

Potassium Sulfate Supplementation with Elevated Electrical Conductivity Was Unproductive for Hydroponic Strawberry at the Original Yamazaki Nutrient Solution Nitrogen Level

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Abstract. The production of strawberries (*Fragaria × ananassa*) in hydroponic systems has been increasing. In hydroponic systems, precise nutrient management is crucial for optimal plant growth and fruit production. Among essential elements, potassium (K) is a key nutrient that affects fruit yield and quality in fruiting crops. The objective of this study was to investigate whether increasing the K concentration in the Yamazaki strawberry nutrient solution could enhance plant growth, fruit yield, and fruit quality in hydroponic strawberries. Bare-root plants of strawberry ‘Monterey’ and ‘San Andreas’ were planted in a deep water culture hydroponic system and grown with initial K concentrations of 117, 194, 271, and 348 mg·L⁻¹ under the same initial nitrogen concentration of 77 mg·L⁻¹. As the K concentration increased from 117 to 348 mg·L⁻¹, the nutrient solution electrical conductivity increased from 1.0 to 1.9 dS·m⁻¹. The experiment was conducted inside an indoor vertical farm at a 23°C air temperature with an extended photon flux density (400–750 nm) of 350 μmol·m⁻²·s⁻¹ under an 18-hour photoperiod. Increasing the K concentration from 117 to 348 mg·L⁻¹ had minimal effects on plant growth characteristics of both cultivars, although root dry mass of ‘Monterey’ increased linearly with increasing K. Increasing the K concentration from 117 to 348 mg·L⁻¹ did not affect the total fruit number or total fruit fresh mass of ‘Monterey’, but for ‘San Andreas’, it reduced the total fruit number by 34% and total fruit fresh mass by 45%. Additionally, increasing the K concentration from 117 to 348 mg·L⁻¹ reduced the individual fruit mass, fruit length, and fruit diameter and increased titratable acidity in both cultivars. These results indicate that increasing the K concentration in the Yamazaki strawberry nutrient solution did not benefit plant growth, fruit yield, or fruit quality of the hydroponically grown strawberries ‘Monterey’ or ‘San Andreas’.

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The use of hydroponic vertical farming systems to produce strawberries (*Fragaria × ananassa*) is increasing as reductions in arable land, increased labor costs, and tightening regulations are making outdoor production more challenging for growers (Samtani et al. 2019). In hydroponic systems, the nutrient solution is the only source of the nutrients provided to plants. The concentration of nutrients is one of the major factors that influences plant development and, ultimately, crop yield (Wada 2019). Strawberries require the precise management of nutrients to effectively produce quality harvestable fruit in a timely manner because they are particularly sensitive to nutrient concentrations (Barroso and Alvarez 1997).

Adequate potassium (K) is necessary for high crop yield and quality, is essential for

many plant growth processes, regulates stomatal opening and closing for gas and water vapor exchange during photosynthesis, maintains cell turgor pressure, and activates more than 60 enzymes crucial for plant growth (Johnson et al. 2022; Zörb et al. 2014). Additionally, K promotes leaf expansion and biomass accumulation by facilitating cell expansion (Oosterhuis et al. 2014), enhances root development, and influences biomass distribution between shoots and roots (Sustr et al. 2019). Generally, in fruiting crops, K controls nutrient movement into fruits, affecting their size and quality (Çalışkan and Çalışkan 2017; Kumar et al. 2006). Enzymes crucial for fruit development, such as sucrose phosphate synthase, invertase, and phosphofructokinase, depend on adequate K (Sardans and Peñuelas 2021). Because its presence at optimal levels improves fruit quality, K has also been considered a quality element in fruiting crops (Kumar et al. 2006; Shen et al. 2017; Wang et al. 2024).

In strawberries, the benefits of adequate K have been demonstrated in terms of improved plant growth, higher fruit yield, and higher fruit quality in hydroponic systems, mainly with soilless substrates. Increasing the K concentration from 200 to 300 mg·L⁻¹ improved individual fruit mass, fruit number, and fruit yield in strawberry ‘Camarosa’, ‘Selva’, and ‘Parus’ using different combinations of peat, cocopeat, sand, and perlite (Ebrahimi et al. 2012). In strawberry ‘Camarosa’ grown in cocopeat and perlite, increasing the K concentration from 235 to 350 mg·L⁻¹ increased leaf area, shoot fresh mass, fruit yield, fruit diameter, and fruit total soluble solids (TSS) (Tohidloo et al. 2018). In strawberry ‘Selva’, shoot fresh mass and fruit yield increased as the K concentration increased from 235 to 450 mg·L⁻¹ (Tohidloo et al. 2018). Increasing the K concentration from 196 to 431 mg·L⁻¹ also increased the fruit yield and TSS of strawberries grown in sand and perlite (Preciado-Rangel et al. 2020). Together, these studies showed that increasing the K concentration up to 300 to 450 mg·L⁻¹ enhanced plant growth, fruit yield, and fruit quality for hydroponic strawberry cultivation using soilless substrates.

In addition to the K concentration, the balance between K and nitrogen (N) is another consideration for strawberry nutrient management because the requirement for K increases as the supplied N increases (Cheng 2013; Preciado-Rangel et al. 2020; Nakro et al. 2023). While the recommended optimal K:N ratio for hydroponic strawberry fertilization is between 1.7:1 and 2.0:1 (Morgan 2006), recent research has shown that increasing the K:N ratio beyond this range can further enhance fruit quality. For example, in strawberries ‘Fortuna’, ‘San Andreas’, and ‘Sabrina’, a high K:N ratio of 2.6:1 with 290 mg·L⁻¹ K during the vegetative stage increased total fruit yield by 42% and total soluble solids by 16% compared with those associated with a K:N ratio of 1.3:1 (Nakro et al. 2023). Increasing the K:N ratio from 0.5:1 to 2.8:1 improved fruit yield and TSS in strawberries

Table 1. Concentrations of potassium (K) and nitrogen (N), K:N ratios, and electrical conductivity (EC) of hydroponic nutrient solution treatments.

K (mg·L ⁻¹)	N (mg·L ⁻¹)	K:N ratios	EC (dS·m ⁻¹)
117	77	1.5	1.0
194	77	2.5	1.3
271	77	3.5	1.6
348	77	4.5	1.9

‘Oso Grande’ and ‘Diamante’ (Maldonado et al. 2012).

The Yamazaki strawberry nutrient solution is widely used for hydroponic strawberry production (Jiang et al. 2023; Jun et al. 2013; Kumar et al. 2020; Yafuso and Boldt 2024; Yu et al. 2023). The Yamazaki strawberry nutrient solution, developed from empirical data of plant nutrient uptake (Wada 2019), supplies 77 mg·L⁻¹ N (or 5.5 mM) and 117 mg·L⁻¹ K (or 3 mM), with a K:N ratio of 1.5:1 (Tsukagoshi and Shinohara 2020). Despite its widespread application, the K concentration and K:N ratio in the Yamazaki strawberry nutrient solution are lower than the desirable values identified by recent research. The potential benefits of increasing the K concentration and the K:N ratio beyond those in the Yamazaki strawberry nutrient solution were unclear. In this study, we investigated whether increasing the K concentration, and consequently the K:N ratio, in the Yamazaki strawberry nutrient solution could further enhance vegetative growth, fruit yield, and fruit quality in two strawberry cultivars.

Materials and Methods

Plant materials. Two ever-bearing strawberry cultivars, Monterey and San Andreas, were obtained as bare-root plants from a commercial nursery (Lassen Canyon Nursery Inc., Redding, CA, USA) on 17 Mar 2023. From each cultivar, 130 bare-root plants with crown diameters between 10 and 13 mm

were selected. The crown diameters of ‘Monterey’ and ‘San Andreas’ bare-root plants averaged 12.0 mm and 11.7 mm, respectively. After selection, the bare-root plants were thoroughly washed with tap water to remove all remaining substrate particles. Then, they were soaked for 15 min in a Zeritol solution (1:100 dilution containing 27.1% hydrogen peroxide and 2.0% peroxyacetic acid; Biosafe Systems, East Hartford, CT, USA) to eliminate any pathogens using the concentration recommended by the manufacturer for a preplant dip.

Growing environment. After being cleaned and sanitized, the plants were moved to a temperature-controlled vertical farm on the Arizona State University Polytechnic Campus (Mesa, AZ, USA). The plants were then transplanted into Styrofoam rafts (32-cell lettuce raft; Beaver Plastics Ltd., Acheson, AB, Canada), that floated in deep water culture hydroponic growing trays (1.12 m × 0.66 m × 0.18 m; GT24X44X7B; Botanicare, Vancouver, WA, USA). The experiment was set up as a randomized complete block design with four K treatments and two replications (blocks) per treatment. It included eight experimental plots,

with each consisting of a hydroponic growing tray placed on one of two tiers across four independent racks. Each tray held 15 plants of each of the two cultivars arranged identically across all trays. The treatments were randomly assigned to the trays within each replication. Replications served as blocks, with the growing reservoirs designated as experimental units for the nutrient solution treatments, and individual plants were treated as subsamples.

Sole-source lighting was supplied using blue (peak = 457 nm) + red (peak = 660 nm) + far-red (peak = 732 nm) light-emitting diode (LED) lamps (T8 Double-Row LED Indoor Grow Light; Homer Farms Inc., Mesa, AZ, USA) with an 18-h photoperiod. On the surface of the floating raft, the blue (400–500 nm), red (600–700 nm), and far red (700–750 nm) photon flux densities were 80, 270, and 50 μmol·m⁻²·s⁻¹, respectively, based on an average of nine measurements taken using a spectroradiometer (PS-300; Apogee Instruments, Logan, UT, USA) at predetermined horizontal positions. The air temperature was maintained at 23 °C, and the relative humidity was ambient, with an average of 65% throughout the experimental

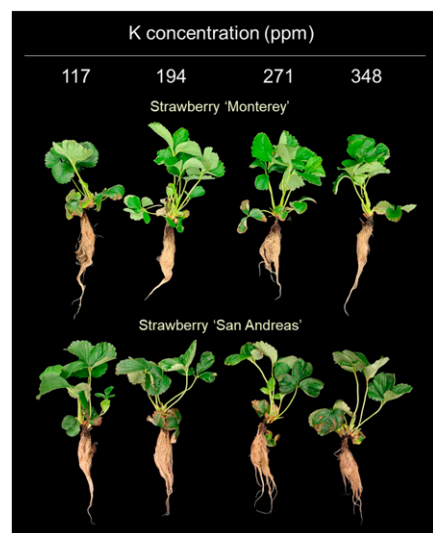


Fig. 1. Representative plants of strawberry ‘Monterey’ and ‘San Andreas’ grown for 3 weeks under potassium (K) concentrations of 117, 194, 271, and 348 mg·L⁻¹.

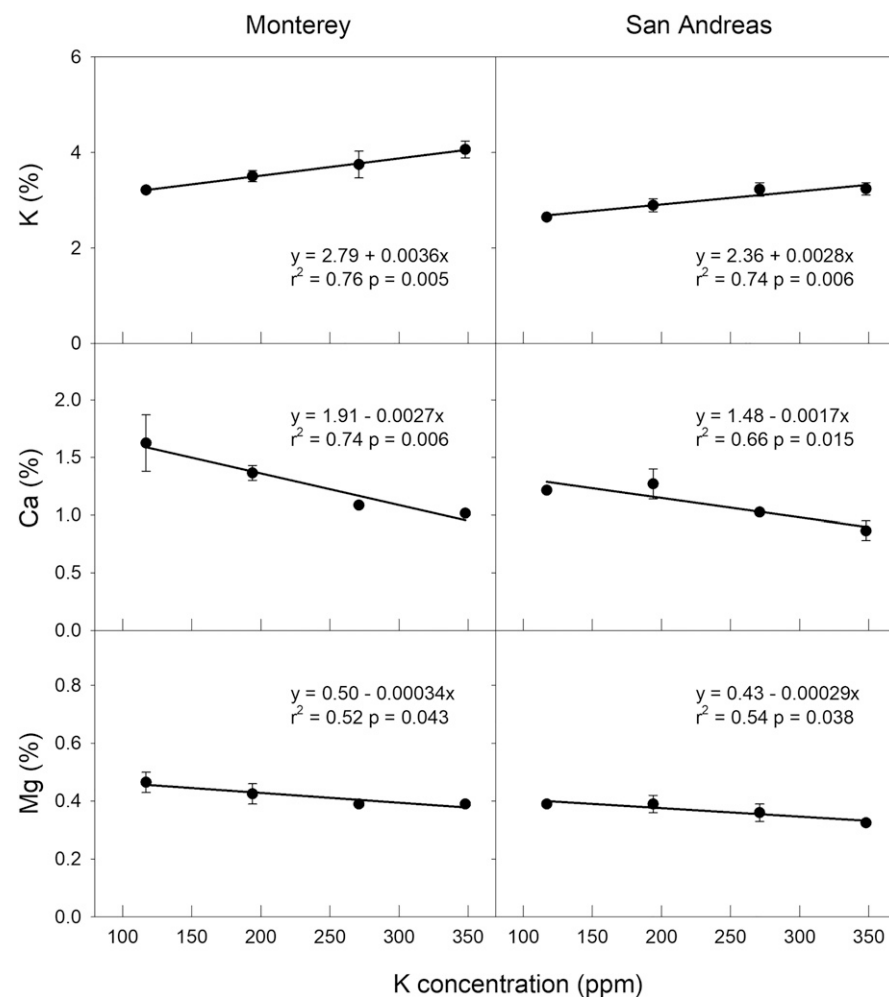


Fig. 2. Effects of potassium (K) concentrations on the concentrations of K, calcium (Ca), and magnesium (Mg) in strawberry ‘Monterey’ and ‘San Andreas’ 3 weeks after treatment. Each data point represents the mean and standard error of two replications (n = 2). Regression equations, r² values, and P values are presented when statistically significant at $P < 0.05$ (solid line).

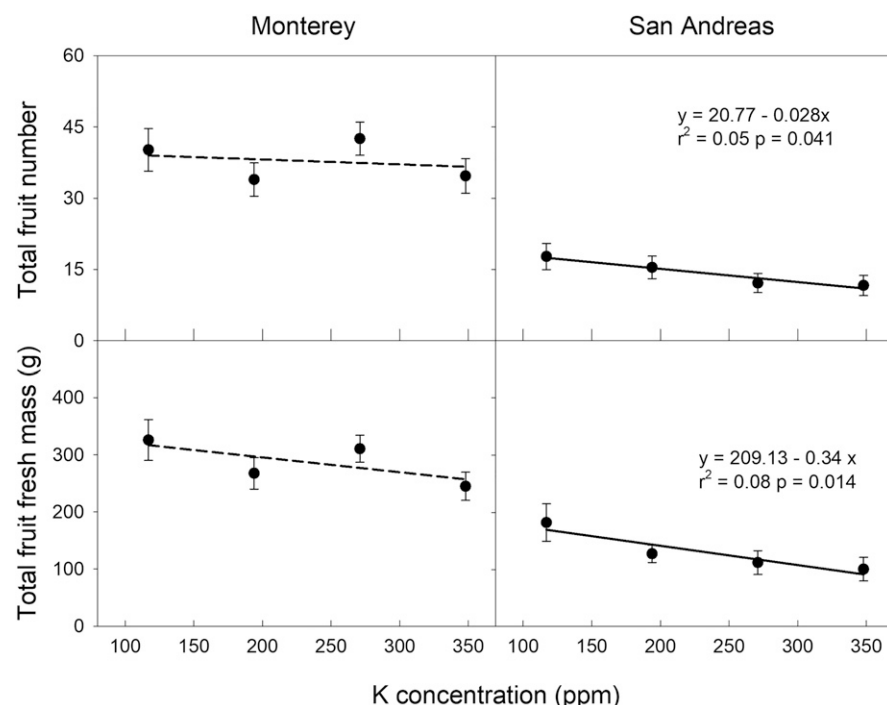


Fig. 3. Effects of potassium (K) concentrations on total fruit number per plant and total fruit fresh mass per plant in strawberries 'Monterey' and 'San Andreas' during the harvesting period. Each data point represents the mean and standard error of two replications with 10 plants per replication ($n = 20$). Regression equations, r^2 values, and P values are presented when statistically significant at $P < 0.05$ (solid line), but not when nonsignificant (dashed line).

period. Both the air temperature and relative humidity were continuously monitored and recorded hourly using a sensor (Smart Thermo-Hygrometer H5075; Govee, Shenzhen, China) placed in the center of each growing tray.

K treatments and hydroponic nutrient solution. For the first 3 weeks after transplanting, the nutrient solution contained a Yamazaki strawberry formula fertilizer (Jack's Strawberry Part A/B; JR Peters Inc., Allentown, PA, USA) dissolved in deionized water to provide (in $\text{mg}\cdot\text{L}^{-1}$) 77 N, 24 P, 117 K, 16 sulfur (S), 40 calcium (Ca), 12 magnesium (Mg), 1.95 iron (Fe), 0.54 manganese (Mn), 0.32 zinc (Zn), 0.38 boron (B), 0.05 copper (Cu), and 0.01 molybdenum (Mo). Subsequently, we evaluated the effects of four K concentrations of 117, 194, 271, and 348 $\text{mg}\cdot\text{L}^{-1}$ (Table 1) with and without the addition of supplemental potassium sulfate (K_2SO_4) to the standard Yamazaki strawberry nutrient solution. Because K_2SO_4 was used, the increase in K also simultaneously increased S from 16 to 111 $\text{mg}\cdot\text{L}^{-1}$. Among the available K supplements, including potassium nitrate (KNO_3), potassium chloride (KCl), potassium hydroxide (KOH), and K_2SO_4 , we chose K_2SO_4 to minimize the impact of anions because sulfur toxicity is rare. In this study, plant tissue analysis results (Supplemental Table 2) further confirmed that S levels remained within the sufficient range and were not high or excessive across all treatments, suggesting that additional S from K_2SO_4 had minimal to no impact on plant growth.

The nutrient solutions were circulated continuously using a water pump (396 GPH Fixed Flow Water Pump; Sunlight Supply

Vancouver, WA, USA) in a single reservoir connected to two trays per rack. The reservoir was oxygenated using an air pump (ACO-050; Vivosun, ON, CA, USA) and an air stone (ASD-200; Pawfly, Guangzhou, Guangdong, China). Each tray had two additional air stones (Aquarium Air Stone Bar 8-in; PawFly) connected to a separate air pump (EcoPlus Air 8 Outlet Air Pump HGC728350; Sunlight Supply Inc.) for increased oxygenation. The pH and electrical conductivity (EC) of the nutrient solutions were monitored daily using a pH and EC meter (HI9814; Hanna Instruments, Smithfield, RI, USA). The pH was readjusted to 5.8 daily using 50% sulfuric acid (H_2SO_4) to lower the pH and potassium bicarbonate (KHCO_3) to increase the pH. Throughout the experiment, nutrient solutions were replenished equally across all reservoirs to compensate for water loss, primarily because of transpiration. The ECs for the K concentration treatments of 117, 194, 271, and 348 $\text{mg}\cdot\text{L}^{-1}$ were maintained at 1.0, 1.3, 1.6, and 1.9 $\text{dS}\cdot\text{m}^{-1}$, respectively, throughout the experiment (Table 1). To maintain consistent EC levels, deionized water was added uniformly to all reservoirs when EC levels increased because of transpirational water loss and nutrient uptake by plants. The pH (mean \pm standard deviation) of the nutrient solution for each K treatment for the duration of the experiment was 5.8 ± 0.1 .

Data collection and analysis. The experiment lasted 17 weeks. Runners and flowers were removed daily during the first 6 weeks after transplanting to promote vegetative growth. Six weeks after transplanting (3 weeks after starting the K concentration treatments), we collected vegetative growth data. Five representative plants

of each cultivar, treatment, and replication were chosen for data collection, with one photographed (Fig. 1). For each plant, the leaf number (the number of fully formed trifoliate leaves), soil plant analysis development (SPAD) index determined using a chlorophyll meter (SPAD-502; Konica Minolta Sensing Inc., Chiyoda, Tokyo, Japan), crown number, crown diameter determined using a caliper (B07DFFYCXS; Adoric, Shenzhen, Guangdong, China), leaf area determined using a leaf area meter (LI-3100; LI-COR Inc., Lincoln, NE, USA), root length, and fresh and dry shoot and root mass obtained using a scale (PB602-S; Mettler Toledo, Columbus, OH, USA) were recorded. The shoot and root dry mass were recorded after plants were dried at $\geq 70^\circ\text{C}$ for ≥ 5 d in a drying oven (Hafco 1600; VWR International LLC, Aurora, CO, USA). For the strawberry plant tissue analysis, dried leaves (four to five of the largest trifoliate leaves per plant) from each treatment within each replication were combined and submitted to an analytical laboratory (Plant Tissue, Waste & Compost, Solutions and Soilless Media Testing Laboratory, Agronomic Division, North Carolina Department of Agriculture and Consumer Services, Raleigh, NC, USA), where the macronutrient and micronutrient concentrations were measured as described previously (McClintic et al. 2024). The plant tissue samples were combined for nutrient analysis because of insufficient leaves from each treatment for separate tissue analyses.

Six weeks after transplanting, the remaining plants (10 of each cultivar, treatment, and replication) were allowed to flower and produce fruits. The date of the first flower bud opening (days to first flower) and the date of the first fully ripened fruit (determined by the visual appearance of fully red fruit) were recorded for each plant. For each plant, once the fruits were fully ripe, they were harvested twice weekly for the rest of the experiment. The harvested fruits were then transported to the laboratory and analyzed on the same day for fresh mass, size, TSS, and titratable acidity (TA). For each fruit, the diameter at its widest point and length from top to bottom were measured using a caliper (B07DFFYCXS; Adoric). Each fruit was weighed using an analytical balance (PB602-S; Mettler Toledo). To analyze TSS and TA, the five fruits with the highest fresh mass from each treatment, replication, and cultivar were selected. After we removed the pedicels, we combined their juice using a pestle and mortar and filtered it through a mesh screen to remove any pulp or seeds. The filtered juice was analyzed for TA with a titrator (HI 84532; Hanna Instruments) and for TSS using a digital refractometer (HI 96801; Hanna Instruments) at a room temperature of 22°C four times during peak harvest.

Data from the two replications were pooled and analyzed using SAS (version 9.4; SAS Institute, Cary, NC, USA). The effects of the K concentration were assessed with PROC MIXED considering one fixed factor (K concentration) and two random factors (blocks and their interaction with K concentration). Linear regression was performed using PROC REG to evaluate relationships between K concentration and plant parameters ($P < 0.05$).

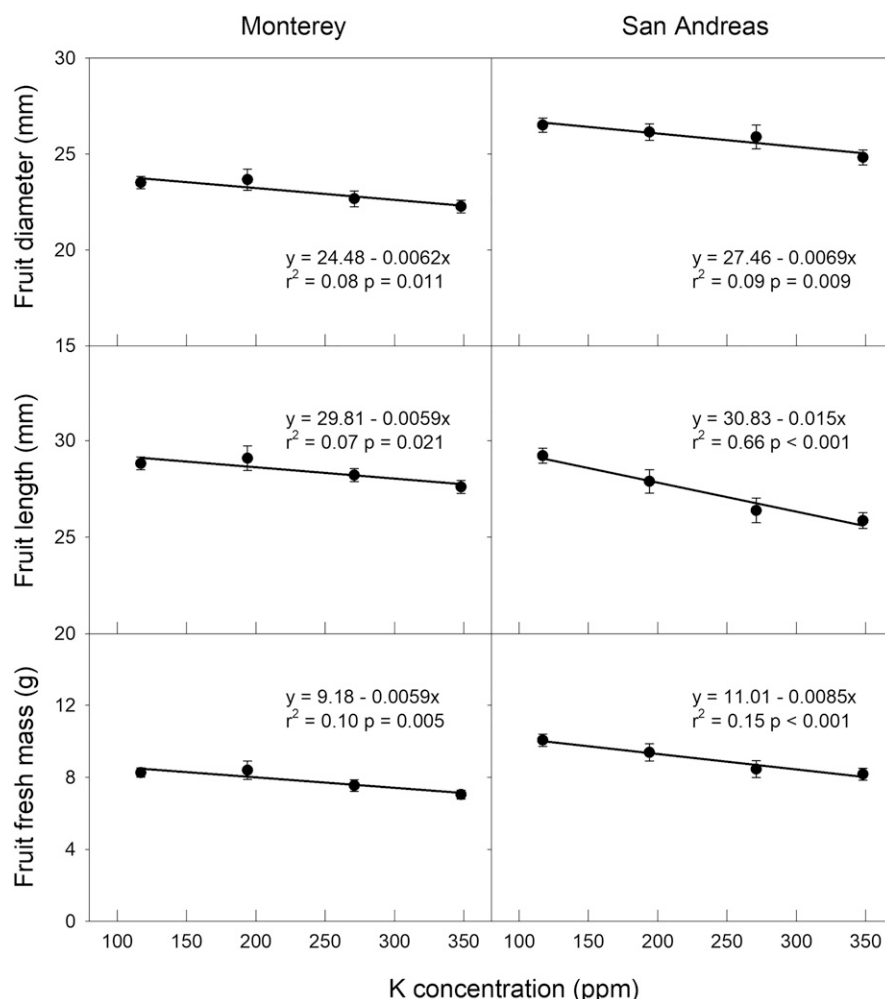


Fig. 4. Effects of potassium (K) concentrations on individual fruit fresh mass, individual fruit diameter, and individual fruit length in strawberries 'Monterey' and 'San Andreas' during the harvesting period. Each data point represents the mean and standard error of two replications with 10 plants per replication ($n = 20$). Regression equations, r^2 values, and P values are presented when statistically significant at $P < 0.05$ (solid line), but not when nonsignificant (dashed line).

The number of data points used for the statistical analysis varied across the different plant parameters as follows: plant growth characteristics ($n = 10$; 2 replications \times 5 plants per replication); days to flower and fruit harvest ($n = 20$; 2 replications \times 10 plants per replication); plant nutrient content ($n = 2$; 2 replications \times 1 combined plant sample per replication); fruit production and characteristics ($n = 2$ replications \times 10 plants per replication), TSS ($n = 8$ for 'Monterey'; 2 replications \times 4 samplings per replication), and TA ($n = 6$ for 'San Andreas'; 2 replications \times 3 samplings per replication). The tests of the effect of the K concentration did not reveal significant differences at $P < 0.05$ in any plant parameters among the treatment groups. Thus, the mean values of the treatments and the P values for each plant parameter are reported in Supplemental Tables 1–3. The results of the linear regression analysis that showed a significant relationship between the K concentration and plant parameters are shown in Figs. 2–5.

Results

Plant growth characteristics. In strawberries 'Monterey' and 'San Andreas', the K

concentration did not influence the crown number, crown diameter, leaf number, leaf area, shoot fresh and dry mass, or root fresh mass after 3 weeks of K treatments (and 6 weeks after transplanting) (Supplemental Table 1, Fig. 1). Increasing the K concentration from 117 to 348 $\text{mg}\cdot\text{L}^{-1}$ linearly increased root dry mass by 26% in strawberry 'Monterey', but not in 'San Andreas'.

Leaf nutrient compositions. Increasing the nutrient solution K concentration in the nutrient solution from 117 to 348 $\text{mg}\cdot\text{L}^{-1}$ linearly increased the leaf K concentration by 26% in 'Monterey' and by 22% in 'San Andreas' (Fig. 2). Conversely, the leaf Ca and Mg concentrations decreased linearly by 37% and 17% in 'Monterey' and 29% and 15% in 'San Andreas', respectively, as the nutrient solution K concentration increased from 117 to 348 $\text{mg}\cdot\text{L}^{-1}$. The nutrient solution K concentration did not affect the leaf concentrations of the other macronutrients and micronutrients (Supplemental Table 2).

Flowering and fruit production. The K concentrations ranging from 117 to 348 $\text{mg}\cdot\text{L}^{-1}$ did not affect the time to flowering or the time for the first fruit to ripen in both

'Monterey' and 'San Andreas' (Supplemental Table 3). However, in 'San Andreas', increasing the K concentration from 117 to 348 $\text{mg}\cdot\text{L}^{-1}$ reduced the total fruit number harvested per plant by 34% and the total fruit fresh mass harvested per plant by 45% (Fig. 3).

Fruit quality. In both cultivars, there was a linear reduction in the fresh mass, diameter, and length of individual strawberry fruits as the K concentration increased from 117 to 348 $\text{mg}\cdot\text{L}^{-1}$ (Fig. 4). In 'San Andreas', but not in 'Monterey', TSS increased linearly with increasing K concentrations (Fig. 5). The TA increased linearly in both cultivars with increasing K concentrations. The TSS:TA ratio decreased linearly in 'Monterey' but remained unaffected in 'San Andreas' as the K concentration increased from 117 to 348 $\text{mg}\cdot\text{L}^{-1}$.

Discussion

In this study, increasing the K concentration from 117 to 348 $\text{mg}\cdot\text{L}^{-1}$ in the nutrient solution did not affect shoot growth in either strawberry cultivar (Supplemental Table 1), but it led to a linear decrease in the total fruit number and fruit fresh mass in 'San Andreas', but not in 'Monterey' (Fig. 3). Typically, increasing the K concentration enhances strawberry plant growth and fruit yield up to an optimum level, beyond which further increases do not provide additional benefits (Afroz et al. 2016; Ahmad 2014; Ebrahimi et al. 2012; Haynes and Goh 1987; Nakro et al. 2022; Tohidloo et al. 2018; Wu et al. 2020). For example, in strawberry 'Camarosa', increasing the K concentration from 250 to 350 $\text{mg}\cdot\text{L}^{-1}$ increased leaf area, shoot fresh and dry mass, and fruit yield, but further increases to 450 and 600 $\text{mg}\cdot\text{L}^{-1}$ did not enhance these characteristics (Tohidloo et al. 2018). Similarly, increasing the K concentration from 200 to 300 $\text{mg}\cdot\text{L}^{-1}$ increased strawberry fruit number and yield, but further increases from 300 to 400 $\text{mg}\cdot\text{L}^{-1}$ led to reductions (Ebrahimi et al. 2012). While the reported optimum K concentrations for hydroponic strawberry cultivation range from 300 to 450 $\text{mg}\cdot\text{L}^{-1}$ in hydroponic systems using soilless substrates (Ebrahimi et al. 2012; Tohidloo et al. 2018), our results suggest that the optimum K concentration for plant growth and fruit yield of the two strawberry cultivars in this study using a deep water culture hydroponic system may be $\leq 117 \text{ mg}\cdot\text{L}^{-1}$.

The discrepancy in the optimum K concentrations for plant growth and fruit yield may be at least partly attributed to the N concentration or the K:N ratio because the crop response to K is influenced by the N concentration (Zhang et al. 2010). Increased biomass accumulation from K applications was enhanced by higher N concentrations, suggesting that sufficient N is needed to fully benefit from higher K concentrations (Li et al. 2022; Ye et al. 2021). In addition, increasing the K concentration under N-deficient conditions did not impact strawberry fruit yield (Li et al. 2013). In previous studies (Ebrahimi et al. 2012; Tohidloo et al. 2018), the optimum K was investigated using the Hoagland solution,

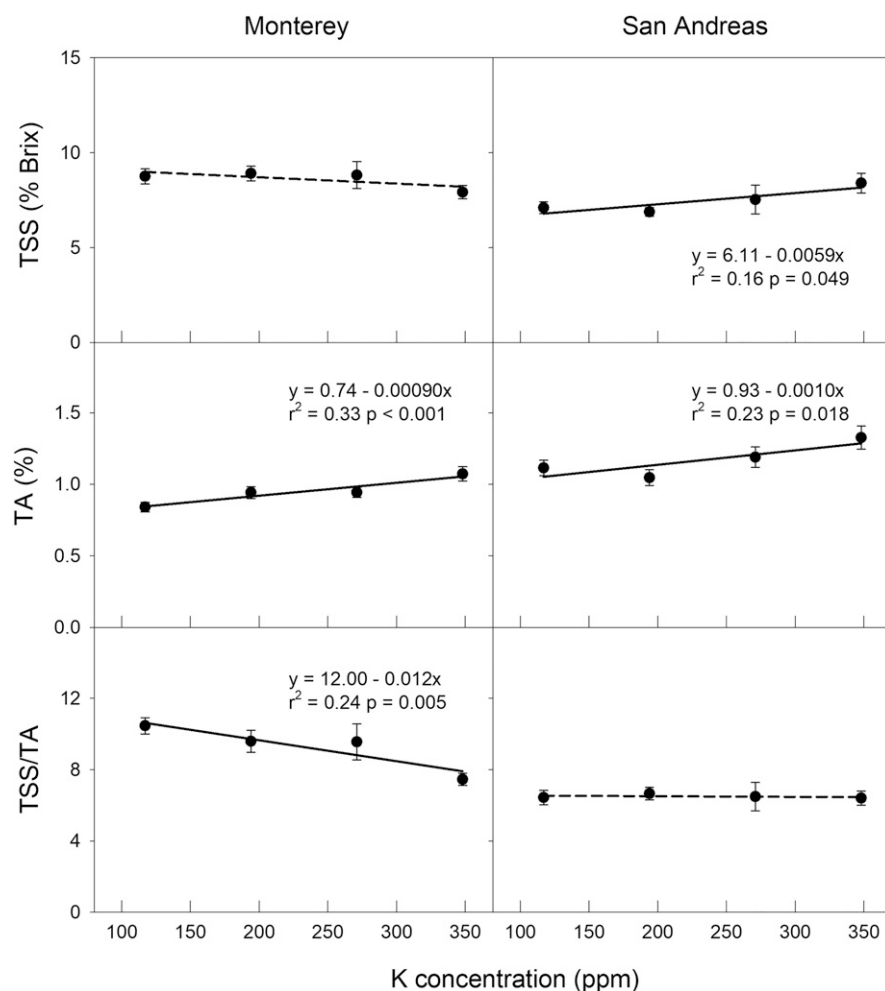


Fig. 5. Effects of potassium (K) concentrations on total soluble solids (TSS), titratable acidity (TA), and TSS:TA ratio in strawberries 'Monterey' and 'San Andreas' during the harvesting period. Each data point represents the mean and standard error of two replications, with four samplings per replication for 'Monterey' (n = 8) and three samplings per replication for 'San Andreas' (n = 6). Regression equations, r^2 values, and P values are presented when statistically significant at $P < 0.05$ (solid line), but not when nonsignificant (dashed line).

which contains an N concentration of approximately 200 mg·L⁻¹ at full strength and K:N ratios ranging from 1.5:1 to 2.25:1 at the optimum K concentration. In our study, we used the Yamazaki strawberry nutrient solution, which provides a lower N concentration of 77 mg·L⁻¹, and tested K:N ratios of 1.5 to 4.5 while keeping N constant. Additionally, previous studies (Ebrahimi et al. 2012; Tohidloo et al. 2018) irrigated soilless media with a nutrient solution, providing a consistent N supply for plants. In contrast, this study used a deep water culture hydroponic system, where N in the nutrient solution may have decreased over time as the plants grew. While the reported optimum K:N ratios vary, including 1.7:1 to 2.0:1 (Morgan 2006), 2.6:1 (Nakro et al. 2023), and 2.8:1 (Maldonado et al. 2012), our results suggest that, given a low N concentration, the tested K:N ratios of 2.5:1 or higher may be too high to realize benefits from increases in the K concentration.

Increasing the K concentration in the nutrient solution from 117 to 348 mg·L⁻¹ resulted in a 22% increase in the leaf K concentration

and decreased the leaf Ca concentration by 29% and the leaf Mg concentration by 17% (Fig. 2). Additionally, K, Ca, and Mg are all cations that compete for uptake by plant roots (Rhodes et al. 2018). High levels of K can hinder the absorption of Ca and Mg because K ions outcompete them for entry into the plant roots (Haynes and Goh 1987; Lieten 2006; Nazarijeljou et al. 2019; Rhodes et al. 2018). In strawberry 'Red Gauntlet', increasing the K application from 0 to 400 kg·ha⁻¹ decreased the leaf Ca concentration by 34% and the leaf Mg concentration by 22% and increased the leaf K concentration by 10% (Haynes and Goh 1987). Therefore, the decrease in leaf Ca and Mg concentrations with increasing K concentrations in this study could be attributed to cationic antagonism, which reduced the uptake of Ca and Mg. Despite the reduced uptake of Ca and Mg at higher K concentrations, leaf Ca and Mg concentrations remained within their sufficient ranges (Campbell 2000) (Supplemental Table 2).

In this study, we observed a linear decrease in fruit diameter, fruit length, and fruit

fresh mass in both cultivars by increasing the K concentration from 117 to 348 mg·L⁻¹ (Fig. 4). Water accumulation in cells is the main factor in fruit volumetric growth (Matthews and Shackel 2005). High salinity in the nutrient solution can limit root water uptake and water movement to the fruit, thereby restricting fruit growth (Zhang et al. 2016). In our study, increasing the K concentration from 117 to 348 mg·L⁻¹ increased the nutrient solution EC from 1.0 to 1.9 dS·m⁻¹ (Table 1). In alpine strawberries (*Fragaria vesca* L.), increasing the EC from 1.3 to 2.2 dS·m⁻¹ decreased plant water uptake by 22% and fruit fresh mass by 9% (Caruso et al. 2011). Moreover, in strawberries 'Albion', 'Benicia', 'Monterey', and 'Ventana', increasing the EC from 0.7 to 2.5 dS·m⁻¹ decreased the percentage of marketable-sized fruits (≥ 10 g) by 30% to 64%, indicating a reduction in individual fruit size (Ferreira et al. 2019). These findings suggest that the concurrent increase in EC with increasing K may have contributed to the reduced fruit size and fresh mass.

The concentrations of sugars and acids in strawberries are considered important quality factors (Kallio et al. 2000). The TSS is a reliable measure of sugar content because soluble sugars make up the majority of the soluble solids in strawberries (Menzel 2022; Pistón et al. 2017). The TA reflects the total acidity in the fruit and correlates well with the levels of organic acids, including citric and malic acids (Ikegaya 2024; Patel et al. 2023). Additionally, K can influence the concentrations of sugars and acids in fruits by regulating sucrose metabolism and sink strength, enzyme activities involved in sugar and organic acid metabolisms, and phloem translocation (Alva et al. 2006; Shen et al. 2017; Wang et al. 2024). Previous studies have shown that increasing the K concentration up to the optimum concentration can enhance TSS and TA. For example, increasing the K concentration from 196 to 431 mg·L⁻¹ increased TSS from 9.3 to 10.6 (Preciado-Rangel et al. 2020). Increasing the K concentration from 235 to 350 mg·L⁻¹ in strawberry 'Camarosa' and 450 mg·L⁻¹ in strawberry 'Selva' increased TSS (Tohidloo et al. 2018). In strawberry 'Parus', increasing the K concentration from 235 to 450 mg·L⁻¹ increased TA (Tohidloo et al. 2018). In this study, increasing the K concentration in the nutrient solution from 117 to 348 mg·L⁻¹ increased the TSS content in 'Monterey' and increased TA in both 'Monterey' and 'San Andreas' (Fig. 5), indicating that K had positive effects on TSS and TA, even at higher concentrations that did not enhance plant growth, fruit yield, or fruit size. Salinity in the nutrient solution can also affect TSS and TA (Zhang et al. 2016). Smaller fruits under salinity stress may have less water content, which can concentrate the sugars and acids, leading to higher TSS and TA (Al-Ismaïly et al. 2014; El-Mogy et al. 2018). In this study, the linear increases in TSS in 'Monterey' and TA in both 'Monterey' and 'San Andreas' were accompanied by linear decreases in fruit fresh mass, fruit diameter, and fruit length

(Fig. 4). This suggests that the increases in TSS and TA were at least partly associated with smaller fruit size, which resulted from the higher EC caused by the increased K concentration. A similar observation was reported for alpine strawberries, for which increasing EC from 1.3 to 2.2 dS·m⁻¹ decreased fruit fresh mass but increased TSS, sucrose, glucose, fructose, and citric acid (Caruso et al. 2011).

A key metric for evaluating overall strawberry fruit flavor is the TSS:TA ratio (Gunness et al. 2009; Ikegaya 2024; Patel et al. 2023). Because organic acids contribute to sourness and can mask sweetness, a higher TSS:TA ratio indicates a sweeter fruit (Ikegaya 2024). A few previous studies reported that K had minimal effects on the TSS:TA ratio (Ebrahimi et al. 2012; Nakro et al. 2023; Wu et al. 2020). In this study, increasing the K concentration from 117 to 348 mg·L⁻¹ did not affect the TSS:TA ratio in 'San Andreas' but linearly decreased the TSS:TA ratio in 'Monterey' (Fig. 5). This was because increasing the K concentration led to a greater increase in TA in both cultivars compared with the slight increase in TSS in 'San Andreas' and the minimal change in TSS in 'Monterey'. Our results indicate that TA was more responsive to K than TSS, suggesting that higher K levels could adversely affect the TSS:TA ratio and, thus, the sweetness of strawberries.

Conclusions

In conclusion, increasing the hydroponic nutrient solution K concentration from 117 to 348 mg·L⁻¹ or the K:N ratio from 1.5 to 4.5 in the Yamazaki strawberry nutrient solution had minimal effects on plant growth in strawberry cultivars Monterey and San Andreas and on total fruit yield in 'Monterey'. Increasing the K concentration reduced total fruit yield in 'San Andreas' and negatively impacted individual fruit fresh mass, fruit diameter, and fruit length in both cultivars. In 'Monterey', increasing the K concentration also decreased the TSS:TA ratio. The N concentration of 77 mg·L⁻¹ in each treatment may have been insufficient for elevated K concentrations to improve plant growth and fruit production. In addition, elevated nutrient solution EC with higher K concentrations may have reduced water movement into fruits and, thus, fruit size. Our results suggest that increasing the K concentration and K:N ratio in the Yamazaki strawberry nutrient solution did not provide any beneficial effects on plant growth, fruit yield, or fruit quality in either cultivar. The lack of positive effects from increasing K could be attributed to the potential N limitation and the increased nutrient solution EC.

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