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Amelioration Effects against Salinity Stress in Strawberry by Bentonite–Zeolite Mixture, Glycine Betaine, and *Bacillus amyloliquefaciens* in Terms of Plant Growth, Nutrient Content, Soil Properties, Yield, and Fruit Quality Characteristics

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Featured Application: In this study, commercially available products were tested, which could be used by strawberry growers to ameliorate toxic effects of salinity on strawberry plants and achieve higher yields.

Abstract: Strawberry, the most significant berry crop, is characterized as a salt-sensitive plant. The present study aimed to examine ways to alleviate salinity symptoms (34 mM of NaCl in irrigation water) in strawberry plants. For this purpose, the osmolyte glycine betaine was foliarly applied, a mixture of bentonite–zeolite was added to the substrate, and a microbial product based on *Bacillys amyloliquefaciens* as a soil drench were tested in terms of plant growth and nutrient status, yield, fruit physiological and organoleptic characteristics, as well as phytochemical properties (phenolic compounds, carbohydrates, organic acids, anthocyanins, and antioxidant capacity), and soil physicochemical properties. Salinity severely reduced plant growth and yield, while the effects on fruit quality were also distinct. Treatments alleviated to some extent these negative effects. Plant nutrient content was not severely affected by product application, and neither were most of the soil physicochemical properties. Among the products applied, the mixture of bentonite plus zeolite and glycine betaine proved to be more efficient in ameliorating toxicity symptoms, as both treatments preserved plant hydric status and plant growth, while glycine betaine resulted in an almost 30% higher yield than the treatment with saline water.

Keywords: *Fragaria x ananassa*; fruit quality; mineral nutrients; phytochemicals; salt stress; hydric status

1. Introduction

Soil salinization and the availability of irrigation water have become major restriction factors for plant growth, productivity, distribution, and survival in many areas during recent decades. The expansion of agriculture, the increased water supply needs of the big cities along with the changes in rainfall volume and distribution due to global warming, have increased soil salinity to a significant problem and stress factor for plants to deal with [1,2].

Strawberry (*Fragaria x ananassa* Duch.) is the most economically important cultivated berry species in the horticultural sector. However, strawberry plants are salt-sensitive [3,4],

and may suffer significant damages when cultivated in salt-affected soils. In this sense, it is necessary to implement new, up-to-date cultural practices as an approach to ameliorate the negative impacts of salinity stress on plants.

Several studies have indicated the positive effects of glycine betaine (GB) on the growth and survival of various plants growing under saline conditions [5–7], as well as zeolite [8], and *Bacillus amyloliquefaciens* [9,10].

GB, as an osmolyte, may ameliorate osmotic stress induced by salinity, by improving the water status of the cells, preserving thus membrane function and water content [1]. Furthermore, exogenous GB application enhances photosynthesis [11–14], improves nutrient homeostasis [15], and induces the concentration of other osmoprotectants such as proline [16]. Moreover, it has been reported that GB application under saline conditions can modify Na^+ and K^+ transport and accumulation, decreasing thus the Na^+/K^+ ratio [7].

Zeolites are crystalline, hydrated aluminosilicates of alkali and earth metals with a porous structure that can retain a variety of cations, such as K^+, Na^+, Ca^{2+}, Mg^{2+} and others [17]. Due to their unique features, such as being abundant and inexpensive, as well as their high cation exchange capacity (200–300 meq per 100 g), along with the selective absorption and structure stability [18], zeolites serve as soil amendments, against water and salinity stress [8,18,19]. Furthermore, zeolite improves soil physicochemical and biological properties, increases soil pH and exchangeable potassium [20]; mitigates soil erosion caused by surface runoff, reducing thus soil loss; and improves degraded pastures [21]. Bentonite, on the other hand, has not been tested so extensively, but reports are presenting beneficial effects on plant growth under salinity stress [22].

The use of bacterial inoculations to mitigate the negative impact of salinity in plant growth and development is an alternative emerging technology to improve the abiotic stress tolerance of plants [23–25]. Several reports have shown that plant growth-promoting rhizobacteria (PGPR) that colonize the rhizospheres of plants, are beneficial microorganisms, capable of increasing the stress tolerance of host plants against both biotic and abiotic factors [26,27].

Bacillus amyloliquefaciens is a Gram-positive, non-pathogenic endospore-forming, soil-inhabiting prokaryote rhizobacterium, which colonizes the plant rhizosphere, promotes plant growth, and suppresses competing phytopathogens, such as bacterial, fungal and fungal-like pathogens. The ability to promote plant growth is linked to the use of diverse mechanisms that include indole-3-acetic acid (IAA) synthesis [28], and phosphorus and potassium solubilization [29].

It is crucial to adopt cultural techniques to alleviate salinity effects on strawberry plants in an eco-friendly way. Since salinity imposes a great sequel of physiological and biochemical disorders in plants, the present study aimed to assess the efficacy of various agents with different modes of action, i.e., changing soil properties, using an osmoprotectant, and using beneficial microbes against salinity stress in strawberry plants. To our knowledge, a mixture of zeolite–bentonite, as well as the foliar application of GB, are here assessed for the first time against salt stress in strawberry, in terms of plant growth, nutrition, and fruit quality, as well as soil physicochemical properties.

2. Materials and Methods

2.1. Plant Material

In early November, fresh strawberry plants of cv. Camarosa were planted in 5 L plastic pots filled with a mixture of soil, commercial compost (commercial name Compost by Biosolids, organic matter 30–50%, pH 6.9–7.7, C/N 14–17, N 1–2% *w*/*w*, P 0.3–0.6% *w*/*w*, K: 0.3–0.8 *w*/*w*, Ca: 1–9% *w*/*w*, Mg: 9000–10,000 mg Kg^{-1}, Zn: 200–210 mg Kg^{-1}, Cu: 45–70 mg Kg^{-1}, EC: 1–3 mS cm^{-1}), and perlite, unless stated otherwise. The soil substrate with a moderately fine texture (clay loam) was characterized by a pH value of 7.26, organic matter 8%, and electrical conductivity of 2.49 mS cm^{-1}. The plants were grown in a glasshouse located at the Agricultural University of Athens (latitude: 378580 N, longitude: 238,320 E, altitude: 30 m above sea level). The same volume of water was

provided to all the plants throughout the trial period. The plants were fertigated with Fe-EDDHA, boric acid, calcium nitrate, and a water-soluble fertilizer (21–21–21 N–P–K, plus micronutrients and vitamins) as needed to ensure optimum nutrient status. The experiment was arranged as a completely randomized block design with three replications of five plants each.

2.2. Treatments

Salt stress started three months after planting, in February, when the plants had developed enough leaves. The salinity treatments consisted of 0 mM (Blank) and 34 mM of NaCl in water (Control). To avoid sudden osmotic stress to plants, the salt concentration was gradually increased by 10–12 mM NaCl per week, to the desired level of 34 mM of NaCl. Plants were irrigated with 0.25 L water (Blank) or the salt solution, on average twice a week, avoiding wilting. Two months later, the substrate was flushed with tap water to leach concentrated salt in the rooting zone and the salinity stress cycle started again, as described earlier.

The treatments against salt stress consisted of (a) the foliar application of Bluestim WP (GB) (glycine betaine 50% w/w)(osmolyte) plus an adjuvant (Tween-20) at the dose rate of 5 g L^{-1} (a total of three applications of GB took place every seven weeks, starting three months after planting, with the beginning of salt stress), (b) the application by soil drenching of Rhizocell GC *(Bacillus amyloliquefaciens* IT45) (BA), at the dose rate of 10.8 g 4 L^{-1} applied at three-week intervals, starting two months after planting (a total of six applications took place during the experimental period and (c) a mixture of zeolite and bentonite (BETZ) (at a ratio of 5:95), comprising the 20% of the substrate at planting. Both products (BlueStim WP and Rhizocell GC) were used at their registered dose rate and at the recommended time of application and intervals, as indicated above.

2.3. Sampling

Three sampling events took place during the harvest period. A sampling event was designated as a period of approximately one and a half months, during which all fully ripe fruits at the red ripe stage were harvested. On average, fruit harvesting took place twice a week during the trial period, and the fruits were transferred to the laboratory for further analysis. At the end of the trial, three soil samples and nine plants (separately the above-ground plant mass (AGPM) and the roots) per treatment, were collected and analyzed for their soil physicochemical properties and plant nutrient status, respectively.

2.4. Evaluation of Fruit Physiological Attributes

Physiological attributes (weight, length, and diameter) of each fruit were determined with a calibrated electronic balance (Kern 470, Kern and Sohn, GmbH, Balingen, Germany) and a digital caliper, respectively. Based on the fruit diameter measured, fruits were classified into two categories, i.e., "Extra", fruits with a diameter above 25 mm, and "I and II" for fruits with a diameter of at least 18 mm (European Community legislation 843/2002 for the strawberry fruit trade). Malformed or diseased fruits were not included in this classification. Fruit firmness was determined with a penetrometer, with a 5 mm conical plunger. Firmness was measured at two opposite points at the equatorial sector of each fruit. Fruit dry weight was measured of at least five fruits per plot at the end of the sampling events, by drying the whole fruit in an oven at 70 °C to constant weight, and the ratio of fresh versus dry weight was determined.

Fruit color was measured at two opposite points of the equatorial region of each fruit, with a Minolta CR 300 reflectance Chroma Meter (Minolta, Osaka, Japan). At the end of measurements, fruits were cleaned from sepals and stored at −25 °C for further analyses. The sample lots per sampling event were homogenized frozen by a food processor, obtaining a homogenous mixture, which was used for the analyses.

2.5. Total Soluble Solids (TSS), Total Titratable Acidity (TA), and pH Determinations

A fraction of the homogenous mixture was centrifuged for 5 min at 14,000 and in the supernatant juice the total soluble solids (TSS), pH, and titratable acidity (TA) were determined. TSS was evaluated at 20 °C with a HI96801 digital refractometer (Hanna Instruments) and expressed as °Brix. TA was determined in diluted juice (1:20 with distilled water) by titrating to pH 8.2 using 0.1 N NaOH and pH was measured in the diluted solution.

2.6. Total Phenol Content, Total Anthocyanin Content, and Antioxidant Capacity

Approximately 0.5 g of the frozen strawberry pulp was extracted twice with 5 mL 75% (*v*/*v*) ethanol in a water bath at 38 °C for 20 min with periodical stirring. After centrifugation, the supernatant was assessed for total phenolic compounds. The total phenols, total *o*-diphenols, total flavanols, and total flavonoids were determined according to [30]. The results were expressed as mg equivalent of gallic acid, caffeic acid, catechin, and caffeic acid per g fresh weight, respectively.

For the total anthocyanin content, 0.5 g of the frozen strawberry pulp was extracted twice with 5 mL of 80% acetone acidified with 1% (*v*/*v*) concentrated HCl for 1 h at 4 °C with periodical stirring. The total anthocyanin content was assessed based on the pH differentiation method, according to Roussos et al. [30]. The results were expressed as pelargonidin 3-glucoside 100 g^{-1} fresh weight. The antioxidant capacity of strawberry fruits was evaluated in the supernatant produced by the extraction of phenolic compounds using the DPPH and FRAP assays based on the method described by Roussos et al. [30] and expressed in μmol Trolox equivalents per g fresh weight.

2.7. Carbohydrate Determination

Carbohydrate extraction and determination were performed according to Roussos et al. [30], using a Shimadzu Nexera X2 HPLC system equipped with an LC-30AD pump. The separation of the carbohydrates was achieved through a Hamilton HC-75 cation exchange column, calcium form (Ca^{2+}) (305 mm × 7.8 mm, 9 μm) (Hamilton, Bonaduz, Switzerland), equilibrated at 80 °C with water as mobile phase, running at a flow of 0.6 mL min^{-1}. Three soluble sugars were detected (HP1047A, refractive index detector, Agilent, Santa Clara, CA, USA) in the strawberry fruits, i.e., sucrose, glucose, and fructose. Total sugar concentration was estimated by summing the concentrations of the individual sugars detected by HPLC. Final concentrations were expressed as mg g^{-1} fresh weight.

The sweetness index (SI) of the fruit, an estimate of the total sweetness perception, was calculated based on the relative amount and sweetness properties of each carbohydrate [31]. Each carbohydrate contributes to sweetness perception as following: fructose is 2.3 and sucrose 1.35 times sweeter than glucose and hence the SI was calculated as 1.00 * (glucose concentration) + 1.35 * (sucrose concentration) + 2.3 * (fructose concentration) [31].

2.8. Organic Acid Determination

Approximately 0.5 g of frozen pulp was extracted two times with 5 mL aqueous 3% (*w*/*v*) metaphosphoric acid at room temperature for 30 min under periodical vortexing. At the end of each 30 min period, the sample was centrifuged, and the two supernatants were combined and filtered through a 0.45-μm-pore nylon syringe filter. The analysis of organic acids took place with a Shimadzu Nexera X2 HPLC system equipped with an LC-30AD pump and SPD-M20A diode array detector (DAD). The analysis was performed on a Li-Chrospher RP18 column (250 mm × 4.6 mm, 5μm, Merck Kenilworth, NJ, USA), eluted isocratically at a flow rate of 1 mL min^{-1}. The mobile phase consisted of 0.02% (*v*/*v*) formic acid in water. The organic acids were detected at 200 nm and identified based on their retention times. Citric, malic, fumaric, and ascorbic acid were detected, and the total organic acid concentration was also calculated. Final concentrations were expressed as mg g^{-1} fresh weight.

2.9. Growth Parameters

At the end of the experiment (7 months after planting), three plants from each replicate (out of five plants per replicate) were randomly uprooted, and data on plant growth parameters such as the number of leaflets, AGPM, and leaflet area (using Image J open-source software), yield efficiency (grams of fruits produced per final AGPM area in cm^2), AGPM fresh weight, root fresh weight, AGPM dry weight, and root dry weight per plant were determined. At the end of each sampling event the overall toxicity symptoms were assessed based on the following scale: 0—no symptoms at all, 1—symptoms such as leaf tip burn in less than 25% of the AGPM, 2—burn symptoms at 25–50% of the AGPM, 3—burn symptoms at 50–75% of the AGPM and 4—symptoms at more than 75% of the AGPM. Furthermore, the salt tolerance index (TI) was evaluated using the following formula:

$$\text{Tolerance index (TI)} = (\text{Treatment dry weight}/\text{Blank dry weight}) * 100.$$

Specific leaf area (SLA) was calculated based on total leaf area versus total AGPM dry weight, while specific leaf weight (SLW) was calculated as total AGPM dry weight versus total AGPM area. The water contents of the AGPM and roots were calculated by subtracting their respective dry weights from their fresh weights.

2.10. Plant Tissue Mineral Analysis

The AGPM and root samples were analyzed to determine the concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), and boron (B). Each sample was appropriately washed—first with tap water and then three times with deionized water. Consequently, it was dried at 80 °C to constant weight and then ground into a fine powder and dry-ashed in a furnace at 500 °C for 5 h. The ash was extracted with 5% v/v HCl. P concentration was determined by the vanado-molybdo-phosphate yellow color method, B concentration by azomethine-H, and K, Ca, Mg, Fe, Mn, Zn, and Cu concentration was determined by atomic absorption spectrometry (Varian SpectrAA, 240 FS) in the dry digest [32,33]. The concentration of N was determined by the indophenol-blue method in the wet digest [32,33].

2.11. Soil Substrate Analysis

The soil substrate samples were air-dried, crushed, sieved through a 2-mm mesh and analyzed for the following parameters as described by Karapouloutidou and Gasparatos [34]: (a) soil texture was determined using a hydrometer, (b) equivalent calcium carbonate percentage was estimated using a digital calcimeter, (c) pH was measured in a suspension with a 1:1 ratio of soil to distilled water with a pH meter, (d) electrical conductivity (EC) was determined in the soil paste extract, (e) soil organic matter (SOM) was determined by the Walkley–Black wet digestion method, (f) exchangeable cations K, Na, Ca, and Mg were extracted by ammonium acetate CH_3COONH_4 1 M, pH = 7, (g) available P was determined using the 0.5 N $NaHCO_3$ extraction method (h) NO_3-N, NH_4-N were extracted by 2 M potassium chloride KCl, (i) extractable Fe, Mn, Zn, and Cu were determined with diethylene-triamine-pentaaceticacid (DTPA) using an atomic absorption spectrophotometer and, (j) soluble Cl was determined volumetrically using 0.05 N silver nitrate $AgNO_3$.

2.12. Experimental Design and Statistical Analysis

All samples were analyzed twice regarding fruit quality characteristics, while each fruit was measured separately for its physiological characteristics. The data collected were analyzed as a one-way ANOVA, with the applied products being the factor. The data were analyzed altogether, with each sampling event serving as replication. Toxicity symptom evaluation based on the scale constructed was subjected to Chi-square analysis. Before analysis, the normality of data distribution was checked, and where needed, suitable data transformation was performed. Correlation analysis was also performed between the

physiological plus the organoleptic characteristics of the fruit and plant growth parameters with (i) soil properties, (ii) AGPM nutrient content, (iii) root nutrient content, and (iv) plant nutrient content, and presented as heatmaps. The same was also performed regarding the phytochemical constituents of the fruits. Additionally, a principal component analysis was performed to enable us to describe the effects of salinity and its alleviating products with a small number of variables. The statistical analysis was performed using the Statgraphics Centurion XVII statistical software (Statpoint Technologies Inc., Warrenton, VA, USA) and JMP 13 (SAS Institute) as needed.

3. Results

3.1. Effect of Salinity and Alleviation Treatments on Fruit Physiological and Quality Parameters

Salt stress negatively affected some of the fruit physiological and quality parameters, such as mean fruit weight, fruit diameter, the fruit percentage in categories Extra and I plus II, the dry:fresh weight ratio, and finally the total yield per plot (Table 1). Mean fruit weight was significantly higher under Blank treatment, followed by the application of the microbial product (without a significant difference) while the other treatments resulted in lower mean fruit weight. Similarly, Blank treatment resulted in the highest mean fruit diameter while Control resulted in the lowest, with significant differences. The highest percentage of fruits belonging to the Extra category was recorded in Blank and microbial product treatments, while Control treatment resulted in the highest percentage of fruits belonging to the I plus II category. The dry:fresh weight ratio was highest under the microbial product treatment, with a significant difference from that determined in the Blank treatment. Finally, the total yield per plot was highest under the use of good-quality water (Blank), followed by GB treatment (with a significant difference), and lowest under the rest of the treatments, which resulted in the lowest total yields per plot. It is noteworthy that GB treatment resulted in an almost 31% higher yield per plot compared with the Control treatment. The mean fruit weight, length, diameter:length ratio, and firmness did not differ significantly among treatments (Table 1). However, the alleviating product applications increased the mean fruit diameter, compared with salt-stressed plants (Table 1).

The alleviating products' applications did not exhibit any significant effects on the fruit juice pH value, TA, and TSS content, or their ratio (TSS:TA) (Table 2). As far as the color of the fruit surface is concerned, there was not any statistically significant difference between treatments in any of the measured variables (Chroma, L* and Hue angle) (Table 2).

Table 1. Salt stress and alleviating product application effects on strawberry mean fruit weight (g), diameter (mm), length (mm), diameter:length ratio, fruit classification (Extra, I and II, %), firmness (N), dry:fresh weight ratio, and mean total yield per plot (g) (fifteen plants).

Parameters	Weight	Diameter	Length	Diameter:Length	Extra	I and II	Firmness	Dry:Fresh Weight	Total Yield/Plot
Blank	12.15 ± 1.1 ^{a}	29.07 ± 1.5 ^{a}	33.54 ± 3.2 ^{a}	0.87 ± 0.0 ^{a}	86 ± 2.9 ^{a}	14 ± 2.9 c	2.86 ± 0.4 ^{a}	0.06 ± 0.0 ^{b}	426 ± 15.4 ^{a}
Control	9.48 ± 0.4 ^{a}	26.12 ± 0.6 ^{b}	29.50 ± 2.0 ^{a}	0.89 ± 0.1 ^{a}	58 ± 2.6 ^{b}	42 ± 2.6 ^{a}	2.87 ± 0.3 ^{a}	0.10 ± 0.0 ^{ab}	239 ± 9.5 c
BETZ	10.07 ± 0.6 ^{a}	27.53 ± 0.7 ^{ab}	28.77 ± 5.8 ^{a}	0.82 ± 0.1 ^{a}	73 ± 5.5 ^{ab}	27 ± 3.5 ^{ab}	2.79 ± 0.3 ^{a}	0.09 ± 0.0 ^{ab}	244 ± 16.2 c
BA	10.73 ± 0.2 ^{a}	27.92 ± 0.3 ^{ab}	32.10 ± 0.7 ^{a}	0.86 ± 0.0 ^{a}	81 ± 7.6 ^{ab}	19 ± 2.9 ^{b}	2.70 ± 0.3 ^{a}	0.11 ± 0.0 ^{a}	261 ± 24.0 c
GB	10.27 ± 0.4 ^{a}	27.54 ± 1.5 ^{ab}	31.43 ± 0.7 ^{a}	0.87 ± 0.0 ^{a}	72 ± 8.6 ^{ab}	28 ± 5.7 ^{ab}	2.92 ± 0.3 ^{a}	0.09 ± 0.0 ^{ab}	314 ± 15.5 ^{b}

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

Table 2. Salt stress and alleviating product application effects on strawberry fruit juice pH; titratable acidity (TA) (g citric acid 100 g^{-1} fresh weight); total soluble solids (TSS) (Brix); the ratio of total soluble solids:titratable acidity (TSS:TA); and on the chroma, L*, and Hue value color parameters.

Parameters	pH	TA	TSS	TSS:TA	Chroma	L*	Hue
Blank	3.47 ± 0.1 [a]	0.93 ± 0.0 [a]	8.31 ± 0.3 [a]	8.98 ± 0.3 [a]	43.24 ± 2.2 [a]	37.02 ± 0.6 [a]	33.78 ± 0.9 [a]
Control	3.35 ± 0.1 [a]	0.93 ± 0.0 [a]	7.41 ± 0.1 [a]	8.02 ± 0.3 [a]	43.19 ± 2.7 [a]	36.85 ± 1.1 [a]	33.58 ± 1.8 [a]
BETZ	3.49 ± 0.1 [a]	0.88 ± 0.0 [a]	7.84 ± 0.3 [a]	8.90 ± 0.2 [a]	43.19 ± 2.7 [a]	36.56 ± 0.1 [a]	33.58 ± 1.8 [a]
BA	3.69 ± 0.2 [a]	0.88 ± 0.1 [a]	8.43 ± 0.9 [a]	9.72 ± 2.0 [a]	41.32 ± 0.1 [a]	36.89 ± 0.7 [a]	32.54 ± 1.3 [a]
GB	3.40 ± 0.2 [a]	1.0 ± 0.2 [a]	8.01 ± 0.2 [a]	8.24 ± 1.4 [a]	40.94 ± 0.4 [a]	35.85 ± 0.3 [a]	32.64 ± 0.9 [a]

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

3.2. Effects of Salt Stress and Alleviating Product Application on Strawberry Fruit Phenolic and Anthocyanin Concentration and the Antioxidant Capacity of Fruit Juice

Salt stress and the application of the various alleviating products had no significant impact on total phenols, total o-diphenols, total flavanols, and total flavonoids concentration (Table 3). On the other hand, the application of BETZ, followed by GB, resulted in the highest concentration of total anthocyanins, with a significant difference from both the Blank and Control treatments. The application of the various products significantly affected the antioxidant capacity of the fruit juice throughout the experimental period (Table 3), as the juice of the fruits derived from plants treated with BETZ primarily and secondarily with GB presented higher antioxidant capacity than juice from fruits harvested from plants that had had Blank treatment (except for GB concerning FRAP assay).

Table 3. Salt stress and alleviating product application effects on strawberry fruit total phenols, total o-diphenols, total flavanols, and total flavonoids concentration (expressed as mg g^{-1} fresh weight), total anthocyanins (expressed as mg 100 g^{-1} fresh weight), and antioxidant capacity of strawberry fruit juice, according to DPPH and FRAP assays (expressed as μmol Trolox g^{-1} fresh weight).

Parameters	Total Phenols	Total O-Diphenols	Total Flavanols	Total Flavonoids	Total Anthocyanins	DPPH	FRAP
Blank	2.69 ± 0.1 [a]	1.34 ± 0.4 [a]	0.54 ± 0.01 [a]	0.82 ± 0.01 [a]	25.43 ± 0.4 [b]	6.98 ± 1.2 [b]	4.49 ± 0.4 [b]
Control	3.18 ± 1.0 [a]	1.46 ± 0.1 [a]	0.61 ± 0.1 [a]	1.13 ± 0.2 [a]	25.55 ± 2.1 [b]	8.73 ± 0.6 [ab]	5.08 ± 0.2 [ab]
BETZ	2.88 ± 0.3 [a]	1.52 ± 0.1 [a]	0.56 ± 0.1 [a]	1.07 ± 0.2 [a]	33.35 ± 2.7 [a]	8.96 ± 0.5 [a]	5.76 ± 0.2 [a]
BA	3.13 ± 0.1 [a]	1.28 ± 0.1 [a]	0.67 ± 0.01 [a]	1.14 ± 0.1 [a]	25.93 ± 3.2 [b]	8.67 ± 1.0 [ab]	4.95 ± 0.4 [ab]
GB	2.87 ± 0.2 [a]	1.35 ± 0.2 [a]	0.67 ± 0.1 [a]	1.17 ± 0.1 [a]	31.85 ± 4.0 [ab]	9.31 ± 0.4 [a]	5.19 ± 0.3 [ab]

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

3.3. Effects of Salt Stress and Alleviating Product Application on the Carbohydrate and Organic Acid Content of Fruits

Salinity did not have any significant effect on the concentration of the detected sugars of the fruits, compared with Blank treatment (Table 4). However, GB application resulted in increased sucrose concentration compared with BETZ, while glucose and fructose were significantly higher in strawberry plants treated with BA compared with BETZ and Control (Table 4). Total sugars concentration did not exhibit any significant change due to the alleviating product application. The sweetness index of the fruits, on the other hand, was highest under the BA treatment followed by the GB one, while those treated with BETZ presented the lowest values.

Table 4. Salt stress and alleviating product application effects on the carbohydrate concentration (expressed as mg g^{-1} fresh weight) and on the sweetness index (SI) of the strawberry fruit.

Parameters	Sucrose	Glucose	Fructose	Total Sugars	SI
Blank	4.25 ± 0.2 ^{ab}	8.09 ± 0.1 ^{ab}	8.70 ± 0.2 ^{ab}	21.28 ± 0.4 ^{a}	33.86 ± 0.4 ^{b}c
Control	4.56 ± 0.1 ^{ab}	7.19 ± 0.1 ^{b}	7.83 ± 0.1 ^{b}	19.20 ± 0.2 ^{a}	31.37 ± 0.^{b}c
BETZ	3.38 ± 0.1 ^{b}	7.24 ± 0.1 ^{b}	8.05 ± 0.1 ^{b}	18.43 ± 0.4 ^{a}	30.32 ± 0.3 c
BA	5.34 ± 0.1 ^{ab}	9.19 ± 0.1 ^{a}	9.90 ± 0.1 ^{a}	24.96 ± 0.1 ^{a}	39.17 ± 0.1 ^{a}
GB	5.45 ± 0.2 ^{a}	8.15 ± 0.1 ^{ab}	8.85 ± 0.1 ^{ab}	21.83 ± 0.2 ^{a}	35.89 ± 0.5 ^{ab}

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

Among the measured organic acids, citric acid was the predominant one, while fumaric acid was detected in a very low amount (Table 5). The fruits deriving from salt-stressed plants presented the highest amounts of ascorbic, malic, citric, and fumaric acids, higher than that determined in fruits after Blank treatment (except for malic acid). Among the alleviating products, fruits from GB-treated plants exhibited a high concentration of all the measured organic acids, while the lowest amount of malic acid was detected in the BETZ-treated plants, lower than that determined in fruits from GB-treated plants.

Table 5. Salt stress and alleviating product application effects on the strawberry fruit organic acid content (expressed as g 100 g^{-1} fresh weight).

Parameters	Ascorbic Acid	Malic Acid	Citric Acid	Fumaric Acid	Total Acids
Blank	0.030 ± 0.01 ^{b}	0.061 ± 0.01 ^{ab}	0.507 ± 0.01 ^{b}	0.0009 ± 0.001 c	0.601 ± 0.1 ^{b}
Control	0.047 ± 0.01 ^{a}	0.095 ± 0.01 ^{a}	0.658 ± 0.01 ^{a}	0.0033 ± 0.001 ^{a}	0.804 ± 0.1 ^{a}
BETZ	0.034 ± 0.01 ^{ab}	0.038 ± 0.01 ^{b}	0.532 ± 0.01 ^{b}	0.0013 ± 0.001 ^{b}c	0.606 ± 0.011 ^{b}
BA	0.033 ± 0.01 ^{ab}	0.058 ± 0.01 ^{ab}	0.513 ± 0.1 ^{b}	0.0024 ± 0.001 ^{ab}	0.608 ± 0.1 ^{b}
GB	0.046 ± 0.01 ^{a}	0.087 ± 0.01 ^{a}	0.594 ± 0.01 ^{ab}	0.0027 ± 0.001 ^{ab}	0.731 ± 0.01 ^{ab}

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

3.4. Effects of Salt Stress and Alleviating Product Application on Strawberry Growth Parameters and Toxicity Symptoms

Salinity reduced leaflet area, while BETZ treatment seemed to be able to alleviate to some extent this negative impact of salt stress (Table 6). Plant AGPM area, and AGPM and root fresh and dry weights were significantly reduced by the imposed salt stress. The AGPM area was reduced on average by 38%, AGPM fresh weight by 60.8%, root fresh weight by 32%, AGPM dry weight by 59%, and root dry weight by 41% in salt-stressed plants compared with Blank treatment.

The application of alleviating products did not result in significant changes concerning AGPM area, the number of leaves, or AGPM fresh or dry weights. Nonetheless, GB application resulted in significantly higher yield efficiency than both in Control and Blank treatments, while BETZ enhanced root fresh and dry weights, compared with Control.

The highest tolerance index among the amelioration products was achieved after the application of either BETZ or GB with a significant difference from the Control treatment (Table 7). GB application resulted in the lowest SLA but the highest SLW, higher than that measured under Blank conditions. The AGPM water content was highest under Blank conditions, without significant differences though from BETZ and GB treatments. The root water content was found to be lowest under BA treatment, while BETZ preserved root water at similar levels to the Blank treatment. On the other hand, none of the amelioration treatments resulted in a similar ratio of AGPM DW to Root DW to the Blank treatment.

Table 6. Salt stress and alleviating product application effects on strawberry mean plant leaflet area (cm^2), above-ground plant mass (AGPM) area (cm^2), number of leaves, yield efficiency (g cm^{-2}), AGPM, and root fresh and dry weights (g).

Parameters	Leaflet Area	AGPM Area	Number of Leaves	Yield Efficiency	AGPM Fresh Weight	Root Fresh Weight	AGPM Dry Weight	Root Dry Weight
Blank	23.02 ± 2.3 ^{a}	711.0 ± 53.3 ^{a}	30 ± 3.5 ^{a}	0.12 ± 0.01 ^{b}	82.0 ± 29.4 ^{a}	38.03 ± 6.0 ^{a}	18.62 ± 4.0 ^{a}	7.63 ± 1.4 ^{a}
Control	18.57 ± 3.4 ^{b}c	439.9 ± 13.6 ^{b}	24 ± 3.0 ^{ab}	0.10 ± 0.01 ^{b}	32.09 ± 2.5 ^{b}	25.89 ± 4.1 ^{b}	7.55 ± 1.2 ^{b}	4.51 ± 0.6 c
BETZ	22.20 ± 1.6 ^{ab}	418.2 ± 32.5 ^{b}	19 ± 6.1 ^{b}	0.11 ± 0.01 ^{b}	50.84 ± 13.4 ^{ab}	41.50 ± 1.6 ^{a}	10.83 ± 1.5 ^{b}	7.05 ± 0.4 ^{ab}
BA	16.68 ± 3.4 c	339.6 ± 67.7 ^{b}	19 ± 4.0 ^{b}	0.15 ± 0.05 ^{ab}	29.87 ± 7.2 ^{b}	24.12 ± 4.6 ^{b}	7.78 ± 1.0 ^{b}	4.69 ± 1.0 ^{b}c
GB	16.24 ± 0.8 c	335.2 ± 19.2 ^{b}	20 ± 1.5 ^{b}	0.18 ± 0.01 ^{a}	41.62 ± 1.3 ^{b}	34.33 ± 4.5 ^{ab}	10.67 ± 1.0 ^{b}	6.10 ± 0.8 ^{b}c

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

Table 7. Salt stress and alleviating product application effects on strawberry plant tolerance index (%), specific leaf area (cm^2 g^{-1} DW), specific leaf weight (mg DW cm^{-2}), leaf water content (g), root water content (g), and the ratio of AGPM dry weight to root wry weight.

Parameters	Tolerance Index	Specific Leaf Area	Specific Leaf Weight	AGPM Water Content	Root Water Content	AGPM D.W./Root D.W.
Blank	100 ± 0.0 ^{a}	58.96 ± 5.5 ^{a}	17.15 ± 3.6 ^{b}	63.38 ± 15.4 ^{a}	30.4 ± 5.0 ^{ab}	2.51 ± 0.4 ^{a}
Control	45.96 ± 6.3 c	38.93 ± 7.4 ^{ab}	26.02 ± 2.3 ^{ab}	24.54 ± 1.3 ^{b}	21.37 ± 3.5 ^{b}c	1.68 ± 0.2 ^{b}
BETZ	68.10 ± 6.8 ^{b}	38.82 ± 2.8 ^{ab}	25.84 ± 1.9 ^{ab}	40.00 ± 12.0 ^{ab}	34.45 ± 1.6 ^{a}	1.53 ± 0.1 ^{b}
BA	47.51 ± 7.4 c	42.34 ± 14.1 ^{ab}	25.03 ± 8.9 ^{ab}	22.09 ± 6.9 ^{b}	19.43 ± 3.6 c	1.68 ± 0.2 ^{b}
GB	63.9 ± 4.7 ^{b}	31.49 ± 1.9 ^{b}	31.83 ± 1.9 ^{a}	30.94 ± 1.4 ^{ab}	28.23 ± 3.7 ^{ab}c	1.77 ± 0.2 ^{b}

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

Toxicity symptoms appeared already from the end of the first sampling event, as can be seen in Figure 1. At the end of the second sampling event, significant differences were detected, as GB-treated plants presented lighter toxicity symptoms than Control plants. Nonetheless, at the end of the third sampling event, treatments did not seem to alleviate significantly the toxicity symptoms, although both GB- and BETZ-treated plants had a better overall appearance, based on their toxicity index.

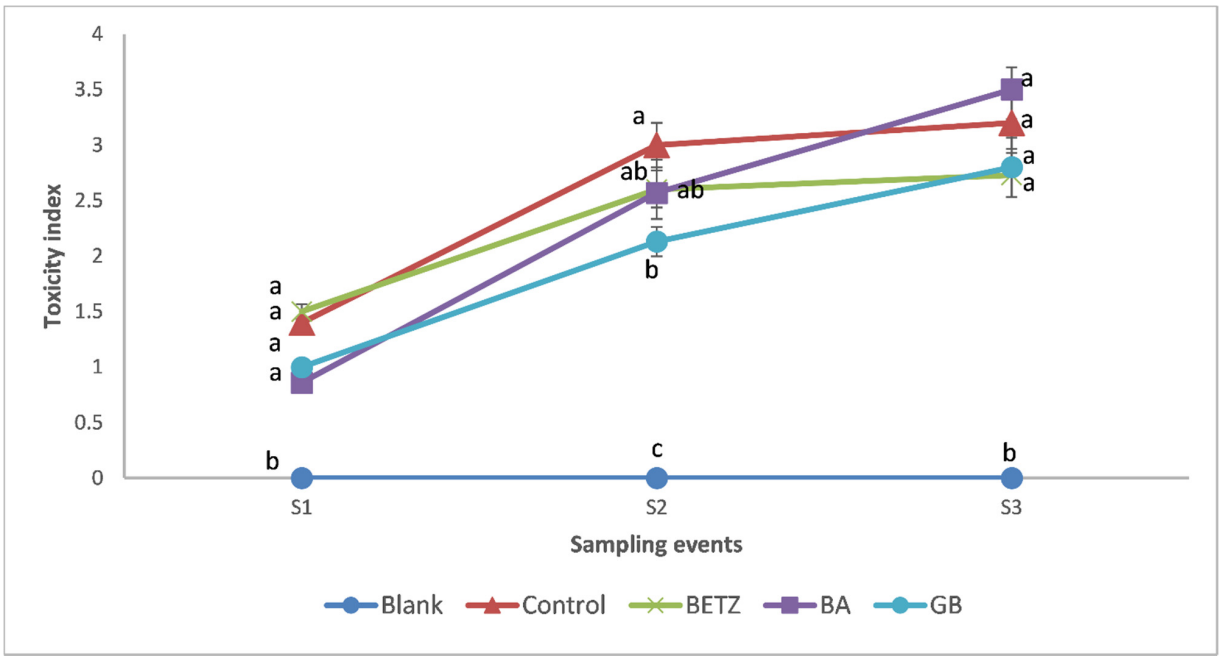

Figure 1. Toxicity symptom severity, depending on sampling event and treatment. Different letters within each sampling event indicate significant differences among treatments, according to the Tukey HSD test at a = 0.05. Bars at each data point represent the SEs.

The severity percentage distribution of the symptoms revealed a significant difference (by the Chi-square test), which is shown in Figure 2. Sixty percent of the Control and BA-treated plants presented symptoms on more than 75% of the AGPM, indicating the severe salt stress of the plants. On the other hand, both GB- and BETZ-treated plants responded better, as only 40% of the plants exhibited severe toxicity symptoms.

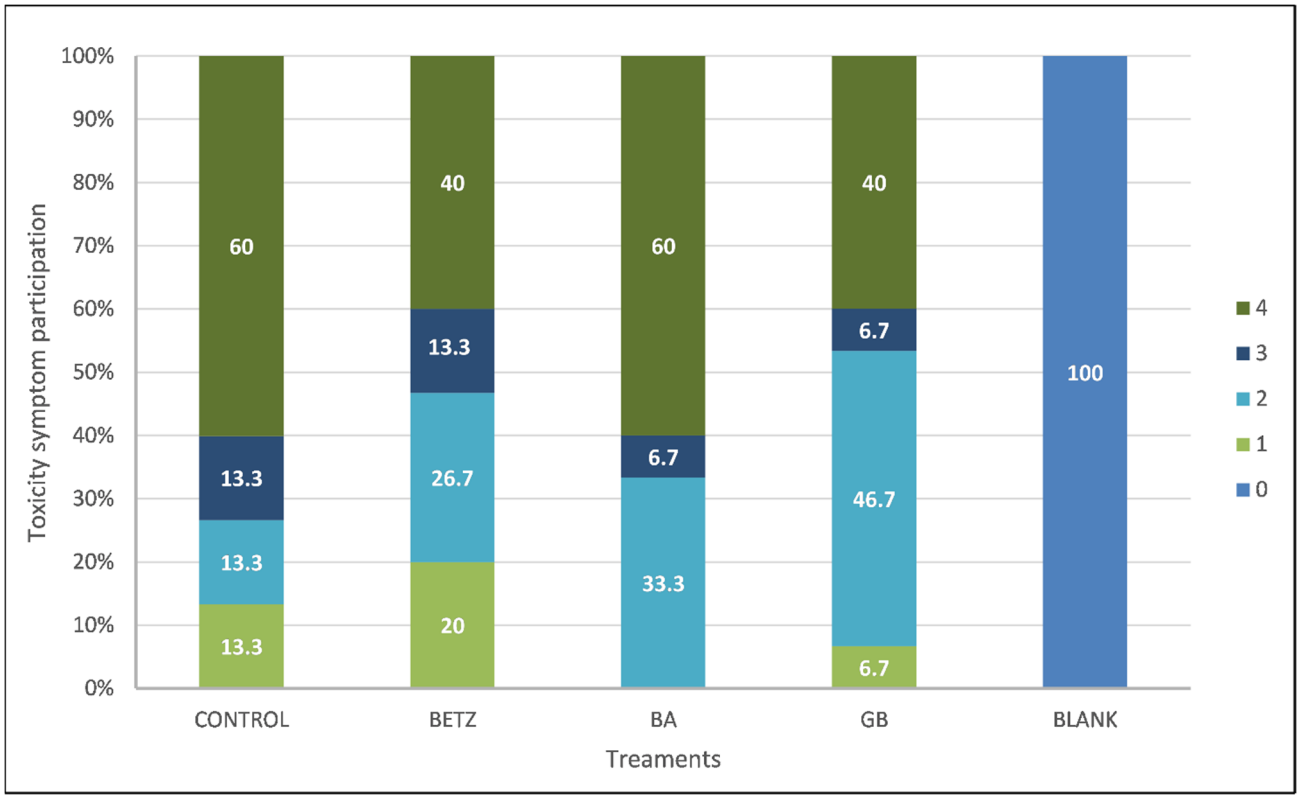

Figure 2. Toxicity symptoms distribution depending on their severity.

3.5. Effects of Salt Stress and Alleviating Product Application on Leaf, Root, and Whole-Plant Nutrient Content

Plants given the Blank treatment exhibited the highest leaf N, P, K, Ca, Mg and B content (Table 8). Salt-stressed plants exhibited, as was expected, an increased Cl and Na content in leaves, while the alleviating products had no significant effect on leaf Na and Cl content. Furthermore, BA-treated plants exhibited the lowest leaf N, Ca, Mg, and B content in their AGPM (Table 8).

N content was found to be highest in the roots of plants from the Blank treatment, though without significant differences from BETZ and GB (Table 9). Cl content was highest in the roots of salt-stressed and BA-treated plants, while BETZ and GB did not differ significantly from the Blank treatment, which exhibited the lowest Cl content. Na content was significantly increased in salt-stressed Control plants, and in BETZ and GB-treated ones, with BA treatment not differing from the Blank-treated plants.

The mineral content per the whole plant showed that N, P, K, Ca, Mn, and B contents were highest following the Blank treatment (Table 10). Salinity resulted in an accumulation of Na and Cl in the plant, without the alleviating products being able to significantly reduce it.

Table 8. Effects of salt stress and alleviating product application on strawberry above-ground plant mass nutrient content (N, P, K, Ca, Mg, and Na expressed as g; Cl, Fe, Mn, Zn, Cu, and B expressed as mg).

Parameters	N	P	K	Ca	Mg	Na	Na/K	Na/Ca	Cl	Fe	Mn	Zn	Cu	B
Blank	0.14 ± 0.01 ^{a}	0.006 ± 0.001 ^{a}	0.122 ± 0.04 ^{a}	0.115 ± 0.023 ^{a}	0.023 ± 0.006 ^{a}	0.010 ± 0.006 ^{b}	0.08 ± 0.02 ^{b}	0.09 ± 0.03 ^{b}	0.24 ± 0.07 ^{b}	1.49 ± 0.6 ^{a}	0.44 ± 0.09 ^{a}	0.29 ± 0.2 ^{a}	0.04 ± 0.01 ^{a}	0.36 ± 0.09 ^{a}
Control	0.08 ± 0.01 ^{b}	0.003 ± 0.001 ^{b}	0.062 ± 0.01 ^{ab}	0.070 ± 0.002 ^{b}	0.015 ± 0.003 ^{b}	0.034 ± 0.009 ^{a}	0.56 ± 0.15 ^{a}	0.48 ± 0.05 ^{a}	0.71 ± 0.15 ^{a}	0.77 ± 0.1 ^{a}	0.22 ± 0.03 ^{a}	0.14 ± 0.01 ^{a}	0.03 ± 0.00 ^{a}	0.23 ± 0.07 ^{ab}
BETZ	0.07 ± 0.01 ^{b}	0.003 ± 0.001 ^{b}	0.068 ± 0.015 ^{ab}	0.063 ± 0.004 ^{b}	0.014 ± 0.001 ^{b}	0.029 ± 0.010 ^{ab}	0.42 ± 0.13 ^{ab}	0.46 ± 0.15 ^{a}	0.73 ± 0.07 ^{a}	0.70 ± 0.2 ^{a}	0.19 ± 0.04 ^{a}	0.10 ± 0.01 ^{a}	0.02 ± 0.00 ^{a}	0.21 ± 0.03 ^{b}
BA	0.05 ± 0.01 ^{b}	0.003 ± 0.001 ^{b}	0.059 ± 0.004 ^{ab}	0.053 ± 0.005 ^{b}	0.012 ± 0.002 ^{b}	0.033 ± 0.007 ^{ab}	0.61 ± 0.21 ^{a}	0.64 ± 0.19 ^{a}	0.52 ± 0.09 ^{ab}	0.52 ± 0.1 ^{a}	0.18 ± 0.02 ^{a}	0.11 ± 0.01 ^{a}	0.02 ± 0.00 ^{a}	0.16 ± 0.02 ^{b}
GB	0.07 ± 0.01 ^{b}	0.003 ± 0.001 ^{b}	0.046 ± 0.011 ^{b}	0.063 ± 0.010 ^{b}	0.013 ± 0.001 ^{b}	0.030 ± 0.011 ^{ab}	0.65 ± 0.06 ^{a}	0.48 ± 0.08 ^{a}	0.69 ± 0.13 ^{ab}	1.20 ± 0.9 ^{a}	0.22 ± 0.02 ^{a}	0.15 ± 0.01 ^{a}	0.03 ± 0.00 ^{a}	0.20 ± 0.01 ^{b}

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

Table 9. Effects of salt stress and alleviating product application on strawberry root nutrient content (N, P, K, Ca, Mg, and Na expressed as g; Cl, Fe, Mn, Zn, Cu, and B expressed as mg).

Parameters	N	P	K	Ca	Mg	Na	Cl	Fe	Mn	Zn	Cu	B
Blank	0.040 ± 0.006 ^{a}	0.004 ± 0.000 ^{a}	0.009 ± 0.004 ^{a}	0.049 ± 0.012 ^{a}	0.005 ± 0.001 ^{a}	0.002 ± 0.001 ^{b}	0.06 ± 0.03 ^{b}	3.91 ± 1.31 ^{a}	0.25 ± 0.13 ^{a}	0.18 ± 0.08 ^{a}	0.09 ± 0.01 ^{a}	0.14 ± 0.01 ^{a}
Control	0.026 ± 0.007 ^{b}	0.004 ± 0.001 ^{a}	0.006 ± 0.001 ^{a}	0.056 ± 0.005 ^{a}	0.004 ± 0.001 ^{a}	0.013 ± 0.002 ^{a}	0.17 ± 0.04 ^{a}	5.00 ± 1.81 ^{a}	0.21 ± 0.03 ^{a}	0.12 ± 0.00 ^{a}	0.08 ± 0.02 ^{a}	0.11 ± 0.00 ^{a}
BETZ	0.028 ± 0.008 ^{ab}	0.004 ± 0.001 ^{a}	0.014 ± 0.007 ^{a}	0.047 ± 0.005 ^{a}	0.004 ± 0.001 ^{a}	0.015 ± 0.005 ^{a}	0.13 ± 0.02 ^{ab}	4.02 ± 0.85 ^{a}	0.22 ± 0.05 ^{a}	0.14 ± 0.02 ^{a}	0.07 ± 0.02 ^{a}	0.11 ± 0.01 ^{a}
BA	0.020 ± 0.004 ^{b}	0.003 ± 0.001 ^{a}	0.007 ± 0.002 ^{a}	0.038 ± 0.005 ^{a}	0.003 ± 0.001 ^{a}	0.011 ± 0.003 ^{ab}	0.19 ± 0.05 ^{a}	3.79 ± 1.10 ^{a}	0.17 ± 0.05 ^{a}	0.16 ± 0.03 ^{a}	0.07 ± 0.01 ^{a}	0.09 ± 0.02 ^{a}
GB	0.028 ± 0.004 ^{ab}	0.003 ± 0.001 ^{a}	0.010 ± 0.009 ^{a}	0.043 ± 0.010 ^{a}	0.004 ± 0.001 ^{a}	0.014 ± 0.005 ^{a}	0.14 ± 0.02 ^{ab}	3.41 ± 1.93 ^{a}	0.25 ± 0.09 ^{a}	0.24 ± 0.06 ^{a}	0.11 ± 0.02 ^{a}	0.11 ± 0.03 ^{a}

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

Table 10. Effects of salt stress and alleviating product application on strawberry whole-plant nutrient content (N, P, K, Ca, Mg, and Na expressed as g; Cl, Fe, Mn, Zn, Cu, and B expressed as mg).

Parameters	N	P	K	Ca	Mg	Na	Cl	Fe	Mn	Zn	Cu	B
Blank	0.18 ± 0.03 ^{a}	0.011 ± 0.002 ^{a}	0.13 ± 0.04 ^{a}	0.16 ± 0.02 ^{a}	0.029 ± 0.006 ^{a}	0.013 ± 0.005 ^{b}	0.30 ± 0.07 ^{b}	5.4 ± 1.9 ^{a}	0.69 ± 0.18 ^{a}	0.48 ± 0.19 ^{a}	0.13 ± 0.02 ^{a}	0.50 ± 0.09 ^{a}
Control	0.10 ± 0.02 ^{b}	0.008 ± 0.002 ^{ab}	0.06 ± 0.01 ^{b}	0.12 ± 0.02 ^{b}	0.020 ± 0.003 ^{b}	0.047 ± 0.009 ^{a}	0.89 ± 0.19 ^{a}	5.7 ± 1.9 ^{a}	0.43 ± 0.05 ^{ab}	0.27 ± 0.03 ^{a}	0.11 ± 0.02 ^{a}	0.15 ± 0.07 ^{b}
BETZ	0.10 ± 0.01 ^{b}	0.008 ± 0.001 ^{ab}	0.08 ± 0.00 ^{ab}	0.11 ± 0.00 ^{b}	0.018 ± 0.002 ^{b}	0.044 ± 0.006 ^{a}	0.80 ± 0.08 ^{a}	4.7 ± 0.8 ^{a}	0.42 ± 0.08 ^{ab}	0.25 ± 0.02 ^{a}	0.10 ± 0.02 ^{a}	0.33 ± 0.02 ^{b}
BA	0.07 ± 0.01 ^{b}	0.006 ± 0.001 ^{b}	0.06 ± 0.02 ^{b}	0.09 ± 0.00 ^{b}	0.018 ± 0.003 ^{b}	0.045 ± 0.005 ^{a}	0.71 ± 0.14 ^{ab}	4.3 ± 1.0 ^{a}	0.35 ± 0.10 ^{b}	0.27 ± 0.06 ^{a}	0.09 ± 0.02 ^{a}	0.26 ± 0.05 ^{b}
GB	0.10 ± 0.01 ^{b}	0.006 ± 0.001 ^{b}	0.05 ± 0.00 ^{b}	0.10 ± 0.01 ^{b}	0.016 ± 0.001 ^{b}	0.045 ± 0.005 ^{a}	0.84 ± 0.33 ^{a}	4.6 ± 1.1 ^{a}	0.48 ± 0.08 ^{ab}	0.40 ± 0.06 ^{a}	0.15 ± 0.02 ^{a}	0.31 ± 0.04 ^{b}

Means (±standard error) within the same column followed by the same letter, are not significantly different based on the Tukey HSD test at a = 0.05.

3.6. Effects of Salt Stress and Alleviating Product Application on Soil Physicochemical Properties

The soil analysis showed that the pH; the $CaCO_3$ content; and the concentrations of NH_4-N, NO_3-N, P, Ca, Mg, and Mn did not differ significantly among treatments (Figure 3a,b). However, the electrical conductivity was significantly increased after salinity imposition, with the BETZ treatment being the only one not differing from the Blank treatment (Figure 3a).

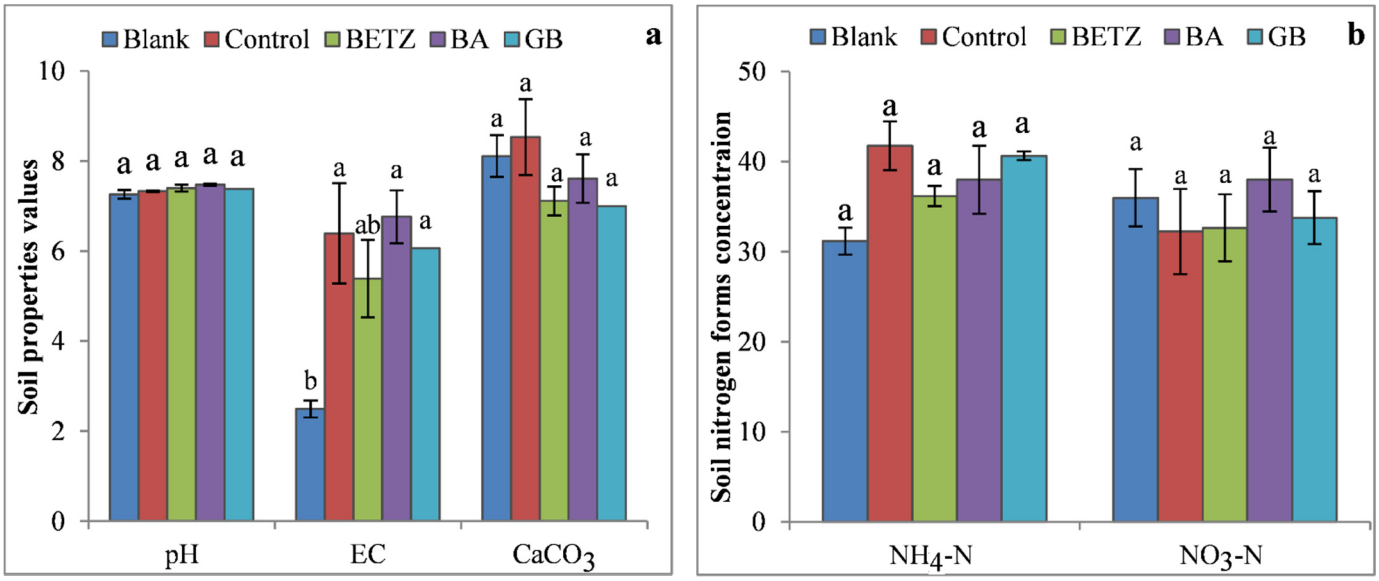

Figure 3. Effects of salt stress and alleviating product application on soil physicochemical properties (**a**) pH, EC, $CaCO_3$ and (**b**) NH_4-N, NO_3-N, (EC expressed as mS cm^{-1}; $CaCO_3$ as %; NH_4-N and NO_3-N as mg Kg^{-1}). Bars on the top of each column represent the standard error of the mean.

The BETZ treatment also resulted in a high concentration of available K, significantly higher than all in other treatments, which did not differ among each other (Figure 4a). Sodium was detected in high amounts in salt-treated soil (Figure 4a), while significant differences between treatments were detected concerning the concentration of soil micronutrients (Figure 4b). Chloride was found in low concentration in Blank treatment, which did not differ from BETZ treatment. On the other hand, Fe was found to be in high concentration in the Control, higher than that determined in GB treatment. Control and BA treatments resulted in a high concentration of Zn in the soil, higher than that determined under BETZ and GB treatments. Copper was found at a significantly lower concentration in the soil of BETZ treatment than that determined in Control.

3.7. Correlations of the Measured Plant Nutrition Parameters with the Physiological and Organoleptic as Well as with the Phytochemical Characteristics of the Fruit

In the heatmap produced from the correlation between physiological–organoleptic plant growth characteristics and the nutrient content of the AGPM it is clear that all nutrients were positively related to the yield, mean fruit weight, and Extra fruit weight, except for Cl and Na, which were negatively related (Figure 5).

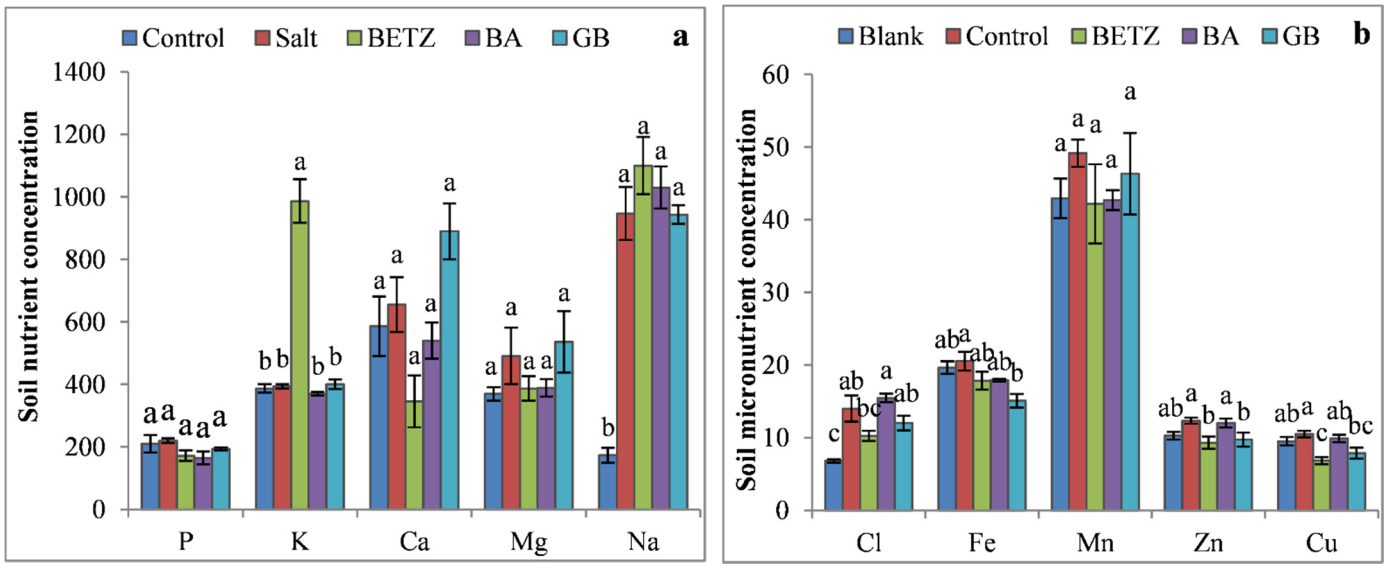

Figure 4. Effects of salt stress and alleviating product application on soil nutrient concentration, (**a**) P, K, Ca, Mg, Na expressed as mg Kg^{-1}, and (**b**) Fe, Mn, Zn, Cu and B expressed as mg Kg^{-1}; Cl as meq L^{-1}. Bars on the top of each column represent the standard error of the mean.

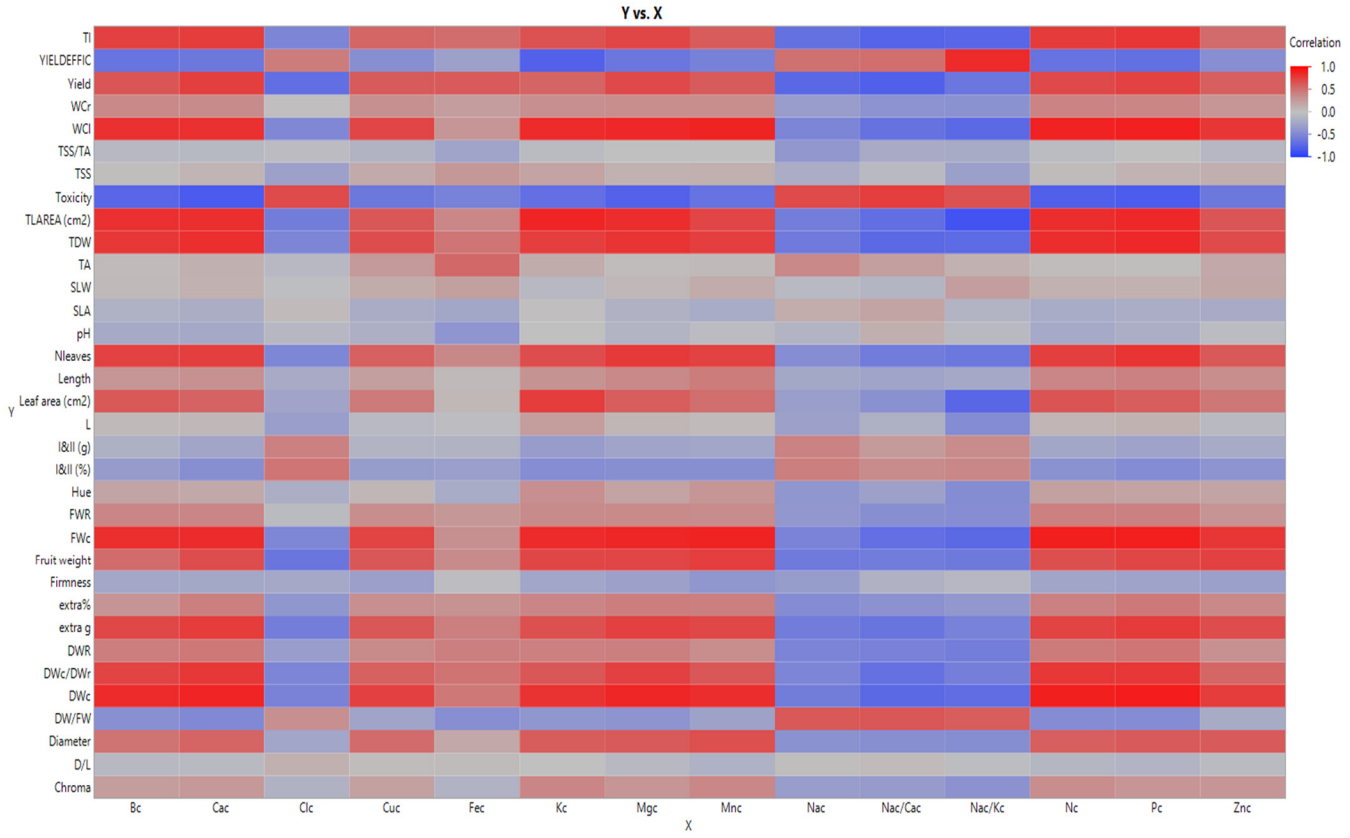

Figure 5. Heatmap of correlation between organoleptic plant growth characteristics and nutrient content of the AGPM.

Concerning root nutrient content, it was evident that both Cl and Na were negatively related to the yield and Extra category fruit weight, while leaf area was positively related to the B and P content of the roots, and yield to the N content (Figure 6). Concerning the nutrient content of the entire plant, the relations revealed were more or less similar to those determined with the nutrient content of the AGPM (Supplementary material, Figure S1). Soil physicochemical properties also revealed significant effects on fruit and plant parameters measured, such as that EC, Cl, and especially Na were negatively related to plant yield but positively to the ratio DW/FW of the fruit (Supplementary material, Figure S2).

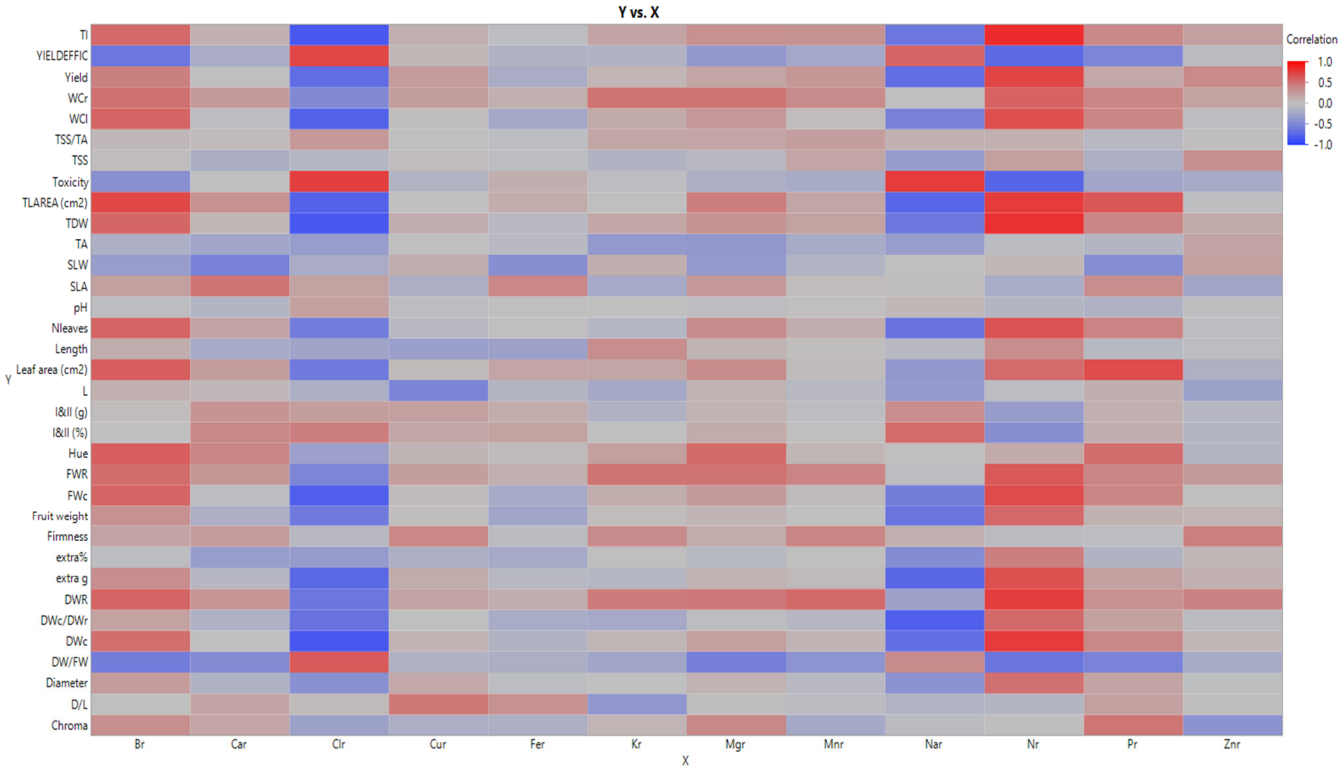

Figure 6. Heatmap of correlation between organoleptic plant growth characteristics and nutrient content of the root.

Concerning the phytochemical properties of the fruit, it was clear that Cl and Na in the AGPM were the only nutrients positively related to some of the parameters studied (Figure 7), such as antioxidant capacity and o-diphenols concentration of the pulp (Cl), total phenols, fumaric acid, and total organic acids concentration (Cl and Na).

The sodium and Cl contents of the roots were positively correlated with the flavonoid concentration and the antioxidant capacity of the fruit (Figure 8), while the overall relations observed regarding fruit phytochemical properties and whole-plant nutrient content were similar to those reported for the nutrient content of the AGPM (Supplementary material, Figure S3). Fumaric acid concentration of the fruit pulp was positively related to the soil EC and Cl concentrations, while antioxidant capacity (FRAP) was positively related to the ECE, K, and Na concentrations of the soil (Supplementary material, Figure S4).

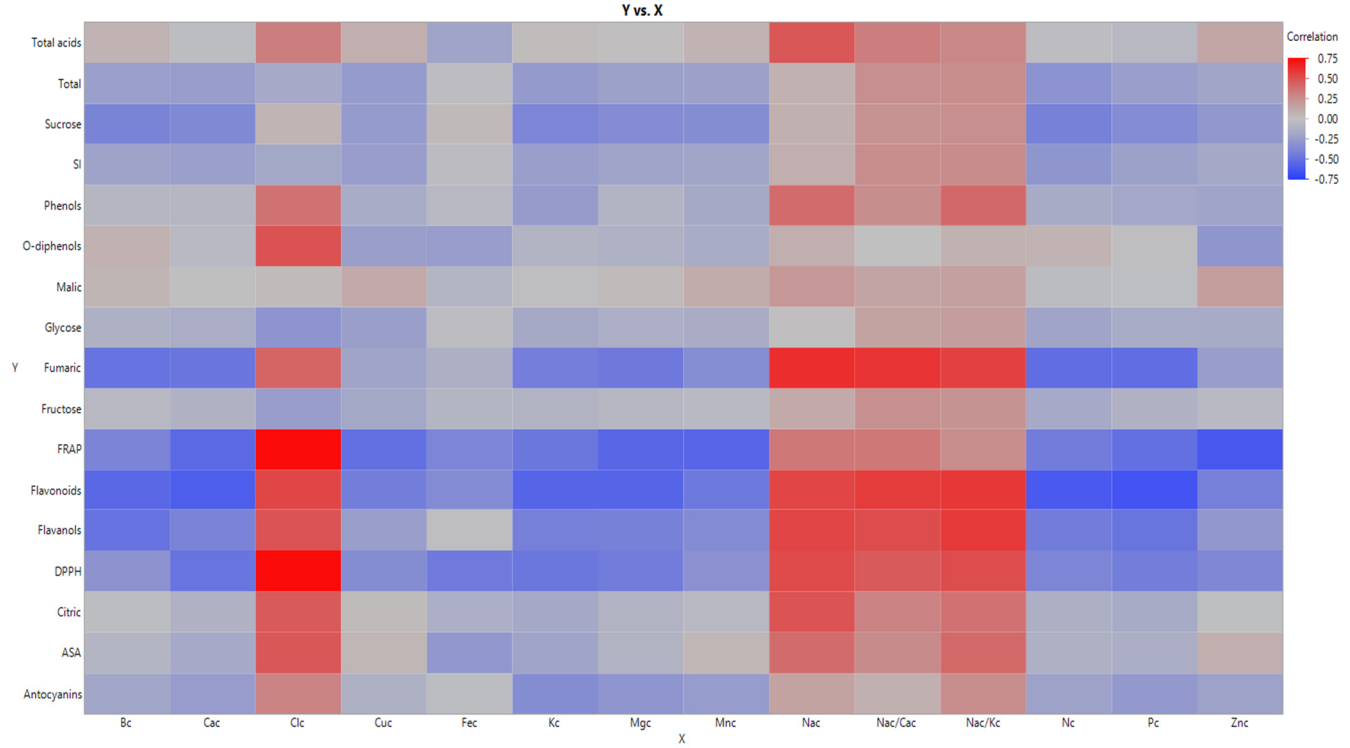

Figure 7. Heatmap of correlation between the phytochemical properties of the fruit pulp and nutrient content of the AGPM.

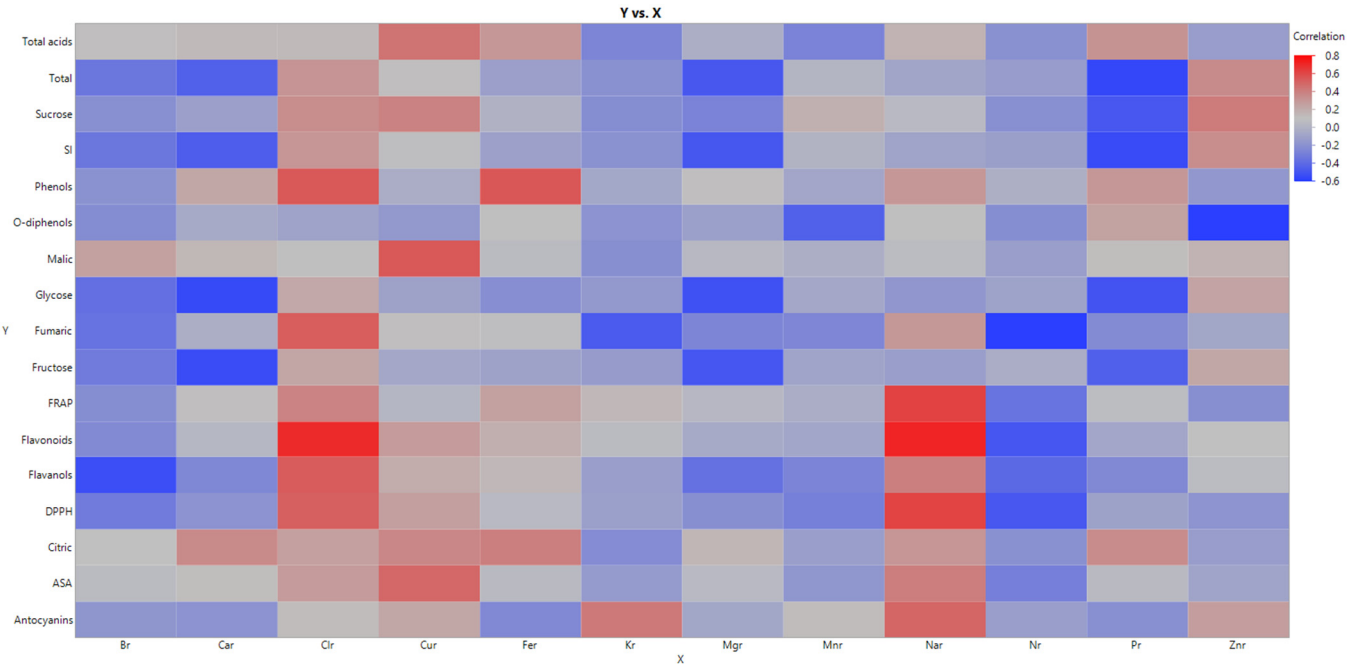

Figure 8. Heatmap of correlation between the phytochemical properties of the fruit pulp and nutrient content of the plant root.

3.8. Principal Components Analysis

The principal component analysis revealed that the first two principal components describe approximately 50.48% of the overall variability of the data, which is considered to be quite low (Figure 9). Nonetheless, all alleviating products (all located on the positive axis of PC1) were distinct from Blank treatment, which was located on the negative side of PC1. On the other hand, though, they were distinct from Control treatment too, with BETZ being the furthest separated one—located on the positive side of PC2, while Control was located on its negative side.

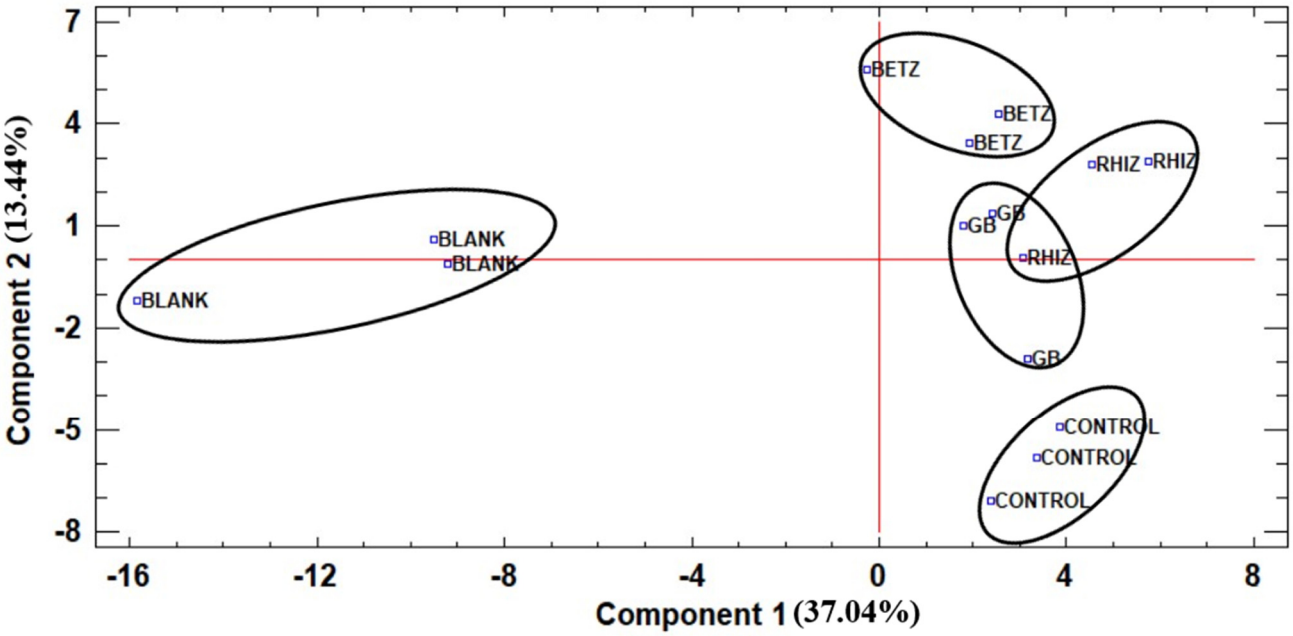

Figure 9. Principal component analysis scatterplot of the measured variables, based on the treatments imposed.

4. Discussion

Salinity reduced strawberry plant growth significantly, as was evident by the reductions of leaflet area, AGPM area, AGPM fresh and dry weights, and root fresh and dry weights. Similar results have been reported for several cultivars, including Camarosa, by many researchers [4,35–40]. According to some researchers [35,36] salinity slows down leaf development, induces deficiencies in nutrients such as N, P, and K, while at the same time causing chlorophyll content to decrease [40], leaf senescence to accelerate, and inducing toxicity symptoms in the older leaves—all of which symptoms lead to reduced photosynthetic activity, low production of photoassimilates, and thus reduced growth. Furthermore, salinity imposes also osmotic stress, by decreasing the osmotic potential of soil solution, hindering thus the absorption of water needed for growth [38]. Ghaderi et al. [36] reported that salinity affected only the number of leaves and not the leaf area per se, while Saied et al. [39] reported the exact opposite, since the number of leaves remained unaltered while the leaf area was reduced. In the present trial, both these parameters were reduced, which indicates the severity of the salinity stress imposed. Furthermore, Ghaderi et al. [36] reported that the ratio of root-to-shoot dry weight was increased in favor of root growth and this was attributed to the greater reduction of the above-ground biomass, which can be attributed to leaf loss [39]. Similar to these findings, in the present experiment, the reduction of AGPM dry weight was greater than that of roots, indicating that roots are more tolerant to salinity than the leaves [36]. The treatments, to some extent, alleviated the negative impacts of salinity, with different effects on the measured parameters. The BETZ treatment resulted in a similar leaflet area to that of Blank treatment, which did not lead to increased total leaf area—the number of leaves being rather significantly reduced.

AGPM dry weight was severely reduced under all alleviation treatments, while BETZ was the only treatment in which root dry weight was not reduced significantly, compared with Blank, being at the same time higher than that with Control, as has been reported in other cases too [41]. Both zeolite and bentonite have been found to increase the water-holding capacity of the substrate [41–45], leading probably to a significant alleviation against low osmotic potential induced by salinity, allowing thus more water to be available for the growth of roots [8,46]. This could partly justify the increased root fresh weight determined in BETZ compared with Control, as roots may have retained higher water mass, as well as the similar root dry weight to Blank, as reported by others too [47,48]. This alleviation efficacy of BETZ treatment was not observed in AGPM fresh and dry weights, leading to the assumption that although there was enough water in the roots, it was not transferred to the above-ground parts of the plants. This could be ascribed to restrictions of vessel hydraulic conductivity due to salinity [49] and/or reduced transpiration rate due to malfunction of the stomata, by the increased Na concentration at the expense of the K concentration (antagonistic effect on both uptake and transport) [47,49,50], which regulates stomatal aperture and thus photosynthesis and growth. The microbial treatment (BA) was less effective than BETZ in most cases, although the same bacillus (not necessarily the same strain though) has been found to induce salinity tolerance to many crops, by increasing the fresh and/or dry weight of the plant [51], its growth and yield [52,53]. The discrepancies found here could be attributed to the different strains used, to the different growth conditions, salt concentration, and applications used. GB, on the other hand, presented the highest yield efficiency and slightly higher AGPM and root dry weights, indicative of its amelioration action. Similar results have been reported in other species too [7,38,54] and were attributed to the impact of GB on the maintenance of plant cell osmotic potential [38], improving water use efficiency [38,49] and relative water content [49]. Similar effects of GB on AGPM and root water content have been found in the present experiment, as GB increased both of them compared with Control treatment, although not significantly.

Toxicity symptoms (such as leaf tip burn, leaf margin necrosis) gradually evolved from the first to the third sampling, on old leaves as has been reported by others too [55–57], with both GB and BETZ showing the least symptoms at the end of the period. Similar results have been observed in other plants too, as these treatments (zeolite, bentonite, and glycine betaine) have reduced leaf burns and retained chlorophyll content [41,47,49,58]. The tolerance index indicated that the best alleviation treatments were BETZ and GB, with a significant difference from the Control treatment, supporting the efficacy of these two treatments on the mentioned growth parameters under salinity stress.

Plant growth was not the only parameter that was affected by salinity. Yield and yield parameters were affected as well, with the yield been significantly reduced by approximately 44%. Reduction of yields has been already reported in strawberries growing under saline conditions [4,55], and this was attributed to the lower number of fruits [4,18,55,59] and/or lower fruit weight [4,59]. Taking into account the mean yield per plot of the present trial divided by the mean fruit weight, it is obvious that salinity greatly reduced the number of fruits produced (35 fruits per Blank plot against only 25 in the Control one), not affecting the mean fruit weight, as reported also by Saied et al. [39]. By the heatmaps produced it was obvious that toxicity and the total leaf area were negatively and positively related, respectively, to the yield, revealing the great importance of the leaves on producing the necessary photoassimilates to support bud differentiation and fruit growth. A significant decrease in the number of flowers produced, reaching almost 50%, i.e., approximately the percentage of yield reduction observed in the present trial has been reported by Zahedi et al. [60]. Marketable fruits have been reported to decrease with salinity too [55], while fruit firmness did not change significantly under salinity stress, although opposite results have been reported [60]. According to Garriga et al. [35], the unaltered fruit firmness suggests that Na and Cl levels in the fruits were not high enough to change the activity of pectinases as well as other cell wall degrading enzymes, thus the fruit retained its desirable firmness.

The dry-to-fresh weight ratio of the fruits increased under saline conditions, but this should be ascribed to the higher fruit water content under Blank conditions and not to increased accumulation of photosynthates into the fruits of Control, as proposed by Keutgen and Pawelzik [31], and Saied et al. [39]. The treatments with the various alleviating products resulted in a slight increase in the percentage of fruits belonging to the Extra category and increased total yield, although not significantly differently from that of Control. On the other hand, though, GB application resulted in a 32% increase in yield compared with Control and did not differ significantly from the Blank treatment, revealing a significant alleviation action, attributable to its osmoprotectant, ion homeostasis, anti-chlorophyllase, and possible antioxidant actions [7,38,54,61].

The organoleptic characteristics of the fruits were not affected by salinity as all pulp pH, titratable acidity, total soluble content, and fruit surface color attributes did not differ among treatments. There are conflicting data in the literature regarding the effect of salinity on strawberry fruit quality attributes. According to Garriga et al. [35] and Saied et al. [39], salinity resulted in significant TSS reduction only under high levels of salt concentration, and increased TA in two strawberry cultivars, while in Camarosa fruit, the TA remained unchanged [35], as in the present trial. On the other hand, according to Keutgen and Pawelzik [31] and Zahedi et al. [60], the TA decreased significantly with salinity, indicating that cultivar and experimental conditions may have a significant influence, as has been also reported for the TSS content by Ferreira et al. [55] and Keutgen and Pawelzik [31].

The color of the fruit remained fairly stable, as reported also by Saied et al. [39], indicating that salinity does not significantly change fruit pigment concentration.

This was also evident as both Blank and Control treatment results exhibited similar anthocyanins concentrations. In general, salinity stress did not change fruit phytochemical content, regarding the concentration of the different groups of phenolic compounds, indicating that the biosynthetic pathways of phenolic compounds were more or less unaffected. This is in contrast to the results obtained by Zahedi et al. [60], who reported significant decreases in total phenolic compound concentrations as well as a significant reduction in the antioxidant capacity of the fruit. Similar results have been reported for lettuce [62]. On the other hand, Galli et al. [63] reported a significant increase in anthocyanins concentration and antioxidant capacity under mild salinity stress in strawberry. A slight increase of all groups of phenolic compounds and antioxidant capacity under saline conditions was also recorded here, but this was not statistically significant. In general, under stress conditions, the plant experiences oxidative stress due to the loss of control of the electron transfer chain, and it has to deploy its defense arsenal, which consists of both enzymatic and non-enzymatic molecules [64]. Non-enzymatic molecules able to confer tolerance against oxidative stress are the various phenolic compounds, which, to a point, protect plant membranes and functions from getting damaged and in the case of fruit, result in its biofortification with molecules beneficial for human health, as reported by Crizel et al. [64] for strawberry fruits. Beyond that point, though, and under continuous stress conditions and as stress elevates, the antioxidant mechanism is not able to protect membranes and functions, as the production of antioxidant molecules is surpassed by that of oxidative ones. Furthermore, the already present antioxidant molecules are used as defense agents, without being the plant able to substitute them. At this point, oxidative symptoms are developing in alignment with a reduction in plant defense molecules, as has been reported in strawberry fruits with increasing salinity stress [60]. Based on the heatmaps produced, it was found that antioxidant capacity (both measured by DPPH and FRAP assays) was positively related to Cl and Na concentration determined in the AGPM (primarily Cl) and roots (primarily Na). This indicates that stress imposition has triggered the antioxidant mechanism of the plant. All alleviation treatments though, enhanced the antioxidant capacity of the fruit compared with Blank treatment, thus fortifying the fruit with beneficial properties for human health [63]. It seems, thus, that some of the treatments act as elicitors of antioxidant defense against salinity, resulting in enhanced nutritional quality of the fruit. Among them, BETZ and GB proved to be more efficient in enhancing the anthocyanin

content (especially BETZ) and the antioxidant capacity of the fruits, as has been observed in other plant species, too [41,62,65].

The sugar content of the fruit was not significantly affected by salinity, as it was slightly reduced. This slight reduction could be ascribed to the reduced leaf area, resulting in lower photosynthetic activity and thus lower supply of photoassimilates to the fruits, as has been proposed by [39], who also detected reductions of fruit carbohydrate content. Furthermore, as oxidative stress might have begun (judging from the toxicity signs on the leaves), photosynthesis might have been impaired to a great extent, contributing also to the reduced carbohydrate concentration found in the fruits.

Individual (apart from malic acid), as well as the total organic acids, were significantly increased under saline conditions. Similar results have been reported by many authors working with strawberry [4,31], while a non-significant change in the levels of ascorbic acid has been also recorded [66]. BETZ and BA primarily, and GB secondly resulted in non-significant differences with the Blank treatment regarding total organic acid concentration. As salinity induced an elevation of organic acid accumulation in the fruits, it can be assumed that the former two treatments alleviated to some extent the negative effects on salt stress, regarding the organic acid content of the fruits.

The mineral content of the plant was significantly affected by salinity, apart from the majority of micronutrients, as has been previously reported [56]. In general, N, K, Mg, and Ca were significantly reduced, while Na, Cl, and the Na/K and Na/Ca ratios were significantly increased, in both leaves, roots, and whole plant. According to several authors, Cl is the element responsible for the toxic symptoms in strawberry, as it is absorbed by cell membranes and it is translocated to the upper part more easily than Na [55,57,67]. In the present experiment, the Na content in the leaves increased by almost 240% in Control compared with Blank, as similarly reported by others [55,56,68], while that of Cl increased by almost 196%. On the other hand, Na content in the roots increased by 550% while that of Cl increased by 183%, indicating that a substantial amount of Na was retained at the root level, as reported by other authors too [55,67]. Furthermore, Cl concentration in the leaves has been related to leaf tissue necrosis [67], as in the present experiment, where Cl both in roots and leaves was positively related to toxicity symptoms and negatively to tolerance index.

Nitrogen content in the leaves of all plants subjected to salinity was significantly reduced and this may be ascribed to the inhibition of NO_3^- translocation from the root to the upper plant part due to competition with Cl [56,67]. According to Suarez and Grieve [67] the anion channels in the xylem parenchymatic cells may exhibit similar permeability for both NO_3^- and Cl^- and under conditions favoring Cl^- concentration (i.e., salinity stress); NO_3^- loading and translocation would be impaired.

Potassium on the other hand is known to compete with Na uptake and translocation and this is usually in favor of Na, as this is the major mineral found in the root zone under saline conditions [47,69]. This leads to reduced K concentration in the leaves as determined also here [69]. Calcium and Mg content were also reduced in leaves and the whole plant, similar to those reported by Saied et al. [39] and Zahedi et al. [60], while Ca content in roots slightly increased in Control, as reported also by Keutgen and Pawelzik [56], indicating that Ca accumulation in the roots acts as a protection mechanism against severe toxicity.

Phosphorus was significantly decreased under saline conditions in leaves while it remained unaffected in roots. Decreased P concentration in the tissues has been reported by others too [47,60], while Demiral [67] and Keutgen and Pawelzik [56] have reported increases of P in strawberry under saline conditions or non-significant changes [67]. In general, the influence of salinity on P is quite variable in plants and depends on many factors, among which cultivar plays a significant role [47].

Micronutrients, both in roots and upper plant part, were more or less unaffected (apart from B in the leaves and total plant mass), similar to the findings of Ferreira et al. [55], Keutgen and Pawelzik [56], and Suarez and Grieve [68] in various strawberry cultivars,

indicating that salinity did not have a significant impact on the uptake and translocation of micronutrients in this plant.

Alleviating treatments did not have any significant impact on leaf, root, and whole-plant nutrient content compared to Control. This possibly indicates that none of them was able to overcome the effects on salinity on plant nutrition and/or restrict Cl as well as Na uptake and translocation to the leaves. GB was not able to maintain a low Na/K and Na/Ca content in the leaves as reported by Mansour and Ali [7] and Estaji et al. [38]. BETZ was also ineffective in decreasing the Na/K ratio and increasing Ca leaf content, unlike the cases reported by others [8,18,41]. Similarly, BA was ineffective in sustaining a better nutrient level than Control, even though the efficiency of rhizobacteria against salinity has been described in several species [52], but this is mainly dependent on bacterium strain, trial conditions, and plant species itself.

Overall, it can be assumed that in the present trial alleviating products did not present any significant impact on plant nutrition. This may be attributed not only to the pre-mentioned factors but also to the increased EC determined in the soil. Soil EC in the present trial was probably too high, as it was similar to the highest [55], or higher than, reported by other authors [57], rendering the products ineffective in alleviating salinity effect on nutrient content reduction.

High salt content adversely affects soil physical and chemical properties and the continuous increase of salinization on a global scale makes saline soils one of the most important categories of degraded soils with severe effects on crops.

According to Figure 3a, the BETZ treatment has the same EC as the Blank treatment, indicating that the application of zeolite + bentonite mixture could alleviate the adverse effects of salinity by lowering the total salt concentration in soils. In accordance with our results, Turan [70] reported that as natural zeolite was added to poultry litter compost, the electrical conductivity values decreased. Noori, et al. [71] observed that the application of natural zeolite in radish cultivation under saline conditions retained the harmful salts preventing their accumulation in the plant. Our results indicate that this mechanism works sufficiently for Cl, which is trapped by the zeolite + bentonite mixture as it enters into the cavities of those aluminosilicate minerals. The effect of BETZ treatment was more pronounced on soil-exchangeable K, which is characterized as excessive. It is well-known that zeolites have a stronger selectivity on K than Na, Ca, and Mg, hence the losses of K from the soil system are reduced by facilitating greater uptake of K by plant root hairs. Recently, Palanivell et al. [72], using 20 g of clinoptilolite zeolite in a Typic Paleudult, found higher K adsorption with lower K desorption suggesting that the zeolite sorbs K effectively. Both zeolite and bentonite have been found to increase the micronutrient use efficiency, alleviating the imbalance in their uptake by plants induced by salinity. Sheta, et al. [73] reported that five natural zeolites and bentonite minerals pose a high potential for Zn and Fe sorption, hence showing a high capacity for slow-release fertilizers. According to our study, the BETZ treatment resulted in significantly lower Zn, and Cu availability in soil as countermeasures to mitigate the salinization impact on plant micronutrients in strawberry leaves.

Numerous studies have suggested that plant-growth-promoting rhizobacteria (PGPR) can be used as biofertilizers inducing tolerance against salt stress [74]. PGPR improves soil nutrient utilization, enhances phosphate solubility, and promotes the production of hydrocyanic acid (HCN), siderophores, chitinase, ammonia, and indole-3-acetic acid (IAA).

In the present study, the concentration of soil-available P under the treatment with *B. amyloliquefaciens* was not significantly different from the various other treatments (Figure 4a). This finding could be attributed to the initial high concentration of available P that was almost ten times higher than the critical level, according to the Olsen method, as the result of fertigation and the high organic matter content of soil substrate.

Recently, Karapouloutidou and Gasparatos [34] found that when the soil organic matter content is above the critical threshold of 3.4%, it masks the possible positive effects

of the various soil amendments on soil properties. This is consistent with our findings, where the content of organic matter in soil-substrate was 8.0%.

5. Conclusions

In conclusion, it seems that apart from the toxic effects of salinity induced by over-accumulation of Cl as well as of Na in plant tissues, osmotic stress, and water deprivation are equally responsible for the adverse effects of salinity on the growth and yield of strawberry plants. This was most evident in BETZ and GB treatments, which, without having any positive effect on the nutrient content of the plants, alleviated symptoms and resulted in increased yield, due to the better hydric status of the plant, based on leaf and root water content.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/app11198796/s1, Figure S1: Heatmap of correlation between the organoleptic plant characteristics and the nutrient content of the whole plant. Figure S2: Heatmap of correlation between the organoleptic plant characteristics and soil physico-chemical properties. Figure S3: Heatmap of correlation between the phytochemical properties of the fruit pulp and the nutrient content of the whole plant. Figure S4: Heatmap of correlation between the phytochemical properties of the fruit pulp and soil physico-chemical properties. Table S1: Component Weights of the principal component analysis.

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