPLC grade) at $38 \text{ }^\circ\text{C}$ for 15 min under periodical agitation. Afterward, the extract was centrifuged at $4000 \times g$ for 6 min; the supernatant was collected into a

new tube, and the pellet was re-extracted under the same conditions; the same procedure was repeated. The two supernatants were combined for the analysis of the total phenolic fractions and the antioxidant activity of the extract.

The concentration of the total phenols, total o-diphenols, total flavanols, and total flavonoids was determined in the supernatants, according to Roussos et al. [24]. The results expressed as mg equivalent gallic acid (GAE), caffeic acid (CAE), catechin (CtE), and CAE per g fresh weight (FW), respectively.

The antioxidant capacity was determined based on the DPPH (2,2-diphenyl-1-picrylhydrazyl), FRAP (Ferric Reducing Antioxidant Power), and ABTS assays, as described by Roussos et al. [24] and Re et al. [25], and are expressed in μmol Trolox equivalents (TE) per g fresh weight.

2.5. Soluble Sugars Determination

The soluble sugars were determined using 100 mg of dry leaf powder which was extracted twice with 4 mL of HPLC-grade water based on a microwave-assisted extraction method, as has been described by Roussos et al. [24]. Sugars were detected and quantified by HPLC using a Waters 510 isocratic pump (Waters, Milford, MA, USA) delivering acetonitrile: water (80:20), as the mobile phase at a flow rate of 1.0 mL min^{-1} to an Adamas Amino 5μ column ($250 \times 4.6 \text{ mm}$) (Sepachrom, Italy), working at 35°C . A refractive index detector (Hewlett Packard HP1047A) (Agilent, CA, USA) was used for the determination of the four soluble sugars in the kiwifruit leaves, i.e., sucrose, glucose, inositol, and fructose. A five-point calibration curve using external standards was used for the quantification of the prementioned soluble sugars, while the total sugar concentrations were estimated by summing the concentrations of the individual sugars.

2.6. Statistical Analysis

The trial was designed as a completely randomized design with four replicates of four vines each (i.e., 16 vines per treatment, where only the two central vines were used, with the two vines at the edges serving as a buffer zone). Significant differences were determined based on Tukey's HSD test at $\alpha = 0.05$ after checking the normal distribution of the raw data using standard skewness and standard kurtosis and the homogeneity of variances. Data, separately from each assessment (sampling event), were analyzed by discriminant analysis to assess any possible discrimination between the treatments based on all available data per sampling event. For the analyses, the statistical software Statgraphics Centurion XV (Statgraphics Technologies, Inc. The Plains, VA, USA) was used.

3. Results

During early August, the leaf sclerophylly indexes had already been influenced by the application of the alleviating products (Table 1). The relative water content (RWC) was significantly higher under the osmolyte (BlueStim) compared to the other alleviating products (the reflectance product, Pureshade, and the antioxidant, Sun Protect). On the other hand, the water saturation deficit was lower under osmolyte treatment, while, at the same time, leaf succulence was higher than those determined under the influence of the other alleviating products.

Table 1. Effects of the alleviating products on kiwifruit leaf sclerophylly indexes during the first sampling event on August 7th (WC, %; RWC, %; LTD, g kg⁻¹; WSD, %; WCS, g H₂O g⁻¹ DW; SLA FW, mm² mg⁻¹; SUC, mg H₂O mm⁻²).

Treatment	WC	RWC	LTD	WSD	WCS	SLA FW	SUC
	ns	***	ns	***	ns	ns	***
Control	70.61 a	67.94 ab	29.39 a	32.06 ab	3.57 a	21.25 a	0.034 ab
BlueStim	72.87 a	73.37 a	27.13 a	26.63 b	3.79 a	19.68 a	0.038 a
Pureshade	71.76 a	66.30 b	28.24 a	33.69 a	3.93 a	21.63 a	0.033 b
Sun Protect	71.48 a	66.14 b	28.52 a	33.87 a	3.87 a	21.65 a	0.033 b

Means within the same column followed by the same letter do not differ significantly according to Tukey's HSD multiple range test at $\alpha = 0.05$. ***, indicate significant differences among treatments at $\alpha = 0.001$, ns, indicates not significant difference.

During the second and third assessments in late August and late September, no significant effects for the alleviating treatments were detected (Tables 2 and 3).

Table 2. Effects of alleviating products on kiwifruit leaf sclerophylly indexes during the second sampling event on August 20th (WC, %; RWC, %; LTD, g kg⁻¹; WSD, %; WCS, g H₂O g⁻¹ DW; SLA FW, mm² mg⁻¹; SUC, mg H₂O mm⁻²).

Treatment	WC	RWC	LTD	WSD	WCS	SLA FW	SUC
	ns	ns	ns	ns	ns	ns	ns
Control	69.73 a	79.53 a	30.27 a	20.46 a	3.02 a	26.79 a	0.027 a
BlueStim	67.01 a	78.56 a	32.99 a	21.44 a	2.67 a	26.17 a	0.026 a
Pureshade	66.39 a	75.50 a	33.61 a	24.50 a	2.61 a	26.92 a	0.025 a
Sun Protect	68.82 a	79.86 a	31.18 a	20.14 a	2.83 a	24.14 a	0.029 a

Means within the same column followed by the same letter do not differ significantly according to Tukey's HSD multiple range test at $\alpha = 0.05$, ns, indicates not significant difference.

Table 3. Effects of the alleviating products on kiwifruit leaf sclerophylly indexes during the third sampling event on September 21st (WC, %; RWC, %; LTD, g kg⁻¹; WSD, %; WCS, g H₂O g⁻¹ DW; SLA FW, mm² mg⁻¹; SUC, mg H₂O mm⁻²).

Treatment	WC	RWC	LTD	WSD	WCS	SLA FW	SUC
	ns	ns	ns	ns	ns	ns	ns
Control	66.93 a	64.98 a	33.07 a	35.02 a	3.15 a	28.79 a	0.024 a
BlueStim	68.69 a	66.91 a	31.32 a	33.09 a	3.32 a	24.89 a	0.028 a
Pureshade	67.43 a	65.05 a	32.57 a	34.95 a	3.23 a	26.14 a	0.026 a
Sun Protect	66.25 a	64.63 a	33.75 a	35.37 a	3.08 a	25.77 a	0.025 a

Means within the same column followed by the same letter do not differ significantly according to Tukey's HSD multiple range test at $\alpha = 0.05$, ns, indicates not significant difference.

Carbon assimilation efficiency was severely affected by the alleviating treatments during the early days of August, as indicated in Figure 1. Photosynthetic efficiency was higher under the osmolyte treatment, with significant differences when compared to all other treatments. Similarly, stomatal conductance was also high under the osmolyte treatment, without any difference observed from the treatment with the antioxidant factor, but this was still higher than the control and reflectance treatment. The ratio of photosynthetic efficiency versus intercellular CO₂ was high under osmolyte treatment, higher than that determined under the effect of the antioxidant factor. Leaf temperature was lower under the reflectance treatment compared to the control and osmolyte treatment.

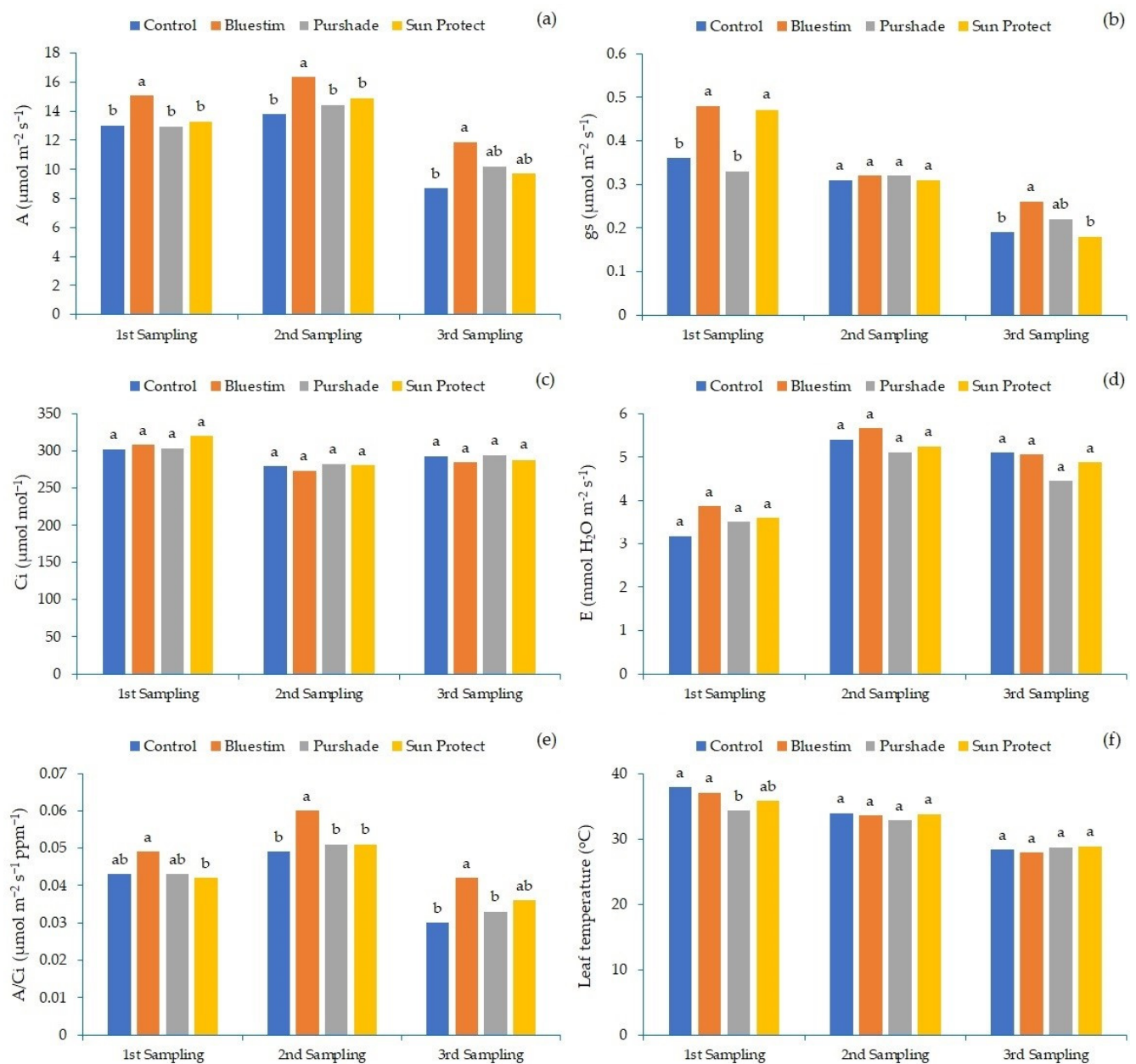


Figure 1. Effect of alleviating products on the photosynthetic parameters (a) A, photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$), (b) gs, stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$), (c) Ci, intercellular CO_2 ($\mu\text{mol mol}^{-1}$) (d) E, transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), (e) A/Ci ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{ppm}^{-1}$) and (f) leaf temperature ($^{\circ}\text{C}$), of kiwifruit leaves during the first (on August 7th), second (on August 20th), and third (on September 21st) sampling events. Different letters above each column under the same sampling event denote statistically significant differences among the treatments according to Tukey's HSD multiple range test at $\alpha = 0.05$.

Similar to that measured during early August, the photosynthetic capacity of the leaf was higher under the osmolyte treatment compared to all other treatments in late August (Figure 1a). The A versus Ci ratio was also higher than that estimated for all other treatments. The osmolyte application resulted in a higher photosynthetic capacity, stomatal conductance, and an A versus Ci ratio than the control during the third assessment in late September. No significant differences were determined among the treatments regarding leaf temperature during the second and third samplings in late August and September, respectively. Similarly, the SPAD index and leaf fluorescence were not significantly affected by any of the treatments applied during all three assessments (Table 4).

Table 4. Effects of alleviating products on kiwifruit leaf chlorophyll (SPAD) and fluorescence (Fv/Fm) (first–third sampling events).

Treatment	1st Sampling (August 7th)		2nd Sampling (August 20th)		3rd Sampling (September 21st)	
	SPAD	Fv/Fm	SPAD	Fv/Fm	SPAD	Fv/Fm
	ns	ns	ns	ns	ns	ns
Control	60.03 a	0.775 a	62.98 a	0.774 a	62.09 a	0.754 a
BlueStim	61.00 a	0.776 a	59.13 a	0.756 a	60.72 a	0.784 a
Pureshade	62.06 a	0.741 a	63.29 a	0.755 a	67.09 a	0.769 a
Sun Protect	58.86 a	0.758 a	62.04 a	0.769 a	60.81 a	0.758 a

Means within the same column followed by the same letter do not differ significantly according to Tukey's HSD multiple range test at $\alpha = 0.05$, ns, indicates not significant difference.

During the first sampling in early August, the total phenol, total flavanols, and total flavonoids concentration in the leaves was significantly affected by the treatments, as the reflectance product resulted in a low concentration (Figure 2a,b,d), lower than that of all other treatments (regarding total phenols and total flavanols concentration). Total flavonoids were also found in a lower concentration in the leaves of the kiwifruit vines treated with the reflectance product during the second assessment in late August, without any significant difference in the concentration found in the leaves of the vines treated with the antioxidant.

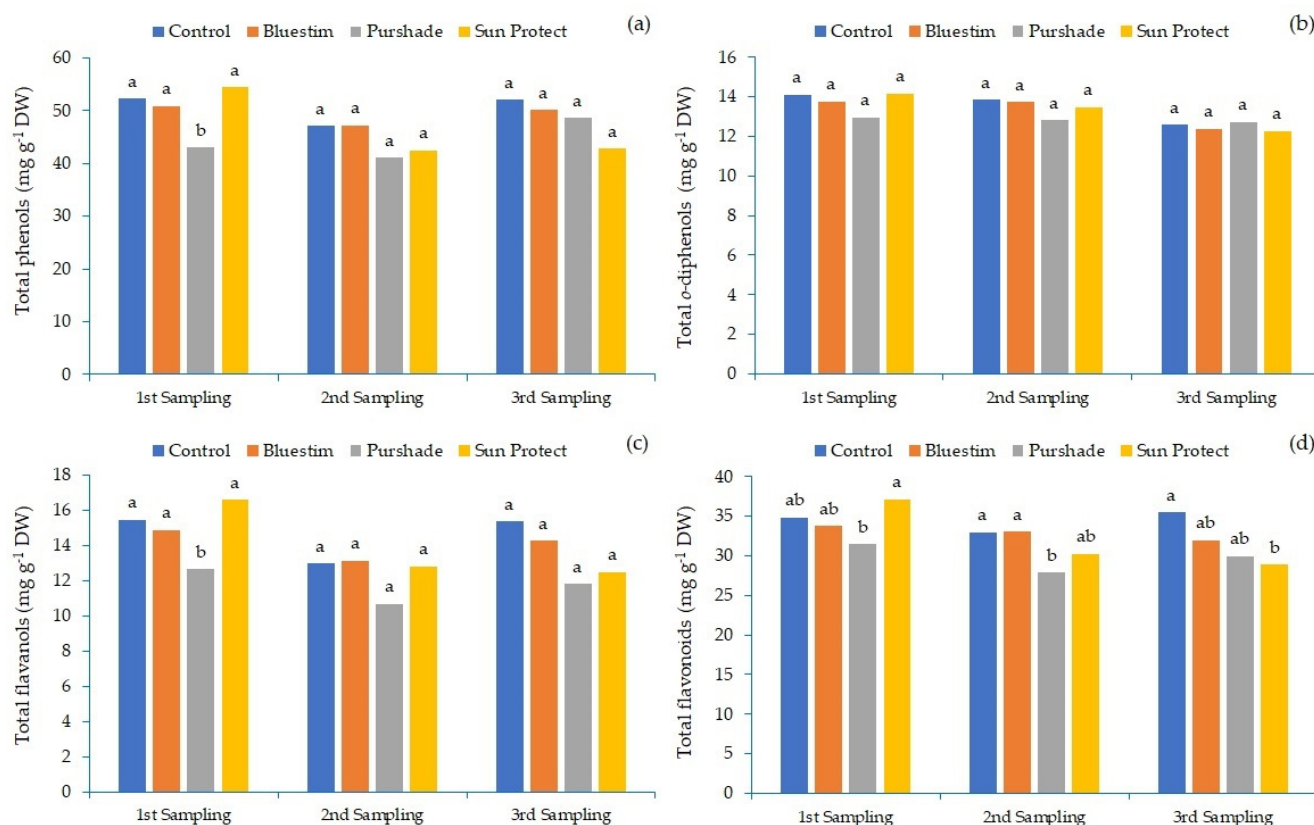


Figure 2. Effects of the alleviating products on the total phenolic compound concentration, (a) total phenols, mg equiv. gallic acid g⁻¹ DW, (b) total o-diphenols, mg equiv. caffeic acid g⁻¹ DW, (c) total flavanols, mg equiv. catechin g⁻¹ DW and (d) total flavonoids, mg equiv. catechin g⁻¹ DW, of the kiwifruit leaves during the first (on August 7th), second (on August 20th), and third (on September 21st) sampling events. Different letters above each column under the same sampling event denote statistically significant differences among the treatments according to Tukey's HSD multiple range test at $\alpha = 0.05$.

The application of the antioxidant resulted in a low concentration of flavonoids in the leaves during the third sampling (Figure 2d), with significant differences from the control.

The antioxidant capacity of the leaves was only significantly affected by the treatments imposed during the first sampling event in early August (Table 5). The control presented high antioxidant capacity in the leaves (determined by DPPH and ABTS assays) with significant differences when compared to the osmoprotectant and reflectance products (based on DPPH assay) and the reflectance product only (based on ABTS assay). The treatment with the reflectance product resulted in the lowest antioxidant capacity values during the first assessment, without a significant difference from the osmoprotectant product (based on both DPPH and ABTS assays). No significant differences were recorded during the last two assessments in late August and September.

Table 5. Effects of alleviating products on kiwifruit leaf antioxidant capacity (FRAP, DPPH, and ABTS are expressed as $\mu\text{mol equiv. Trolox g}^{-1}$ DW).

Treatment	1st Sampling (August 7th)			2nd Sampling (August 20th)			3rd Sampling (September 21st)		
	FRAP ns	DPPH ***	ABTS **	FRAP ns	DPPH ns	ABTS ns	FRAP ns	DPPH ns	ABTS ns
Control	313.21 a	56.54 a	439.17 a	298.67 a	45.20 a	370.12 a	358.66 a	57.76 a	416.41 a
BlueStim	274.91 a	35.08 bc	405.74 ab	336.91 a	58.27 a	394.74 a	331.45 a	33.23 a	386.63 a
Pureshade	281.05 a	23.99 c	381.87 b	289.71 a	44.91 a	351.32 a	313.48 a	31.25 a	378.28 a
Sun Protect	344.32 a	54.07 ab	442.38 a	290.54 a	46.68 a	371.98 a	346.37 a	41.81 a	336.10 a

Means within the same column followed by the same letter do not differ significantly according to Tukey's HSD multiple range test at $\alpha = 0.05$. **, indicates significant differences among treatments at $\alpha = 0.01$, ***, indicates significant differences among treatments at $\alpha = 0.001$, ns, indicates not significant difference.

Leaf carbohydrate concentration was significantly affected by the alleviating products during the first assessment in early August, as can be seen in Figure 3. Sucrose was the dominant carbohydrate in the leaves, and it was found in higher concentrations in the control, with significant differences when compared to the other treatments. Glucose, on the other hand, was higher in the leaves treated with the reflectance product, with significant differences from the control, while the total carbohydrates concentration was lower under osmolyte treatment when compared to the leaves from control and antioxidant treatment.

Similar to the first assessment, sucrose was the major carbohydrate found in the leaves, with its concentration being similar under all treatments (Figure 3c). Glucose, on the other hand, presented a high concentration in the leaves of the vines treated with the reflectance product, followed by those treated with the osmoprotectant, which resulted in the highest concentration of fructose in the leaves (without any significant difference when compared to the leaves from control treatment). Inositol was found in high concentrations in the leaves treated with the reflectance product, with a significant difference from that determined in the leaves treated with the antioxidant. The highest total sugar concentration was determined in the leaves of the vines treated with the reflectance product, with a significant difference when compared to the control and antioxidant treatment.

During the last assessment at the end of September, there were fewer differences, as the concentration of the total sugars, inositol, and sucrose were similar under all treatments (Figure 3c–e). Nonetheless, glucose concentration was high under the antioxidant effect, with a significant difference when compared to the control, which also presented the lowest fructose concentration, significantly lower than that determined under the influence of the reflectance product.

The discriminant analysis of the data collected during the three assessments separated the four treatments, which did not present any common area (Figures 4–6, respectively), indicative of the fact that the effects of each alleviation treatment were distinctly different from the others.

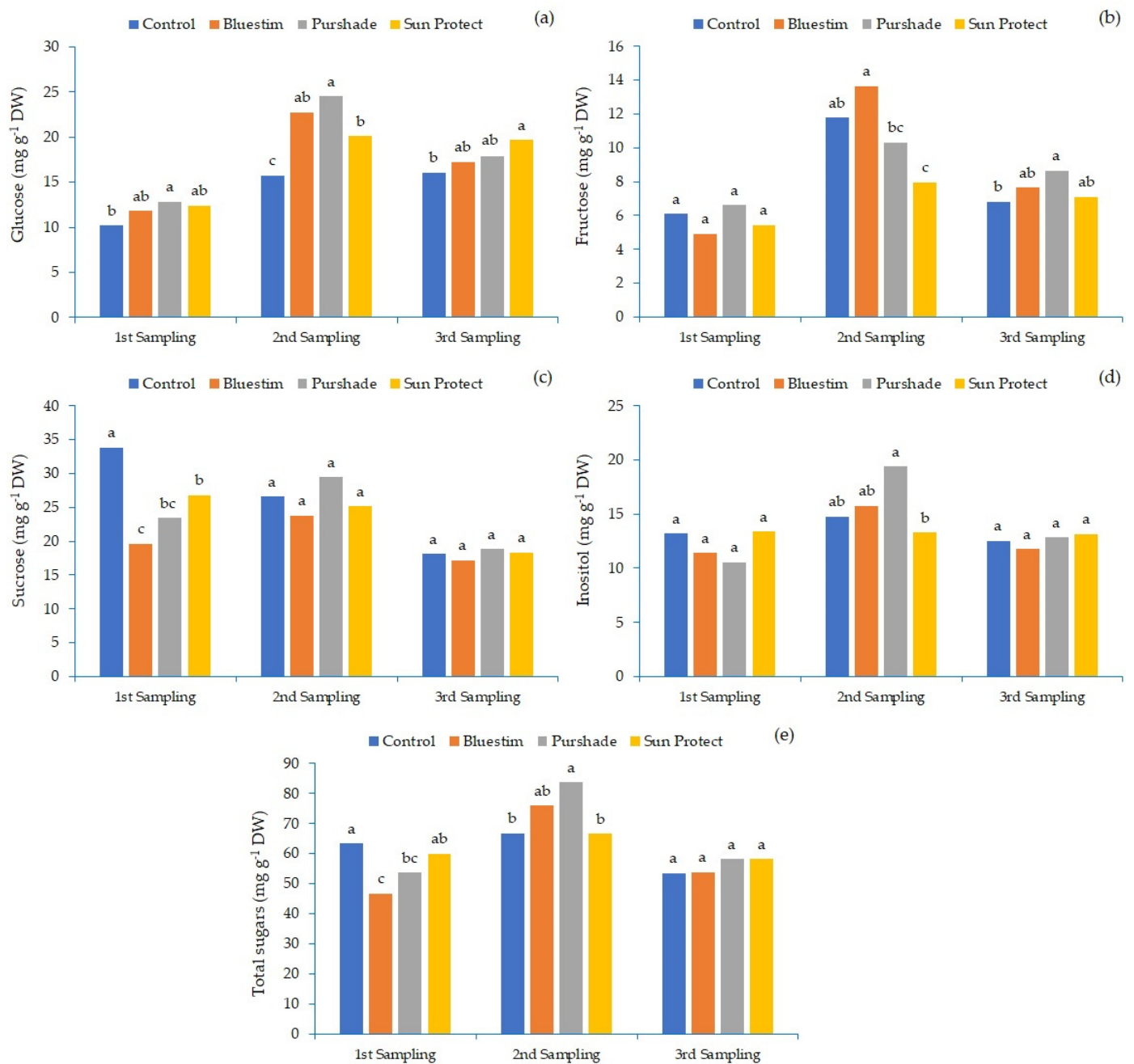


Figure 3. Effects of the alleviating products on kiwifruit leaf carbohydrate concentration (a) sucrose, (b) fructose, (c) glucose, (d) inositol, and (e) total sugars are expressed as mg g⁻¹ D.W., during the first (on August 7th), second (on August 20th), and third (on September 21st) sampling events. Different letters above each column under the same sampling event denote statistically significant differences among the treatments according to Tukey's HSD multiple range test at $\alpha = 0.05$.

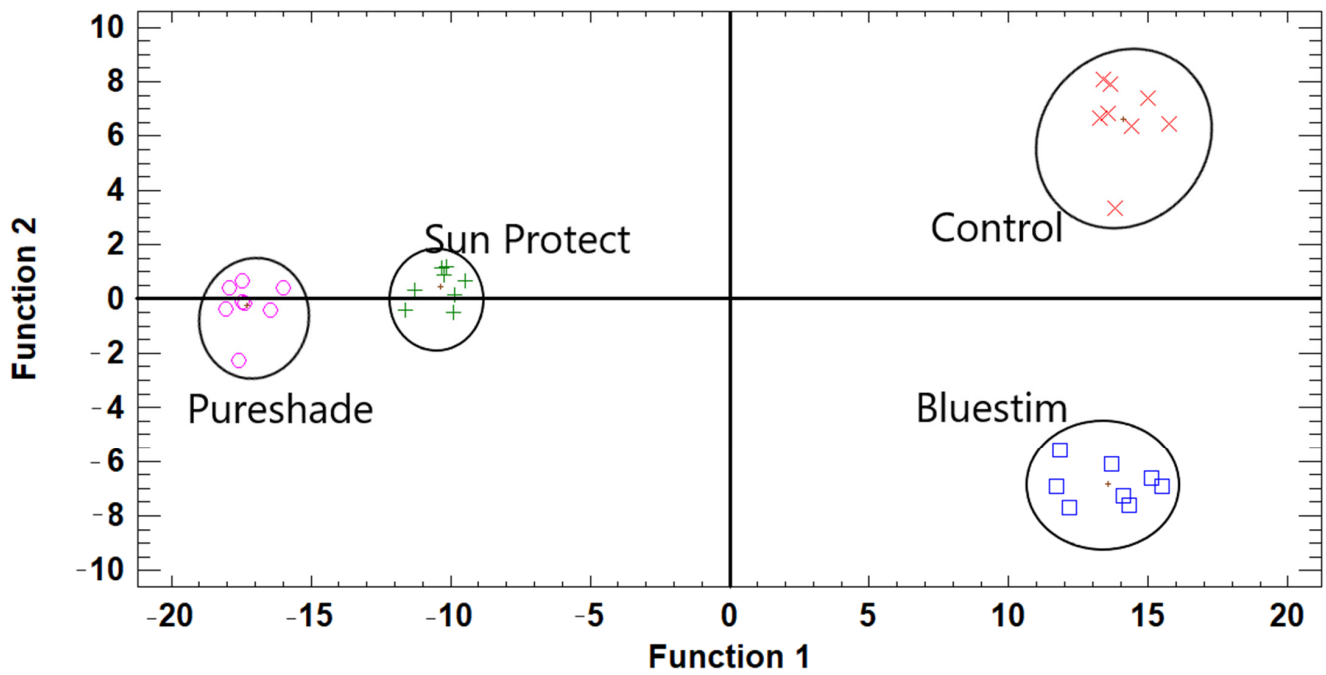


Figure 4. Plot of discriminant functions produced from the data of the first sampling on August 7th.

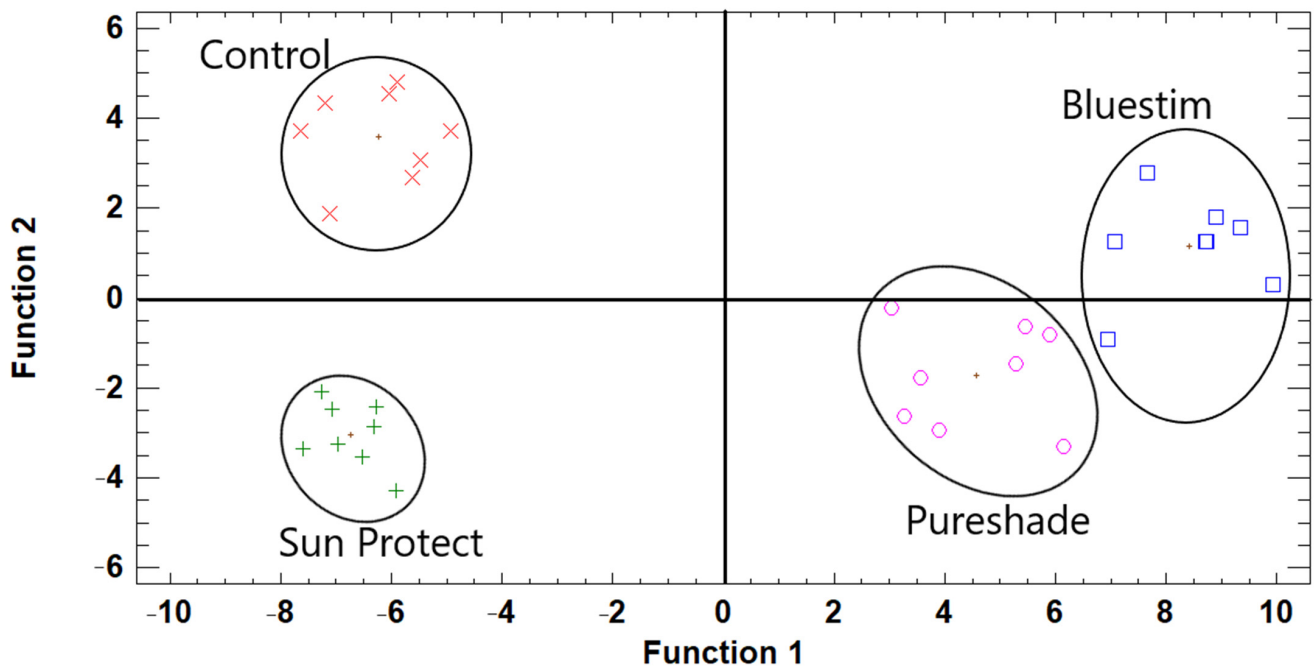


Figure 5. Plot of discriminant functions produced from the data of the second sampling on August 20th.

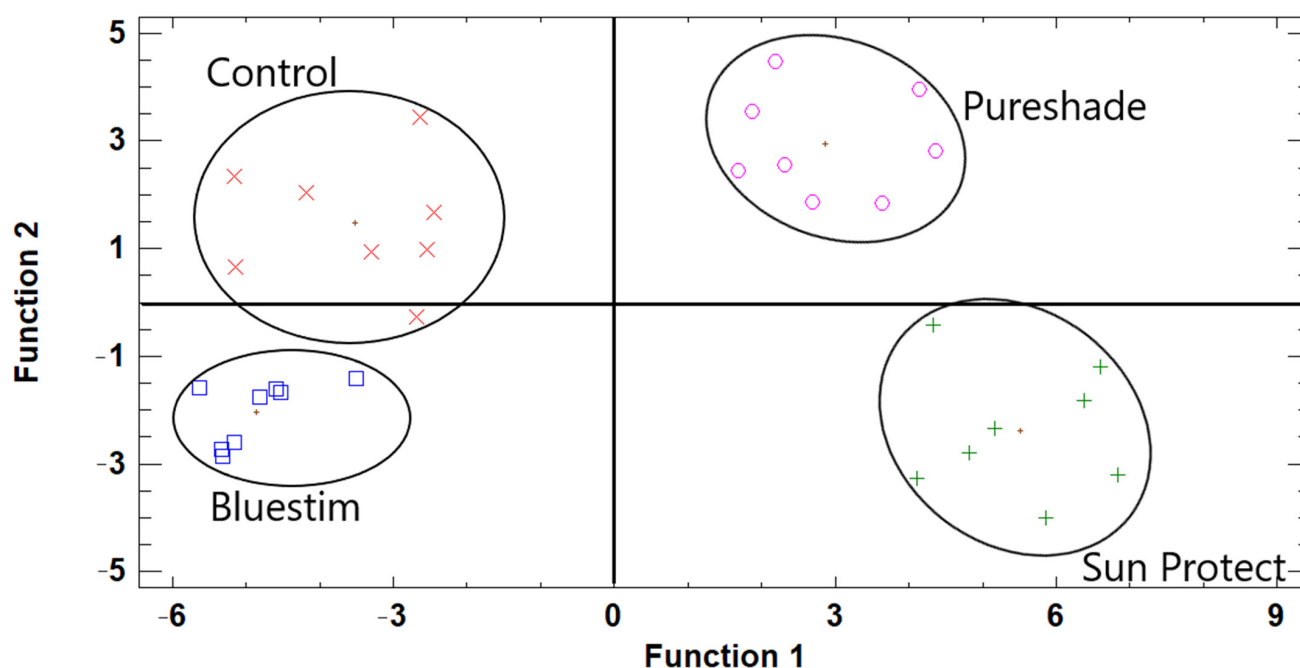


Figure 6. Plot of discriminant functions produced from the data of the third sampling on September 21st.

4. Discussion

The Mediterranean basin, an area where kiwifruit has been greatly cultivated during recent decades, is characterized by high summer temperatures (often exceeding 40 °C) and solar irradiance, provoking significant morphological, anatomical, and physiochemical alterations in plants, with subsequent growth and yield reductions [7,8,25]. Treatments aiming to alleviate this kind of stress proved to be efficient in various ways, depending on the mode of action of the alleviating factor used, as well as the measured parameter [26,27].

The eco-physiological changes experienced due to high temperatures are closely related to plants' water content [25]. The osmoprotectant glycine betaine (BlueStim product) retained high leaf relative water content during early August and, subsequently, a low water saturation deficit, while the other treatments did not exhibit such a significant effect on the leaf water indexes. Similarly, many researchers have reported higher RWC under GB treatment in various species grown under stress conditions [28–30], while Karaat and Denizhan [22] did not find any significant effect of Sun Protect on RWC. As the summer progressed to its end and the temperature was getting milder, the positive effect of the osmoprotectant gradually disappeared, possibly due to a reduction in the severity of the stress imposed. Heat stress is thought to cause physiological perturbations [31], which may be prevented or, to some extent, overcome by the use of compatible solutes, such as glycine betaine. GB application induces various metabolic changes within the cell [30] while, at the same time, it increases the proportion of bound water in the cell due to its hydrophilic features, therefore resulting in a higher RWC. According to Salinger, Kenny, and Morley-Bunker [31], exogenously applied GB can also trigger the expression of stress-response genes and enhance stress tolerance to multiple abiotic stresses, thus delaying leaf senescence and preserving a high photosynthetic rate, which has been found in many species [30,32].

The preservation of carbon assimilation rate was also observed here, as the photosynthetic activity of kiwifruit leaves treated with GB was higher during all three assessments, which has been described for other species too [30]. At the same time, stomatal conductance and A/Ci ratio were high in the GB-treated leaves, indicating that both stomatal and nonstomatal limitations were, to some extent, alleviated by GB application. GB is thought to improve g_s through an improved guard cell size, as well as stomatal width [30]. As a

result, there is more efficient control of the gas exchange and a high level of RWC. Similarly, Sorwong and Sakhonwasee [33] reported that exogenously applied GB alleviated the heat stress-induced reduction of photosynthesis, as well as g_s , and retained high levels of RWC in marigold.

Although Islam et al. [30] and Ahmed et al. [34] reported higher chlorophyll content and RWC by GB application and considered these as the main reasons for higher photosynthetic performance, this is not exactly the case in the present trial as there were no significant differences among the treatments concerning the SPAD index. It seems that the method of action of GB in kiwi may not be based on maintaining chlorophyll levels but, among others, on a better leaf water status. According to Ali et al. [32], GB protects photosynthetic activity by raising stomatal conductance, preserving the RuBisCo enzyme activity, and conserving the ultrastructure of chloroplasts, fully justifying the increase in photosynthetic performance and the A/Ci ratio of the GB-treated leaves in the present trial. Furthermore, according to Zulfigar, Ashraf, and Siddique [35], it is thought that calcium-dependent protein kinases (CDPKs), as well as mitogen-activated protein kinases (MAPKs), are activated by GB, which, in turn, are responsible for the activation of heat-shock transcription factor genes (HSF), preparing the plant to withstand stress conditions.

On the other hand, mineral particle film application is thought to reduce leaf temperature by reflecting much of the excessive ultraviolet and infrared radiation, which might otherwise induce heat injury [36]. In the present trial, the application of calcium carbonate succeeded in reducing leaf temperature during the hottest days of the summer (first assessment) by almost 3 °C compared to the control, which is in accordance with Patanè, Pellegrino, and Di Silvestro [36] and Tsai, Lee, and Chang [37]. Although this was not evident during the latter assessments, when the stress conditions were becoming milder, similar to Patanè, Pellegrino, and Di Silvestro [36], photosynthetic capacity slightly increased compared to the control, probably due to the release of CO₂ from calcium carbonate [38]. On the other hand, the antioxidant did not induce any significant change in the SPAD index, similar to that reported by Karaat and Denizhan [22]. It also resulted in a slight but not significant decrease in leaf temperature compared to the control during the first assessment, in accordance with the findings of Montanaro, Dichio, and Xiloyannis on the effects of shade [15].

The total phenolic compounds assessed in this experiment were significantly affected by the applied products. Calcium carbonate seems to negatively affect (in most cases) the concentration of phenolic compounds in kiwifruit leaves. On the other hand, phenolic compounds were found in high concentrations in the leaves of the control treatment during all sampling events. According to Hassan et al. [4] and Ul Hassan et al. [7], the activity of phenylalanine ammonia-lyase (PAL), one of the enzymes responsible for phenolic compounds biosynthesis, is enhanced under heat stress, justifying the high concentration found in the leaves of control treatment. Calcium carbonate was used as an alleviating agent against heat stress, working to reduce leaf temperature, as was clearly shown during the first two assessments based on its properties to act as a reflecting agent [39]. Based on the fact that high or increased temperatures enhance phenolic biosynthesis and reduce their oxidation through the reduction of peroxidase and polyphenol oxidase activities [30], it can be assumed that calcium carbonate application resulted in reduced secondary metabolite synthesis by reducing leaf temperature. Phenolic compounds are nonenzymatic antioxidants that can be part of the defense arsenal of plants against abiotic stresses [40,41]. In some cases, they have been detected in lower concentrations in stressed plants compared to controls, but this could be partially ascribed to their role as antioxidant compounds—protectors, helping the plant to overcome the oxidation imposed by the stress [40,42]. Thus, under mild stress, phenolic compounds could accumulate to serve as antistress agents, but as soon as the stress conditions become more severe, they are oxidized to prevent cell component oxidation. It is fair to assume that if the plant is partly relieved from stress, there is no need to spend extra energy on the biosynthesis of compounds, which are not needed anymore to defend itself. Therefore, a relatively lower concentration of phenolic compounds can be

expected under the influence of any factor alleviating stress. Although on the other hand, if the alleviating factor protects the phenolic compounds from oxidation (i.e., an antioxidant such as Sun Protect), then it could be assumed that phenolic compound concentration could increase, not through increased biosynthesis, but through reduced oxidation. Sun Protect is a formulation containing phenols, so it seems reasonable to assume that it increased leaf phenol concentration through its own phenolic compounds. Furthermore, according to Linić et al. [43], ferulic acid application (a constituent of Sun Protect) increased the levels of phenolic compounds in leaves, conferring extra antioxidant protection against oxidative stress. According to Lalarukh and Shahbaz [44], the application of α -tocopherol, also a constituent of Sun Protect, enhanced the total phenolic compound concentration in the presence or absence of stress in sunflowers, further justifying the increase in their concentration that was determined in the present experiment. In the present trial, during the first sampling event when the conditions (elevated leaf temperature) would trigger phenolic compound oxidation [4], the application of the antioxidant could have prevented their catabolism while, at the same time, conferring phenols itself, thus increasing their concentration. Similar to phenolic compound concentration, the antioxidant capacity of the leaves slightly increased under the control and antioxidant treatments. It seems that the antioxidant capacity of kiwifruit leaves is closely linked to phenolic compounds, as the latter are efficient radical scavengers with high antioxidant properties [41].

Carbohydrates, on the other hand, are the direct products of photosynthesis. During the first sampling event, even though the photosynthetic rate was higher under the osmoprotectant treatment, the glucose, sucrose, and total carbohydrate concentration in the leaves were among the lowest. Although this looks rather controversial at first, it seems that the kiwifruit trees treated with GB must have used the carbohydrates produced through photosynthesis to support the growing organs, such as fruits, shoots, and roots [42]. The level of sucrose, which is the main sugar transported to the fruit during development [45], was significantly lower under all the alleviating product treatments. This could partly justify the assumption that alleviation of stress could result in higher and earlier carbohydrate production in the leaves, which are readily translocated to the growing organs, as their growth has not ceased under the stress-relieved conditions imposed by the products used [30]. Similar results have been reported in many plants, where GB stimulated the partitioning of photosynthetic products towards the reproductive and growing organs [31,46,47], supporting their growth with carbon skeletons.

It is noteworthy that early fruit growth in kiwifruit depends on carbohydrate supply and especially glucose [48,49]. The vines treated with GB presented a high photosynthetic capacity, which should have resulted in high glucose production, which is used to support fruit growth. During the second and third sampling events, when the osmolyte-treated leaves continued to present higher photosynthetic activity, their glucose and fructose concentration was high, which is in contrast to the total carbohydrates when compared to the control. On the other hand, the leaves treated with calcium carbonate presented a high carbohydrate concentration, significantly higher than the control, during the second assessment, without presenting any significant difference in photosynthetic activity. As fruit growth depends on carbohydrate supply [48,49], it could be assumed that the alleviating products altered not only the photosynthetic capacity of the leaves but also the temporal accumulation of carbohydrates to pool within the organs, although this needs to be ascertained with further experiments.

Overall, the carbohydrate concentration in the leaves was not steady during the three sampling events, which took place almost 100–145 days after full bloom, in accordance with the findings of Bolding, Smith, and Klages [49].

5. Conclusions

Climate change greatly affects the agricultural sector, with plants being quite vulnerable to these changes. While progress in the production of new cultivars and hybrids able to withstand abiotic stresses is slow, especially in the perennial species, the adaptation of

stress mitigation measurements seems to be the most immediate effective solution. Alleviation products have been extensively studied in many plant species under multiple abiotic stresses with variable success. In the present trial, the application of the alleviation products resulted in multiple physiological and biochemical changes in the leaves of kiwifruit. The leaves retained their hydration level and photosynthetic capacity, especially during the first assessment in the middle of summer, while, during the autumn assessment, the effect of the alleviation products seemed to be less impressive, probably due to milder climatic conditions. Carbohydrate concentration in the leaves seemed to be altered by the products used, indicating the possible enhancement or earlier translocation of carbohydrates to the growing organs. The present work emphasizes the role of the alleviating product used in kiwifruit culture under the prism of a changing environment due to climate change. Alleviating products can be a valuable tool for growers when harsh conditions prevail, inhibiting plant physiological mechanisms from functioning properly. However, further research is needed in order to assess their effects on fruit yield and quality, both at harvest and after the storage period.

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