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Research Article

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Growth and Physiological Response of Strawberry under Salt Stress: Role of Glycine Betaine and Seaweed Extract

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A B S T R A C T

Strawberry is one of the most salt-sensitive horticultural economic crops. In our study, strawberry cv. Festival plants were subjected to salt stress (8 dS/m EC) to investigate the individual and combined effects of Glycine betaine (GB) (60 mM) and Seaweed extract (SWE) (8 ml/L) with different number of applications (one, two, three times) on growth, chlorophyll content, antioxidant activity, some fruit-quality parameters and yield. This research aims to alleviate salt stress-induced growth inhibition and to advance sustainable strategies for improving crop tolerance and yield under saline conditions. This experiment followed three replications and seven treatments in pots, including a control, individual GB/SWE applications, their combinations, and a salt stress level. The results indicated that GB and SWE treatments significantly improved growth characteristics, i.e. leaf area, root and vegetative growth, total yield, and fruit quality characters under salinity stress. Notably, the combined GB+SWE treatment outperformed individual applications, demonstrating 98% greater fruit weight per plant compared to salt-stressed plant and 80% over non-stressed plant, and a synergistic efficacy in restoring physiological functions by increasing antioxidant activity around 59% in the salt-stressed plant. This approach represents a highly effective strategy to mitigate salinity stress on strawberry cultivation, offering eco-friendly alternatives to maximize yield under salinity without needing freshwater-intensive practices, supporting water-scarce or saline-affected areas.

INTRODUCTION

During growth and development, plants often encounter many abiotic stresses like salinity, drought, and cold stress, which can negatively impact their growth and metabolism (Gómez-del-Campo *et al.*, 2015). Among them one of the most significant environmental issues that hinders the plants growth is salinity (Latif and Mohamed, 2016), since it still causes substantial crop losses across the globe (Singh and Takhur, 2018). It is crucial to find ways to promote plant growth and productivity in salinity stress conditions in order to achieve global food security. Salinity generally inhibits DNA, RNA, protein synthesis, lipid metabolism, mitosis, photosynthesis, and seed germination (Niu *et al.*, 2013; Ghonaim *et al.*, 2021). Salinity affects plants by limiting their ability to absorb water through oxidative stress, osmotic stress, ion toxicity (Balasubramaniam *et al.*, 2023; Nikolić *et al.*, 2023), and dehydration of plant cells (Hasegawa *et al.*, 2000). These negative phenomena affect fruit's physical and quality parameters, including its length, mean weight, and diameter, as well as its diameter/length ratio, dry/fresh weight ratio, number of fruits per plant, and eventually its overall production (Denaxa *et al.*, 2022).

Strawberry (*Fragaria ananassa* Duch.) is one of the most commonly consumed fruits worldwide because of its taste and nutritional value, which are attributed to the existence of potentially beneficial elements like phenolic compounds

(Giampieri *et al.*, 2012). However, the plants are categorized as salt sensitive (Crizel *et al.*, 2020; D'anna *et al.*, 2003). Their optimum electric conductivity ranges from 1 to 1.5 dS; values above this cause adverse effects on metabolism (D'anna *et al.*, 2003). It has been demonstrated that salinity causes strawberry plants to produce a smaller number of fruits by reducing the size and number of leaves, the shoot weight and number of branch crowns (Pirlak and Esitken, 2004). Therefore, in order to lessen the negative effects of salt stress and ensure optimal strawberry production in saline conditions, new, sustainable, and innovative strategies must be put into place.

The best approach to handle the global food security issue in the current climate change paradigm seems to be developing new crop varieties with enhanced abiotic stress tolerance through conventional breeding, genetic engineering or genome editing (Fita *et al.*, 2015). However, other tactics, including the use of biostimulants, can aid in improving our current crop varieties' tolerance and lessen the effect of climate change. A wide range of chemicals and microorganisms known as agricultural biostimulants can be applied to plants to enhance crop quality traits, nutritional efficiency, and tolerance to abiotic stress (Van Oosten *et al.*, 2017). Although biostimulants are not nutrients themselves, they help in nutrient uptake or contribute positively to growth promotion or stress tolerance (Brown and Saa, 2015). The goal of this study was to assess two biostimulants, Glycine Betaine (GB) and Seaweed (SWE), on strawberry plants cultivated under salt stress conditions. Numerous studies have demonstrated the positive effects of GB (Türkan and Demiral, 2009; Mansour and Ali, 2017) and seaweed (Weber *et al.*, 2018) on the survival and growth of various plants growing under saline conditions. For plant stress protection, GB has been reported as one of the most attractive biostimulants due to its natural synthesis, low cost, and non-toxicity (Dutta *et al.*, 2018). Additionally, according to literature, this compound can function as an osmoprotectant, maintaining cellular osmolarity, protecting thylakoid membranes and photosynthetic machinery (photosystem II), reducing oxidative damage to cells, and stabilizing protein structures (Dutta *et al.*, 2018; Wani *et al.*, 2013). Furthermore, GB application in saline condition has been shown to alter the transit and accumulation of Na^+ and K^+, lowering the Na^+/ K^+ ratio in the process (Mansour and Ali, 2017).

Several seaweed species (macroalgae) have been utilized in their raw form for crop production since ancient times due to their growth-promoting properties. These marine organisms are widely used in horticultural crops because they exhibit positive effects on fresh products' flowering, yield and nutritional value (Battacharyya *et al.*, 2015) while also enhancing plants' ability to withstand the biotic and abiotic challenges (Parađiković *et al.*, 2019). They are widely employed as plant biostimulants because they possess bioactive substances such as proteins, phytohormones, phenolic compounds, polysaccharides, pigments, and a variety of micro and macronutrients (Hariharan *et al.*, 2024). In treated plants, SWE also raises the endogenous concentrations of salt-related chemicals, such as cytokinins, proline, and antioxidants (Fan *et al.*, 2013).

It is essential to use cultural methods to reduce the detrimental effects of salinity on strawberry plants in a sustainable way. Since salt contributes to a large number of physiological and biochemical problems in plants, the current study sought to evaluate the impact of GB and SWE on the physiological and morphological characteristics of strawberry plants. To the best of our knowledge, the effects of combination of GB and SWE on strawberry plant growth, nutrition, and fruit quality assessed here for the first time against salt stress.

MATERIALS AND METHODS

Plant materials, growing conditions and treatments

The present study was carried out under a netting house where the average temperature was 23±2°C in daytime and 13±2°C at night, with a relative humidity of 65 to 70%, and approximately 11 h local natural photoperiod with no artificial lighting (Sher-e-Bangla Agricultural University Horticulture farm, Dhaka, Bangladesh; 23.7714º N, 90.3754º E, altitude 9 m). Strawberry Festival, as a short-day vigorous cultivar, with an apparent lesser susceptibility to powdery mildew (caused by *Sphaerotheca macularis*) and to botrytis fruit rot (caused by *Botrytis cinerea*) compared to other varieties, have been selected for this experiment (Chandler *et al.*, 2000). Strawberry plantlets were obtained from the commercial nursery at Agargaon in Dhaka. Thirty (30) days old healthy and well-established plantlets were transplanted in 12 L plastic pot following addition of the recommended dose of urea, compost, muriate of potash, triple super phosphate, and boron (BARI, 2021). The GB and SWE was applied three times (14, 28, and 35 d after transplanting) on the foliage of plants at the concentrations of 60 mM and 8 ml/L respectively. The sets of plants were exposed to salt stress by irrigating 8 dS/m EC NaCl solutions at 20 d after germination which lasted for 21 days, and the control plants were irrigated only with water. Regular application of saline or normal water was made when the soil moisture content was less than 10%. The experiment comprised of 7 different treatments viz., T_0= Control (only water), T_1= Salt (8 dS/m EC), T_2= Glycine Betaine (60 mM) + No salt, T_3= Seaweed extract (8 ml/L) + No salt, T_4= Salt (8 dS/m EC) + Glycine Betaine (60 mM), T_5= Salt (8 dS/m EC) + Seaweed extract (8 ml/L), T_6= Salt (8 dS/m EC) + Glycine Betaine (60 mM) + Seaweed extract (8 ml/L). The experiment was laid out in a one factor completely randomized design (CRD) having three replications thus comprising 63 pots to which the treatment was assigned randomly. Each pot contains one strawberry plant. every important cultural practice and plant protection procedures were observed in each pot during the experiment. In each replication, growth, yield and physicochemical parameters were assessed on randomly selected plants.

Dry matter content of fruit (%)

After harvesting, a randomly selected 100 g fruit sample was sliced into very thin pieces, placed into an envelope, and put in an oven maintained at 80°C for 72 hours. The sample was then transferred into a desiccator and allowed to cool to room temperature. The final weight of the sample was recorded. The dry matter content was computed using the following formula:

$$Dry\ matter\ content\ (\%) = \frac{Dry\ weight\ of\ fruit\ (g)\ \times\ 100}{Fresh\ weight\ of\ fruit\ (g)}$$

Chlorophyll content (SPAD value)

Leaf chlorophyll content was measured using SPAD-502 chlorophyll meter in the first fully expanded leaves (Minolta, Tokyo, Japan). For both treated and control plants, measurements were taken from the middle of the leaf lamina.

Relative water content (RWC)

The relative water content (RWC) was measured from each replication. Leaves were weighed to obtain the fresh weight. Then, the leaves were floated in water under light until the weight remained constant to attain full turgidity, after which the turgid weight was recorded. The leaves were then kept in a hot air oven at 80°C for 48 hours and the dry weight was recorded. Finally, the leaf RWC was calculated using the formula below:

$$RWC\ \% = \frac{(FW - DW) \times 100}{(TW - FW)}$$

Vitamin-C content (mg/100g FW)

The vitamin C content was determined according to the method of AOAC International (2005) with some modification using 2,6-Dichlorophenol indophenol (DCPIP), sodium bicarbonate, a 5% oxalic acid solution, and a standard L-ascorbic acid solution. The 5% oxalic acid solution was prepared by dissolving 50 g of oxalic acid powder in 1000 ml of distilled water. For the standard L-ascorbic acid solution, 10 mg of L-ascorbic acid was dissolved in 100 ml of the 5% oxalic acid solution. Subsequently, 10 ml of this solution was combined with 90 ml of the 5% oxalic acid solution in a volumetric flask to create the standard ascorbic acid Vit C solution. The dye solution was prepared by dissolving 260 mg of the sodium salt of 2,6-dichlorophenol indophenol in approximately 1000 ml of hot distilled water containing 210 mg of sodium carbonate.

Additionally, a 5% oxalic acid solution was prepared by dissolving 5g of oxalic acid in 100 ml of water. The standard L-ascorbic acid solution was prepared by taking 100 mg of L-ascorbic acid in a conical flask and adding 1 L of oxalic acid to it. Subsequently, 5 ml of the standard L-ascorbic acid solution was transferred to a 100 ml volumetric flask and topped up to 100 ml using oxalic acid. For the titration process, 5% of this solution was utilized.

The preparation of the Strawberry solution involved weighing the Strawberry, blending it without adding any water, filtering it, and transferring it to a 100 ml volumetric flask which was then filled up to 100 ml using oxalic acid. During the titration process, 5 ml of the standard L-ascorbic acid solution was placed in a conical flask, and the dye solution was added to a burette. The content of the conical flask was titrated with the dye until the endpoint was reached, indicated by a color change from pink to blue. The volume of dye solution required to complete the titration was then recorded. L-ascorbic acid in solution calculated from

$$Unknown\ solution = \frac{0.5 \times y \times 100}{x \times 5}$$

x = Amount of dye for standard L-ascorbic

y = Amount of dye for Strawberry solution

DPPH (2.2 Diphenyl-1-picrylhydrazyl) radical scavenging activity

DPPH free radical scavenging activity of the methanol extracts of the leaf sample of strawberry fruit were analysed according to the method suggested by the Sanchez-Moreno *et al.,* (1998). Three grams (3 g) of fresh sample was taken and homogenized with 25 ml methanol (99.8%) The sample was then centrifuged at 4000 rpm for 30 minutes and kept it at 4°C for 12 hours, aliquot of the plant extract (0.1 ml) was added to 3.9 ml of DPPH solution containing 0025 g/L in methanol. Samples absorbance was measured at 515 nm by UV-spectrophotometer after 30 minutes of incubation in darkness. Violet colour of the DPPH solution disappears in the presence of antioxidants, as a result of free radical scavenging in the measured medium. The standard curve for this assay was also constructed using Trolox (Sigma-Aldrich, Steinhen, Germany) in the concentration ranging from (0 to 0.330) mM. The dilution of the Troloxution was made by using PBS (phosphate buffer saline) solution whose pH value was 7.4. Each sample and standard concentration had triplicate analysis. The antioxidant activity was reported in µmoles of Trolox equivalents per gram fresh sample (µmol TE-g fw).

Electrolyte leakage (%)

Electrolyte leakage (EL) was used to assess membrane permeability. Leaf samples were taken and cut into 1 cm^2 segments. EL was measured using an Electrolyte Conductivity Meter (EC). The samples were placed into a container with 10 ml of distilled water and washed three times to avoid contamination. They were then incubated on a shaker at 100 rpm at room temperature for 24 hours. The EC of the bathing solution (EC_1) was recorded after incubation. Next, the samples were placed in an autoclave at 120°C for 20 minutes, and a second reading (EC_2) was taken after cooling the solution to room temperature. Electrolyte leakage was calculated using the following formula:

$$Electrolyte\ Leakage\ (EL\ \%) = \frac{EC_1}{EC_2}$$

Total soluble solids (%)

The TSS content of strawberries was measured by a hand refractometer. A drop of strawberry juice was obtained by dropper and placed on the refractometer prism. The refractometer showed a reading of total soluble solids.

Data analysis

The data collected underwent statistical analysis through the utilization of the Statistics 10 (IBM Corp, Armonk, NY, USA) computer package program. The mean values for each treatment were computed, and an analysis of variance was conducted for each character using the F-test (Variance Ratio). The disparity between treatments was evaluated using the Least Significant Difference (LSD) test at a significance level of 5% (Gomez and Gomez, 1984). The graphs were made with the Microsoft Excel program.

RESULTS

Plant height

The treatments had a significant effect on the plant height of strawberry plants under salinity stress at various days after treatment (DAT) (Figure 1). The results showed clear trends

in the effectiveness of different treatments in promoting plant height over time. At 15 DAT, the lowest plant height was observed in the treatment with only salt (T_1), with a height of 5.68 cm. This was followed by the combined treatment of salt and SWE (T_5) at 6.82 cm and the treatments with salt and Glycine Betaine (T_4) at 6.97 cm, respectively. The highest plant height at 15 DAT was achieved with the combined treatment of salt, GB, and SWE (T_6), with a height of 8.25 cm which was statistically at par with T_2 (7.67 cm) and T_3 (7.54 cm).

Similarly, at 30 DAT, the lowest plant height was again observed in the treatment with only salt (T_1) at 9.03 cm, statistically similar with the treatments of salt and SWE (T_5) at 10.12 cm and salt and Glycine Betaine (T_4) at 10.45 cm. The control treatment (T_0) had an intermediate value of 11.37 cm. The treatments with SWE alone (T_3) and Glycine Betaine alone (T_2) resulted in plant heights of 11.86 cm and 12.05 cm, respectively. The highest plant height at 30 DAT was observed in the combined treatment of salt, GB and SWE (T_6), with a height of 13.02 cm. Similar trends of plant height were also observed in 45, 60 and 75 DAT, where tallest plants were found from T_6 treatment and T_1 produced the shortest plant.

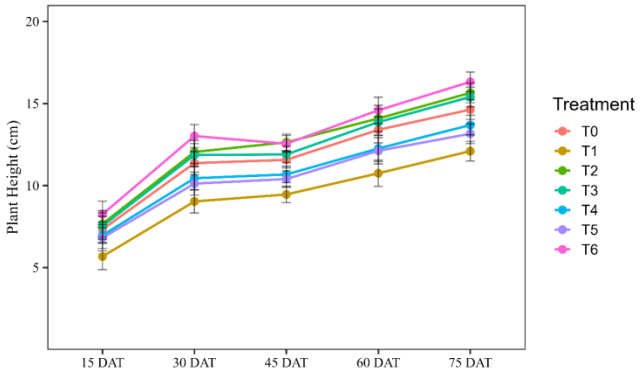

Figure 1: Effect of Glycine Betaine and Seaweed extract on plant height of strawberry under salinity stress. [Here, T_0= Control, T_1= Salt (8 dS/m EC), T_2= Glycine Betaine (60 mM) + No salt, T_3= Seaweed extract (8 ml/L) + No salt, T_4= Salt (8 dS/m EC) + Glycine Betaine (60 mM), T_5= Salt (8 dS/m EC) + Seaweed extract (8 ml/L), T_6= Salt (8 dS/m EC) + Glycine Betaine (60 mM) + Seaweed extract (8 ml/L)]

Foliage coverage

The treatments had a significant effect on the foliage coverage of strawberry plants under salinity stress from 30 DAT onwards (Table 1). The results illustrated clear trends in the effectiveness of different treatments in enhancing foliage coverage over time. At 15 DAT, the lowest foliage coverage was observed in the treatment with only salt (T_1), which resulted in a value of 11.14 cm which was followed by the combined treatment of salt and SWE (T_5) at 13.56 cm, and the treatment with salt and Glycine Betaine (T_4) at 14.23 cm. The highest foliage coverage at 15 DAT was achieved with the combined treatment of salt, Glycine Betaine, and SWE (T_6), with a coverage of 18.29 cm which was statistically similar with the treatment containing only GB (T_2) and only SWE (T_3) of 17.32 cm and 16.84 cm, respectively. Similarly, at 30, 45, 60 and 75 DAT, the highest foliage coverage of 18.90 cm, 18.57 cm, 22.11 cm and 22.20 cm, respectively were recorded from T_6 treatment combination and the lowest foliage coverage 12.19 cm, 12.39, 14.31 and 15.41 cm at the same DAT, respectively were found from T_1 treatment. Overall, the trend in foliage coverage among the treatments can be summarized as $T_6 > T_2 > T_3 > T_0 > T_4 > T_5 > T_1$.

Table 1: Effect of Glycine Betaine and Seaweed extract on foliage coverage of strawberry under salinity stress

Treatments	Foliage coverage (cm) at				
	15 DAT	30 DAT	45 DAT	60 DAT	75 DAT
T_0	16.27 b	16.38 bcd	16.97 bcd	18.05 c	18.11 c
T_1	11.14 d	12.19 e	12.39 e	14.31 e	15.41 d
T_2	17.13 ab	17.32 ab	18.00 ab	20.01 b	20.08 b
T_3	16.84 abc	16.94 b	17.75 abc	19.57 bc	19.73 bc
T_4	14.23 c	15.24 d	15.35 d	15.54 cde	16.38 bcd
T_5	13.56 c	14.73 d	14.82 d	15.13 de	16.29 cd
T_6	18.29 a	18.90 a	18.57 a	22.11 a	22.20 a
LSD (0.05)	1.63	1.60	1.61	1.68	1.67
Level of sig.	*	**	**	**	**
CV%	5.76	5.53	5.97	5.50	5.44

[In a column means having similar letter (s) are statistically similar and those having dissimilar letter (s) differ significantly as per 0.05 level of probability. [Here, T_0= Control, T_1= Salt (8 dS/m EC), T_2= Glycine Betaine (60 mM) + No salt, T_3= Seaweed extract (8 ml/L) + No salt, T_4= Salt (8 dS/m EC) + Glycine Betaine (60 mM), T_5= Salt (8 dS/m EC) + Seaweed extract (8 ml/L), T_6= Salt (8 dS/m EC) + Glycine Betaine (60 mM) + Seaweed extract (8 ml/L); **: Significant at 0.01 level of significance; *: Significant at 0.05 level of significance. LSD= Least Significant Difference; CV= Coefficient of Variation]

Days to flower initiation

The experiment evaluated the effect of GB and SWE on the days to flower initiation in strawberries under salinity stress. The results demonstrated that the days to flower initiation varied significantly across treatments (Table 2). Treatment T_1 (Salt, 8 dS/m EC) had the longest days to flower initiation, with an average of 51.43 days, which was significantly higher than all other treatments and statistically different from all other treatments. In contrast, the shortest days to flower initiation were observed in treatment T_6 (Salt, 8 dS/m EC + Glycine Betaine, 60 mM + Seaweed extract, 8 ml/L), with an average of 38.59 days. This was followed by T_2 (Glycine Betaine, 60 mM + No salt) at 42.85 days, and T_3 (Seaweed extract, 8 ml/L + No salt) at 44.83 days. The control treatment T_0 recorded 45.38 days, while T_4 (Salt, 8 dS/m EC + Glycine Betaine, 60 mM) and T_5 (Salt, 8 dS/m EC + Seaweed extract, 8 ml/L) recorded 46.08 and 47.50 days, respectively. The trend observed in the treatments based on days to flower initiation was $T_6 < T_2 < T_3 < T_0 < T_4 < T_5 < T_1$.

Table 2: Effect of Glycine Betaine and Seaweed extract on different growth parameters of strawberry under salinity stress

Treatments	Days to flower initiation	No. of flowers plant^{-1}	No. of fruits plant^{-1}	Fruit setting (%)	Individual fruit weight (g)	Total fruit weight plant^{-1} (g)
T_0	45.38 cd	27.89 d	23.33 c	83.64 bc	10.62 cd	247.99 c
T_1	51.43 a	17.16 f	4.37 f	25.38 f	9.20 e	40.53 f
T_2	42.85 e	39.03 b	32.67 b	83.70 bc	11.78 ab	384.85 b
T_3	44.83 d	37.93 c	31.58 b	83.26 bc	11.12 bc	351.17 b
T_4	46.08 c	27.41 de	19.30 d	70.38 d	10.31 d	198.75 d
T_5	47.50 b	26.48 e	15.40 e	58.14 e	9.50 e	146.03 e
T_6	38.59 f	40.48 a	36.48 a	90.11 a	12.20 a	445.30 a
LSD $_{(0.05)}$	0.96	0.94	1.45	4.04	0.70	21.79
Level of sig.	**	**	**	**	**	**
CV%	1.21	1.73	3.56	3.27	3.73	4.80

[In a column means having similar letter (s) are statistically similar and those having dissimilar letter (s) differ significantly as per 0.05 level of probability. [Here, T_0= Control, T_1= Salt (8 dS/m EC), T_2= Glycine Betaine (60 mM) + No salt, T_3= Seaweed extract (8 ml/L) + No salt, T_4= Salt (8 dS/m EC) + Glycine Betaine (60 mM), T_5= Salt (8 dS/m EC) + Seaweed extract (8 ml/L), T_6= Salt (8 dS/m EC) + Glycine Betaine (60 mM) + Seaweed extract (8 ml/L); **: Significant at 0.01 level of significance; *: Significant at 0.05 level of significance**.** LSD= Least Significant Difference; CV= Coefficient of Variation]

Number of flowers plant^{-1}

The treatments had a significant effect on the number of flowers plant^{-1} of strawberries (Table 2). Treatment T_6 (Salt, 8 dS/m EC + Glycine Betaine, 60 mM + Seaweed extract, 8 ml/L) produced the highest number of flowers plant^{-1}, with an average of 40.48 flowers. This was followed by T_2 (Glycine Betaine, 60 mM + No salt) with 39.03 flowers, and T_3 (Seaweed extract, 8 ml/L + No salt) with 37.93 flowers. The control treatment T_0 recorded 27.89 flowers, while T_4 (Salt, 8 dS/m EC + Glycine Betaine, 60 mM) and T_5 (Salt, 8 dS/m EC + Seaweed extract, 8 ml/L) recorded 27.41 and 26.48 flowers, respectively. Treatment T_1 (Salt, 8 dS/m EC) had the lowest number of flowers plant^{-1}, with an average of 17.16 flowers.

Number of fruits per plant

The number of fruits produced by every plant of strawberry was significantly affected by the various treatments (Table 2). This finding suggests that both salinity stress and the introduced compounds (GB and SWE) influenced fruit production. Treatment T_6 (Salt, 8 dS/m EC + Glycine Betaine, 60 mM + SWE, 8 ml/L) produced the highest number of fruits plant^{-1} (36.48). This was closely followed by T_2 (32.67 fruits plant^{-1}) and T_3 (31.58 fruits plant^{-1}). The control treatment T_0 yielded 23.33 fruits per plant, whereas T_4 and T_5 recorded 19.30 and 15.40 fruits, respectively. Treatment T_1 (Salt, 8 dS/m EC) resulted in the lowest number of fruits plant^{-1} (4.37).

Fruit setting (%)

The percent fruit setting of strawberry was significantly affected by the various treatments (Table 2). This finding suggests that both salinity stress and the introduced compounds (GB and SWE) influenced the fruit setting of strawberries. The results revealed that the treatment combining salt, glycine betaine, and Seaweed extract (T_6) achieved the highest fruit setting percentage at 90.11%, making it the most effective treatment. This was followed by GB treatment without salt (T_2) achieved an 83.70% fruit setting, placing it next in effectiveness. The SWE treatment without salt (T_3) and the control treatment (T_0), which resulted in an 83.26% and 83.64% fruit setting, respectively. The treatment (T_4) resulted in a 70.38% fruit setting, followed by the treatment (T_5), which had a 58.14% fruit setting. The salt-exclusive treatment (T_1) had the poorest result, with only a 25.38% fruit setting.

Individual fruit weight

The individual fruit weight of strawberry was significantly affected by the various treatments (Table 2). Here, we saw the interplay between salinity stress and the introduced compounds (GB and SWE). Plants exposed to salt stress (T_1) produced the lightest fruits (9.20 g), followed by those with salinity stress and SWE (9.50 g) and salinity stress with GB (10.31 g). These results point to the detrimental effect of salinity on strawberry fruit weight. Conversely, the heaviest fruits were observed in plants receiving the combination of GB and SWE under salinity stress (T_6) (12.20 g). This was followed by those with just glycine betaine (T_2) (11.78 g), Seaweed extract (T_3) (11.12 g) and the control group (T_0) (10.62 g).

Total fruit weight per plant

The total fruit weight per plant was significantly affected by the various treatments. This finding indicated that both salinity stress and the introduced compounds (GB and SWE) influenced overall fruit yield (Figure 2). Plants exposed to the treatment with only salt (T_1) produced the lowest total fruit weight plant^{-1} (40.53 g), highlighting the detrimental effect of salinity on strawberry production. Similarly, the addition of either glycine betaine (T_4) (198.75 g) or Seaweed extract (T_5) (146.03 g) to salinity stress resulted in only a moderate increase in total fruit weight compared to T_1. This suggests that while these compounds may offer some protection against the negative effects of salinity on individual fruit weight (as seen in Table 1), their impact on total yield under salinity stress may be limited. The greatest total fruit weight plant^{-1} under salinity stress conditions was observed in plants receiving the combination of both Seaweed extract and glycine betaine (T_6) (445.30 g), demonstrating 998% greater fruit weight per plant compared to salt-stressed plant (T_1) and was significantly higher (80%) than the control group (T_0) (247.99 g) though it's important to note the absence of salinity stress in the control group. However, treatment T_2 (GB without salinity stress) also yielded a substantial fruit weight plant^{-1} (384.85 g), suggesting a benefit of GB application for yield improvement even under normal conditions.

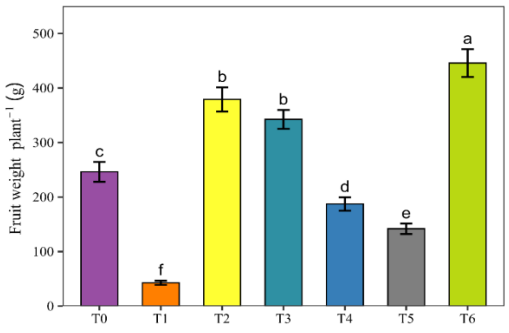

Figure 2: Effect of Glycine Betaine and Seaweed extract on fruit weight of strawberry under salinity stress. [Here, T_0= Control, T_1= Salt (8 dS/m EC), T_2= Glycine Betaine (60 mM) + No salt, T_3= Seaweed extract (8 ml/L) + No salt, T_4= Salt (8 dS/m EC) + Glycine Betaine (60 mM), T_5= Salt (8 dS/m EC) + Seaweed extract (8 ml/L), T_6= Salt (8 dS/m EC) + Glycine Betaine (60 mM) + Seaweed extract (8 ml/L)]

Dry matter content of fruit (%)

The dry matter content of strawberry fruit was significantly affected by the various treatments (Figure 3A). Treatment containing only salt (T_1) resulted in the lowest dry matter content (5.21%), indicating a dilution effect caused by increased water uptake in response to stress. This aligns with the observed decrease in individual fruit weight under salinity stress (Table 3). Interestingly, the addition of either glycine betaine (T_4) or Seaweed extract (T_5) under salinity stress did not significantly improve dry matter content compared to T_1. The most notable result was the significant increase in dry matter content observed in plants receiving the combination of both SWE and GB under salinity stress (T_6) (8.13%). This value was considerably higher than the control group (T_0) (6.81%) and suggests a potential benefit of this treatment for maintaining fruit quality under salinity stress. While individual GB application (T_2) (7.64%) also increased dry matter content compared to the control, the combination with SWE under salinity stress (T_6) appears to have a synergistic effect.

Chlorophyll content

The analysis of chlorophyll content revealed a significant influence of the various treatments (Figure 3B). Plants exposed to only salt (T_1) exhibited the lowest chlorophyll content (SPAD value of 38.73). This finding aligns with the detrimental effect of salinity on chlorophyll production or its degradation within the leaves. Salinity stress might disrupt nutrient uptake, induce oxidative stress, or hinder enzyme activity related to chlorophyll synthesis. But the most favorable outcome for chlorophyll content under salinity stress emerged with the combined application of glycine betaine and Seaweed extract (T_6; SPAD value of 55.61). This value was significantly higher compared to all other salinity stress treatments (T_4 & T_5) and the control group (T_0). This finding suggests a potential synergistic effect between GB and SWE in mitigating the negative effects of salinity on chlorophyll content and photosynthetic function. While not the absolute highest, the application of glycine betaine without salinity stress (T_2) (SPAD value of 52.95) resulted in a higher chlorophyll content compared to the control group (T_0).

Relative water content

Statistical analysis of relative water content (RWC) revealed a significant impact of the treatments. Only salt treatment (T_1) led to the lowest RWC (64.73%), highlighting its detrimental effect on water retention. Interestingly, several treatments mitigated this stress (Figure 3C). The most successful strategy (T_6) involved the combined application of GB and SWE under salinity stress, resulting in the highest RWC (90.65%). Notably, both glycine betaine (T_2) and Seaweed extract (T_3) individually improved RWC compared to the control group even under non-salinity conditions. These findings suggest a trend: salinity stress reduced RWC (T_1), while glycine betaine (T_2) and Seaweed extract (T_3) improved it even without stress. Furthermore, the combined treatment (T_6) displayed a synergistic effect, exhibiting the highest RWC under salinity stress.

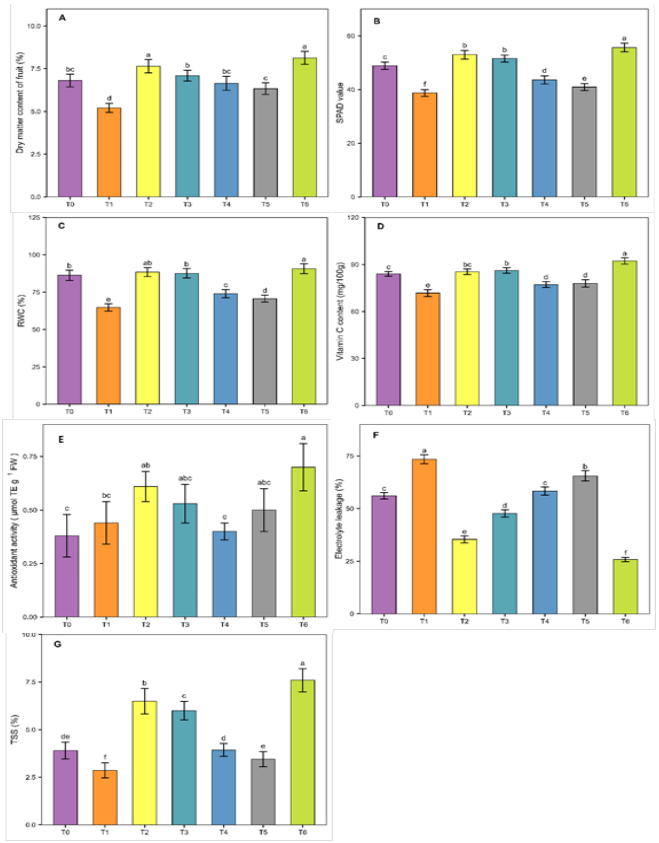

Figure 3: Effect of Glycine Betaine and Seaweed extract on different quality parameters of strawberry under salinity stress. A. Dry matter content of fruit; B. SPAD value; C. Relative water content; D. Vitamin C content; E. Determination of antioxidant activity; F. Electrolyte leakage; G. Total soluble solid; [Here, T_0= Control, T_1= Salt (8 dS/m EC), T_2= Glycine Betaine (60 mM) + No salt, T_3= Seaweed extract (8 ml/L) + No salt, T_4= Salt (8 dS/m EC) + Glycine Betaine (60 mM), T_5= Salt (8 dS/m EC) + Seaweed extract (8 ml/L), T_6= Salt (8 dS/m EC) + Glycine Betaine (60 mM) + Seaweed extract (8 ml/L)]

Vitamin C content

The treatments had a significant effect on the vitamin C content of strawberry fruit under salinity stress (Figure 3D). The lowest result was observed with the salt only treatment (T_1), which resulted in a vitamin C content of 71.77 mg/100 g. This was followed by the combined treatments of salt and Glycine Betaine (T_4) and salt and Seaweed extract (T_5),

which produced vitamin C contents of 77.21 mg/100 g and 77.92 mg/100 g, respectively. These treatments, although better than the salt-exclusive treatment, still showed reduced vitamin C levels compared to the control. On the other hand, the highest result was achieved with the combined treatment of salt, Glycine Betaine, and Seaweed extract (T_6), which significantly increased the vitamin C content to 92.24 mg/100 g. This was followed by the individual treatment with Seaweed extract (T_3) at 86.21 mg/100 g and GB (T_2) at 85.35 mg/100 g. The control treatment (T_0) resulted in a vitamin C content of 83.97 mg/100 g, which was higher than the treatments involving salt but lower than the best-performing treatments.

DPPH radical scavenging activity/Antioxidant activity

The treatments had a significant effect on the DPPH radical scavenging activity (antioxidant activity) of strawberry fruit under salinity stress (Figure 3E). The lowest result was observed in the control treatment (T_0), which had a DPPH radical scavenging activity of 0.38 µmol TE/gFW. This was followed by the combined treatment of salt and Glycine Betaine (T_4) at 0.40 µmol TE/gFW. The salt-exclusive treatment (T_1) showed a slight increase in antioxidant activity, with a value of 0.44 µmol TE/gFW. In contrast, the highest result was achieved with the combined treatment of salt, GB and SWE (T_6), which significantly increased the DPPH radical scavenging activity to 0.70 µmol TE/gFW, 59% greater than salt treatment (T_1). The synergistic result was statistically identical with the individual treatment of GB (T_2) at 0.61 µmol TE/gFW, Seaweed extract (T_3) at 0.53 µmol TE/gFW and the treatment with salt and Seaweed extract (T_5) at 0.50 µmol TE/gFW, respectively.

Electrolyte leakage (%)

The treatments had a significant effect on the electrolyte leakage of strawberry fruit under salinity stress (Figure 3F). The highest electrolyte leakage was observed in the only salt treatment (T_1), which had a value of 73.43% which was statistically different from all other treatments and followed by the combined treatment of salt and SWE (T_5) at 65.51%. The treatment with salt and GB (T_4) also showed a relatively high electrolyte leakage of 58.26%, indicating the detrimental effects of these treatments in cell membrane damage under salinity stress. Conversely, the lowest electrolyte leakage was observed in the combined treatment of salt, GB and SWE (T_6), which resulted in a value of 25.18%. This was followed by the treatment with only GB (T_2) at 35.37%. The treatment with only SWE (T_3) and the control treatment (T_0) showed intermediate values of 47.71% and 56.07%, respectively. The trend in electrolyte leakage among the treatments can be summarized as $T_6 < T_2 < T_3 < T_0 < T_4 < T_5 < T_1$.

Total Soluble Solids (TSS %)

The treatments had a significant effect on the total soluble solids (TSS) content of strawberry fruit under salinity stress (Figure 3G). The results demonstrated a clear trend in the effectiveness of the different treatments in enhancing the TSS content of strawberries. The lowest TSS content was observed in the salt treatment (T_1), which resulted in a value of 2.86%. This was followed by the combined treatment of salt and SWE (T_5) with a TSS content of 3.45%. The control treatment (T_0) and the combined treatment of salt and GB (T_4) showed intermediate values of 3.90% and 3.93%, respectively. In contrast, the highest TSS content was achieved with the combined treatment of salt, GB and SWE (T_6), which significantly increased the TSS content to 7.60%. This was followed by the treatment containing only GB (T_2) at 6.49% and the treatment containing only SWE (T_3) at 6.00%. The trend in the TSS content among the treatments can be summarized as $T_6 > T_2 > T_3 > T_4 > T_0 > T_5 > T_1$.

DISCUSSION

Salinity dramatically slowed the strawberry plant growth, as seen by the decrease in leaflet area and above-ground plant mass (AGPM) area. Many researchers have observed similar results for several cultivars (Zahedi *et al.*, 2019; Garriga *et al.*, 2017; Ghaderi *et al.*, 2018; Estaji *et al.*, 2019; Roshdy *et al.*, 2021). Some researchers (Garriga *et al.*, 2017; Ghaderi *et al.*, 2018) claim that salinity slows down the development of leaves, causes deficiencies in nutrients such as N, P, and K, and also causes a decrease in chlorophyll content decrease (Roshdy *et al.*, 2021), which accelerates leaf senescence and inducing toxicity symptoms in the older leaves. These symptoms all contribute to a decrease in photosynthetic activity, a low production of assimilates and a reduction in growth. Additionally, by lowering the osmotic potential of soil solution, salinity imposes osmotic stress and impedes the absorption of water needed for growth (Estaji *et al.*, 2019). According to Ghaderi *et al.* (2018), salinity only has an effect on the number of leaves rather than their leaf area. Leaf area was decreased significantly in the present study, demonstrating the intensity of the salt stress. It was not just plant growth that was affected by salinity. Both yield and yield parameters also affected, with the yield being considerably decreased by about 30%. Strawberries grown in saline conditions have already been shown to have lower yields in several studies (Zahedi *et al.*, 2019; Ferreira *et al.*, 2019), and this was attributed to the lower number of fruits (Zahedi *et al.*, 2019; Ferreira *et al.*, 2019) and/or lower fruit weight (Zahedi *et al.*, 2019).

A notable drop in the number of flower production, which reached almost 60%, or roughly the yield loss percentage observed in the present study, has been reported by Zahedi *et al.* (2020). Marketable fruits have also been found to decline as a result of salinity (Ferreira *et al.*, 2019), while under salt stress, fruit firmness did not change substantially, despite reports of opposite outcomes (Zahedi *et al.*, 2020). According to Garriga *et al.* (2017), the fruit's firmness was maintained because the levels of Na and Cl in the fruit were not high enough to alter pectinases and other enzyme activity that break down cell walls.

Individual GB application demonstrated the significant yield efficiency and moderately increased AGPM, which were indicative of its ameliorating activity. Similar results have been documented in other species as well (Mansour and Ali, 2017; Estaji *et al.*, 2019; Alasvandyari *et al.*, 2017), and they were ascribed to GB's impact on the maintenance of plant cell osmotic potential (Estaji *et al.*, 2019), improving relative water content and water use efficiency (Estaji *et al.*, 2019). In another experiment (Ntanos *et al.*, 2021), GB had similar effects on AGPM and root water content, increasing both although not much as compared to the control treatment.

It is evident from above tables that under salt stress, GB at both levels raised morphological parameters, SPAD value, and RWC. In this regard, Gorham (1995) showed that GB establishes the structure and function of enzymes and protein

complexes and protects membranes from the damaging effects of extremes in heat, cold, salt and freezing. Wyn Jones (1984) and Agboma *et al.* (1997) suggested that the GB's activity as a non-toxic cytoplasmic osmolyte during osmotic change is linked to its protective effect on Sorghum growth. Moreover, Bohnert and Jensen (1996) revealed that GB protects enzymes from denaturation by preferentially excluding inorganic ions such as sodium from the hydration sphere of proteins. On the other hand, Heuer (2003) pointed out that GB is a well-known compatible solute that contributes to the process of osmotic balance in many crops that have accumulated under abiotic stress. The primary role was likely to protect plant cells from the negative effects of salt by maintaining osmotic balance, stabilizing the structure of important proteins such as Rubisco, protecting the photosynthetic apparatus, and functioning as an oxygen free radical. GB application increased yield when compared to the Control, although it did not differ substantially from the salt combined treatment.

The obtained results from Figure 1 and Table 2, of vegetative growth characteristics are in agreement with those reported by Spinelli *et al.* (2010) and Abdel-Mawgoud *et al.* (2010) on watermelon, Fawzy *et al.* (2012) on garlic and Alam *et al.* (2013) on strawberry who found that SWE foliar spray also increased plant height, leaf area, number of leaves per plant, and fresh and dry weight of biomass of these crops. Research has also shown that applying SWE helps plants root growth and development (Crouch and Staden, 1992; Mancuso *et al.*, 2006; Thompson, 2004). Both endogenous auxins and other substances in the extracts may contribute to a better root system (Crouch *et al.*, 1992). Endogenous growth compounds and other substances in the extract may be responsible for the improved vegetative growth traits. These substances may affect the cellular metabolism of the treated plants, resulting in enhanced growth and crop yield. Additionally, SWEs improve nutrient uptake by roots (Crouch *et al.*, 1990), increasing the water and nutrient efficiency of root systems and, ultimately, the overall growth and vigor of plants.

In the present study, even SWE by itself was unable to effectively perform well against salt stress, as was also the case with GB alone. Surprisingly, the combination of GB and SWE in salt treated plant uplifted the parameters significantly, revealing a significant alleviation action, due to its osmoprotectant, anti-chlorophyllase, ion homeostasis, and potential antioxidant properties mentioned in the earlier studies (Mansour and Ali, 2017; Estaji *et al.*, 2019; Alasvandyari *et al.*, 2017).

CONCLUSION

Combined application of glycine betaine and seaweed extract significantly enhanced salt stress tolerance, outperforming individual treatments by enhancing vitamin C content, photosynthetic efficiency, antioxidant defense, and TSS content, while reducing oxidative damage, advocating as a promising biostimulant combination for commercial strawberry production in salinity-affected regions.

Conflict of interest

The authors declare that they have no conflicts of interest.

Ethics statement

This study was conducted in accordance with all relevant ethical guidelines and regulations.

Authors' contributions

M.H.K. designed and supervised the experiment, M.A.A.R. and M.S. conducted the research, F.T.Z and N.I analyzed the data and performed the statistical analysis, S.A., I.N.H. and M.S. wrote the original draft, M.A.A.R. and M.H.K. reviewed and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

Availability of data and materials

All data generated or analyzed during this study are included in this published article.

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