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Yield and Fruit Quality of 'Albion' and 'San Andreas' Strawberry in Hydroponic Culture in Alabama, United States Over a Single Season

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Abstract

Day-neutral strawberry cultivars Albion and San Andreas were cultivated hydroponically in a climate-controlled greenhouse (temperature and light regulated) to assess fruit quality and anthocyanin composition, which are important attributes for flavor and color (visual appeal), respectively. Fruits were collected from 6 Feb 2023, until 18 May 2023, at Auburn University, AL. Soluble solids content (SSC), titratable acidity (T_{acid}), pH, total phenolics (TPC), and anthocyanins [total anthocyanins (TAC), cyanidin-3-glucoside (C3G), pelargonidin-3-glucoside (P3G), pelargonidin-3-rutinoside (P3R), pelargonidin-3-malonylglucoside (P3M)] were determined from the juice of thawed frozen fruits. Average fruit yield (F_{yield}; g·plant^{-1}) was similar between cultivars. Both cultivars were similar for SSC, T_{acid}, TPC, TAC, and the major pigment (P3G) when averaged across days after transplanting (DAT). Pelargonidin-based pigments predominantly characterized the anthocyanin profile. Minor pigments differed, with more C3G (mg 100 g/fresh weight) in 'Albion' than in 'San Andreas' (0.39 and 0.18, respectively), whilst 'San Andreas' had more P3R (mg 100 g/fresh weight) than 'Albion' (2.26 and 1.81, respectively). Plant age (DAT, non-replicated) influenced SSC, T_{acid}, and most of the anthocyanins. F_{yield}, T_{acid}, and SSC were higher in plants at 140 DAT (early spring), but lower in plants at 180 DAT (late spring), indicating a potential plant age effect on fruit productivity and quality. Correlation analysis indicated a robust positive correlation between TAC, C3G, pelargonidin anthocyanins (P3G, P3R, P3M), and F_{yield}, whereas F_{yield} was inversely correlated with T_{acid} and TPC. Our results indicate that strawberry fruit quality is influenced by cultivar-specific pigment profiles, seasonal variations, and yield interactions, highlighting the need to balance productivity with market-preferred traits in hydroponic greenhouse systems.

Introduction

The increasing global demand for strawberries is reflected in a 200% rise in production over the past three decades, rising from 3.49 MMT in 1994 to 10.49 MMT in 2023 (FAO 2023). Strawberries (*Fragaria* × *ananassa* Duch.) are valued for their flavor, aroma, and texture. They are also abundant in nutrients and phytochemicals, including vitamin C, anthocyanins and phenolic compounds like ellagic acid, all of which are linked to potential health advantages (Zeliou et al. 2018). In comparison to other small fruits, strawberries are relatively low in anthocyanins; yet these pigments provide fruit coloration, consumer attractiveness, and possible antioxidant benefits (Cai et al. 2023).

Strawberry fruit quality is determined by genetic and environmental factors (Matsushita et al. 2016). Cultivar genetics can impact anthocyanin amount and composition, phenolic content, sweetness, and acidity, whereas production strategies influence nu-

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trient availability, temperature, and light exposure (Pinheiro et al. 2021). Hydroponic crop production method relies on nutrient solutions instead of soil, providing precise control of environmental and nutritional parameters, reduces the prevalence of soilborne diseases, and prolongs the production period (Agrawal et al. 2020). Nonetheless, a hydroponic system does not eradicate all abiotic and biotic stresses, and its influence on fruit biochemical profiles may vary by cultivar (Alavi et al. 2025; Whitaker et al. 2011). In 2019, strawberry production utilization in the U.S. under hydroponic systems was 83.32 MT (USDA-NASS 2020), accounting for only 0.008% of the total 1,020,582.83 MT (USDA-NASS 2022).

Global interest in hydroponic strawberry cultivation is rising as producers pursue sustainable methods to produce high-quality fruit in controlled environments (Agrawal et al. 2020). Understanding the biochemical responses of cultivars to hydroponic environments is crucial for optimizing production strategies and meeting consumer quality standards (Alavi et al. 2025). Day-neutral cultivars respond to temperature rather than day length are ideal for a hydroponic system under temperature control and offer a prolonged (up to a year) season for production (Mazon et al. 2023).

In this study, two day-neutral cultivars, Albion and San Andreas were selected for their proven adaptability to controlled hydroponic systems (Chaves et al. 2017). Plants were cultivated in a greenhouse hydroponic system with supplemental lighting and temperature regulation. The fruit of ‘Albion’ is conical and dark red (Shaw and Larson 2006) with a soluble solids content (% SSC) ranging from 8.9 to 9.0 (Parehwa et al. 2021). In contrast, ‘San Andreas’ produces large, wedge-shaped light red fruit (Shaw and Larson, 2009) with a % SSC range of 8.0 to 8.8 (Parehwa et al. 2021). Both cultivars were chosen to evaluate their performance under regulated hydroponic conditions.

Previous evaluations of ‘Albion’ and ‘San Andreas’ strawberries have centered on yield and fruit size as key factors influencing production under hydroponic system (Hernandez Martinez 2023; Parehwa et al. 2021). This research hypothesized that: 1) cultivar differences exist between quality and color attributes in strawberries; 2) these various quality and color variables differ in how much they vary over the season; and 3) quality variables are related to yield. Therefore, in this study, we examined fruit quality and yield aspects of these two cultivars cultivated hydroponically under greenhouse in Alabama growing conditions.

Materials and Methods

Plant material and growing conditions. Plug plants of the day-neutral strawberry cultivars Albion and San Andreas (Balamore Farm Ltd., Great Village, NS, Canada) were planted on 13 Sep 2022, in soilless coir substrate slabs (Riococo Worldwide, Irving, TX, USA) within a greenhouse at the Plant Science Research Center, Auburn University, Auburn, AL, USA (32°35′17″N 85°29′20″W). The experimental design employed was a randomized complete block design with three blocks per cultivar (64 plants per block per cultivar) with a total of 192 plants per cultivar. Plants were cultivated on an elevated gutter system measuring 20 cm in width, 65 cm in height, and 894 cm in length, organized on metal tables, with eight plants allocated per slab. The greenhouse measured 11 m x 10 m and was outfitted with forced-air natural gas heating, evaporative cooling, and supplementary high-pressure sodium lighting (100 $W \cdot m^{-2}$, positioned 2 m above the plant canopy) to sustain a daily light integral of 20 $mol \cdot m^{-2} \cdot d^{-1}$. Day and night temperatures were maintained at 15–25 °C and 12–20 °C, respectively, with a relative humidity of 60–70%. The average photosynthetic photon flux density (PPFD) of the light system for the entire season was 210 $\mu mol \cdot m^{-2} \cdot s^{-1}$. White cloth (polypropylene) was applied as a shade to regulate the increase of temperature from ambient light at 200 days after transplanting (DAT; mid-spring). The air temperature and photosynthetic active radiation (PAR) were recorded at 15 minutes interval using a mini weather station (Watchdog, Spectrum Technologies, Inc. San Dimas, CA, USA) placed at the center of the greenhouse. Plants were fertigated bi-hourly by drip irrigation. Three stock solutions were used by filling water in a 20 L bucket per stock solution. The first bucket was filled with fertilizer solution (ppm) which contained 80,000 nitrogen (N), 120,000 phosphorus (P), 320,000 potassium (K), 3,500 magnesium (Mg), 5,000 sulfur (S), 2,800 iron (Fe), 1,000 manganese (Mn), 200 zinc (Zn), 200 copper (Cu), 500 boron (B), and 7 molybdenum (Mo). The second bucket was filled with calcium nitrate $Ca(NO_3)_2$ containing 190,000 ppm calcium (Ca) and 155,000 ppm N. The third bucket was filled with 35% sulfuric acid (H_2SO_4) for pH regulation (Hernández-Martínez et al. 2023). Ten individual leaf blade samples per cultivar were collected per month for leaf tissue macronutrient (N, P, K, Ca, Mg, S) analysis using inductively coupled plasma analysis (Brookside Laboratories, New Bremen, OH, USA) following the method of Odom and Koné (1997). Plants produced fruit from 6 Feb 2023 (146 DAT) to 18 May 2023 (247 DAT).

Fruit harvest and analysis. Mature fruits were harvested and weighed three times per week to obtain fruit yield (F_{yield}; g·plant^{-1}) from 192 plants per cultivar. Marketable fruit was defined as exceeding 12 grams per fruit, possessing an optimal shape, and devoid of flaws or disease (Hernández Martinez 2023). Biochemical analysis utilized weekly harvests from 6 Feb 2023, until 18 May 2023 (146 to 247 DAT) with data from ten samples from each harvest recorded separately for statistical analysis (n = 18 harvests).

For sample preparation and analysis, bags of frozen fresh fruit (6-10 berries per bag per cultivar per harvest) were thawed and juice collected and spun in a centrifuge (Sorvall Legend RT, Waltham, MA, USA) at 1800 ×*g* and 5 °C to remove debris. SSC was determined with a PAL-1 refractometer (Atago, Bellevue WA, USA). For titratable acidity, 0.5 mL juice was diluted with 24.5 mL distilled water, mixed, and a 0.5 mL aliquot placed on an Atago F5 acid refractometer using the 'strawberry' setting. Juice pH was determined via a pH meter (Thermo Scientific™ Orion Star™ A211, Waltham, MA, USA) and electrode (Thermo Scientific™ Orion™ Ross, Waltham, MA, USA). Aliquots of 0.4 mL strawberry juice mixed with 1 mL of acidified solvent were used for anthocyanin and total phenolics content (TPC; Haynes et al. 2025). TPC was determined using a microplate (Biotek Powerwave XS, Wanooski, VT, USA) using the Folin-Ciocalteu method (Lester et al. 2012).

Anthocyanin content and profiles were determined using a Hitachi LaChrom HPLC (Hitachi Ltd., Tokyo, Japan), equipped with a UV-VS diode array detector (DAD), controlled temperature auto sampler (4 °C), and column compartment (30 °C). D-2000 software (Hitachi Ltd., Tokyo) was used as the system run controller and for data processing. Aliquots for HPLC were spun at 13,500 ×*g* 25 °C in a microfuge (Eppendorf, Framingham, MA, USA) prior to LC preparation. Supernatant aliquots of 1 mL were filtered through 0.2 µm PTFE membranes (Fisher Scientific, Pittsburgh, PA) into 2 mL amber vials (Agilent), flushed with nitrogen gas and capped. Samples of 10 µL were injected into a reversed phase C18 column (Synergi 4µ Hydro-RP 80Å, 250 x 4.6 mm, Phenomenex, Torrance, CA, USA). The mobile phase consisted of 5% formic acid in water (A) and 100% methanol (B) with a flow rate of 1 mL/min using a step gradient of 0 min, 10% B; 5 min, 15% B; 15 min, 20% B; 20 min, 25% B; 25 min, 30% B; 45 min, 60% B; 47 min, 10% B; 60 min, 10% B. Compound concentrations were determined using standard curves generated by injecting 5 µL of 0.0625 to 0.5 mg·mL^{-1} preparations of cyanidin 3-glucoside, pelargonidin-3-glucoside and pelargonidin-3-rutinoside as external standards. Content is reported as mg of pelargonidin-3-glucoside equivalents per 100 g fresh weight (fwt). Sums of anthocyanins were calculated to obtain total anthocyanin content and each anthocyanin calculated as a percentage of the total anthocyanin content to normalize values across genotypes.

Statistical analysis. Data analysis was performed using SAS 9.4 (SAS Institute, Cary, NC, USA) employing several statistical approaches. Variations in anthocyanin and phenolic content were analyzed using the Generalized Linear Mixed Models Procedure (PROC GLIMMIX) with mean comparisons between cultivars and DAT conducted using Tukey's Honestly Significant Difference (HSD) test at $P < 0.05$. *P*-values for each parameter by cultivar and DAT were obtained from the Type III tests table to evaluate the overall significance of each fixed effect. Pearson correlation and principal component analysis (PCA) were performed using the PROC CORR and PROC PRINQUAL procedures, respectively in SAS 9.4. A monotonic transformation was applied to the variables soluble solids content (SSC), pH, titratable acidity (T_{acid}), total phenolics (TPC), total anthocyanin (TAC), cyanidin-3-glucoside (C3G), pelargonidin-3-glucoside (P3G), pelargonidin-3-rutinoside (P3R), pelargonidin-3-malonylglucoside (P3M) and F_{yield} to preserve the rank order of the data and satisfy linearity assumptions. Two principal components were extracted (n=2), accounting for 76.74% of the total variance (PC1 = 58.62%, PC2 = 18.12%). The PCA was used to assess correlations among anthocyanins, phenolic compounds, F_{yield}, and fruit quality characteristics across cultivars and DAT.

Results and Discussion

Air temperature, light condition, and leaf macronutrient concentration over the season. The air temperature and PAR over DAT were depicted in Fig. 1A and Fig.1B, respectively. Leaf macronutrient concentrations (%) range over DAT were the following: N (2.05 - 3.09 and 2.05 - 2.93), P (0.42 - 0.62 and 0.32 - 0.62), K (1.68 - 2.67 and 1.53 - 2.85), Ca (0.51 - 1.33 and 0.73 - 1.35), Mg (0.25 - 0.51 and 0.29 - 0.44), S (0.16 - 0.31 and 0.17 - 0.33) for 'Albion' and 'San Andreas', respectively. N and S (except during early plant age) were not within the sufficiency range (N: 3.0 - 4.0, P: 0.2 - 0.4, K: 1.5 - 3.0, Ca: 0.4 - 1.5, Mg: 0.25 - 0.5, and S: 0.20 - 0.31) (Mills and Jones 1996) for both cultivars.

Cultivar differences between quality and color attributes. Mean values of fruit composition variables including SSC, T_{acid}, and pH were similar for 'San Andreas' and 'Albion' strawberries (Table 1). In this hydroponic greenhouse setting, 'Albion' and 'San Andreas' showed no significant differences in total anthocyanin content (Table 1). Pelargonidin-3-glucoside was dominant in both strawberry cultivars (23.09 mg/100 g, representing 90.4% of total anthocyanin content (Fig. 2A). The pigments P3R, C3G and P3M (Fig. 2B-D) made up a minor fraction with values of 1 to 4 mg/100 g (9.6 %). The two cultivars displayed contrasting profiles for the minor anthocyanins. 'San Andreas' had elevated levels of P3R relative to 'Albion' (2.26 ± 0.15 vs. 1.8 ± 0.15 mg/100 g) (Fig. 2B; Table 1), whereas 'Albion' contained a substantially higher concentration of C3G compared to 'San Andreas' (0.39 ± 0.04 vs. 0.18 ± 0.04 mg/100 g) (Fig. 2C; Table 1). While no significant difference found on P3M between the two cultivars Albion and San Andreas (0.15 ± 0.02 and 0.09 ± 0.02 mg/100 g, respectively; Fig. 2D; Table 1).

No significant differences were found in TPC between 'Albion' and 'San Andreas' (Table 1) with mean values of about 100 mg/100 g fwt, and with slight differences with DAT. Higher TPC values (170-233 mg/100 g) were reported for these cultivars grown in greenhouses (Chaves et al. 2017; Mazon et al., 2023). Chiomento et al. (2023) reported higher values of TPC as rutin equivalents in greenhouse grown 'San Andreas' compared to 'Albion' strawberries, which corresponds to 333 and 202 mg/100 g fwt. 'Albion' and 'San Andreas' fruit grown in field production in low tunnels were considerably higher (290-590 mg/100 g fwt) and were higher for the earlier harvest date (Lester et al. 2012). Our lower val-

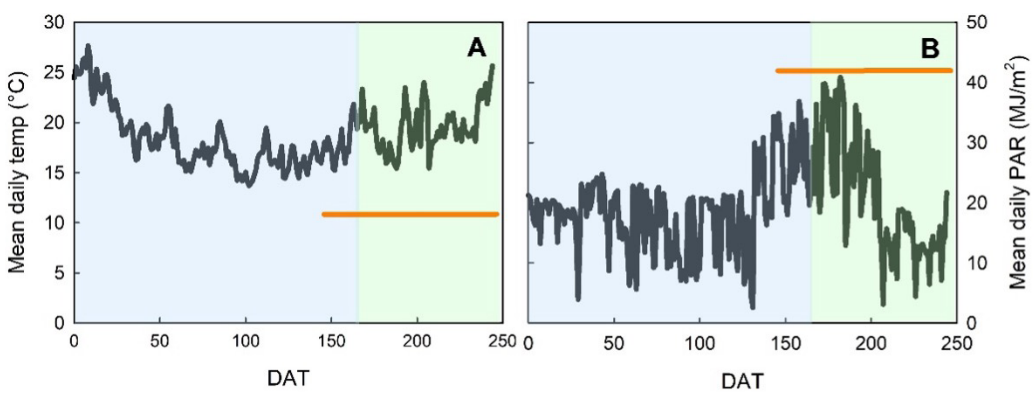

Figure 1. Mean daily temperature (**A**) and photosynthetic active radiation (PAR) (**B**) from 13 Sep 2022 to 18 May 2023. Strawberry transplants were placed in greenhouse at 0 days after transplanting (DAT). The light blue shaded area signifies late winter season while the light green shaded area indicates the spring season. Shade cloth was applied at 184 DAT. Orange line indicates fruit harvest period.

Table 1. Cultivar and DAT effects on composition of fully ripe strawberries grown in a non-recirculating hydroponic system in Auburn, AL, in 2023.

Source of Variation	Cultivar (1 df)			DAT (17 df)	
Variable[i]	CV		P values	Mean ± SE	P values
	'Albion'	'San Andreas'			
SSC	15.46	20.57	ns[ii]	6.93 ± 0.55	0.002**
pH	1.94	2.15	ns	3.42 ± 0.04	0.024*
T_{acid}	9.78	10.13	ns	0.88 ± 0.04	0.001***
SSC/T_{acid}	17.18	19.22	ns	7.91 ± 0.73	0.011*
TPC	7.37	9.06	ns	101.46 ± 3.28	<0.001***
TAC	31.50	25.83	ns	25.54 ± 2.66	<0.001***
C3G	50.70	77.61	0.001**	0.29 ± 0.15	0.651ns
P3G	31.23	25.57	ns	23.09 ± 2.47	<0.001***
P3R	32.45	28.89	0.039*	2.04 ± 0.28	0.001**
P3M	80.37	86.09	ns	0.12 ± 0.04	<0.001***

[i]**SSC** = % Soluble solids content, **T_{acid}** = Titratable acidity (% citric acid equivalents), **TPC** = Total phenolic content [mg gallic acid equivalents per 100 g fresh weight (fwt)], **TAC** = Total anthocyanin (mg P3G equivalents per 100 g fwt), **C3G** = cyanidin-3-glucoside (mg/100 g fwt), **P3G** = pelargonidin-3-glucoside (mg/100 g fwt), **P3R** = pelargonidin-3-rutinoside (mg/100 g fwt), **P3M** = pelargonidin-3-malonylglucoside (mg/100 g fwt), and **DAT** = days after transplanting.
[ii]Asterisks *, **, and *** indicate significant difference using Tukey's Honestly Significant Difference (HSD) multiple comparison test applied to LS-means at $p < 0.05$, $p < 0.01$, or $p < 0.001$, respectively. ns (not significant) indicates that the statistical difference was $p > 0.05$.

ues may be from use of juice rather than fruit flesh, as achenes can add to TPC value (Aaby et al. 2007).

In red strawberry fruit, P3G is the predominant pigment (Haynes et al. 2025). In this study, the average TAC was similar for the fruit of day neutral cultivars 'Albion' and 'San Andreas' (Table 1). Values varied from 10 to 40 mg/100 g over DAT, with mean values of 20-25 similar to those reported by Chaves et al. (2017), but higher than the reports of Chiomento et al. (2023) (4.6 and 2.1 for 'Albion' and 'San Andreas', respectively). Discrepancies in TAC are prevalent and can be attributed to genetic-environment interactions and/or methodologies (Whitaker et al. 2011).

Reported amounts of P3G in 'Albion' and 'San Andreas' vary among studies. Chaves et al. (2017) reported slightly elevated P3G (18.6 vs 16.2 mg/100 g of fresh weight) in 'Albion' as compared to 'San Andreas'. These values are slightly lower than the average 22.7-23.5 mg/100 g of fresh weight found in our study and may reflect the higher greenhouse temperatures in our study. In contrast, Mazon et al. (2023) noted greatly increased levels of P3G (mg/100 g of fresh weight) in 'San Andreas' compared to 'Albion' (77.4 and 42.5, respectively). In that study, strawberries were grown in plastic tunnels in Brazil and may have had more UV light. Strawberry anthocyanin content can be greatly affected by small differences in ripeness, relative season (late vs early), and environmental factors such as light intensity and temperature. Intense light exposure, together with warm days and cool nights, is optimal for anthocyanin formation, as these conditions stimulate essential biosynthetic genes such as *FaMYB10*, *FaHY5*, and *FaBBX22*, which are pivotal to the flavonoid pathway (Wang et al. 2025). Furthermore, elevated air temperatures from 20/15 °C to 30/15 °C, day/night, have been shown to inhibit anthocyanin accumulation in strawberries by downregulating the expression of biosynthetic genes, especially in fruit skin and flesh (Matsushita et al. 2016).

Other pelargonidin pigments such as P3R and P3M, have been reported in varying amounts among strawberry cultivars (Perkins-Veazie et al. 2016). C3G, which is derived from cyanidin anthocyanidins rather than from pelargonidin anthocyanidins, is commonly found in small amounts in strawberry fruit, with content differing with cultivar (Lin et al. 2018). While C3G is thought to have a negligible impact on strawberry color (Lin et al. 2018), this pigment may augment color intensity (Chaves et al. 2017). In this study, C3G levels were elevated in

'Albion' compared to 'San Andreas'.

P3R markedly elevated in 'San Andreas' compared to 'Albion', can significantly influence fruit coloration, intensifying red-orange colors (Lin et al. 2022). Shading markedly influences strawberry fruit coloration, indirectly suggesting that P3R accumulation may be susceptible to light conditions, necessitating further research on environmental sensitivity of P3R (Tang et al. 2020). The anthocyanin P3M was numerically higher in 'Albion' than 'San Andreas' (Fig. 2D), marking potentially the first report directly contrasting this pigment between the two cultivars.

Fruit quality and color variables over the season. DAT had a significant influence on SSC, pH, T_{acid}, SSC/T_{acid} ratio, TPC, TAC, and pelargonidin anthocyanins (P3G, P3R, P3M; Table 1). The concentrations of anthocyanins and phenolics displayed a bimodal pattern with peaks at 167 and 247 DAT for anthocyanins (Fig. 3A) and at 197 and 223 DAT for phenolics (Fig. 3B). When plotted against plant age from late winter to spring, all assessed anthocyanins (Fig. 3C-F) exhibited temporal variation, with the two cultivars adhered to comparable overall patterns over DAT. Although the extent of change differed marginally between cultivars, the timing of peaks and the overall trend of rise or decline were predominantly uniform (Figs. 3A-F). Conversely, SSC and T_{acid} exhibited a unimodal distribution, peaking at 197 and 223 DAT, respectively (Figs. 3G, H).

SSC reached a maximum between 180 and 220 DAT (Fig. 3G), corresponding to minimal harvest weights (Fig. 3A). Overall, SSC was generally 6-8%, especially between 140 and 180 DAT. Although below the desired 10% SSC for strawberries (Jouquand et al. 2008), values are similar to those reported by others for these cultivars (Chaves et al. 2017; Parehwa et al. 2021). 'San Andreas' was slightly lower than 'Albion' in SSC; this has also been noted by Chaves et al. (2017) and Parehwa et al. (2021) in other studies. Titratable acidity increased from 0.8% to >1% for both cultivars at 180 to 240 DAT, and declined slightly after 240 DAT. This T_{acid} fluctuation might be due to the gradual increase of temperature in late spring (Fig. 1A). The slight reduction of fruit

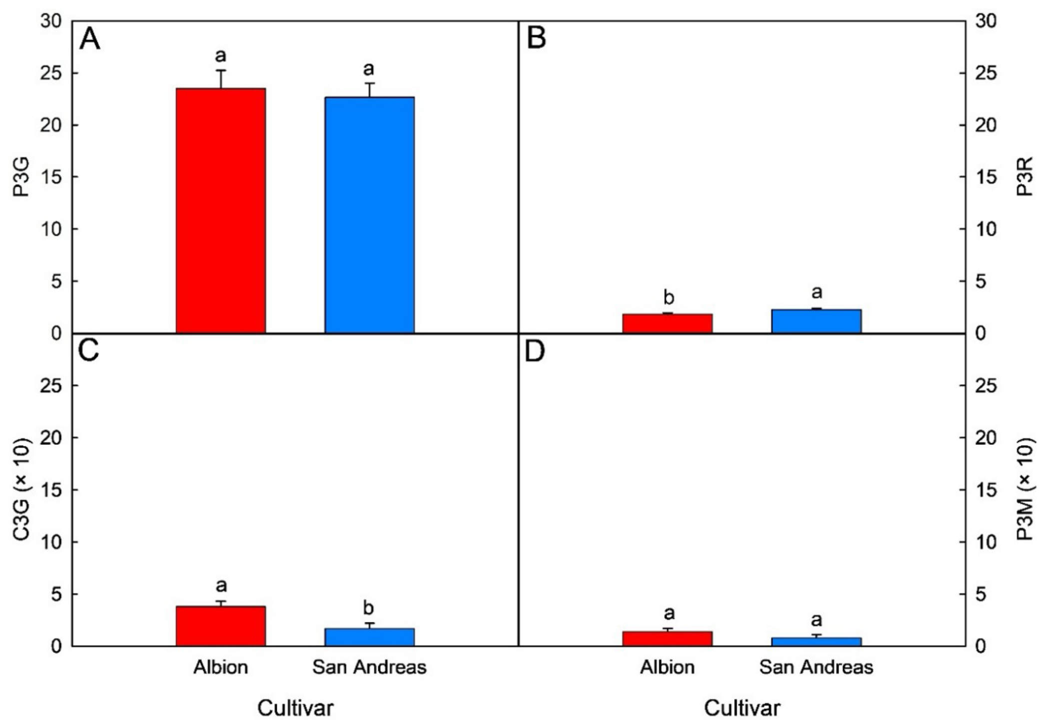

Figure 2. Mean values for 'Albion' and 'San Andreas' anthocyanin profiles (mg/100 g fresh weight) pelargonidin-3-glucoside (P3G; **A**), pelargonidin-3-rutinoside (P3R; **B**), cyanidin-3-glucoside (C3G; **C**) and pelargonidin-3-malonylglucoside (P3M; **D**) averaged over days after transplanting. Data represent the mean ± standard error (represented as bars) of 18 harvest dates for each cultivar. Data for cultivars were subjected to Generalized Linear Mixed Models Procedure (PROC GLIMMIX) and compared with Tukey's Honestly Significant Difference (HSD) test, where different letters represent significant differences, P<0.05. Pigment values C3G and P3M were multiplied x 10 to enable comparison to P3G and P3R.

SSC found between 197 to 247 DAT could be due to the infestation of spider mites and thrips during this period. Mite damage can hinder photosynthetic efficiency and nutrient absorption, whereas regrowth frequently results in a temporary dilution of assimilates, both of which can exacerbate the decrease in SSC (Livinali et al. 2014).

A gradual rise in temperature (Fig. 1A) can in-

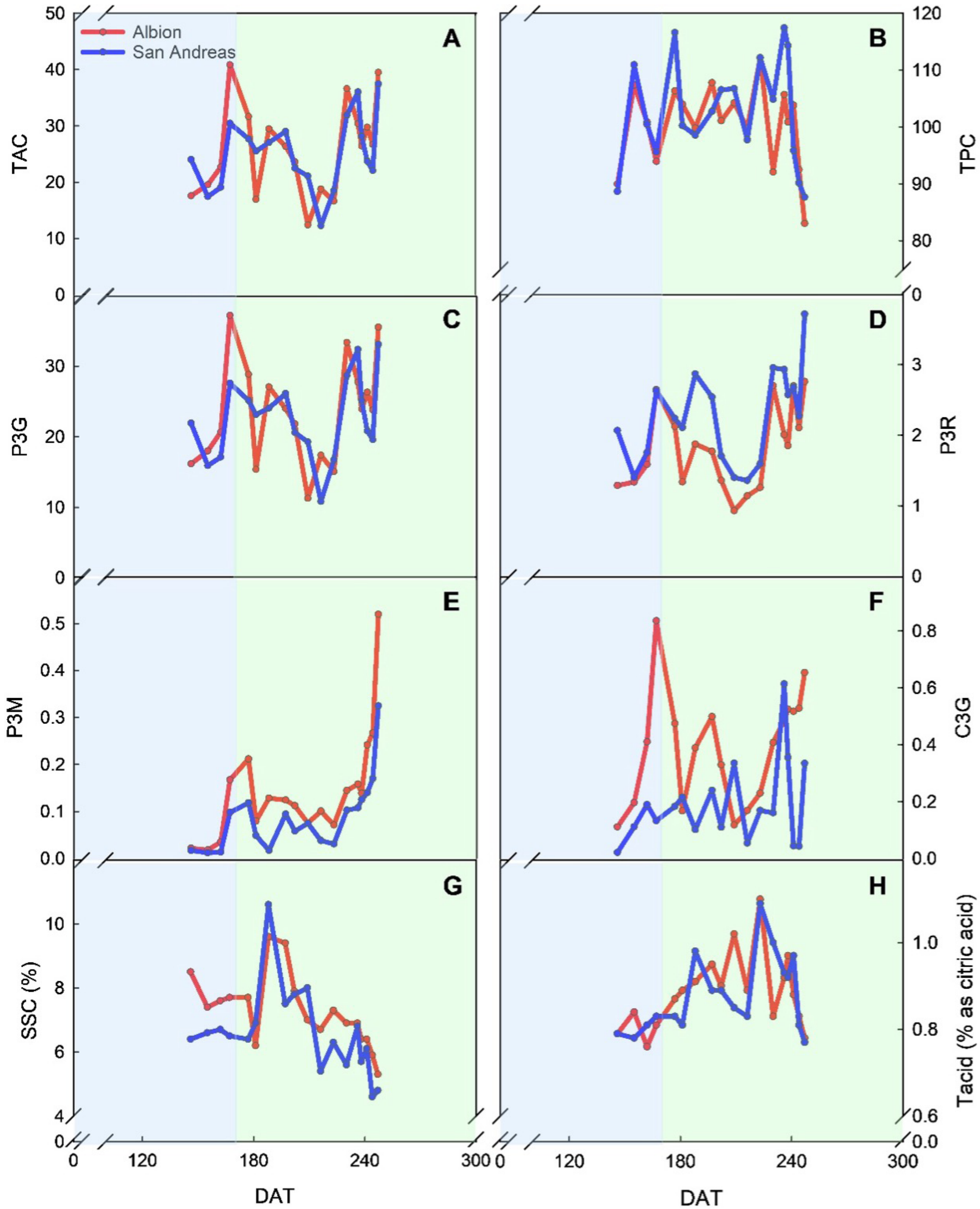

Figure 3. Days after transplanting (DAT) influence on composition of fully ripe fresh strawberry cultivars Albion and San Andreas grown in the greenhouse, with (**A**) TAC (mg P3G equiv/100 g fwt); (**B**) TPC (mg GA/100 g fwt), and anthocyanins (mg/100 g fwt) of (**C**) pelargonidin-3-glucoside, (**D**) pelargonidin-3-rutinoside, (**E**) pelargonidin-3-malonylglucoside, (**F**) cyanidin-3-glucoside. Soluble solids content of fruit is shown in (**G**) and titratable acidity in (**H**). The light blue shaded area signifies late winter season while the light green shaded area indicates the spring season.

crease fruit respiration, leading to the degradation of carbohydrates, and a decline in minerals (Menzel 2022). In addition, increased light intensity between 150 and 200 DAT before shade installation likely led to enhanced T_{acid} (Qiu et al. 2024). Subsequent shading diminished PAR from 28–33 to 10–18 $MJ \cdot m^{-2} \cdot day^{-1}$, presumably decreasing SSC (Qiu et al. 2024). The reduction in SSC from 197 to 247 DAT may be associated with diminishing leaf macronutrient concentrations, particularly P, which exhibits a strong correlation with SSC ($r = 0.95$; Cao et al. 2015) and consistently low N levels, which can hinder photosynthesis and carbohydrate production, resulting in decreased SSC and smaller fruit (Livinali et al. 2014). Moreover, infestations of spider mites and thrips during this period may have further intensified SSC loss (Livinali et al. 2014). T_{acid} and SSC exhibited no significant differences between cultivars, indicating that environmental factors in greenhouse production may supersede genetic variations, despite the recognized heritable component for titratable acidity (Mishra et al. 2015; Pinheiro et al. 2021).

The bimodal pattern of anthocyanin and phenolic concentration (Figs. 3A-F) indicates two separate phases of metabolic activity (affected by spider mites and thrips infestation), potentially associated with environmental stimuli throughout the fruiting stage, signifying a particular phase of optimal sugar buildup and acidity (Mazon et al. 2023; Parehwa et al. 2021). Contrarily, the unimodal distribution of SSC (Fig. 3G) and T_{acid} (Fig. 3H) indicates that the response of cultivars to DAT is regulated by common physiological mechanisms which may affect the degree of accumulation (Parehwa et al. 2021).

Fruit quality variables in relation to yield. The marketable fruits per harvest were 11 to 282 for 'San Andreas' and 20 to 252 for 'Albion' with an average of 94 and 92 marketable berries per harvest, respectively. Yields ($g \cdot plant^{-1}$) averaged over DAT were not significantly different between 'Albion' and 'San Andreas' (28.4 ± 4.1 and 29.9 ± 4.1, respectively), although slightly higher fruit yield occurred with 'San Andreas' (Fig. 4). Fruit yield of strawberry cultivars increased at 162 DAT, decreased at 202 DAT, and increased again at 230 DAT (Fig. 4).

Yield fluctuations between 197 and 223 DAT (Fig. 4) could be due to a peak infestation of spider mites and thrips (Livinali et al. 2014). The installation of shade (Fig. 1B) to reduce excessive heat did not adversely affect the 20-40 $MJ \cdot m^{-2}$ (Fig. 1B) needed for adequate anthocyanin production (Matsushita et al. 2016; Tang et al. 2020). Notably, SSC levels were comparatively low at this period, although anthocyanin concentrations were elevated, a trend frequently observed in strawberries (Chiomento et al. 2023). This phenomenon has been noted in specific cultivars that produce deeply pigmented red fruit with elevated anthocyanin levels but relatively low sugar content (Wang et al. 2025). The inverse correlation between SSC and anthocyanin may in-

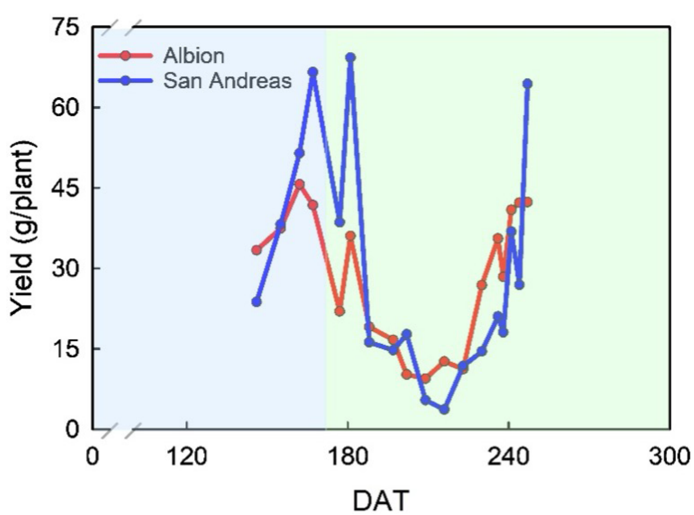

Figure 4. Effect of days after transplanting (DAT) and cultivar on fruit yield ($g \cdot plant^{-1}$) of fully ripe strawberries. The light blue shaded area signifies late winter season while the light green shaded area indicates the spring season. Fruit yield data were collected at 18 harvest dates and analyzed in relation to DAT.

dicate cultivar-specific metabolic prioritizing under stress or high light circumstances, wherein carbon flux is preferentially allocated to secondary metabolite formation rather than sugar accumulation (Chiomento et al. 2023).

A highly positive association was found for TAC, C3G and pelargonidin compounds (P3R, P3G, and P3M) and a negative correlation between P3M with SSC and TPC was found (Table 2; Fig. 5). F_{yield} exhibited a highly positive correlation with TAC and P3R implying that higher anthocyanin content was strongly associated with increased productivity (Chiomento et al. 2023). On the otherhand, F_{yield} was inversely correlated with T_{acid} and TPC. A negative relationship was found between T_{acid} and pH and a positive correlation with TPC. Moreover, a strong positive correlation was observed between SSC and pH.

The PCA demonstrated distinct correlations between strawberry fruit anthocyanin, phenolic con-

Table 2. Combined correlation coefficients of 'Albion' and 'San Andreas' between fruit yield and quality of fully ripe strawberries grown in a non-recirculating hydroponic system in Auburn, AL, in 2023.

Index	F_{yield}	SSC	pH	T_{acid}	TPC	TAC	C3G	P3G	P3R	P3M
F_{yield}	1.000									
SSC	–0.278	1.000								
pH	0.092	0.538**	1.000							
T_{acid}	–0.571**	0.199	–0.392*	1.000						
TPC	–0.351*	0.187	–0.168	0.507**	1.000					
TAC	0.037**	–0.049	–0.060	–0.213	–0.242	1.000				
C3G	0.146	0.092	–0.051	–0.093	–0.014	0.687**	1.000			
P3G	0.328	–0.026	–0.030	–0.217	–0.236	0.999**	0.693**	1.000		
P3R	0.380**	–0.249	–0.315	–0.144	–0.270	0.836**	0.312	0.813**	1.000	
P3M	0.266	–0.383*	–0.233	–0.199	–0.423*	0.647**	0.590**	0.634**	0.525**	1.000

*, ** Significant correlations at 5% and 1% level, respectively, using Pearson correlation coefficients (n=36).

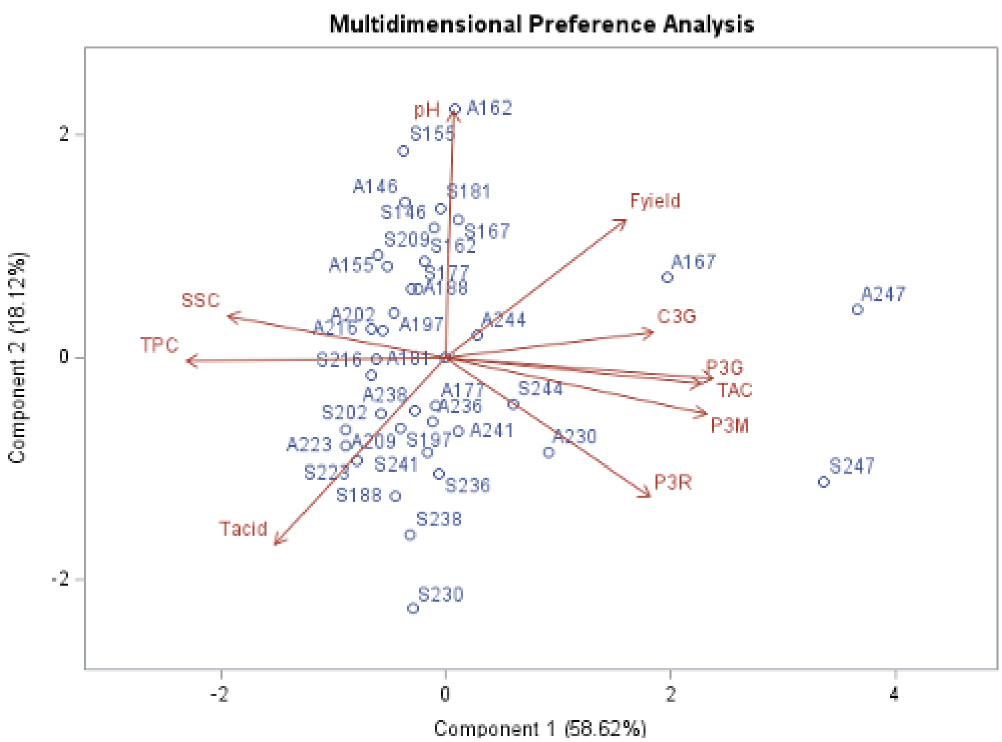

Figure 5. Principal Component Analysis of anthocyanins, phenolics and fruit yield across days after transplanting (DAT) in strawberries. Arrows pointing in the same direction are positively correlated and arrows pointing in opposing direction are negatively correlated, while arrows that form near 90°C angles are neither positively nor negatively correlated. Principal Components of Qualitative Data (PROC PRINQUAL) was applied for all variables.

tents and fruit yield (Fig. 5). As fruit yield increased, T_{acid} decreased, and TAC decreased as TPC and SSC increased. Total anthocyanins, C3G, and pelargonidin derivatives (P3R, P3G, and P3M) exhibited a positive correlation, in agreement with a coordinated pigment production within the flavonoid pathway (Chiomento et al. 2023). T_{acid} and pH, indicators of fruit acidity and ripeness (Jouquand et al. 2008), demonstrated moderate or negligible associations with anthocyanin content, soluble solids concentration (SSC), and total phenolics (Table 2; Fig. 5). These findings correspond with earlier studies by Cai et al. (2023) and Zeliou et al. (2018), which also noted that T_{acid} and pH are predominantly independent of pigment and sugar accumulation in strawberries.

As reported in other studies, anthocyanin profiles and fruit quality characteristics can be significantly influenced by genetic background and production environment (Parehwa et al. 2021; Vinson III et al. 2022). Additionally, the physiological age of transplants and day-neutral classification can affect fruit quality dynamics (Jouquand et al. 2008; Parehwa et al. 2021). In this study, the results indicate a possible bimodal response (Fig. 3), with differences in fruit quality in late winter/early spring compared to late spring. Changes in temperature (Fig. 1A), light (Fig. 1B) and macronutrient content during late spring may have influenced the observed variability, in conjunction with potential impacts of extended flowering on carbon allocation and assimilate dilution (Figs. 3A and B; Hernández-Martínez et al. 2023).

The results indicated that strawberry growers must meticulously regulate harvest timing, environmental conditions, and insect management to optimize output, sweetness, and color development (Alavi et al. 2025). Anthocyanin peaks when sugar levels are reduced, indicating that growers may prioritize either flavor or visual appearance based on consumer demand (Chiomento et al. 2023). 'San Andreas' was characterized by elevated P3R, in contrast to 'Albion', which was characterized by elevated P3M, underscoring cultivar-specific response on these minor pigments. Pest infestations and nutrient deficiency (N and S) decrease SSC, highlighting the necessity for integrated pest management (IPM) and fertilization (N and S) approaches (Livinali et al. 2014). Effects between 180 and 222 DAT may have affected strawberry quality, due to removal of fruit during treatment of plants for heavy infestation of spider mites and thrips, corresponding with the established timing of pest management interventions during this interval. This trade-off underscores the need of evaluating transplant age, flowering behavior, and fruit yield when analyzing variations in color profiles and flavor characteristics between experiments. Environmental management is crucial, in addition to cultivar selection. Growers in warmer or high-UV regions can adjust practices, including shading or cooling, to improve fruit flavor, consumer-preferred berries, or enhanced antioxidant content for premium markets.

Conclusion

This study revealed that the quality of strawberry fruit is influenced by cultivar variations, seasonal fluctuations, and yield correlations. Cultivars exhibited unique characteristics in anthocyanins cyanidin-3-glucoside (C3G) and pelargonidin-3-rutinoside (P3R), with fruit quality traits (except C3G) varying more significantly across days after transplanting (DAT), indicating susceptibility to environmental factors. Furthermore, yield was associated with total anthocyanins demonstrating trade-offs where increased productivity correlated with diminished titratable acidity and phenolic content. These findings emphasize the intricate interaction of genetics, environment, and yield in influencing strawberry quality, highlighting the necessity to reconcile productivity with preferred consumer attributes in management strategies. Tracking pigment composition, flavor characteristics, and environmental factors of strawberry cultivars helps ensure documentation of fruit quality and yield in hydroponic system under greenhouse conditions.

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