Discover Plants

Research

Intermittent salt application enhances total soluble solids of strawberries (*Fragaria* × *ananassa*) in hydroponics

Christopher Pascual[1,3] · Lirong Xiang[1] · Steven Hall[1] · Ricardo Hernandez[2]

Received: 19 February 2025 / Accepted: 16 April 2025
Published online: 28 April 2025
© The Author(s) 2025 OPEN

Abstract
Abiotic stress, such as salinity in irrigation water, impacts plant growth and yield, with severe stress potentially causing plant death. However, controlled stress can improve plant fortification. This study explored the effects of intermittent salt applications (43 and 77 mM for durations of 24 and 72 h) during the fruiting stage of strawberries in hydroponics (Kratky and substrate-based systems) to enhance total soluble solids (TSS). Alternating freshwater and 77 mM saltwater every 72 h in substrate-based systems resulted in the highest total soluble solids (TSS), reaching 13.28 °Brix (°Bx)—approximately 24% higher than the control (10.72 °Bx). However, this value was not statistically different from the other salt-stressed treatments within the same hydroponic system, with TSS values ranging from 10.85 to 12.98 °Bx. Yield and fruit weight were unaffected in either hydroponic technique. However, the plants applied for 72 h of 77 mM salinity under the Kratky method resulted in a significantly higher percentage of fruit deformities, with over 10%. In the substrate-based technique, the deformed fruits under the salt-treated plants were not significantly different from the control, with percentages ranging from 5.08 to 7.16%. These results indicate that the substrate-based hydroponic strawberries, irrigated intermittently with 43–77 mM saltwater every 24–72 h during fruiting, can enhance sugar content without negatively impacting yield and causing significant fruit deformities.

Keywords Abiotic stress · Food fortification · Saltwater use · Coastal agriculture · Controlled salt stress

1 Introduction

Strawberries (*Fragaria* × *ananassa*) are among the most widely cultivated and economically valuable fruit crops worldwide [1]. Strawberries are rich in nutrients and minerals, such as vitamin C, folate, and manganese, which support the immune system [2–4]. Additionally, strawberries contain dietary fiber, which promotes digestive health and regulates glucose levels, making them an excellent fruit for preventing diabetes [5–7]. These characteristics of strawberry fruit are just some of the many reasons for its popularity among consumers and researchers. However, abiotic stressors, including drought, salinity, and temperature fluctuations, are increasingly challenging strawberry production, adversely impacting plant growth, development, and fruit quality. Because of this, several studies focused on innovations, adaptation, and mitigation strategies to sustain production.

✉ Christopher Pascual, cspascua@ncsu.edu; Lirong Xiang, lxiang3@ncsu.edu; Steven Hall, shall5@ncsu.edu; Ricardo Hernandez, rhernan4@ncsu.edu | [1]Department of Biological and Agricultural Engineering, North Carolina State University, Campus Box 7621, Raleigh, NC 27695-7621, USA. [2]Department of Horticultural Science, North Carolina State University, Campus Box 7609, Raleigh, NC 27695-7609, USA. [3]Department of Agricultural and Biosystems Engineering, Central Luzon State University, 3120 Science City of Munoz, Nueva Ecija, Philippines.

The adoption of hydroponic systems and greenhouse cultivation for strawberries has increased to meet consumer demands for higher quality produce during off seasons [8–10]. In controlled greenhouse and hydroponic systems, precise regulation of the environment offers significant potential for improving crop production and nutritional quality [11]. Among the strategies gaining interest is using abiotic stresses, such as salinity, temperature, drought, light, and nutrient concentration, not only to understand plant responses but also to enhance the health benefits of crops [12]. While excessive and prolonged abiotic stresses affect plant growth and yield negatively, carefully controlled exposure to these stresses can improve certain nutritional attributes of plants, such as increased sugar content in fruits, enhanced levels of antioxidants, and higher concentrations of phytochemical compounds [12–17]. This approach represents a novel form of food fortification, where plants are subjected to specific conditions designed to boost their nutritional value, particularly in high-demand crops like strawberries. Several studies on salinity stress have been conducted on strawberries and were known to impact strawberries, particularly under soil-grown systems [18–20]. However, substantial information on its impact on hydroponic systems, especially during crucial phases like fruiting remains unexplored.

This study explores the impact of an intermittent salt application on the total soluble solids (TSS) of strawberries grown under two hydroponic techniques (Kratky and substrate-based systems) during the fruiting stage. Total soluble solids (TSS) represent the concentration of dissolved substances in a liquid, often expressed as Brix (°Bx) in fruits, where it primarily indicates sugar content and sweetness [21]. This approach aligns with the principles of aquaponics, where crops are grown in nutrient-loaded wastewater from aquaculture systems [22]. Marine aquaponics offers a sustainable solution for food production in coastal areas and regions affected by saltwater intrusion [23]. It presents an opportunity to utilize the saline environment to fortify crops like strawberries. By integrating aquaculture effluents rich in nutrients with controlled intermittent salt stress, growers can enhance the nutritional value of crops while promoting circular, resource-efficient agriculture.

2 Materials and methods

2.1 Site and duration of experiment

The experiment was conducted at D. S. Weaver Laboratory and Greenhouse, Department of Biological and Agricultural Engineering, North Carolina State University, Raleigh, North Carolina, USA. The stolons (daughter plants) were produced indoors, with temperatures ranging from 19 to 24 °C, relative humidity (RH) between 35 and 65%, and carbon dioxide (CO_2) levels ranging from 350 to 520 mg/L. These environmental parameters were measured directly above the plant canopy using an Arduino-based data logging instrument equipped with an Adafruit SCD-30 sensor that simultaneously reads and records temperature, RH, and CO_2. This custom-built instrument was calibrated using a standard CO_2 controller (DanoPlus) and a 3-in-1 thermometer-hygrometer (Neoteck) to ensure accurate CO_2 concentration, temperature, and relative humidity measurements. During the crop growth to the fruiting stage, the strawberries were transferred to the greenhouse with a temperature range between 10 and 34 ℃. The relative humidity inside the greenhouse fluctuated between 26 and 85%, while the CO_2 mainly relied on the atmospheric conditions, ranging between 400 and 610 mg/L. The same Arduino-based data logging instrument was used and installed in the middle of the greenhouse.

2.2 Experimental design

The strawberry plants were arranged in a completely randomized design with two factors: hydroponics techniques (two levels: A1—Kratky and A2—substrate-based) and intermittent saltwater applications (five levels). For A1 (Kratky technique), the salt applications were: (C1) control-no salt, (B1) 24-h alternate exposure to 43 mM saltwater and 24-h freshwater, (B2) 24-h alternate exposure to 77 mM saltwater and 24-h freshwater, (B3) 72-h alternate exposure to 43 mM saltwater and 72-h freshwater, and (B4) 72-h alternate exposure to 77 mM saltwater and 72-h freshwater. For the substrate-based technique, the salt applications were: (C2) control-normal irrigation every 24 h with no salt, (T1) alternate irrigation of 43 mM saltwater and freshwater every 24 h, (T2) alternate irrigation of 77 mM saltwater and freshwater every 24 h, (T3) alternate irrigation of 43 mM saltwater and freshwater every 72 h, and (T4) alternate irrigation of 77 mM saltwater and freshwater every 72 h. This study used a 4-L black plastic pot for the substrate-based system filled with a mixture of coco coir and perlite in a 70:30 ratio by volume. The Kratky system used a 5.7-L food-grade rectangular plastic box wrapped with black plastic to cover the nutrient solution from light exposure and avoid algae growth. The Kratky method is a passive hydroponic system where seedlings in net pots sit over a nutrient

solution. Initially, roots are partially submerged for nutrient uptake, and as the water level drops, they access oxygen, ensuring healthy growth [24]. A total of 30 setups were used with three replications per treatment.

2.3 Crop care, monitoring, and maintenance

Strawberry stolons were produced from a mother plant ('Albion') indoors from December 2023 to February 2024. Albion variety was chosen for its moderate salt stress tolerance [25]. Thirty vigorous and uniform strawberry stolons were selected, and fifteen were planted in two hydroponics setups (Kratky method and substrate-based). After 30 days indoors, the plants were transferred to a greenhouse until the end of the experiment in May 2024. The strawberry plants were nourished with a Masterblend strawberry formula (9-12-34 NPK, Masterblend International) mixed with calcium nitrate (15.5-0-0 NPK) and agricultural-grade Epsom salt (magnesium sulfate). The nutrient formulation and recommended mixing ratio were summarized in Table 1 based on manufacturers' data [26].

Mixing a 2.4 g of Masterblend, 2.4 g of calcium nitrate, and 1.5 g of Epsom salt make up an electrical conductivity (EC) of 2.0 mS/cm in 4 L of tap water. During the stolon productions, a lower EC was maintained (1.0–1.2 mS/cm) and increased to 1.5–2.0 mS/cm during the vegetative to the fruiting stage. The strawberry stolons were illuminated using 9–60W T8 LED lights (6FT, 8000LM, 6000K Cool White, V-Shape, Linkable T8 LED Ceiling Light Fixtures, SHOPLED). The LED lights were installed 8 cm apart and 20 cm from the topmost leaves of the plants. It maintained a 350 µmol m^{-2} s^{-1} light intensity for 18 h throughout the stolon production period. The stolons were clipped into a Rockwool growing substrate (3 × 3 × 2.5 in.—Grodan block) and remained there for 4 weeks before finally cutting off from the mother plant. It used a 3-inch net pot to hold the Rockwool in place. Spider mites were seen in the plants during indoor stolon production but were controlled using neem oil spray. Also, some spider mites still occurred when the plants were transferred to the greenhouse but were easily washed off by water spray with neem oil. A pH adjuster (pH Up and pH Down from General Hydroponics, Santa Rosa, CA, USA) was used to maintain a range between 5.6 and 6.8. The EC and pH were measured using a multi-parameter tester (ExStik EC500, EXTECH Instruments, Waltham, MA, USA). The strawberry plants were not applied with salt during the stolon production up to the growing stage. When the flower emerged, intermittent salt was applied according to the designed treatments. The water salinity was measured using PINPOINT Salinity Monitor (American Marine Inc., Ridgefield, CT, USA). For the 43 mM salinity treatment, 2.5 g of Instant Ocean salt (Blacksburg, VA, USA) was dissolved in 1 L of nutrient solution with an initial electrical conductivity (EC) of 2.0 mS/cm, resulting in a final EC of 5.9 mS/cm. For the 77 mM salinity treatment, 4.5 g of salt was added to 1 L of the same nutrient solution, increasing the final EC to 9.0 mS/cm.

Table 1 Nutrient composition of hydroponics fertilizer used in this study

Nutrient	Masterblend 4-18-38 (%)	Calcium nitrate ($Ca(NO_3)_2$) (%)	Magnesium sulfate ($MgSO_4$) (%)
Nitrate nitrogen	9.00	15.50	0.00
Available phosphate (P_2O_5)	12.00	0.00	0.00
Soluble potash (K_2O)	34.00	0.00	0.00
Calcium (Ca)	0.00	19.00	0.00
Water Soluble Magnesium (Mg)	0.50	0.00	9.80
Sulfur (S)	4.00	0.00	13.00
Chelated iron (Fe)	0.40	0.00	0.00
Boron (B)	0.08	0.00	0.00
Chelated zinc (Zn)	0.03	0.00	0.00
Chelated copper (Cu)	0.05	0.00	0.00
Molybdenum (Mo)	0.008	0.00	0.00
Mixing ratio in 4 L of water	2.4 g	2.4 g	1.5 g

https://www.masterblend.com/9-12-34-strawberry-formula/

2.4 Data collection

The total yield per plant and individual fruit weight were recorded. The fruits were sorted, and the deformed fruits, including those weighing less than 3 g, were separated. Three fruits from each replicate every harvest period were randomly selected for the TSS measurement using a handheld Brix meter (Atago 3810 PAL-1, COLE-PARMER). Weekly harvesting was done for four consecutive weeks, starting 28 days after the first emergence of flowers. Strawberries grown using two hydroponic techniques: (a) the Kratky method and (b) the substrate-based technique, are shown in Fig. 1.

2.5 Statistical analysis

Statistical analysis was performed to evaluate the effects of different treatment combinations on yield, total soluble solids (TSS), and the percentage of deformed fruits under two hydroponic systems. The dataset was first grouped according to hydroponic technique (Kratky and substrate-based), and a one-way analysis of variance (ANOVA) was conducted separately within each group to determine the significance of the applied salinity treatments. Post hoc comparison was performed using pairwise *t*-tests for each group at a significance level of $p < 0.05$. All statistical analyses and visualizations were conducted using R software, 2013 [27].

3 Results and discussion

3.1 Total soluble solids

Figure 2 presents the TSS of strawberries cultivated under two hydroponic techniques subjected to intermittent salt stress. Under the Kratky method (Fig. 2a), plants alternately exposed to 77 mM saltwater and freshwater every 72 h (A1B4) produced the highest TSS value at 10.91 °Bx (Table 2), which was significantly higher ($p < 0.001$) than all other Kratky treatments (Table 3). In contrast, the control (A1C1) and the treatment with 43 mM saltwater exposed every 24 h (A1B1) resulted in the lowest TSS values, ranging from 7.78 to 7.96 °Bx. Under the substrate-based technique (Fig. 2b), plants alternately irrigated with 77 mM saltwater every 72 h (A2T4) recorded the highest TSS value (13.28 °Bx), which was significantly higher than the control (A2C2; $p = 0.027$), but not significantly different from the other salt-treated plants (A2T1–A2T3).



Fig. 1 Strawberries grown under two hydroponics techniques: **a** Kratky method and **b** substrate-based technique

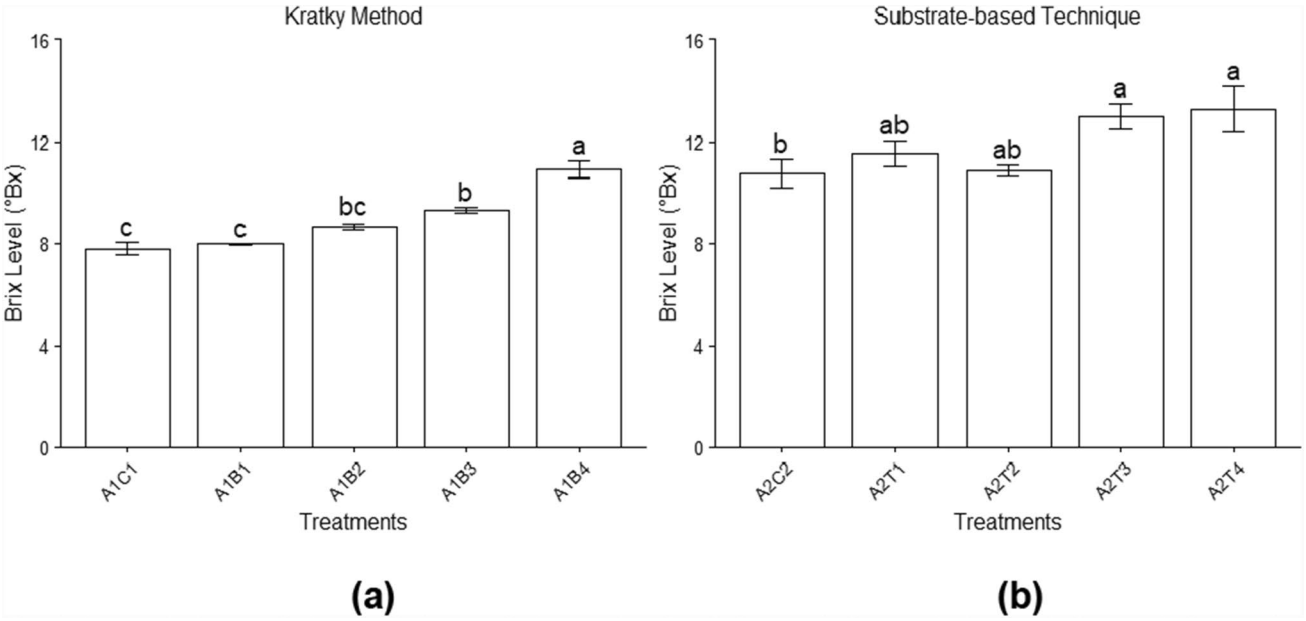


Fig. 2 Total soluble solids (°Bx) of strawberries under different salinity treatments in **a** Kratky method and **b** substrate-based hydroponic systems. Error bars represent standard error. Means indicated with the same letters on each plot were not significantly different at $p < 0.05$ using pairwise *t*-test

Table 2 Pairwise *t*-test analysis of the yield and fruit quality parameters (TSS, yield, fruit weight, and percentage deformed fruits) of the strawberries under two hydroponics techniques subjected to different salt stress treatments during the fruiting stage

Treatment	TSS, °Bx	Yield, g/plant	Fruit weight, g/fruit	Percentage deformed fruits, %
Kratky hydroponics				
A1C1	7.78^{c}	149.83^{a}	10.66^{a}	6.25^{c}
A1B1	7.96^{c}	137.53^{a}	10.44^{a}	7.49^{b}
A1B2	8.67^{bc}	133.29^{a}	11.11^{a}	9.53^{a}
A1B3	9.28^{b}	136.11^{a}	11.34^{a}	9.69^{a}
A1B4	10.91^{a}	126.84^{a}	10.57^{a}	10.17^{a}
Substrate-based hydroponics				
A2C2	10.72^{b}	160.14^{a}	11.65^{a}	5.08^{a}
A2T1	11.53^{ab}	160.07^{a}	13.34^{a}	5.80^{a}
A2T2	10.85^{ab}	152.51^{a}	12.71^{a}	5.61^{a}
A2T3	12.98^{a}	149.92^{a}	13.98^{a}	6.29^{a}
A2T4	13.28^{a}	142.62^{a}	11.89^{a}	7.16^{a}

Means indicated with the same letters on each plot were not significantly different at $p < 0.05$ using *t*-test

Table 3 One-way ANOVA results showing the effects of intermittent salt applications (43 and 77 mM) alternated with fresh water every 24 and 72 h on the total soluble solids (TSS) and yield of strawberries grown under two hydroponic techniques (Kratky method and substrate-based technique)

Parameters	Factor	DF	F-value	*p*-value
Total soluble solids (°Bx)	Kratky method	4	40.56	<0.001***
	Substrate-based	4	4.30	0.027*
Average yield, g	Kratky method	4	1.44	0.290^{ns}
	Substrate-based	4	0.81	0.547^{ns}
Fruit weight average, g	Kratky method	4	0.23	0.911^{ns}
	Substrate-based	4	1.05	0.427^{ns}
Deformed fruits (%)	Kratky method	4	4.01	0.033*
	Substrate-based	4	1.02	0.442 ns

ns not significant, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ****$p < 0.0001$

Further comparison using a *t*-test (Fig. 3) revealed that, on average, salt-stressed plants grown under the substrate-based technique had significantly higher TSS content (12.15 °Bx; $p < 0.0001$) than those grown using the Kratky method (9.20 °Bx). Salt stress, particularly under the Kratky method, significantly influenced the TSS content of strawberry fruits ($p < 0.001$), with varying effects observed across different salinity levels and exposure durations as indicated by the different letters of significance shown in Fig. 2a. Under the substrate-based technique, although the highest salinity level of 77 mM applied every 72-h produced the highest TSS, salinity levels between 43 and 77 mM applied every 24–72 h did not significantly influence the accumulation of TSS on strawberry fruits as indicated by the overlapping letters of significance shown in Fig. 2b. This indicates that TSS accumulation in strawberry fruits was more responsive and variable under the Kratky method, particularly with alternating exposure to 43–77 mM saltwater applied every 24 to 72 h. In contrast, the substrate-based technique exhibited more stable TSS levels, showing less sensitivity to the intermittent saltwater irrigation treatments.

The lack of significant difference between treatments suggests that using a substrate-based hydroponic technique effectively maintains fruit quality across a range of salinity levels between 43 and 77 mM applied every 24–72 h, highlighting its potential adaptability in optimizing TSS in strawberry fruits. The increase in TSS observed, particularly in higher salinity (77 mM) could be the result of salt and water stress, which induce osmotic stress, leading to water loss and sugar concentration in the fruits [28, 29]. Moreover, salt stress increases TSS in fruits, which aligns with previous studies conducted in tomatoes, wherein salinity stress increased TSS and elevated sucrose and anthocyanin levels in strawberries [30, 31]. Furthermore, water stress likely contributed to the elevated sugar content in 72-h irrigation intervals due to the plant's osmotic adjustment, which increases sugar accumulation to maintain cell turgor and improve drought tolerance. This process may have resulted in higher sugar concentrations in fruits. This corroborates previous studies on strawberries under water stress conditions wherein the concentrations of glucose and fructose under deficit irrigation-treated strawberry fruits contributed to a sweeter taste [32, 33]. While TSS is a useful indicator of sugar content and, by extension, fruit sweetness, its composition is influenced by multiple factors that can shift under environmental stresses, such as salinity. This complexity implies that TSS alone may not reliably reflect sweetness, particularly under conditions involving osmotic adjustment, where plants accumulate various solutes to maintain cellular balance. It is important to note that some solutes—such as soluble proteins, organic acids, and starches—contribute to TSS measurements but do not directly enhance sweetness [34, 35].

3.2 Yield

The average yield of strawberries under the two hydroponic growing techniques subjected to intermittent salt stress is shown in Fig. 4. Within the substrate-based technique (Fig. 4b), the control group and treatment A2T1 (43 mM salinity applied every 24 h) achieved the highest yields among all treatments across both hydroponic techniques, averaging 160 g/plant (Table 2). However, these values were not significantly different ($p = 0.547$) from the other treatments in the same system (Table 3). The lowest yield under this technique was recorded in treatment A2T4 (77 mM salinity applied every 72 h), averaging 143 g/plant. Similarly, within the Kratky method (Fig. 4a), the control group produced the highest yield at approximately 150 g/plant (Table 2). However, it was not significantly different ($p = 0.290$) from the other

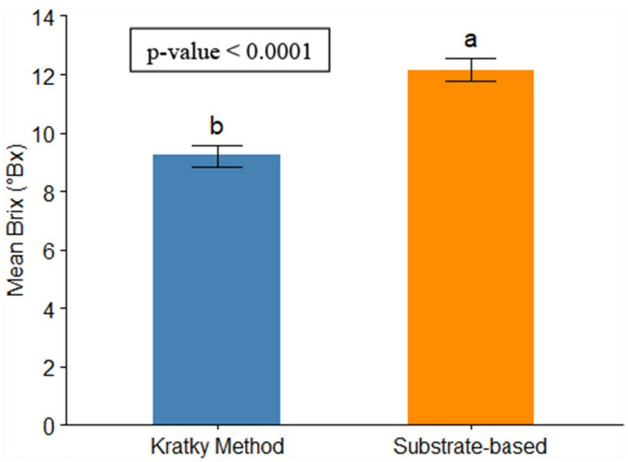


Fig. 3 Comparison of TSS (°Bx) levels in strawberries grown under two different hydroponic techniques (Kratky method and Substrate-based) subjected to salt stress treatments. Error bars represent standard error. Means indicated with the same letters on each plot were not significantly different at $p < 0.05$ using *t*-test

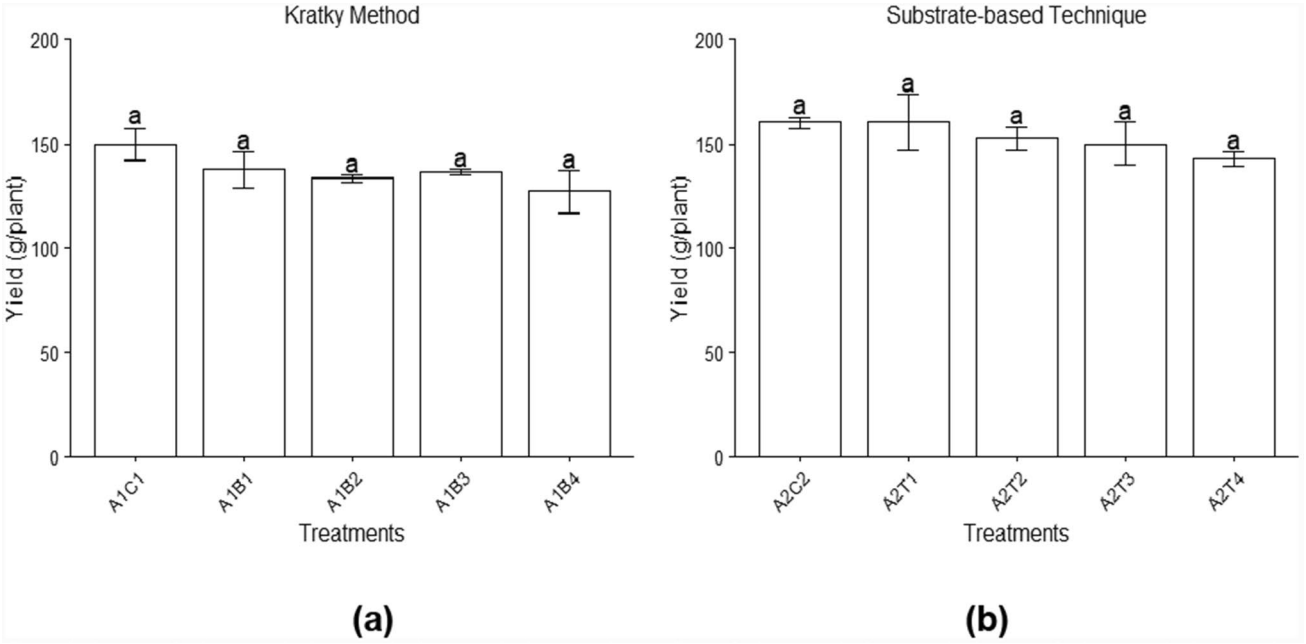


Fig. 4 Average yield per plant (g/plant) of strawberries under different salinity treatments in **a** Kratky method and **b** substrate-based hydroponic systems. Error bars represent standard error. Means indicated with the same letters on each plot were not significantly different at $p < 0.05$ using pairwise *t*-test

treatments in the same system (Table 3). The lowest yield was recorded in the treatment exposed to 77 mM salinity every 72 h, averaging 126.84 g/plant.

By comparison (Fig. 5), the average yield under the substrate-based technique subjected to salt stress was significantly higher (151 g/plant; $p = 0.0032$) than the yield of plants grown under the Kratky method subjected to salt stress, with 133 g/plant. The different salinity stress employed within the hydroponics growing techniques did not significantly influence the yield of the strawberries. However, the overall effects of salt stress between the two hydroponics growing techniques were significantly different, with the Kratky method responding more negatively to salt stress.

Albion cultivar is considered a moderately salt-tolerant variety [25]. However, the effectiveness of its tolerance largely depends on the cultivation system. Substrate-based hydroponics offers a distinct advantage in mitigating salt stress by providing a buffering medium that dilutes and regulates ion availability around the root zone. The substrate acts as a physical and chemical barrier, reducing the immediate exposure of roots to high concentrations of sodium (Na^+) and chloride (Cl^-) ions. This controlled root environment supports more stable water and nutrient uptake and minimizes osmotic shock and ion toxicity caused by the salt [36, 37]. In contrast, the Kratky method, a non-circulating, passive hydroponic system, exposes roots directly to the nutrient solution without the buffering effect of a substrate. As salt is mixed into

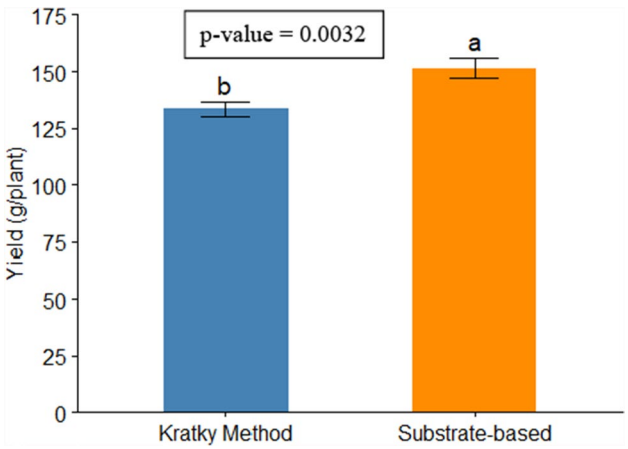


Fig. 5 Comparison of yield of strawberries grown under two different hydroponic techniques (Kratky method and Substrate-based) subjected to salt stress treatments. Error bars represent standard error. Means indicated with the same letters on each plot were not significantly different at $p < 0.05$ using *t*-test

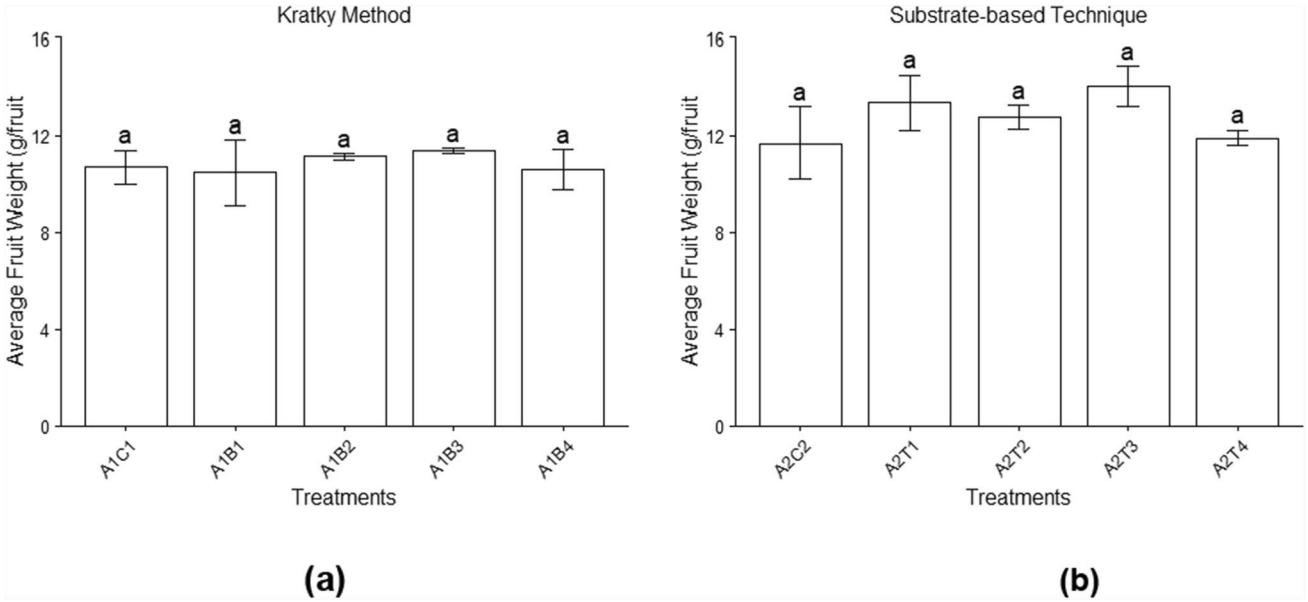


Fig. 6 The average fruit weight of strawberries under different salinity treatments in **a** Kratky method and **b** substrate-based hydroponic systems. Error bars represent standard error. Means indicated with the same letters on each plot were not significantly different at $p < 0.05$ using pairwise *t*-test

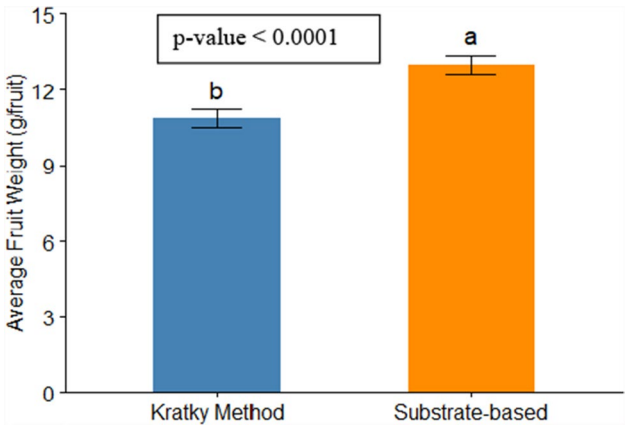


Fig. 7 Comparison of average fruit weight of strawberries grown under two different hydroponic techniques (Kratky method and Substrate-based) subjected to intermittent salt stress treatments. Error bars represent standard error. Means indicated with the same letters on each plot were not significantly different at $p < 0.05$ using *t*-test

the water where the plant's roots are directly submerged, ion toxicity can become more severe, impairing root function and disrupting photosynthetic processes due to reduced stomatal conductance and chlorophyll degradation [38, 39].

3.3 Fruit weight

Figure 6 presents the average fruit weight of strawberries grown using two hydroponic techniques under intermittent salt stress. In the Kratky method (Fig. 6a), the average fruit weights under salt stress ranged from 10.44 to 11.34 g per fruit (Table 2), while the control measured 10.66 g/fruit, with no statistically significant differences among treatments ($p = 0.911$). In the substrate-based system (Fig. 6b), fruits from salt-stressed plants were slightly heavier on average, ranging from 11.89 to 13.98 g per fruit, while the control averaged 11.65 g/fruit (Table 2); however, these differences were also not statistically significant ($p = 0.427$).

A *t*-test comparison of the average fruit weights of salt-stressed plants between the two hydroponic techniques revealed that fruits from the substrate-based system were significantly heavier (12.98 g/fruit; $p < 0.0001$) than those from the Kratky method, which averaged 10.86 g/fruit (Fig. 7).

The salt stress applied to the hydroponic systems did not influence the fruit size of the strawberries; however, the type of hydroponic system did. Previous studies have shown that moderate salinity levels do not always affect yield and can

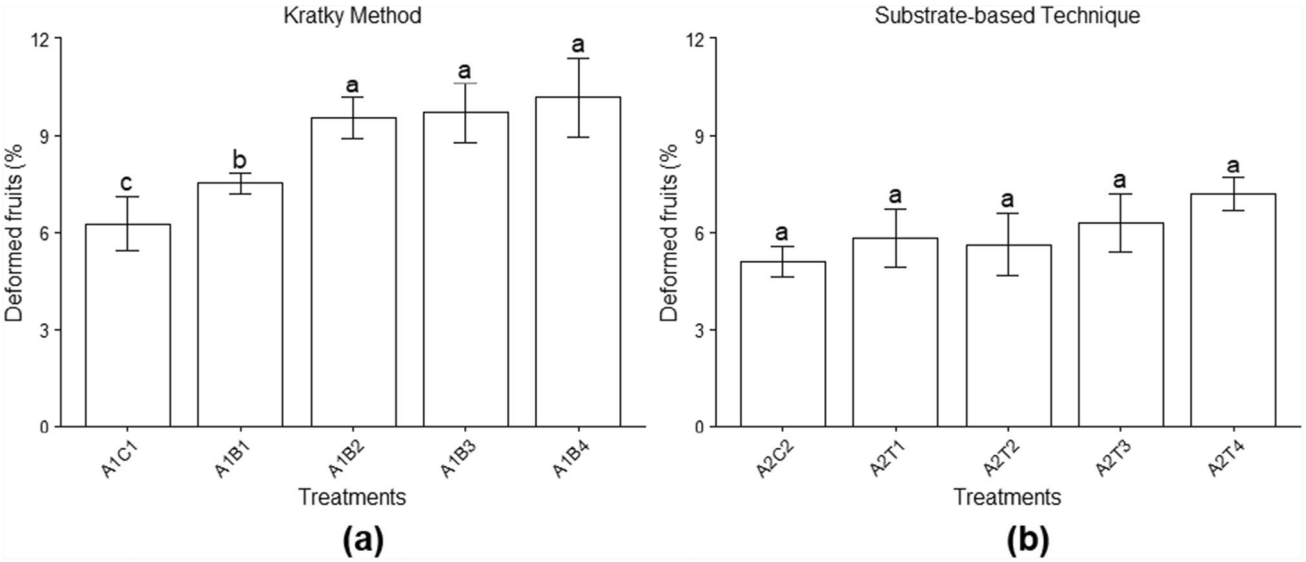


Fig. 8 Percentage of deformed strawberry fruits (%) under different salinity treatments **a** Kratky method and **b** substrate-based hydroponic systems. Error bars represent the standard error of the mean. Means labelled with the same letter within each hydroponic system are not significantly different at $p < 0.05$ based on pairwise *t*-tests

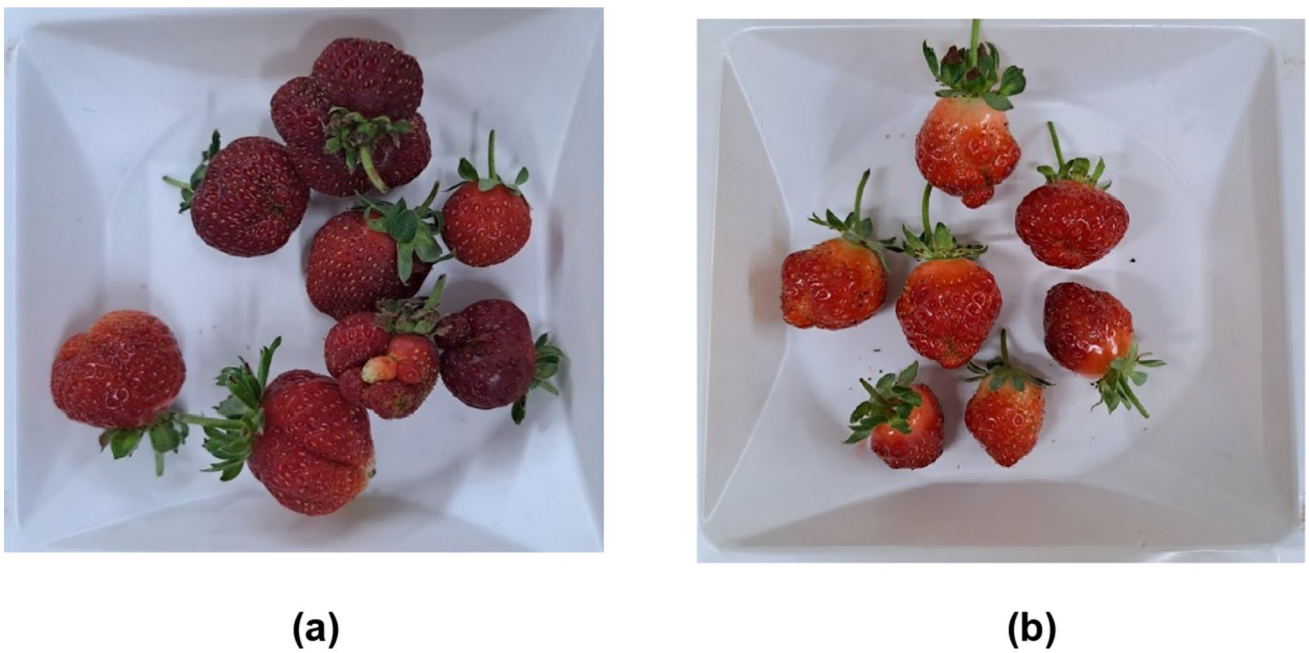


Fig. 9 Deformed fruits of strawberries as affected by the salinity treatments in **a** Kratky method and **b** substrate-based hydroponic systems

be cultivar-dependent. For example, it was observed that increasing the EC beyond 2.5 mS/cm reduced fruit yield in the cultivar Tudla [40]. The yield stability observed in this study across salinity treatments underscores the importance of selecting an appropriate hydroponic technique when growing in salt-stressed environments—with the substrate-based system showing a more favorable performance compared to the Kratky method.

3.4 Deformed fruits

Figures 8 and 9 illustrate the percentage and examples of deformed fruits. Among all treatments in both hydroponic techniques, the highest percentage of deformed fruits (> 10%) was observed in strawberries subjected to 72-h intervals

of 77 mM salinity under the Kratky method (Fig. 8a). This was significantly higher ($p = 0.033$) than the control and the A1B1 treatment (43 mM salinity applied every 24 h) within the same system (Table 2). However, it was not significantly different from the A1B3 (43 mM every 72 h) and A1B4 (77 mM every 24 h) treatments (Table 3). In contrast, no significant differences were found among treatments in the substrate-based system ($p = 0.442$), where the percentage of deformed fruits ranged from 5.08 to 7.16%.

A comparison of the two hydroponic systems (Fig. 10) using *t*-test analysis revealed that the percentage of deformed fruits from salt-stressed plants was significantly higher under the Kratky method (9.22%; $p < 0.001$) compared to the substrate-based system, which averaged 6.21%. The results indicate that salinity negatively impacted fruit quality in the Kratky system, particularly in treatments exposed to higher salinity levels (77 mM). In contrast, fruit deformity in the substrate-based system remained comparable to the control (no salt), suggesting a buffering effect of the substrate in mitigating salt stress on fruit quality.

Fruit deformation is a common problem in strawberry production, often caused by abiotic factors, such as temperature, relative humidity, water, and salt stress [41]. When salt levels exceed a plant's tolerance, nutrient, and water balance, disruption can lead to incomplete fruit formation. This may explain the deformities observed in the Kratky method, particularly in higher salinity (77 mM) and more prolonged exposure (72 h). The increased percentage of deformed fruits under these conditions suggests that the Kratky method's direct root exposure and limited buffering capacity amplify the effects of osmotic stress, leading to cellular damage and abnormal development. This concurred with the previous findings that moderate salinity (2.5 mS/cm) is optimal for balancing strawberry yield and quality, while higher salinity levels (3.5–4.5 mS/cm) improve firmness but reduce yield and increase the percentage of unmarketable fruit [40]. Excessive salt levels lead to osmotic stress, reducing water uptake and causing cellular damage [42–44]. In contrast, the substrate-based system showed fewer deformities, likely due to its ability to more effectively buffer and moderate salinity levels. In the substrate-based technique, the coco coir and perlite mixture help retain moisture and nutrients, providing more consistent root-zone conditions. This buffering capacity can mitigate sudden osmotic stress, ensuring more stable water and nutrient uptake and promoting healthier fruit development. Salt stress manifests in fruit deformities such as reduced size, poor shape, and developmental abnormalities [28, 43, 45].

4 Conclusions

This study highlights the potential of controlled salt stress to enhance the total soluble solids (TSS) of strawberries grown in Kratky and substrate-based hydroponic systems during the fruiting stage. In the substrate-based system, alternate irrigation with 77 mM saltwater and freshwater every 24–72 h significantly increased TSS to 13 °Bx, compared to 10 °Bx in the control. In the Kratky method, the highest TSS was observed in plants exposed to 77 mM salinity every 72 h, reaching nearly 11 °Bx—significantly higher than other treatments within the same system, indicating more variability in the effects of salinity treatments in the Kratky system. Yields within each hydroponic technique were not significantly different. Average yields ranged from 126 to 149 g/plant in the Kratky system and 142 to 160 g/plant in the substrate-based system. On a per-fruit basis, weights ranged from 10.57 to 11.34 g in Kratky, and 11.65 to 13.98 g in the substrate-based system. On average, the substrate-based system demonstrated significantly better performance, producing higher TSS

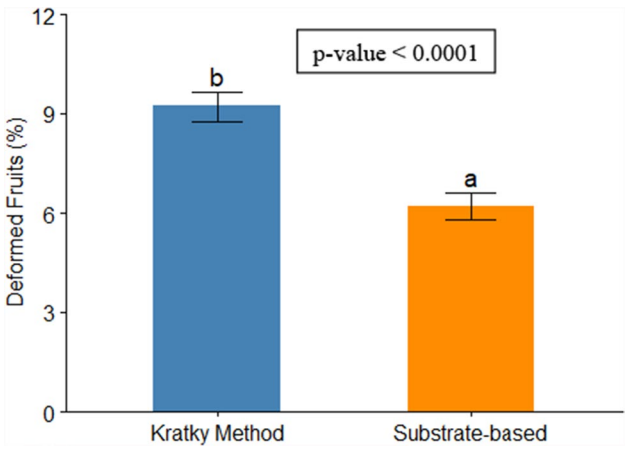


Fig. 10 Comparison of the percentage of deformed strawberry fruits (%) grown under two different hydroponic techniques (Kratky method and substrate-based), subjected to intermittent salt stress treatments. Error bars represent the standard error of the mean. Means labelled with the same letter within each hydroponic system are not significantly different at $p < 0.05$ based on *t*-tests

(12.15 °Bx), greater yield (151 g/plant), heavier fruits (12.98 g/fruit), and a lower percentage of deformed fruits (6.21%) compared to the Kratky method, which recorded a TSS of 9.20 °Bx, yield of 133 g/plant, average fruit weight of 10.86 g/fruit, and 9.22% deformed fruits.

While this study was limited to examining the effects of intermittent salt stress ranging from 43 to 77 mM, applied every 24–72 h for one month during the fruiting stage under two hydroponic growing techniques, future research should explore a season-long experiment on salt stress to fully understand the extent of its effects on the yield and fruit quality. Another key area for further study is the development of genetically improved cultivars with enhanced resilience, especially as salinity stress is expected to intensify due to climate change. Additionally, understanding nutrient ion absorption under saline conditions is essential. Salinity can disrupt nutrient uptake by inducing ionic imbalances and osmotic stress, ultimately affecting plant growth and fruit quality.

Acknowledgements The first author wishes to extend his sincerest appreciation to the Engineering Research and Development for Technology (ERDT), Philippines, for providing scholarship support, and to the William White Endowment of North Carolina Agricultural Foundation, Inc. for the materials and equipment that made this research possible. All individuals have consented to be acknowledged in this paper.

Author contributions C.P. and S.H. conceptualized and experimented, collected, analyzed and wrote the first draft of manuscript. All authors edited and reviewed the manuscript.

Funding This research received no external funding.

Data availability The authors confirm that the datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publications Not applicable.

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by-nc-nd/4.0/.

References

1. Chen P, Liu Q. Genome-wide characterization of the WRKY gene family in cultivated strawberry (*Fragaria* × *ananassa* Duch.) and the importance of several group III members in continuous cropping. Sci Rep. 2019;9(1):8423.
2. Battino M, Forbes-Hernandez TY, Gasparrini M, Afrin S, Mezzetti B, Giampieri F. The effects of strawberry bioactive compounds on human health. In: VIII International Strawberry Symposium 1156 [Internet]. 2016 [cited 2024 Oct 19]. p. 355–62. Available from: https://www.actahort.org/books/1156/1156_54.htm
3. Giampieri F, Forbes-Hernandez TY, Gasparrini M, Alvarez-Suarez JM, Afrin S, Bompadre S, et al. Strawberry as a health promoter: an evidence based review. Food Funct. 2015;6(5):1386–98.
4. Han Y, Song M, Gu M, Ren D, Zhu X, Cao X, et al. Dietary intake of whole strawberry inhibited colonic inflammation in dextran-sulfate-sodium-treated mice via restoring immune homeostasis and alleviating gut microbiota dysbiosis. J Agric Food Chem. 2019;67(33):9168–77.
5. Basu A, Lyons TJ. Strawberries, blueberries, and cranberries in the metabolic syndrome: clinical perspectives. J Agric Food Chem. 2012;60(23):5687–92.
6. Giampieri F, Alvarez-Suarez JM, Battino M. Strawberry and human health: effects beyond antioxidant activity. J Agric Food Chem. 2014;62(18):3867–76.
7. Hannum SM. Potential impact of strawberries on human health: a review of the science. Crit Rev Food Sci Nutr. 2004;44(1):1–17.
8. Pascual CS, Agulto IC, Espino AN, Malamug VU. Effect of ground heat exchanger for root-zone cooling on the growth and yield of aeroponically-grown strawberry plant under tropical greenhouse condition. IOP Conf Ser Earth Environ Sci. 2019;301(1): 012006.

9. Samtani JB, Rom CR, Friedrich H, Fennimore SA, Finn CE, Petran A, et al. The status and future of the strawberry industry in the United States. HortTechnology. 2019;29(1):11–24.
10. Kempler C. 'Out-of-season'greenhouse production of raspberry and strawberry. In: XXVI International Horticultural Congress: Protected Cultivation 2002: In Search of Structures, Systems and Plant Materials for 633 [Internet]. 2002 [cited 2024 Jan 16]. p. 459–65. https://www.actahort.org/books/633/633_57.htm
11. Geilfus CM. Controlled environment horticulture: improving quality of vegetables and medicinal plants. Cham: Springer International Publishing; 2019. https://doi.org/10.1007/978-3-030-23197-2
12. Toivonen PM, Hodges DM. Abiotic stress in harvested fruits and vegetables. abiotic stress in plants-mechanisms and adaptations [Internet]. 2011 [cited 2024 Oct 19]; https://books.google.com/books?hl=en&lr=&id=RQmQDwAAQBAJ&oi=fnd&pg=PA39&dq=abiotic+stress+enhance+fruit+quality&ots=j4XzYgstz-&sig=cXYcPiuMh4JE005jbAZ7jUNHjYQ
13. Egea I, Estrada Y, Flores FB, Bolarín MC. Improving production and fruit quality of tomato under abiotic stress: genes for the future of tomato breeding for a sustainable agriculture. Environ Exp Bot. 2022;204: 105086.
14. González-Chavira MM, Herrera-Hernández MG, Guzmán-Maldonado H, Pons-Hernández JL. Controlled water deficit as abiotic stress factor for enhancing the phytochemical content and adding-value of crops. Sci Hortic. 2018;234:354–60.
15. Ortega-Hernández E, Antunes-Ricardo M, Jacobo-Velázquez DA. Improving the health-benefits of kales (*Brassica oleracea* L. var. acephala DC) through the application of controlled abiotic stresses: a review. Plants (Basel). 2021;10(12):2629.
16. Sener S, Saygı H, Duran CN. Responses of in vitro strawberry plants to drought stress under the influence of nano-silicon dioxide. Sustainability. 2023;15:15569.
17. Şener S. Abiotic stress factors and strawberry cultivation. In: Impact of Climate Change on Agriculture. 2021. p. 111–25.
18. Demiral MA. Effect of salt stress on concentration of nitrogen and phosphorus in root and leaf of strawberry plant. Eurasian J Soil Sci. 2017;6(4):357–64.
19. Saied AS, Keutgen AJ, Noga G. The influence of NaCl salinity on growth, yield and fruit quality of strawberry cvs. 'Elsanta' and 'Korona.' Sci Hortic. 2005;103(3):289–303.
20. Turhan E, Eris A. Changes of growth, amino acids, and ionic composition in strawberry plants under salt stress conditions. Commun Soil Sci Plant Anal. 2009;40(21–22):3308–22.
21. Kimball D. Brix and Soluble Solids. In: Kimball D, editor. Citrus processing: quality control and technology. Dordrecht: Springer Netherlands; 1991. p. 7–33. https://doi.org/10.1007/978-94-011-3700-3_2
22. Rakocy JE. Aquaponics—integrating fish and plant culture. In: Tidwell JH, editor. Aquaculture production systems. 1st ed. New York: Wiley; 2012. p. 344–86. https://doi.org/10.1002/9781118250105.ch14
23. Fronte B, Galliano G, Bibbiani C. From freshwater to marine aquaponic: new opportunities for marine fish species production. In SVN; 2016. https://arpi.unipi.it/handle/11568/844495. Accessed 31 Dec 2024
24. Kratky BA. A suspended net-pot, non-circulating hydroponic method for commercial production of leafy, romaine, and semi-head lettuce. Veg Crops. 2010;1:1–19.
25. Ferreira JFS, Liu X, Suarez DL. Fruit yield and survival of five commercial strawberry cultivars under field cultivation and salinity stress. Sci Hortic. 2019;243:401–10.
26. 9-12-34 Strawberry Formula • Masterblend International. Masterblend International. 2018. https://www.masterblend.com/9-12-34-strawberry-formula/. Accessed 31 Mar 2025.
27. Team RC. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. 2013.
28. Yadav S, Irfan M, Ahmad A, Hayat S. Causes of salinity and plant manifestations to salt stress: a review. J Environ Biol. 2011;32(5):667–85.
29. Zhao KF, Harris PJC. The effects of iso-osmotic salt and water stresses on the growth of halophytes and non-halophytes. J Plant Physiol. 1992;139(6):761–3.
30. Galli V, da Silva MR, Perin EC, Borowski JM, Bamberg AL, Rombaldi CV. Mild salt stress improves strawberry fruit quality. LWT. 2016;1(73):693–9.
31. Wu M, Buck JS, Kubota C. Effects of nutrient solution EC, plant microclimate and cultivars on fruit quality and yield of hydroponic tomatoes (*Lycopersicon esculentum*). Acta Hortic. 2004;659:541–7.
32. Adak N, Gubbuk H, Tetik N. Yield, quality and biochemical properties of various strawberry cultivars under water stress. J Sci Food Agric. 2018;98(1):304–11.
33. Terry LA, Chope GA, Bordonaba JG. Effect of water deficit irrigation on strawberry (Fragaria × Ananassa) fruit quality. Acta Hortic. 2009;842:839–42.
34. Ikegaya A, Toyoizumi T, Ohba S, Nakajima T, Kawata T, Ito S, et al. Effects of distribution of sugars and organic acids on the taste of strawberries. Food Sci Nutr. 2019;7(7):2419–26.
35. Scott G, Williams C, Wallace RW, Du X. Exploring plant performance, fruit physicochemical characteristics, volatile profiles, and sensory properties of day-neutral and short-day strawberry cultivars grown in Texas. J Agric Food Chem. 2021;69(45):13299–314.
36. Grattan SR, Grieve CM. Salinity–mineral nutrient relations in horticultural crops. Sci Hortic. 1998;78(1–4):127–57.
37. Savvas D, Gruda N. Application of soilless culture technologies in the modern greenhouse industry—A review. Eur J Hortic Sci. 2018;83(5):280–93.
38. Munns R, Tester M. Mechanisms of salinity tolerance. Annu Rev Plant Biol. 2008;59:651–81.
39. Taiz L, Zeiger E, Møller IM, Murphy A. Plant physiology and development. 2015. 761 p. https://doi.org/10.5555/20173165866
40. D'Anna F, Incalcaterra G, Moncada A, Miceli A. Effects of different electrical conductivity levels on strawberry grown in soilless culture. In: Pardossi A, Serra G, Tognoni F, editors. Proceedings of the International Symposium on Managing Greenhouse Crops in Saline Environment. Leuven 1: International Society Horticultural Science; 2003. p. 355–60. Acta Horticulturae. https://www.webofscience.com/wos/woscc/summary/499a3f82-76c6-4c50-92b7-ba952e1a2ac1-0113fa2d63/relevance/1
41. Larson KD. Strawberry. In: Handbook of environmental physiology of fruit crops. CRC Press; 2018. p. 271–97. https://doi.org/10.1201/9780203719299-10/strawberry-kirk-larson

42. Djanaguiraman M, Prasad PVV. Effects of salinity on ion transport, water relations and oxidative damage. In: Ahmad P, Azooz MM, Prasad MNV, editors. Ecophysiology and responses of plants under salt stress. New York, NY: Springer; 2013. p. 89–114. https://doi.org/10.1007/978-1-4614-4747-4_3
43. Munns R. Comparative physiology of salt and water stress. Plant, Cell Environ. 2002;25(2):239–50.
44. Rasool S, Hameed A, Azooz MM, Muneeb-u-Rehman, Siddiqi TO, Ahmad P. Salt stress: causes, types and responses of plants. In: Ahmad P, Azooz MM, Prasad MNV, editors. Ecophysiology and responses of plants under salt stress. New York, NY: Springer; 2013. p. 1–24. https://doi.org/10.1007/978-1-4614-4747-4_1
45. Shabala S, Munns R. Salinity stress: physiological constraints and adaptive mechanisms. In: Plant stress physiology. 2017;p.24–63.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.