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Seaweed Extract and Microbial Biostimulants Show Synergistic Effects on Improving Organic Strawberry Production

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***Abstract.* The application of seaweed extract and microbial biostimulants has been suggested as a promising approach to overcome yield-limiting factors in organic farming. Yet, information regarding their impact on organic strawberry production is limited. This 2-year field study evaluated the effect of seaweed extract and microbial biostimulants and their synergistic effects on strawberry plant growth, nutrient uptake, fruit yield, and quality under organic production. The biostimulant effects were compared on two strawberry cultivars: Sweet Sensation® Florida127 and Florida Brilliance. Over two seasons, the combination of seaweed extract plus microbial biostimulants applied biweekly consistently resulted in a significant increase of whole-season marketable and total strawberry fruit yields by 23% and 20% on average, respectively, compared with the no-biostimulant control. Application of either biostimulant alone did not consistently show positive effects on strawberry productivity. Modified strawberry root system architecture, enhanced N uptake, increased number of crowns, and higher soil respiration were observed in the biostimulant combination treatment in contrast to the no-biostimulant control. The biostimulant impact was not influenced by strawberry cultivar, but genotypic difference in yield performance under organic production was observed. 'Florida Brilliance' produced significantly higher total fruit number and yield than 'Florida127' by 26% and 12%, respectively, in the first season, and by 34% and 11%, respectively, in the second season. Marketable fruit number (by 18%) and yield (by 9%) of 'Florida Brilliance' were also higher in the first season, along with greater marketable fruit number (by 31%) in the second season. In addition, 'Florida Brilliance' showed significantly higher values of SPAD index, photosynthetic rate (early harvest), and fruit mineral contents based on dry weight (late harvest) than 'Florida127' in both seasons. Although the biostimulant treatments exhibited little influence on the fruit quality attributes including soluble solids content (SSC), titratable acidity (TA), SSC/TA, and total anthocyanin content, varietal differences were observed with significantly higher levels of SSC and lower contents of total anthocyanins in 'Florida 127' vs. 'Florida Brilliance' during each season. The benefits of combined application of seaweed extract and microbial biostimulants demonstrated in this study suggest the need to further elucidate their synergistic functions in promoting nutrient uptake and fruit yield in organic strawberry production systems under different soil and environmental conditions.**

Organic strawberry (*Fragaria ×ananassa* Duch.) production has increasingly gained interest among growers worldwide. In the United States, the harvested organic strawberry acreage reached 2145 ha in 2021 with California as the top producing state followed by Florida (USDA-NASS 2022). Florida Brilliance (Fig. 1A and C) and Sweet Sensation® Florida127 (Fig. 1B and C) are two strawberry cultivars that have dominated Florida strawberry production in recent years (The Packer 2019); however, little research-based information is available regarding their performance in organic cropping systems. Evaluating yield performance and fruit quality of these two leading cultivars in different organic management systems would aid further development of the organic strawberry industry. Compared with conventional production, the yield potential of organically grown strawberry can be 20% to 50% less (Conti et al. 2014; Lesur-Dumoulin et al. 2017; Macit et al. 2007). In addition to challenges associated with disease, pest, and weed management, nutrient supply and synchronizing nutrient availability with crop uptake also represent major constraints in organic strawberry production.

The beneficial effects of biostimulant application have been investigated on various horticultural crops, including improving vegetative growth (Polo and Mata 2018), enhancing nutrient uptake (Mutale-joan et al. 2020), promoting fruit yield (Drobek et al. 2019), and increasing tolerance to biotic and abiotic stresses (Van Oosten et al. 2017). In 2018, the US Farm Bill provided the first legal definition for "plant biostimulant" (US Congress 2018), which promoted interests from both researchers and producers in the use of different biostimulants in sustainable crop production. Depending on specific ingredients, biostimulants are generally classified into six main categories, including humic substances (e.g., humic and fulvic acids), seaweed extracts, beneficial microbes (bacteria and fungi), protein hydrolysates, chitosan, and inorganic compounds (e.g., silicon) (Yakhin et al. 2017).

Most commercially available seaweed extract biostimulants are derived from brown algae species (e.g., *Ascophyllum nodosum*, *Ecklonia maxima*, *Macrocystis pyrifera*, and *Durvillaea potatorum*) and may contain various components, such as mineral elements, amino acids, vitamins, betaines, cytokinins, sterols, and other organic compounds (Khan et al. 2009; Sivasankari et al. 2006; Zheng et al. 2016). Seaweed extract biostimulants have been reported to improve organic vegetable productivity, such as for leafy greens (i.e., lettuce, mustard, kale, Swiss chard, and collards; Sandhu et al. 2018) and okra (Zamana et al. 2021). However, few field studies using seaweed extract biostimulants have been conducted on organic strawberry systems, and the action mechanisms of seaweed extract biostimulants are still poorly understood due to their complex biochemical compositions and possibilities of multifaceted effects.

Microbial biostimulants mainly consist of plant growth-promoting microbes (PGPM), such as beneficial bacteria (e.g., *Bacillus*, *Burkholderia*, *Pseudomonas*), arbuscular mycorrhizal (AM) fungi (*Glomeromycota*), and other beneficial fungi (e.g., *Trichoderma*). Previous studies showed that the application of PGPM can improve plant growth and yield performance of crops like peanut (Dey et al. 2004), strawberry (Esitken et al. 2010; Sangiorgio et al. 2023), and raspberry (Orhan et al. 2006). The proposed functions of PGPM include increasing plant access to nutrients; mediating soil nutrient cycling, such as asymbiotic N_2 fixation (Sahin et al. 2004) and nitrogen (N) mineralization; enhancing pathogen resistance, such as production of siderophores (Gull and

Fig. 1. (**A**) Florida Brilliance strawberry cultivar during the harvest season of the organic strawberry production field trial in Citra, FL. (**B**) Sweet Sensation® Florida127 strawberry cultivar during the harvest season of the organic strawberry production field trial in Citra, FL. (**C**) Containerized transplants of Florida Brilliance and Sweet Sensation® Florida127 strawberry cultivars before planting for the organic strawberry production field trial in Citra, FL. (**D**) Samples of the microbial biostimulant (left) and the seaweed extract biostimulant (right) evaluated in the organic strawberry production field trial in Citra, FL.

Hafeez 2012) and antibiotics (Beneduzi et al. 2012); and releasing plant hormones, such as auxins (Ahmed and Hasnain 2014), cytokinins (García de Salamone et al. 2001), and gibberellins (Gutiérrez-Mañero et al. 2001). Nevertheless, the efficacy of commercial microbial biostimulants on organic strawberry production under field conditions has yet to be determined.

Interestingly, it has been indicated in many reports that biostimulants could work synergistically to enhance crop productivity. Weber et al. (2018) reported that seaweed extract and silicon demonstrated synergistic effects for improving early-season marketable fruit yield of greenhouse-grown organic strawberries. According to another greenhouse study by Roussos et al. (2009), a mixture of a seaweed extract plus a commercial product of nitrophenolates significantly enhanced marketable strawberry fruit yield. In a greenhouse experiment of lettuce, plant fresh weight was increased by the combined application of microbial biostimulant (*Rhizophagus intraradices* and *Trichoderma atroviride*) and plant-derived protein hydrolysates (Rouphael et al. 2017). Combining seaweed extract biostimulant application and iodine biofortification increased strawberry yield and fruit quality in conventional strawberry production under field conditions (Consentino et al. 2023); however, little is known about the synergistic potential of combined use of seaweed extract and microbial biostimulants in organic strawberry production in field cropping systems.

With a focus on seaweed extract and microbial biostimulants (Fig. 1D), this 2-year organic strawberry production field study was conducted to determine the response of short-day strawberry cultivars to single and combined use of commercial biostimulants. Specifically, the objectives of our study were to examine the effects of seaweed extract and microbial biostimulants on organic strawberry plant growth, nutrient uptake, and fruit yield and quality of 'Florida Brilliance' and Sweet Sensation® 'Florida127' in Florida's sandy soils.

Materials and Methods

Experimental design and field trial setup. This 2-year study was conducted on certified organic land at the University of Florida Plant Science Research and Education Unit in Citra, FL, during the 2018–19 and 2019–20 production seasons. The soil type at the research site is Gainesville loamy sand (hyperthermic, coated Typic Quartzipsamments) with 97.0% sand, 2.2% clay, and 0.8% silt, and an average soil organic matter content at 0.8%. In both seasons, granular organic fertilizer Nature Safe 10N–0.9P–6.6K (Darling Ingredients Inc., Irving, TX, USA) was applied preplant at an N rate of 84.1 $kg \cdot ha^{-1}$. False raised beds were formed first and then followed by granular organic fertilizer application on the bed top, and tillage was used to mix organic fertilizer with soil at a depth of 15 cm on 3 Oct 2018 and 30 Sep 2019. On the same day, the final raised beds were made and covered with 0.03 mm black totally impermeable film plastic mulch (Intergro, Inc., Clearwater, FL, USA) and a single drip tape (30.5 cm emitter spacing, 3.4 $L \cdot h^{-1} \cdot m^{-1}$ flow rate; Jain Irrigation, Inc., Haines City, FL, USA) was put on the soil surface in the middle of each bed.

In both years, a split-plot design with four replications of each biostimulant treatment was used for the field trials. In the 2018–19 season, biostimulant treatments were arranged in the whole plots following a randomized complete block design. Three biostimulant treatments were assessed along with a no-biostimulant (water) control, including seaweed extract biostimulant Stimplex® (4.7 $L \cdot ha^{-1}$ biweekly application rate; Acadian Seaplants Limited, Dartmouth, NS, Canada), microbial biostimulant TerraGrow® (1.1 $kg \cdot ha^{-1}$ biweekly application rate; BioSafe Systems, LLC, East Hartford, CT, USA), and a combination of Stimplex® plus TerraGrow®. According to the product label, the seaweed extract biostimulant is derived from *Ascophyllum nodosum*; the microbial biostimulant contained *Bacillus subtilis*, *Bacillus pumilus*, *Bacillus licheniformis*, *Bacillus megaterium*, *Bacillus amyloliquefaciens*, and *Trichoderma harzianum*. The subplots consisted of two strawberry cultivars: Sweet Sensation® Florida127 and Florida Brilliance. In the 2019–20 season, the Sweet Sensation® Florida127 and Florida Brilliance strawberry cultivar treatments were arranged in the whole plots according to a randomized complete block design. The subplots consisted of the no-biostimulant control and the same biostimulant treatments evaluated in the 2018–19 season.

In both years, the experimental unit consisted of 40 plants in each subplot. Strawberry plants were grown in a staggered pattern with two rows (30.5-cm spacing between two rows) in each bed at 30.5 cm spacing between plants, and bed centers were spaced at 1.5 m. Containerized strawberry plants were transplanted on 4 Oct 2018 and 9 Oct 2019. Before strawberry transplanting, all seedling roots were dipped in water, TerraGrow® solution (7.5 $g \cdot L^{-1}$), Stimplex® solution (1 $mL \cdot L^{-1}$), or a combination solution of TerraGrow® and Stimplex® for 2 min, respectively. After transplanting, the strawberry plants in each plot receiving the microbial biostimulant treatment were immediately treated again with TerraGrow® solution at a rate of 1.7 $kg \cdot ha^{-1}$ (dissolved in 7014 $L \cdot ha^{-1}$ water to thoroughly drench the root zone with the product) through drip irrigation lines. The biostimulant combination treatment was drip applied on a biweekly basis from 18 Oct 2018 to 19 Apr 2019 and from 24 Oct 2019 to 13 Mar 2020. Liquid fish fertilizer Aqua Power™ 5N–0.4P–0.8K (JH Biotech, Inc., Ventura, CA, USA) in combination with Big-K™ sulfate of potash 0N–0P–41.5K (JH Biotech, Inc.) were used for in-season fertigation through drip irrigation lines for the strawberry production season. In-season fertigation was applied weekly at 4.71 $kg \cdot ha^{-1}$ N and 4.71 $kg \cdot ha^{-1}$ K for 1 to 3 weeks after

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transplanting (WAT) in both seasons and then increased to 7.85 $kg \cdot ha^{-1}$ N and 6.28 $kg \cdot ha^{-1}$ K for 4 to 29 WAT in the 2018–19 season and for 4 to 22 WAT in the 2019–20 season. Total organic fertilizer application rates were 302.3 and 247.4 $kg \cdot ha^{-1}$ N, 232.9 and 189.0 $kg \cdot ha^{-1}$ K, 25.0 and 20.6 $kg \cdot ha^{-1}$ P in 2018–19 and 2019–20 seasons, respectively.

All strawberry plants were covered using the AgroFabric® System frost protection fabric (Agrifabrics LLC, Alpharetta, GA, USA) for 7 nights in the 2018–19 season and 14 nights in the 2019–20 season when the night air temperature was projected to be below 4 °C.

Biochemical analyses of seaweed extract biostimulant Stimplex®. The presence and abundance of proteins, lipids, and metabolites in the seaweed extract were qualitatively analyzed using liquid chromatography–tandem mass spectrometry (LC-MS/MS). Biostimulant samples (100 μL each) were extracted for proteins, lipids, and metabolites. The proteins were extracted by acetone/methanol precipitation, lipids were extracted with a modified Folch method (Folch et al. 1957), and metabolites by ice-cold methanol. The details of the biochemical analysis protocols were described by Li et al. (2021).

Photosynthetic parameters and vegetative growth. Photosynthetic parameters including photosynthetic rate (A, $\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2), transpiration rate (E, $mmol \cdot m^{-2} \cdot s^{-1}$ H_2O), intercellular CO_2 concentration (c_i, $\mu mol \cdot mol^{-1}$), and stomatal conductance (gsw, $mol \cdot m^{-2} \cdot s^{-1}$) were measured twice (early harvest and peak harvest) in each season. Three representative plants were randomly chosen from each subplot and measurements were conducted on the most recent, fully developed, mature leaf from the top of the canopy of each plant with an LI-6800 portable photosynthesis system (Software Version 1.2.; LI-COR Inc., Lincoln, NE, USA). The light intensity and the CO_2 reference concentration in the leaf chamber (6 cm^2 aperture) were set at 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 400 $\mu mol \cdot mol^{-1}$, respectively.

The leaf relative chlorophyll content was measured at 1, 30, 60, 90, 120, 150, and 180 (first season only) d after transplanting (DAT) on fully developed and most recent mature leaves on the top of plants using a SPAD-502 Plus chlorophyll meter (Konica Minolta, Inc., Tokyo, Japan) in both seasons. Nine SPAD readings were randomly taken from the trifoliate leaves of three different plants in each subplot and then nine readings were averaged and used for the SPAD value of each subplot. Crown diameter at the base of the plant (including all crowns) was measured at 1, 30, 60, 90, 120, 150, and 180 (first season only) DAT using a caliper in both seasons. Destructive sampling was conducted at 50 and 200 DAT in the 2018–19 season and at 60 and 155 DAT during the 2019–20 season for measuring crown number, leaf number, leaf area, and aboveground biomass. The aboveground tissues of two representative plants were removed from each subplot and plants were separated into two parts: crowns (with petioles included) and leaves (fully expanded leaf blades). The numbers of crowns and fully expanded trifoliate leaves were counted and recorded, respectively. The total area of fully expanded trifoliate leaves of two strawberry plants were measured using an LI-3100 Area Meter (LI-COR Inc.). The average leaf area per leaf was determined based on the total leaf area and the total number of leaves.

Fruit yield evaluation. Strawberry harvests started on 4 Dec 2018 (61 DAT) and 6 Dec 2019 (58 DAT) and ended on 25 Apr 2019 (203 DAT) and 16 Mar 2020 (159 DAT). Ripe fruit with 75% to 100% red color from all plants were harvested twice per week in each experimental unit (subplot) and then classified into marketable and unmarketable categories following the US Department of Agriculture standards for grades of strawberries (Santos et al. 2009; USDA-AMS 2006). The small (less than 10 g) and deformed, diseased, and pest damaged fruit were considered to be unmarketable fruit. Fresh marketable and unmarketable fruit were counted and weighed, and data were reported on a per-plant basis. Total fruit yield included marketable and unmarketable fruit yield.

N accumulation in aboveground biomass and fruit mineral content. After measuring growth parameters as aforementioned, samples of crown and leaf parts collected from destructive sampling at 200 DAT in the 2018–19 season and at 155 DAT during the 2019–20 season were dried at 65 °C for 7 d to determine dry weight. Dried plant biomass was then ground through a 1-mm sieve using a Wiley laboratory mill (Model 4; Thomas Scientific, Swedesboro, NJ, USA), before plant tissue N content analysis (by Waters Agricultural Laboratories, Inc., Camilla, GA, USA). Ten ripe fruit were collected in the early (20 Dec 2018 and 19 Dec 2019), peak (21 Feb 2019 and 13 Feb 2020), and late (4 Apr 2019 and 2 Mar 2020) harvest seasons for determination of dry matter and N contents. The drying procedure and N content analysis for fruit followed the same protocol of plant biomass measurement. In addition, the fruit collected in the late season (4 Apr 2019 and 2 Mar 2020) were analyzed for the contents of macronutrients P, K, Ca, Mg, and S and micronutrients B, Fe, Mn, and Zn using the ICAP-open vessel wet digestion Digi Block 3000 (by Waters Agricultural Laboratories, Inc.). The N accumulation in crown and leaf parts was estimated by multiplying the plant tissue N content with the tissue dry weight per plant (g/plant). The N accumulation in fruit during early, peak, and late harvest seasons was estimated by multiplying the corresponding fruit N content of the fruit sample with the total fruit dry weight for the harvest period (g/plant). The total N accumulation (kg/ha) was then calculated by multiplying the amount of N accumulated in crown, leaf, and fruit tissues per plant by the plant population (43,056 plants/ha).

Root growth parameters. Root architecture was also compared between the water control and the biostimulant combination treatment. Two representative strawberry plants from each of the corresponding subplots were sampled for root assessment at 201 DAT on 23 Apr 2019 and at 155 DAT on 12 Mar 2020. The whole root system was collected from the field using a shovel. The samples were submerged in plastic bags filled with deionized water for 1 h. The root system was carefully washed to remove the soil particles and then scanned using a root scanning apparatus (EPSON color image scanner LA1600+; EPSON, Toronto, ON, Canada). The determination of the root system characteristics, including total root length (cm/plant), average root diameter (mm), total root surface area (cm^2/plant), and numbers of tips, forks, and crossings was performed using the WinRhizo image analysis system (Version 2012b; Regent Instruments, Quebec, QC, Canada). Then the strawberry roots were dried at 65 °C for 7 d to determine the dry weight.

Soil respiration. Soil respiration measurements were conducted at 60, 90, and 130 DAT during the 2019–20 strawberry growing season. One cylindrical PVC collar (20 cm in diameter and 10 cm in height) was inserted into the soil to a depth of 2 cm between the strawberry plants in each subplot. Soil collars were installed 1 week before the CO_2 measurements to get stabilized CO_2 flux inside collars. Soil CO_2 efflux was measured using an LI-6800 portable photosynthesis system with an LI-6800 soil CO_2 flux chamber (LI-COR Inc.). Measurements were consecutively replicated three times at each collar and the duration of each measurement was 160 s. All weeds inside the collar were removed immediately once the collar was placed in the field and the inside of the collars was kept weed free during the strawberry growing season. Soil moisture content and temperature as useful ancillary data were measured with a Stevens HydraProbe (Stevens Water Monitoring Systems, Inc., Portland, OR, USA) inserted into the soil in the vicinity of the collar. The soil respiration rate was expressed as $\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2.

Fruit quality attributes. Fruit quality attributes including titratable acidity (TA), soluble solids content (SSC), and total anthocyanin content (TAC) were measured during the early, peak, and late harvest periods in each production season. After removal of the calyxes, 20 fully ripe strawberries per biostimulant treatment replicate with marketable fruit quality were homogenized in a blender (Model: HBB908; Hamilton Beach Brands, Inc., Glen Allen, VA, USA). A portion (~45 g) of the homogenized mixture was centrifuged at 4 °C for 20 min at 19,319 g_n using a Sorvall LYNX 4000 refrigerated centrifuge (Thermo Fisher Scientific, Waltham, MA, USA). The supernatant from the centrifuged sample was filtered through double-layer cheesecloth before further analysis.

The filtered supernatant clear juice was analyzed to measure TA and SSC. The determination of TA was conducted using an automated titrator (905 Titrando; Metrohm, Riverview, FL, USA) by titrating 6 mL strawberry juice (filtered supernatant) with a solution of 0.1 $mol \cdot L^{-1}$ sodium hydroxide (NaOH) to an endpoint of pH 8.2. The TA was expressed as a percentage based on citric acid equivalents. The SSC was assessed using an automatic, temperature compensated refractometer (r^2i300; AMETEK Reichert Technology, Munich, Germany) and expressed as °Brix.

TAC was measured based on the pH differentiation method (Giusti and Wrolstad 2001). Briefly, anthocyanins were extracted using acidified methanol solution. A 2.0-g sample of the blended mixture was added into 5 mL of HCl (1%)-methanol solution and shaken by a vortex for 20 s. The samples covered with aluminum foil were equilibrated at 4 °C for 15 min and then centrifuged at 4 °C for 20 min at 19,319 g_n using a Sorvall LYNX 4000 refrigerated centrifuge to collect the supernatant. The extractions were conducted in duplicate. Two dilutions of the same extractant sample were prepared by adding 600 μL of extract to 2.4 mL of potassium chloride (0.025 M, pH = 1.0) and to 2.4 mL of sodium acetate (0.4 M, pH = 4.5), respectively. All samples were vortexed for 10 s and then equilibrated in the dark at room temperature for 15 min. Their absorbance was measured in triplicate (200 μL for each) at 515 nm and 700 nm for each solution mixture at pH = 1.0 and pH = 4.5, respectively, using a microplate reader (Epoch 2; BioTek Instruments, Inc., Winooski, VT, USA). Results were expressed as milligrams of pelargonidin 3-glucoside equivalents 100 g^{-1} fresh strawberry. TAC was calculated as follows:

$$\mathrm{TAC} = (\mathrm{A} \times \mathrm{MW} \times \mathrm{DF} \times 1000)/(\mathrm{L} \times \varepsilon)$$

where A is the final total absorbance calculated by ($A_{515} - A_{700}$) (pH = 1.0) – ($A_{515} - A_{700}$) (pH = 4.5); MW is the molecular weight (433.2 g·mol^{-1}) of the reference anthocyanin compound (pelargonidin-3-glucoside); DF is the dilution factor; 1000 is the factor for conversion from g to mg; L is the pathlength (1 cm); and ε is molar absorptivity coefficient (36,000 M·cm^{-1}).

Statistical analyses. Data analyses were conducted separately for the two production seasons due to significant seasonal effects shown in a preliminary analysis (Linear Mixed Model). A linear mixed model with the GLIMMIX procedure in SAS (Version 9.4; SAS Institute, Cary, NC, USA) was used for data analysis. Data transformation was not needed after checking normality, homogeneity of variance, and linearity for each dataset. In both seasons, a two-way Linear Mixed Model was performed with strawberry cultivar, biostimulant, and their interactions as the fixed effects and block as the random effect in the model. Multiple comparisons of different measurements among treatments were performed using Tukey's test at $P \leq 0.05$.

Results

Biochemical composition of the seaweed extract biostimulant. The seaweed extract biostimulant contained a minimal number of proteins based on the total spectral counts (less than 10) for each identified protein (Supplemental Fig. 1A); however, metabolomic identification was dominated by polyphenols (Supplemental Fig. 1B). Other categories of metabolites identified included amines, amides, organic acids, isoprenoids, steroids, and plasticizers. According to the manufacturer, cytokinin was an active ingredient with a 0.01% concentration (by volume) in this seaweed extract biostimulant product; however, it was not detected in our study using LC-MS/MS. The lipids identified were classified into four main categories including glycerolipids, glycerophospholipids, sphingolipids, and sterol lipids (Supplemental Fig. 1C). As the major lipid compounds detected, triglyceride, diglyceride, and phosphatidylcholine lipids accounted for 38.2%, 29.2%, and 15.0% of the lipids in the seaweed extract biostimulant, respectively (Supplemental Fig. 1D).

Photosynthetic parameters and vegetative growth. Biostimulants did not affect the photosynthetic parameters of strawberry leaves in either trial (data not shown). Photosynthetic rate (Fig. 2A), transpiration rate (Fig. 2B), and stomatal conductance (Fig. 2C) were significantly higher in 'Florida Brilliance' than 'Florida127' in the early season, by 10%, 12%, and 18%, respectively, in the 2018–19 trial and by 17%, 20%, and 27%, respectively, in the 2019–20 trial.

SPAD values and crown diameter did not differ significantly among biostimulant treatments in either season (data not shown). Overall, 'Florida Brilliance' exhibited significantly higher SPAD values than 'Florida127', by 5% on average in both seasons (Fig. 3A and B). The crown diameter of strawberry plants increased dramatically between 1 and 90 DAT and 'Florida127' had a significantly larger crown size than 'Florida Brilliance' starting from 90 DAT in the 2018–19 season and 60 DAT in the 2019–20 season until the end of each strawberry growing season (Fig. 3C and D).

Overall, the biostimulant treatments were similar to the no-biostimulant control in terms of crown and leaf numbers per plant, average individual leaf area, and total leaf area per plant in the early growing period (50 or 60 DAT) of both seasons (Fig. 4A–D). However, assessment at 200 DAT in the 2018–19 season and 155 DAT in the 2019–20 season indicated significantly greater numbers of crowns (by 35% and 27%, respectively) and leaves (by 42% and 27%, respectively) in plants treated with the biostimulant combination in contrast to the no-biostimulant control (Fig. 4A and B). Compared with the control, the microbial biostimulant alone significantly increased the crown number by 23% at 200 DAT in the first season, while the seaweed extract alone resulted in greater leaf numbers, by 30% at 200 DAT in the first season and by 17% at 155 DAT in the second season. The biostimulant combination treatment significantly increased the crown number compared with the seaweed extract alone and increased the plant leaf number compared with the microbial biostimulant alone by 29% and 25%, respectively, at 200 DAT in the first season, and by 18% and 13%, respectively, at 155 DAT in the second season. During the late growing period in both seasons, the combination treatment consistently maintained larger leaves than the control (Fig. 4C), and the leaf area per plant was significantly increased by all biostimulant treatments (Fig. 4D).

The two strawberry cultivars did not differ in crown number (Fig. 5A). Compared with 'Florida Brilliance', 'Florida127' had significantly greater total leaf number per plant by 12% and 20% at 50 and 200 DAT, respectively, in the first season, and by 18% and

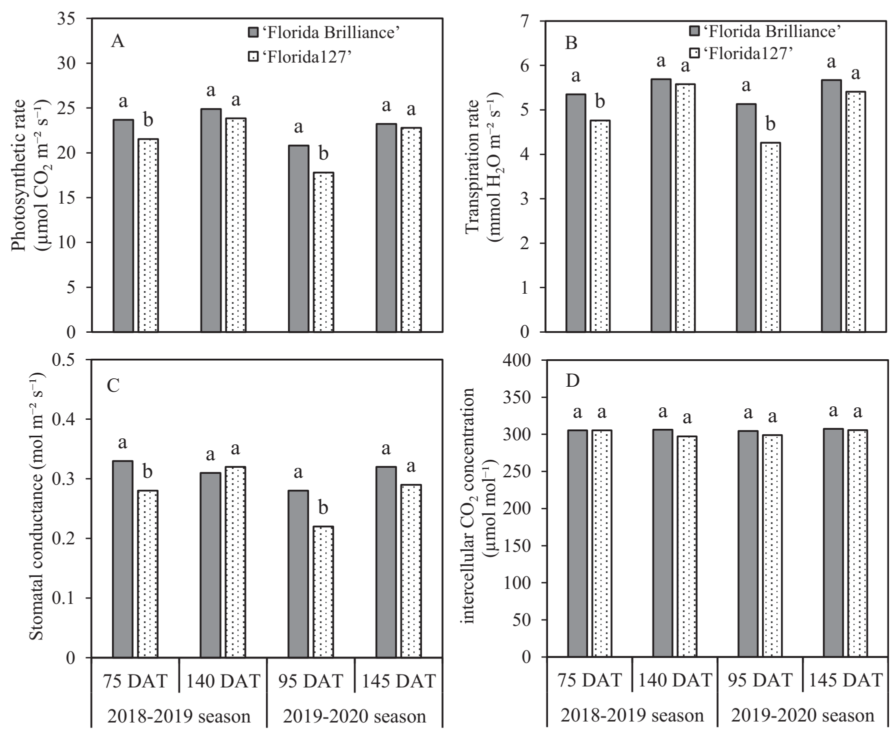

Fig. 2. Strawberry cultivar effects on (**A**) photosynthetic rate, (**B**) transpiration rate, (**C**) stomatal conductance, and (**D**) intercellular CO_2 concentration during 2018–19 and 2019–20 production seasons in Citra, FL. DAT = days after strawberry transplanting. Bars with the same letter at each sampling date do not differ significantly at $P \leq 0.05$ according to Tukey's test.

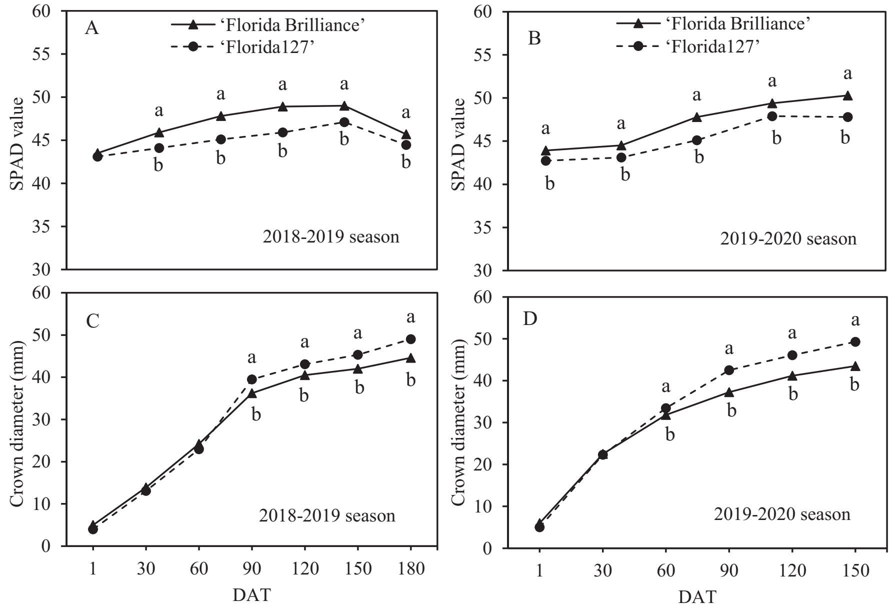

Fig. 3. Effects of strawberry cultivars on leaf relative chlorophyll content (expressed as SPAD value) and crown diameter during 2018–19 (**A** and **C**) and 2019–20 (**B** and **D**) production seasons in Citra, FL. DAT = days after strawberry transplanting. Treatment values with the same letter at each sampling date do not differ significantly at $P \leq 0.05$ according to Tukey's test.

13% at 60 and 155 DAT, respectively, in the second season (Fig. 5B). The average individual leaf area of 'Florida Brilliance' was significantly larger than 'Florida127', by 10% at 50 DAT in the first season and by 5% at 60 DAT in the second season, but 'Florida Brilliance' leaf area was 8% lower than 'Florida127' at 200 DAT in the first season (Fig. 5C). In contrast to average individual leaf area, total leaf area per plant was significantly higher for 'Florida127' than 'Florida Brilliance', by 31% at 200 DAT in the first season and by 14% at 155 DAT in the second season (Fig. 5D).

Organic strawberry fruit yield components. For the whole-season fruit yield in the 2018–19 season, the biostimulant combination treatment led to significantly higher marketable and total fruit yields per plant (Tables 1 and 2) than that of the seaweed extract (by 23% on average) or the microbial biostimulant (by 17% on average) alone, and the no-biostimulant control (by 25% on average). The marketable and total fruit numbers per plant were also significantly increased by the combined biostimulant application, compared with applying the microbial biostimulant alone (by 21% and 19%, respectively) and the without biostimulant control (by 27% and 32%, respectively). For the 2019–20 whole-season fruit yield, the biostimulant combination treatment showed significantly higher marketable (by 22%) and total (14%) fruit yields relative to the no-biostimulant control; however, no-biostimulant effect was observed in fruit number.

For the 2018–19 season monthly fruit yield, the combined biostimulant application significantly increased marketable fruit number in December compared with the seaweed extract treatment alone (by 25%) and the no-biostimulant control (by 15%), whereas the increases in marketable fruit number and yield in April reached 162% and 165%, respectively, compared with the control (Table 1). In addition, the combined biostimulant application significantly increased total fruit number (by 44%) and yield (54%) in March, relative to the control (Table 2). It also produced higher levels of total fruit number (by 107%) and yield (by 94%) in April than microbial biostimulant alone treatment, and the increase rose to 122% and 143%, respectively, when compared with the no-biostimulant control. In the 2019–20 season, the combination treatment led to increases of 21% and 22% in December marketable fruit number and yield, respectively, compared with the control (Table 1). It also significantly increased marketable fruit yield in January compared with the microbial biostimulant alone (by 35%), the seaweed extract alone (by 23%), and the no-biostimulant control (by 59%). In addition, it produced 23% and 27% more berries in December with respect to total fruit number and yield, respectively, compared with the control (Table 2). It also led to significantly higher total fruit yield in January than the microbial biostimulant alone (by 22%) and the control (by 26%).

Strawberry yield responses to biostimulant treatments did not vary with cultivars; however, fruit yield differed significantly between the two cultivars (Tables 1 and 2). In both seasons, 'Florida Brilliance' yielded significantly higher than 'Florida127' in total fruit number (by 26% during 2018–19 and 34% during 2019–20) and yield (by 12% during 2018–19 and 11% during 2019–20) as well as marketable fruit number (by 18% during 2018–19 and 31% during 2019–20). Although 'Florida Brilliance' showed higher marketable fruit yield than 'Florida127' by 9% in the 2018–19 season, no varietal difference was found in the second season.

The monthly fruit yield comparison between cultivars showed that in the first season, 'Florida Brilliance' produced significantly higher marketable fruit number than 'Florida127' for the December (by 26%), January (by 69%), and March (by 32%) harvests, along with higher marketable fruit yield in December (by 14%) and January (by 60%), whereas 'Florida127'

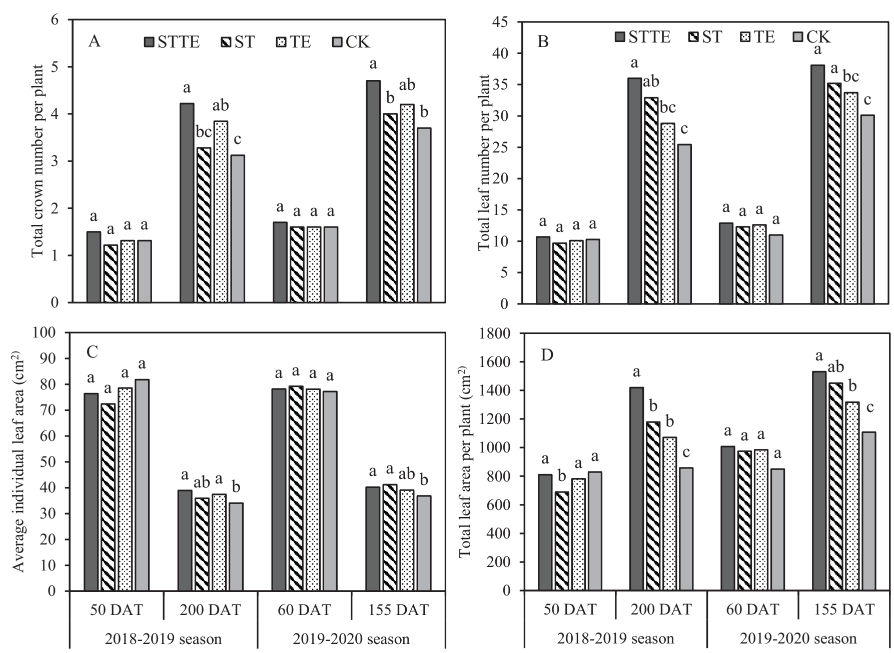

Fig. 4. Effects of biostimulant treatments on (**A**) total crown number per plant, (**B**) total leaf number per plant, (**C**) average individual leaf area, and (**D**) total leaf area per plant at different growth stages during 2018–19 and 2019–20 production seasons in Citra, FL. STTE = combined application of Stimplex® plus TerraGrow®; ST = Stimplex®; TE = TerraGrow®; CK = water control. DAT = days after strawberry transplanting. Bars with the same letter at each sampling date do not differ significantly at $P \leq 0.05$ according to Tukey's test.

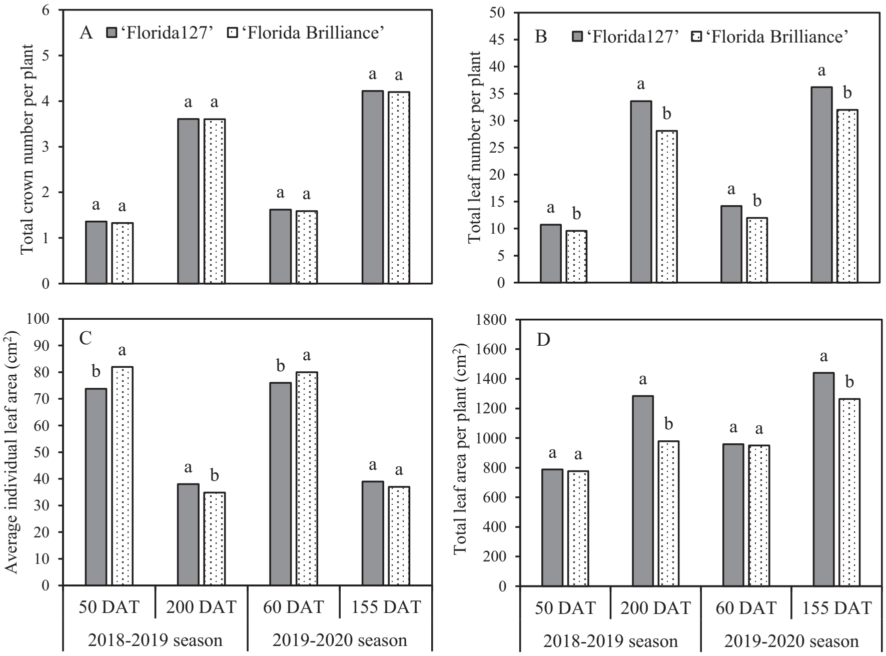

Fig. 5. Effects of strawberry cultivars on (**A**) total crown number per plant, (**B**) total leaf number per plant, (**C**) average individual leaf area, and (**D**) total leaf area per plant at different growth stages during 2018–19 and 2019–20 production seasons in Citra, FL. DAT = days after strawberry transplanting. Bars with the same letter at each sampling date do not differ significantly at $P \leq 0.05$ according to Tukey's test.

produced more marketable fruit number (by 59%) and yield (by 81%) in April (Table 1). Compared with 'Florida127', 'Florida Brilliance' also exhibited significant increases in monthly total fruit number (23% to 67%) and yield (13% to 50%) for the December, January, and March harvests (Table 2). In contrast, 'Florida127' yielded more than 'Florida Brilliance' in total fruit number (by 63%) and yield (by 85%) in April. In the second season, marketable fruit numbers were significantly greater for 'Florida Brilliance' vs. 'Florida127' in December (by 17%) and January (by 128%) (Table 1). The January yield advantage for 'Florida Brilliance' reached 70% for marketable fruit yield. The total fruit numbers in December, January, and March were also significantly higher for 'Florida Brilliance' vs. 'Florida127', by 14%, 93%, and 71%, respectively (Table 2). The January total fruit yield favored 'Florida Brilliance' over 'Florida127' by 61%.

Nitrogen accumulation in aboveground biomass and fruit mineral content. In the 2018–19 season, the biostimulant combination significantly increased N accumulation in leaves, fruit, and total aboveground tissue (including crown, leaves, and fruit), by 63%, 16%, and 29%, respectively, compared with the microbial biostimulant alone, and by 69%, 26%, and 38%, respectively, compared with the no-biostimulant control (Fig. 6). In the 2019–20 season, the combined application also resulted in greater levels of N accumulation in leaves (by 36%), fruit (by 16%), and total aboveground tissue (by 22%), relative to the control (Fig. 6). Moreover, the seaweed extract alone treatment significantly increased N accumulation in leaves (by 25%) and total aboveground tissue (by 14%) compared with the control.

The N accumulation in crowns and leaves was significantly higher in 'Florida127' vs. 'Florida Brilliance', by 26% and 38%, respectively, in the first season, and by 14% and 17%, respectively, in the second season. Compared with 'Florida127', 'Florida Brilliance' showed greater fruit N accumulation, by 15% in the first season and by 12% in the second season. However, the two cultivars did not differ significantly in total aboveground plant N accumulation in either season (Fig. 6).

Contents of N, P, K, Mg, S, Ca, and Mn (dry weight basis) at the end of both seasons were significantly higher in fruit of 'Florida Brilliance' vs. 'Florida127' (Table 3). The biostimulant combination and the seaweed extract alone treatments significantly increased fruit S and K contents compared with the no-biostimulant control in both seasons.

Root morphology. To better understand the potential synergistic effects of seaweed extract and microbial biostimulants, strawberry roots from the combination treatment and the no-biostimulant control plots were sampled at 201 DAT in the 2018–19 season and 155 DAT in the 2019–20 season to compare root dry weight, total root length and surface area, average root diameter, and numbers of root tips, forks, and crossings (Table 4). Root dry weight in the biostimulant combination treatment was significantly higher than that in the water control by 32% and 19% in 2018–19 and 2019–20 seasons, respectively. Total root surface area was significantly increased by the combination treatment in both seasons by 25% (first season) and 28% (second season). In addition, the biostimulant combination significantly increased the number of root forks in the 2018–19 season and the number of root tips and forks in the 2019–20 season. There was a trend (P = 0.06) of more root tips in strawberry plants from the plots receiving the combined application in the 2018–19 season. Root assessment did not reveal any differences between the two strawberry cultivars evaluated.

Soil respiration. Soil respiration rate was only measured at 60, 90, and 130 DAT in the second season (Fig. 7). During the soil respiration measurements, the average soil temperature and moisture (volumetric water content) were 21 °C and 12% at 60 DAT, 15 °C and 10% at 90 DAT, and 22 °C and 11% at 130 DAT, respectively. Compared with the control, the seaweed extract alone and biostimulant combination treatments significantly increased soil respiration rate, by 52% and 28% at 60 DAT, 93% and 60% at 90 DAT, and 33% and 44% at 130 DAT, respectively. The microbial biostimulant alone also led to significant increases at 60 DAT (by 24%) and 130 DAT (by 22%) relative to the control. In addition, soil respiration rate was significantly higher in the seaweed extract alone treatment than that of the microbial biostimulant alone (by 23%) and the combined application (by 19%) at 60 DAT as well as the microbial biostimulant alone (by 59%) at 90 DAT. Compared with the microbial biostimulant alone, the combination treatment significantly increased soil respiration rate by 32% and 18% at 90 DAT and 130 DAT, respectively.

Fruit quality attributes of organic strawberry. In both seasons, 'Florida127' had a significantly higher level of fruit SSC than 'Florida Brilliance' regardless of the sampling date (Table 5). In the first season, 'Florida127' also showed significantly higher fruit TA compared with 'Florida Brilliance', by 12% at 75 DAT (early harvest stage) and by 7% at 180 DAT (late harvest stage). The SSC/TA ratio of 'Florida127' was also significantly higher than that of 'Florida Brilliance', by 15% at 140 DAT (peak harvest stage) in the first season and by 16% at 140 DAT (peak harvest stage) and by 24% at 160 DAT (late harvest stage) in the second season. 'Florida Brilliance' consistently exhibited significantly higher TACs than 'Florida127', by 35% in the first season and 18% in the second season on average (Table 5). The fruit from the seaweed extract alone treatment had a significantly lower SSC/TA ratio compared with the combination (by 13%) and microbial alone (by 8%) treatments and the no-biostimulant control (by 7%) at 180 DAT in the first season. In contrast, the combination and seaweed alone treatments significantly increased the SSC/TA ratio of strawberry fruit by 20% and 28%, respectively, compared with the microbial biostimulant alone, and by 13% and 20%, respectively, compared with the control, at 140 DAT in the second season (Table 5). The biostimulant treatments did not demonstrate any significant effect on total anthocyanin content.

Table 1. Marketable fruit yield components of organic strawberry as affected by biostimulant and strawberry cultivar treatments during the 2018–19 and 2019–20 production seasons in Citra, FL.

	2018–19 season												2019–20 season									
	Marketable fruit number (no./plant)						Marketable fruit yield (g/plant)						Marketable fruit number (no./plant)					Marketable fruit yield (g/plant)				
Treatment[i]	Dec	Jan	Feb	Mar	Apr	WS[ii]	Dec	Jan	Feb	Mar	Apr	WS	Dec	Jan	Feb	Mar	WS	Dec	Jan	Feb	Mar	WS
Biostimulant (B)																						
STTE	4.5 a	4.1	10.2	6.7	3.4 a	28.9 a	101.2	123.5	238.1	93.4	54.4 a	611.1 a	4.1 a	3.3	7.6	1.6	16.5	96.3 a	90.5 a	165.2	16.1	368.1 a
ST	3.6 b	3.3	9.2	5.6	2.2 ab	23.9 b	82.0	93.5	212.5	76.4	34.4 ab	498.7 b	3.8 ab	3.0	6.9	1.6	15.3	85.8 ab	73.8 b	144.9	15.8	320.2 b
TE	4.0 ab	3.2	9.9	5.0	1.8 ab	23.9 b	94.0	94.7	237.8	65.8	29.6 ab	521.8 b	3.9 ab	3.3	7.1	1.7	16.0	89.5 ab	66.9 bc	154.7	21.1	332.2 ab
CK	3.9 b	3.4	9.7	4.4	1.3 b	22.7 b	92.0	102.2	223.0	58.2	20.5 b	495.8 b	3.4 b	2.2	6.6	1.4	13.6	79.0 b	57.0 c	146.3	18.9	301.2 b
Cultivar (C)																						
Florida Brilliance	4.4 a	4.4 a	10.2	6.2 a	1.7 b	26.9 a	98.4 a	127.2 a	226.7	78.5	24.7 b	555.5 a	4.1 a	4.1 a	7.4	1.8	17.4 a	88.0	90.8 a	147.1	19.6	345.5
Florida127	3.5 b	2.6 b	9.3	4.7 b	2.7 a	22.8 b	86.4 b	79.7 b	229.0	68.4	44.7 a	508.2 b	3.5 b	1.8 b	6.7	1.3	13.3 b	87.3	53.3 b	158.5	16.4	315.4
P value																						
B	0.005	0.18	0.55	0.08	0.02	0.003	0.06	0.07	0.35	0.13	0.02	0.004	0.03	0.25	0.41	0.85	0.12	0.03	<0.001	0.41	0.19	0.005
C	<0.001	<0.001	0.09	0.01	0.03	0.001	0.02	<0.001	0.89	0.16	0.009	0.04	0.01	<0.001	0.48	0.21	0.02	0.86	<0.001	0.52	0.31	0.26
B×C	0.07	0.21	0.39	0.36	0.51	0.32	0.10	0.33	0.58	0.45	0.52	0.57	0.12	0.35	0.32	0.17	0.74	0.24	0.15	0.18	0.15	0.39

[i] STTE = combined application of Stimplex® plus TerraGrow®; ST = Stimplex®; TE = TerraGrow®; CK = water control.

[ii] WS = whole season.

Means followed by the same letter within a column are not significantly different at $P \leq 0.05$ according to Tukey's test.

Discussion

Effects of seaweed extract and microbial biostimulants on plant vegetative growth and fruit yield and cultivar response. The two strawberry cultivars did not exhibit differential responses to the biostimulant treatments with respect to plant growth and fruit yield components in the present study focused on organic production systems. Compared with 'Florida127', 'Florida Brilliance' plants had fewer leaves, smaller total leaf area, and smaller crowns, yet showed higher levels of leaf relative chlorophyll content and photosynthetic rate (early harvest). We did not observe any marked impacts of biostimulant treatments on strawberry crown diameter, leaf relative chlorophyll content, and photosynthetic parameters. Plant growth measurements toward the end of the production season revealed some positive effects of seaweed extract (alone) application on plant total leaf number and area, and the individual microbial biostimulant treatment also increased plant total leaf area. Previous studies have demonstrated the benefits of plant biostimulants in overcoming abiotic stress such as N and P deficiency (Mola et al. 2019; Soppelsa et al. 2019), drought (Spann and Little 2011), and salinity (Ertani et al. 2013). However, in the present field trials, influence of the individual biostimulant treatment was generally inconsistent between the two seasons and did not translate into detectable yield increases.

Interestingly, the biostimulant combination treatment consistently increased plant crown number, total leaf number, and area as well as individual leaf size as measured toward the end of each production season, indicating a synergistic effect of these seaweed extract and microbial biostimulants on organic strawberry plant growth. To date, few studies have been conducted to evaluate the impact of combined application of different biostimulants in organic strawberry production systems. Our 2-year study indicated that applying seaweed extract and microbial biostimulants together could have synergistic effects with regard to improving whole-season strawberry fruit yield, resulting in an average increase of 23% in marketable yield and 20% in total yield as compared with the no-biostimulant control. In contrast, no statistical difference was detected in whole-season marketable and total yields between each of the biostimulant alone vs. the no-biostimulant control. The whole-season fruit yield increase in the 2018–19 season was mainly contributed by the increase of fruit number because the biostimulant treatments did not affect average fruit weight (data not shown). In contrast, the fruit number did not differ between biostimulant treatments in the 2019–20 season and the whole-season yield increase was primarily due to the greater average fruit weight (data not shown). The influence of the biostimulants on monthly yield varied during the harvest period in each season, likely owing to the dynamics of the environmental conditions and disease and pest pressure during December to March and April. Regardless, the synergistic effects of biostimulants in enhancing marketable and total fruit

Table 2. Total fruit yield components of organic strawberry as affected by biostimulant and strawberry cultivar treatments during the 2018–19 and 2019–20 production seasons in Citra, FL.

	2018–19 season												2019–20 season									
	Total fruit number (no./plant)						Total fruit yield (g/plant)						Total fruit number (no./plant)					Total fruit yield (g/plant)				
Treatment[i]	Dec	Jan	Feb	Mar	Apr	WS[ii]	Dec	Jan	Feb	Mar	Apr	WS	Dec	Jan	Feb	Mar	WS	Dec	Jan	Feb	Mar	WS
Biostimulant (B)																						
STTE	4.9 a	4.6	13.4	16.6 a	6.0 a	45.5 a	107.6 a	134.8	294.0	172.2 a	76.2 a	784.8 a	5.8 a	6.1	15.1	3.1	30.0	126.6 a	141.6 a	284.6	26.0	578.8 a
ST	4.1 b	3.9	11.6	15.2 ab	4.1 ab	38.9 ab	88.6 b	103.5	249.0	146.6 ab	49.7 ab	637.2 b	5.4 ab	6.1	14.4	3.0	28.9	113.5 ab	125.9 ab	268.6	25.7	533.6 ab
TE	4.2 b	3.9	12.8	14.3 ab	2.9 b	38.1 b	98.5 ab	109.9	288.0	136.6 ab	39.2 b	672.2 b	5.5 ab	5.9	14.7	3.0	29.1	115.2 ab	116.0 b	281.9	28.9	542.0 ab
CK	4.1 b	4.0	12.4	11.5 b	2.7 b	34.6 b	96.6 ab	113.5	265.7	111.6 b	31.3 b	618.7 b	4.7 b	5.3	14.9	2.5	27.4	100.0 b	112.1 b	267.9	27.2	507.2 b
Cultivar (C)																						
Florida Brilliance	4.8 a	4.9 a	13.1	18.0 a	3.0 b	43.8 a	103.8 a	138.4 a	271.9	168.4 a	34.5 b	717.0 a	5.6 a	7.7 a	15.1	3.6 a	32.4 a	113.5	152.8 a	269.4	32.0	567.7 a
Florida127	3.9 b	3.3 b	12.0	10.8 b	4.9 a	34.8 b	91.8 b	92.5 b	276.5	115.1 b	63.7 a	639.5 b	4.9 b	4.0 b	13.2	2.1 b	24.2 b	114.2	95.0 b	282.0	22.0	513.1 b
P value																						
B	0.01	0.29	0.25	0.01	0.002	0.005	0.05	0.07	0.14	0.04	0.01	0.001	0.02	0.41	0.87	0.58	0.28	0.01	0.003	0.58	0.78	0.003
C	<0.001	<0.001	0.10	<0.001	<0.001	<0.001	0.01	<0.001	0.75	<0.001	<0.001	0.009	0.008	0.005	0.16	0.04	<0.001	0.88	<0.001	0.39	0.06	0.02
B×C	0.17	0.17	0.71	0.39	0.46	0.54	0.11	0.24	0.73	0.64	0.39	0.73	0.71	0.62	0.57	0.12	0.96	0.67	0.09	0.16	0.11	0.39

[i] STTE = combined application of Stimplex® plus TerraGrow®; ST = Stimplex®; TE = TerraGrow®; CK = water control.

[ii] WS = whole season.

Means followed by the same letter within a column are not significantly different at $P \leq 0.05$ according to Tukey's test.

numbers and yields were more consistent for December harvests in both seasons, suggesting that the combined application of both biostimulants might be more beneficial for promoting early-season yield to target the early market with its high premium prices.

The synergistic effects of the biostimulants on crop yield performance in this study could be attributed to several plant physiological and morphological factors including enhanced total root length and surface area, improved nutrient uptake (e.g., N), enlarged total and single leaf area, and increased numbers of crowns and leaves during the production season. Because all flower stalks of strawberry plants originate in crowns, strawberry plants with increased crown numbers tend to produce more fruit (Cocco et al. 2011). Furthermore, the resulting increased leaf number and enlarged leaf area could have produced and supplied more carbohydrate assimilates to the strawberry fruit (Weraduwage et al. 2015). Negi et al. (2021) also reported that an increase in number of leaves resulted in enhancement of strawberry fruit yield. Similarly, Sani et al. (2020) reported the synergistic effect of a combination of seaweed extract (*Ascophyllum nodosum*) and *Trichoderma*-based biostimulants on increasing total fruit number and yield and average fruit weight of organic tomato, which was ascribed to improved N and K uptake and plant growth attributes including root dry weight and numbers of leaves and branches. Meanwhile, it is important to note that the efficacy of biostimulant products may also depend on their formulations, extraction methods, and other intrinsic factors (Cristofano et al. 2021). Given the nature of Florida's sandy soils, keeping the seaweed extract biostimulant in the rhizosphere might be a practical challenge. Moreover, strawberry roots with fibrous and shallow architecture may respond poorly to the liquid seaweed extract biostimulant in deep sandy soils (Dong et al. 2020). In this case, the beneficial microorganisms from the microbial biostimulant may have assisted the strawberry plant roots in absorbing the seaweed extract biostimulant more effectively and efficiently by stimulating root growth and improving root system architecture as indicated by the increased total root length and surface area (Dias et al. 2009; Rouphael et al. 2017). On the other hand, the complex ingredients contained in seaweed extract (e.g., polyphenols and organic acids) as identified in our study could potentially promote the activity of extraneous microbes from the microbial biostimulant as well as the indigenous communities of soil organisms by providing carbon (C) and N sources (Alam et al. 2014; Renaut et al. 2019). For example, Schmidt et al. (2013) reported an increase in soil respiration rate in response to application of exogenous polyphenols based on a laboratory incubation study. A similar laboratory experiment by Qu and Wang (2008) also showed that soil amended with different types of phenolic acids had higher soil microbial activities as indicated by increased soil respiration rates. The enhancement of organic strawberry yield observed in the combined seaweed extract plus microbial biostimulants treatment may also stem from the multifunctional network of root-

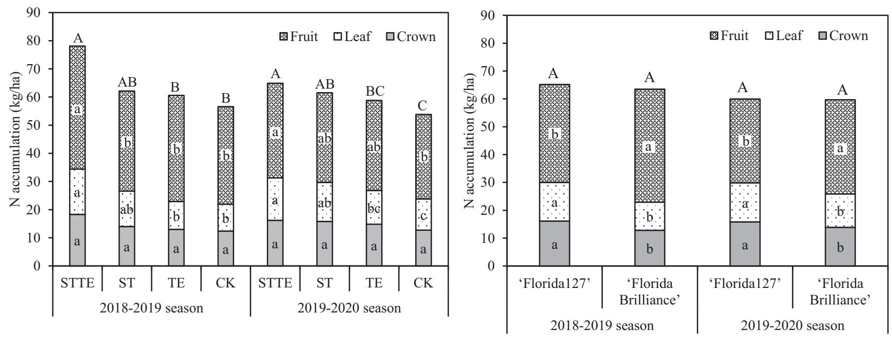

Fig. 6. Effects of biostimulant treatments (left) and strawberry cultivars (right) on N accumulation in fruit, leaf, and crown tissues during 2018–19 and 2019–20 production seasons in Citra, FL. STTE = combined application of Stimplex® plus TerraGrow®; ST = Stimplex®; TE = TerraGrow® CK = water control. Bars with the same uppercase letter for total accumulation of N in all aboveground tissues and bars with the same lowercase letters for N accumulation in a given type of tissue do not differ significantly at $P \leq 0.05$ according to Tukey's test.

soil-microbe interactions (Zhang et al. 2017). To fully understand the synergistic benefits of seaweed extract and microbial biostimulants, more studies are needed to explore their effects on soil chemical and physical properties, soil microbial communities, soilborne pathogens, root-soil-microbe interactions in the rhizosphere, and plant tolerance to abiotic stresses such as drought and temperature extremes. As pointed out by a recent meta-analysis by Li et al. (2022), yield improvement by different biostimulants can be more pronounced with soil treatment vs. foliar application, while greater yield benefits have been observed in less humid environments and sandy soils with low organic matter content and insufficient nutrient conditions.

The biostimulant effects on fruit yield did not differ between the two strawberry cultivars and our results suggested that Florida Brilliance generally outperformed Florida127 under organic production. In particular, 'Florida Brilliance' showed better yield performance in the early harvest season (December and January) when the strawberry market is more profitable. We did not observe any major cultivar differences in terms of disease and pest problems except that 'Florida Brilliance' plants were less affected by angular leaf spot (caused by *Xanthomonas fragariae*) than 'Florida127' in the 2018–19 season (data not shown). Both cultivars were developed for conventional strawberry production in Florida, and this study provided research-based evidence for differential adaptation of these strawberry cultivars to organic production systems. More studies are warranted to further understand specific traits that help promote strawberry productivity in organic growing conditions.

Effects of seaweed extract and microbial biostimulants on root morphology and soil respiration. The increased total root surface area and root length of strawberry plants as a result of combined use of the seaweed extract and microbial biostimulants in the present study might lead to more absorbing area with a greater chance of root contact with water, nutrient ions, hormones, and other beneficial compounds in the soil (Fan et al. 2011). The number of root tips and forks can also considerably impact root architecture, and more root tips and forks might have positive effects on plant uptake of soil nutrients by improving root penetration through soil layers (Wijewardana et al. 2015). It would be intriguing to further explore how the seaweed extract and microbial biostimulants altered strawberry root systems for improved functions.

Although soil respiration was only measured in the second season, it was found that as an indicator of soil microbial activity and soil health, soil respiration rate was consistently increased by the seaweed extract biostimulant and the combination of seaweed extract plus

Table 3. Nutrient contents of strawberry fruit (dry weight basis) as affected by biostimulant and strawberry cultivar treatments at the late harvest season of the 2018–19 and 2019–20 trials in Citra, FL.

	Macronutrient ($g \cdot kg^{-1}$)						Micronutrient ($mg \cdot kg^{-1}$)			
Treatment[i]	N	P	K	Mg	S	Ca	B	Zn	Mn	Fe
	2018–19 season									
Biostimulant (B)										
STTE	11.19	2.86	16.97 a	1.48	0.93 a	2.01	10.3	23.5	26.6	1.9
ST	10.98	2.74	16.30 a	1.45	0.91 a	1.94	10.5	26.8	27.1	2.6
TE	10.84	2.77	15.91 ab	1.41	0.89 ab	1.91	9.8	21.5	26.2	1.9
CK	10.39	2.61	14.69 b	1.36	0.81 b	1.83	10.5	21.9	25.1	2.5
Cultivar (C)										
Florida Brilliance	12.22 a	3.04 a	17.49 a	1.56 a	0.95 a	2.02 a	10.4	24.0	27.9 a	2.5
Florida127	94.84 b	2.44 b	14.45 b	1.29 b	0.82 b	1.83 b	10.2	22.8	24.5 b	2.0
P value										
B	0.27	0.18	0.04	0.12	0.04	0.26	0.88	0.37	0.43	0.39
C	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.81	0.60	<0.001	0.19
B×C	0.31	0.12	0.56	0.43	0.23	0.29	0.56	0.43	0.61	0.12
	2019–20 season									
Biostimulant (B)										
STTE	12.01	3.32	16.34 a	1.45	0.94 a	2.12	13.1	24.7	27.2	3.4
ST	11.53	3.21	15.90 a	1.41	0.92 a	2.01	13.0	26.5	28.7	3.2
TE	11.50	3.12	15.76 ab	1.37	0.83 b	1.97	12.0	24.4	26.1	3.6
CK	11.01	3.21	14.99 b	1.32	0.82 b	1.91	12.8	25.7	26.6	3.0
Cultivar (C)										
Florida Brilliance	12.98 a	3.42 a	16.59 a	1.50 a	0.93 a	2.02 a	12.6	25.1	28.6 a	3.7
Florida127	10.05 b	3.01 b	14.91 b	1.20 b	0.83 b	1.83 b	12.5	23.8	25.7 b	2.9
P value										
B	0.16	0.12	0.02	0.09	0.03	0.18	0.56	0.57	0.45	0.67
C	0.02	0.01	0.02	0.003	0.001	0.03	0.67	0.35	0.04	0.45
B×C	0.65	0.45	0.21	0.18	0.67	0.35	0.55	0.63	0.18	0.38

[i] STTE = combined application of Stimplex® plus TerraGrow®; ST = Stimplex®; TE = TerraGrow®; CK = water control.
The fruit were sampled on 4 Apr 2019 and 2 Mar 2020.
Means followed by the same letter within a column are not significantly different at $P \leq 0.05$ according to Tukey's test.

Table 4. Root dry weight, total root length, average root diameter, total root surface area, and numbers of root tips, forks, and crossings of strawberry plants in the 2018–19 and 2019–20 trials in Citra, FL.

Treatment[i]	Root dry wt (g)	Total root length (cm/plant)	Avg root diam (mm)	Total root surface area (cm^2/plant)	Tips (no.)	Forks (no.)	Crossings (no.)
				2018–19 season			
Biostimulant (B)							
STTE	10.22 a	1,160	1.11	393.5 a	1,648	9,401 a	661
CK	7.76 b	992	1.05	313.6 b	1,361	7,360 b	555
Cultivar (C)							
Florida Brilliance	8.78	1,115	1.06	355.5	1,563	8,543	625
Florida127	9.20	1,037	1.10	353.5	1,446	8,219	591
P value							
B	0.003	0.08	0.33	0.002	0.06	0.03	0.19
C	0.55	0.25	0.07	0.93	0.32	0.62	0.57
B×C	0.45	0.31	0.22	0.65	0.47	0.34	0.11
				2019–20 season			
Biostimulant (B)							
STTE	9.54 a	1,198 a	0.97	413.6 a	1,625 a	9,219 a	692
CK	8.01 b	1,012 b	0.89	322.2 b	1,412 b	7,528 b	631
Cultivar (C)							
Florida Brilliance	7.94	1,100	0.87	370.1	1,549	8,493	682
Florida127	8.43	1,094	0.98	364.7	1,488	8,254	642
P value							
B	0.04	0.03	0.76	0.01	0.04	0.02	0.23
C	0.44	0.78	0.34	0.26	0.24	0.34	0.41
B×C	0.56	0.12	0.42	0.21	0.76	0.34	0.12

[i] STTE = combined application of Stimplex® plus TerraGrow®; CK = water control.
The plant roots were sampled on 23 Apr 2019 and 12 Mar 2020.
Means followed by the same letter within a column are not significantly different at $P \leq 0.05$ according to Tukey's test.

microbial biostimulants throughout the season. The increase in soil respiration rate was likely due to various compounds identified in the seaweed extract biostimulant, such as polyphenols, organic acids, proteins, fatty acids, and steroids (Supplemental Fig. 1). Those organic compounds can affect soil microbial communities by providing substrates (C and N sources) to stimulate metabolism activities of soil microbes (Cleveland et al. 2007). The increased soil respiration suggested a possible enhancement of nutrient availability through increased decomposition of organic matter mediated by soil microbes (bacteria and fungi) and soil fauna (e.g., microarthropods and nematodes) (Reynolds and Hunter 2001). Our results are in agreement with the conventional strawberry study by Alam et al. (2013), which also reported increased soil respiration rates in the field as a result of the application of seaweed extracts derived from *Ascophyllum nodosum*. However, more research is warranted to elucidate the direct linkage of increased soil microbial activities to improvement of strawberry growth and yield performance.

Effects of strawberry cultivar and seaweed extract and microbial biostimulants on N accumulation in aboveground biomass and fruit mineral content. The increase in plant aboveground N accumulation by the combined application of seaweed extract and microbial biostimulants was largely related to the greater level of biomass contributed by leaves and fruit. The total N accumulation in the aboveground biomass was similar in the two strawberry cultivars. However, 'Florida127' accumulated more N in crowns (26% of total aboveground N accumulation) and leaves (22% of total aboveground N accumulation) and less N in fruit (52% of total aboveground N accumulation) than 'Florida Brilliance', which showed 22%, 18%, and 60% of accumulated N in crowns, leaves, and fruit, respectively. This implies that these two strawberry cultivars grown under the same organic management conditions in the present study had similar overall N uptake capacities, but how the N was allocated differed between the two cultivars. The higher yielding potential of 'Florida Brilliance' compared with 'Florida127' could be at least partly attributable to its greater N allocation and assimilation into fruit, making 'Florida Brilliance' more advantageous for organic production systems.

Our study showed that both the seaweed extract application and the combination of seaweed extract and microbial biostimulants increased the contents of K and S in strawberry fruit in the late harvest season. Seaweed extracts have been reported to increase nutrient uptake by plants, possibly due to the improved root system architecture (Mattner et al. 2018). Our results provided further evidence that the combined use of seaweed extract and microbial biostimulants could promote strawberry uptake of some nutrients (N, K, and S) by increasing total root length and surface area. The fruit contents of N, P, K, S, Ca, Mg, and Mn were consistently higher in 'Florida Brilliance' vs. 'Florida127' in both seasons, which is in accordance with previous studies that the levels of macro- and micronutrients in strawberry fruit

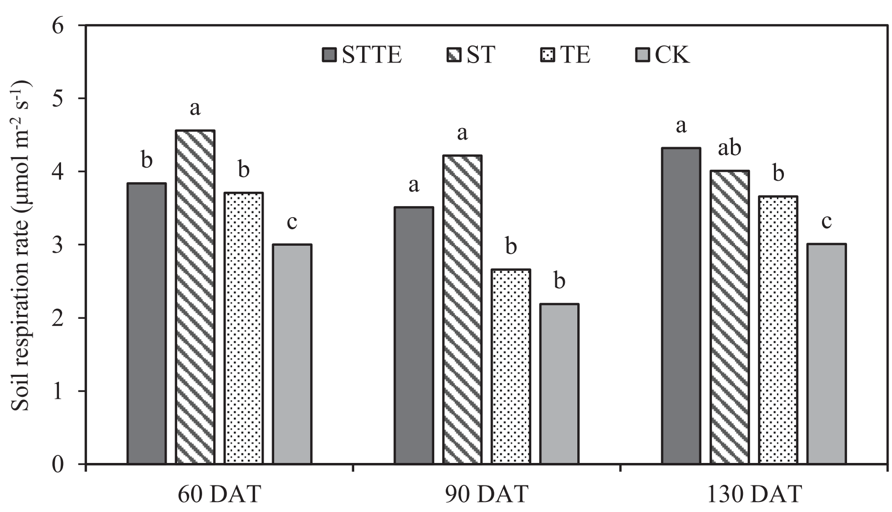

Fig. 7. Effects of biostimulant treatments on soil respiration rate in organic strawberry field during 2019–20 in Citra, FL. STTE = combined application of Stimplex® plus TerraGrow®; ST = Stimplex®; TE = TerraGrow®; CT = water control. Bars with the same letter at each sampling date do not differ significantly at $P \leq 0.05$ according to Tukey's test.

Table 5. Soluble solids content (SSC), titratable acidity (TA), SSC/TA ratio, and total anthocyanin content (TAC) of organic strawberry fruit as affected by biostimulant and strawberry cultivar treatments during the 2018–19 and 2019–20 production seasons in Citra, FL.

	SSC (°Brix)			TA (%)			SSC/TA			TAC (mg/100 g FW)		
	2018–19 season											
Treatment[i]	75 DAT[ii]	140 DAT	180 DAT	75 DAT	140 DAT	180 DAT	75 DAT	140 DAT	180 DAT	75 DAT	140 DAT	180 DAT
Biostimulant (B)												
STTE	6.7	7.2	7.1	0.79	0.68	0.70	8.5	10.6	10.2 a	29.5	30.6	30.5
ST	6.8	7.2	6.7	0.80	0.70	0.76	8.5	10.3	8.9 b	28.9	25.9	29.4
TE	6.7	7.2	6.9	0.78	0.69	0.71	8.7	10.4	9.7 a	28.2	26.1	29.0
CK	6.7	7.1	6.9	0.79	0.67	0.73	8.5	10.6	9.6 a	27.3	28.9	28.6
Cultivar (C)												
Florida Brilliance	6.3 b	6.5 b	6.5 b	0.73 b	0.66	0.70 b	8.6	9.9 b	9.5	30.1 a	32.2 a	33.8 a
Florida127	7.0 a	8.1 a	7.2 a	0.82 a	0.71	0.75 a	8.5	11.4 a	9.7	23.9 b	23.0 b	24.2 b
P value												
B	0.69	0.10	0.15	0.39	0.38	0.06	0.49	0.14	0.006	0.15	0.13	0.67
C	<0.001	<0.001	<0.001	<0.001	0.07	<0.001	0.27	<0.001	0.34	0.02	0.01	0.03
B×C	0.13	0.34	0.25	0.19	0.16	0.23	0.45	0.21	0.43	0.68	0.41	0.16
	2019–20 season											
	75 DAT	140 DAT	160 DAT	75 DAT	140 DAT	160 DAT	75 DAT	140 DAT	160 DAT	75 DAT	140 DAT	160 DAT
Biostimulant (B)												
STTE	7.3	7.4	6.8	0.78	0.69	0.71	9.5	11.3 a	9.6	30.5	27.4	27.3
ST	7.0	7.3	6.8	0.73	0.64	0.70	9.8	12.0 a	9.7	29.9	28.1	27.2
TE	6.6	6.8	6.7	0.72	0.67	0.71	9.2	9.4 b	9.5	29.1	26.9	29.1
CK	6.7	6.6	6.5	0.74	0.66	0.69	9.0	10.0 b	9.4	25.9	27.1	28.2
Cultivar (C)												
Florida Brilliance	6.7 b	6.8 b	5.9 b	0.73	0.66	0.69	9.4	10.3 b	8.6 b	30.9 a	29.3 a	30.9 a
Florida127	7.4 a	8.0 a	7.6 a	0.78	0.67	0.71	9.3	11.9 a	10.7 a	26.9 b	25.4 b	24.9 b
P value												
B	0.09	0.07	0.15	0.65	0.24	0.65	0.63	0.03	0.27	0.34	0.21	0.19
C	0.01	0.02	0.006	0.06	0.76	0.34	0.70	0.01	0.02	<0.001	0.003	0.001
B×C	0.20	0.41	0.18	0.22	0.35	0.17	0.18	0.28	0.45	0.79	0.61	0.53

[i] STTE = combined application of Stimplex® plus TerraGrow®; ST = Stimplex®; TE = TerraGrow®; CK = water control.

[ii] DAT = days after strawberry transplanting.

Means followed by the same letter within a column are not significantly different at $P \leq 0.05$ according to Tukey's test.

are cultivar dependent (Celiktopuz et al. 2021; Jurgiel-Małecka et al. 2017). Strawberry cultivar adaptation to organic systems with respect to nutrient uptake, assimilation, and allocation deserves more studies for identifying and developing genotypes suitable for organic production.

Effects of strawberry cultivar and biostimulant treatments on fruit quality attributes. The application of biostimulant treatments did not have a significant impact on strawberry fruit quality in our study. Notably, despite the increased yield resulting from these treatments, there was no observed decline in fruit quality. 'Florida127' strawberries had consistently higher SSC than 'Florida Brilliance' regardless of the sampling date in both production seasons even though 'Florida127' showed lower yield potential than 'Florida Brilliance' in this study. The SSC/TA ratio has been reported to positively correlate with strawberry flavor (Jouquand et al. 2008). The higher SSC/TA ratio of 'Florida127' fruit detected at 140 DAT in the 2018–19 trial and at 140 and 160 DAT in the second season might indicate enhanced strawberry flavor compared with 'Florida Brilliance'. Similarly, a 3-year study conducted in a conventional production system showed that 'Florida127' possessed significantly higher levels of SSC and SSC/TA than 'Florida Brilliance' (Whitaker et al. 2018, 2019). Overall, the strawberry fruit SSC/TA ratios detected in the present study are consistent with the typical range (8.5–13.0) for strawberries with acceptable fruit quality (Kafkas et al. 2007; Wu et al. 2020).

In our study, 'Florida Brilliance' fruit exhibited greater levels of TAC throughout the harvest season during both trials. As the anthocyanin content in strawberry fruit is closely related to red fruit color intensity, the lower TAC found in 'Florida127' reflected its lighter red color as reported previously (Kelly et al. 2016). The higher TAC level in 'Florida Brilliance' also suggests improved nutritional quality and benefits for human health, particularly due to the antioxidant capacities associated with anthocyanins (Giampieri et al. 2012). The fruit anthocyanin levels measured in our study fall within the range of 23 to 45 mg of pelargonidin 3-glucoside per 100 g of fresh weight for different strawberry cultivars reported previously (Wang and Zheng 2001). Balancing yield and fruit quality is another area of interest in future research for improving organic strawberry production systems. Overall, our study suggests that compared with 'Florida127', 'Florida Brilliance' was better adapted to organic production systems in Florida as reflected by the improved photosynthetic ability, increased N accumulation in fruit, and enhanced early-season fruit yield performance along with acceptable fruit quality with higher levels of total anthocyanins.

Conclusions

Our findings indicate that overall 'Florida Brilliance' outperformed 'Florida127' for fruit yield under organic production and produced strawberries with higher anthocyanin contents, whereas 'Florida127' might have better flavor as reflected by higher values of fruit SSC and SSC/TA. The seaweed extract and microbial biostimulants exhibited synergistic effects in improving strawberry fruit yield, suggesting their integrative potential as a promising measure to enhance strawberry productivity in organic systems. The combined application of seaweed extract plus microbial biostimulants also resulted in greater numbers of crowns and leaves, enlarged leaf area, modification of root morphology with increased total root length and surface area, enhanced N accumulation in aboveground tissue, and increased soil respiration rates. Further research is warranted to investigate the synergistic effects of different types of biostimulants on crop productivity improvement in addition to their individual impacts and the underlying mechanisms.

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