HortScience 60(3):435–445. 2025. https://doi.org/10.21273/HORTSCI18245-24

Adjusting the Percentage of Nitrate in Nutrient Solution to Optimize Strawberry Stolon and Daughter Plant Production

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Keywords. ammonium, controlled environment agriculture, fertilizer, *Fragaria* ×*ananassa*, propagation, runner tips

Abstract. **Year-round production of disease-free strawberry (*Fragaria* ×*ananassa*) daughter plants can be achieved by growing mother plants in controlled environments. However, a lack of protocols exists for nutrient management of mother plants to optimize the production of stolons and daughter plants. Our objective was to identify the optimal percentage range of nitrogen (N) supplied as nitrate (%NO_3^-) in a nutrient solution to maximize strawberry stolon and daughter plant production. Three cultivars (Albion, Fronteras, and Monterey) were grown in 20.3-cm pots filled with a peat-based soilless substrate. A strawberry-specific nutrient solution (Yamazaki) provided 100 mg·L^{-1} N, and the N form supplied ranged from 0% to 100% NO_3^-, with the remainder supplied as ammonium (NH_4^+). In Expt. 1, 'Fronteras' stolon and daughter plant numbers were assessed every 4 weeks for 16 weeks. The harvest interval was too frequent to identify any treatment effects. In Expt. 2, 'Albion', 'Fronteras', and 'Monterey' stolon and daughter plant numbers were assessed at 8 and 16 weeks. Cumulative stolon number and cumulative daughter plant number exhibited linear or quadratic responses to the percentage of NO_3^-, and the responses were cultivar dependent. Maximum calculated cumulative stolon number occurred at 64% NO_3^- for 'Fronteras' and at 100% NO_3^- for 'Albion' and 'Monterey'. Maximum calculated cumulative daughter plant number occurred at 66% NO_3^- for 'Fronteras', 81% NO_3^- for 'Monterey', and 100% NO_3^- for 'Albion'. The percentage of NO_3^- generally did not affect daughter plant quality, such as root number, crown diameter, dry mass, and foliar %N. Total aboveground biomass (mother plant + stolons + daughter plants) increased as the percentage of NO_3^- increased from 0% to 100%. 'Monterey' had more total aboveground biomass than 'Albion' or 'Fronteras'. A calculated range in which all three cultivars overlapped with ≥95% of maximum daughter plant number occurred between 81% to 87% NO_3^-. A strawberry fertilizer recipe in this target range would allow growers the opportunity to use a single fertilizer recipe to support high daughter plant productivity across multiple cultivars. Our results indicate that optimal strawberry daughter plant production occurs at a lower percentage of NO_3^- than recommended for inflorescence or fruit production.**

In the United States, strawberry (*Fragaria* ×*ananassa*) fruit production was valued at $3.2 billion in 2022 (US Department of Agriculture, National Agricultural Statistics Service 2023). Although this popular fruit is primarily a field crop, controlled environments have helped expand local and seasonal availability of strawberry fruit. High tunnels can extend the field growing season, and greenhouses and vertical farms allow for year-round fruit production.

Strawberries are predominantly propagated vegetatively in the United States using field nurseries. In these nurseries, strawberry plants produce stolons (i.e., runners) with attached daughter plants, and these daughter plants root when they contact the field soil. The rooted daughter plants are harvested in the fall and sold either as freshly dug bare root plants or placed in cold storage for up to 1 year (i.e., "frigo" plants) (Hokanson et al. 2004; Neri et al. 2012; Takeda and Newell 2007). However, plant material originating from the field may harbor various plant pests and diseases such as *Colletotrichum* spp., *Phytophthora cactorum*, or *Neopestalotiopsis* spp. (Baggio et al. 2021a, 2021b; Maas 1998). The plants may appear asymptomatic initially and present symptoms after transplant in the field or a controlled environment system. This can be economically costly due to chemical application costs and labor to treat plants, yield losses, and plant death. Therefore, a need exists to develop strategies that provide clean starting material to growers.

A controlled environment agriculture (CEA) strawberry nursery, such as a greenhouse or indoor growth room, can generate clean, healthy, actively growing daughter plants (i.e., runner tips) year-round for CEA and field producers. Daughter plants can be propagated immediately or placed in cold storage for up to 2 months before propagation (Hokanson et al. 2004). Propagating daughter plants in a controlled environment can also ensure clean and well rooted liners or tray plants (Hokanson et al. 2004). Strawberry plants—grown for fruit or for daughter plants—in controlled environments are typically grown in soilless substrates. Research has evaluated daughter plant yield from mother plants growing in various substrates, including coconut coir, peat, perlite, pine bark, rockwool, sand, or wood fibers (Cantliffe et al. 2007; Rivera-del Rio et al. 2017; Taghavi et al. 2017; Tehranifar et al. 2007). Some research has evaluated the impact of environmental conditions, such as light intensity (Xu and Hernández 2020), on stolon and daughter plant yield. However, additional research on other aspects of CEA strawberry production, including environmental, cultural, and nutrient management strategies to optimize daughter plant yield and quality, would be beneficial.

Optimization of the growing environment and crop management practices is crucial to economically produce a high number of high-quality daughter plants while supporting robust mother plant growth. Studies show that nutrient management may influence stolon development in strawberry, including nitrogen (N) form (Cárdenas-Navarro et al. 2006; Shi et al. 2021) and nutrient solution concentration (Andriolo et al. 2014; Cantliffe et al. 2007; Schmitt et al. 2016). In CEA-grown strawberries, supplying 90% of total N as nitrate (NO_3^-) is recommended for inflorescence development and fruit production (Kubota n.d.); anecdotally, decreasing the %NO_3^- to 80% may increase stolon production (Kubota C, personal communication).

However, no consensus exists on the range of %NO_3^- to supply in nutrient solutions to optimize strawberry daughter plant yield and quality. This information will be valuable to support the developing CEA strawberry industry. Therefore, the objective of this research was to identify the optimal range of %NO_3^- to include in a strawberry nutrient solution to optimize 1) daughter plant yield and 2) mother plant growth. Three cultivars (Albion, Fronteras, and Monterey) were evaluated to assess cultivar sensitivity to %NO_3^-. They were selected to include photoperiodic cultivars with both long-day (or "everbearing"; 'Albion' and 'Monterey') and short-day ('Fronteras') responses.

Materials and Methods

Two experiments were conducted to evaluate the impact of nutrient solution %NO_3^--N on strawberry stolon and daughter plant production. An initial study (Expt. 1) was conducted in Fall 2022 and used only 'Fronteras'. A follow-up experiment (Expt. 2) was conducted in Spring 2023 and included 'Albion', 'Fronteras', and 'Monterey'. In both experiments, the nutrient solution %NO_3^--N treatments remained consistent; however, some adjustments in cultural practices and harvest interval occurred between Expts. 1 and 2, which are noted below.

Stock plant growth conditions. Stock plants of 'Albion', 'Fronteras', and 'Monterey'

were grown in a glass-glazed greenhouse (Toledo Botanical Garden, Toledo, OH, USA) and replaced yearly with new plant material to maintain plant vigor and active stolon development. Daughter plants harvested from these stock plants were propagated and used as the starting material for the two research experiments. Stock plants were planted in 20.3-cm diameter pots filled with a peat-based substrate. Greenhouse conditions were maintained at 26/19 °C day/night air temperature and a 16-h photoperiod (0600 to 2200 HR). Light-emitting diode (LED) fixtures (Icarus Ti2; BIOS Lighting, Carlsbad, CA, USA) provided 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density (PPFD) when ambient light intensities were <300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD at canopy level. The plants were irrigated as needed. At every other irrigation, they were fertilized with a 15N–2.2P–12.5K water soluble fertilizer (Jack's Professional 15-5-15 Ca-Mg; JR Peters, Inc., Allentown, PA, USA) at 100 $mg \cdot L^{-1}$ N, supplemented with 306 $mg \cdot L^{-1}$ magnesium sulfate heptahydrate (Magriculture; Giles Chemical, Waynesville, NC, USA). Substate solution pH and electrical conductivity (EC) were checked monthly (HANNA HI9814 GroPro; Hanna Instruments, Woonsocket, RI, USA). If EC drifted above 2.0 $mS \cdot cm^{-1}$, the containers were leached to get rid of excess salts. If pH drifted below 5.5, 1.04 $L \cdot m^{-3}$ flowable lime (CalOx; BioSafe Systems, LLC, East Hartford, CT, USA) was applied to increase pH by approximately 0.5 units. Inflorescences were removed weekly, and stolons containing daughter plants were harvested as needed for research studies. About every 2 months, extra stolons containing at least one daughter plant were removed to maintain crown vigor but ensure a continuous supply of daughter plants that could be harvested and propagated for research studies.

Propagation of starting plant material. Stolons of strawberry 'Fronteras' were harvested from stock plants on 27 May 2022 (Expt. 1) and from 'Albion', 'Fronteras', and 'Monterey' on 20 Dec 2022 (Expt. 2). The harvested stolons were stored in a cooler in the dark at 4 °C for 7 d before propagating. Daughter plants were cut from the stolon approximately 1 cm above and below the node and graded into size categories. Daughter plants with a crown diameter of 5 to 7 mm, visible root initials, and two to three unfolded leaves were selected; this crown diameter corresponded to the small to medium size categories described by Xu and Hernández (2020). Daughter plants were stuck in 50-cell count propagation trays (100-mL cell volume) filled with a commercial peat-based substrate (LM-111 All Purpose Mix; Lambert, Rivière-Ouelle, QC, Canada). Plants were propagated in a reach-in growth chamber (BDR16; Conviron, Winnipeg, MB, Canada) for 5 weeks (Expt. 1) or 4 weeks (Expt. 2). Environmental conditions were set to a constant 24 °C air temperature, a 16-h photoperiod, and a relative humidity (RH) of 80%. Humidity domes were placed over the trays for 7 d to maintain a high RH, and plants were hand misted twice daily. After 7 d, the humidity domes were removed, and the chamber RH setpoint was decreased to 70% for the remainder of the propagation interval. Initial PPFD was approximately 125 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for the first 2 weeks and then increased to approximately 225 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for the remaining 3 (Expt. 1) or 2 (Expt. 2) weeks of propagation. The plants were initially irrigated with tap water and then fertigated as needed with a diluted formulation of the 15N–2.2P–12.5K + magnesium sulfate fertilizer blend provided to the stock plants. The fertilizer was diluted to supply 30 $mg \cdot L^{-1}$ N for the first 14 d, 50 $mg \cdot L^{-1}$ N from days 15 to 28, and 75 $mg \cdot L^{-1}$ N after 28 d. Stolons and inflorescences were removed as they became visible during the propagation phase. These rooted daughter plants were the starting plant material for the research studies.

Transplant and acclimation of research plants. On 8 Jul 2022 (Expt. 1) and 26 Jan 2023 (Expt. 2), the rooted strawberry plants were transplanted into 20.3-cm diameter pots (2.90-L; mum pan; HC Companies, Middlefield, OH, USA), with one plant per pot. We refer to these rooted plants, after transplant, as the mother plants in our research studies. In Expt. 1, the pots were filled with a commercial peat: perlite substrate (85/15 v/v) (LM-111; Lambert). In Expt. 2, the commercial substrate (LM-111) was amended with additional coarse perlite (P.V.P. Industries, Inc., North Bloomfield, OH, USA) to increase porosity, and the final peat: perlite composition was 70/30 (v/v). The plants were grown in a glass-glazed greenhouse (Toledo Botanical Garden) for a 3-week acclimation period. The pots were irrigated as needed with 75 $mg \cdot L^{-1}$ N from a 15N–2.2P–12.5K nutrient solution supplemented with magnesium sulfate. Visible stolons and inflorescences were removed twice weekly.

Greenhouse environmental conditions for Expts. 1 and 2. Greenhouse setpoints were 26 °C day/23 °C night (25 °C average daily air temperature), ambient RH, and a 16-h photoperiod. LED fixtures (Icarus Ti2; BIOS Lighting) provided 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD when ambient light intensities were <300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD at canopy level. Actual conditions were measured with an aspirated thermocouple, RH sensor, and quantum light sensor. The values were recorded every 10 min using a data logger (WatchDog 2475; Spectrum Technologies, Aurora, IL, USA), and mean values [± standard deviation (*SD*)] are reported in Table 1.

Experimental design and treatments. Six $\%NO_3^-$ treatments (0%, 20%, 50%, 60%, 80%, and 100% NO_3^-) were evaluated in both experiments. As mentioned previously, Expt. 1 evaluated only one strawberry cultivar (Fronteras), whereas Expt. 2 evaluated three strawberry cultivars (Albion, Fronteras, and Monterey) at each $\%NO_3^-$ treatment. Each pot (containing one plant) was an experimental unit. There were six pots per treatment combination, arranged in a randomized complete block design, for a total of 36 pots (Expt. 1) or 108 pots (Expt. 2). Treatments started on 4 Aug 2022 (Expt. 1) and 15 Feb 2023 (Expt. 2). The nutrient solution was a modified strawberry nutrient solution (Yamazaki 1982) comprised of 100 $mg \cdot L^{-1}$ total N. The $\%NO_3^-$ treatments were 0%, 20%, 50%, 60%, 80%, or 100% NO_3^-, with the remaining N supplied by ammonium (NH_4^+); this maintained the same total N across treatments (Table 2). The nutrient solutions were mixed using ultra-purified water (18 MΩ), then pH was checked (HANNA HI9814 GroPro; Hanna Instruments) and adjusted to a range of 5.6 to 5.9 ± 0.1 (Table 2) using 1 M potassium hydroxide (KOH). The target nutrient solution pH increased as the $\%NO_3^-$ supplied decreased (and $\%NH_4^+$ supplied increased) to help minimize pH drift in the pots (Table 2). A sample of each batch of nutrient solution was collected, stored at 4 °C until analysis, and analyzed using inductively coupled plasma-optical emission spectroscopy (ICP-OES) (iCAP 6300 Duo; Thermo Electron Corp., Waltham, MA, USA) (Supplemental Table 1).

Drip emitters (slimline EZ close plastic weights; Netafim, Fresno, CA, USA) delivered 77 ± 8 $mL \cdot min^{-1}$ (± *SD*) to the pots every other day for the first 8 weeks of treatment and then daily for the second 8 weeks of the 16-week trial. The pots were irrigated for approximately 6 to 7 min to reach container

Table 1. Daily mean air temperature, relative humidity, and daily light integral of strawberry plants grown in the greenhouse (± standard deviation).

Growing period	Expt.	Air temp (°C)	Relative humidity (%)	Daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$)
Acclimation	1	25.9 ± 1.8	66.5 ± 9.9	15.0 ± 7.7
	2	22.4 ± 1.1	27.4 ± 8.7	19.6 ± 4.2
Treatment	1	22.7 ± 2.9	57.3 ± 16.2	15.8 ± 3.7
	2	22.7 ± 1.4	39.2 ± 10.1	25.5 ± 6.2

The acclimation period was 3 weeks, and the treatment period was 16 weeks.

Received for publication 3 Oct 2024. Accepted for publication 23 Dec 2024.
Published online 26 Feb 2025.
This research was funded by the US Department of Agriculture, National Institute of Food and Agriculture Specialty Crop Research Initiative Grant 2021-51181-35857. We acknowledge Mona-Lisa Banks, Morgan Jones, Mohamad Moussa, Favour Ohaezu, and Douglas Sturtz for assistance with data collection and nutrient analysis. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA. The USDA is an equal opportunity provider and employer.
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Table 2. Modified strawberry nutrient solution (Yamazaki 1982), mixed to a final concentration of 100 mg·L^{-1} N.

Nutrient	0% NO_3^-	20% NO_3^-	50% NO_3^-	60% NO_3^-	80% NO_3^-	100% NO_3^-
Macronutrients (mM)						
NH_4NO_3	0.0	0.0	0.5	1.0	0.4	0.0
$(NH_4)_2SO_4$	3.0	2.3	1.0	0.4	0.0	0.0
$NH_4H_2PO_4$	1.0	1.0	1.0	1.0	1.0	0.0
$Ca(NO_3)_2$	0.0	0.0	0.0	0.1	1.1	2.5
KNO_3	0.0	1.4	3.0	3.0	3.0	2.0
$CaCl_2$	2.0	2.0	2.0	2.4	1.4	0.0
K_2SO_4	1.5	0.8	0.0	0.0	0.0	0.0
KH_2PO_4	0.0	0.0	0.0	0.0	0.0	1.0
$MgSO_4$	0.5	0.5	0.5	0.5	0.5	0.5
Micronutrients (μM)						
$Na_2FeDTPA$	8.17	8.17	8.17	8.17	8.17	8.17
$MnSO_4$	10	10	10	10	10	10
$ZnSO_4$	0.8	0.8	0.8	0.8	0.8	0.8
$CuSO_4$	0.5	0.5	0.5	0.5	0.5	0.5
$(NH_4)_6Mo_7O_{24}$	0.085	0.085	0.085	0.085	0.085	0.085
H_3BO_3	50	50	50	50	50	50
pH	5.9 ± 0.2	5.8 ± 0.1	5.8 ± 0.1	5.8 ± 0.1	5.7 ± 0.1	5.6 ± 0.2
EC (mS·cm^{-1})	1.8 ± 0.2	1.6 ± 0.2	1.5 ± 0.2	1.5 ± 0.2	1.3 ± 0.1	1.1 ± 0.1

EC = electrical conductivity.

capacity plus an approximately 10% leaching fraction. Beginning at 8 weeks of treatments, the pots were flushed with 18 MΩ water once every other week (approximately 20% leaching fraction). Additionally, flowable lime (CalOx; BioSafe Systems) was applied twice during Expt. 2 to increase the substate pH of the 0% to 60% NO_3^- treatments. On 16 May 2023, flowable lime application rates were 3 mL per pot (0% and 20% NO_3^- treatments), 1.5 mL per pot (50% NO_3^-), or 0.8 mL per pot (60% NO_3^-). On 25 May 2023, treatment applications were 3 mL per pot (0% and 20% NO_3^-) and 1.5 mL per pot (50% and 60% NO_3^-). The flowable lime was suspended in water, and a final volume of 250 mL was applied to each pot; nontreated plants received an equivalent volume of water. Plant canopies were sprayed weekly with 3.6 mM of calcium chloride (Sigma-Aldrich, St. Louis, MO, USA) (Expt. 2) to alleviate tip burn (Kroggel and Kubota 2017).

Data collection. Leachates were collected every 4 weeks (Expt. 1) or at 8 and 16 weeks of treatment (Expt. 2) using the pour-through technique (LeBude and Bilderback 2009). Leachate pH and EC were measured (HANNA HI9814 GroPro; Hanna Instruments), and then the leachates were stored at 4 °C until they could be further analyzed using ICP-OES to quantify nutrient concentrations.

Inflorescences were counted and removed weekly. Stolon number, daughter plant number, and daughter plant morphology were assessed every 4 (Expt. 1) or 8 weeks (Expt. 2). Stolon number was counted at each interval. On nonfinal harvest intervals, stolons containing at least one daughter plant were harvested; stolons without a daughter plant remained on the plant until the next harvest interval. At the final harvest, all stolons (with and without daughter plants) were harvested. For Expt. 2 only, the presence of secondary branching was noted when stolons were harvested, as well as the number of daughter plants that formed on primary vs. secondary (or higher) branches. Daughter plant crown size (mm) was measured at the widest point using digital calipers (Fisher Traceable; Fisher Scientific, Pittsburgh, PA, USA) and later categorized using previously published size categories (Xu and Hernández, 2020), defined as extra small (XS; <3.5 mm), small (S; 3.5 to 6.0 mm), medium (M; 6.0 to 8.5 mm), large (L; 8.5 to 11.0 mm), and extra large (XL; >11.0 mm). Root number, daughter plant fresh mass, and stolon fresh mass (aggregated by pot) were also collected. Daughter plants and stolons, separately, were dipped into 0.1 M HCl-acidified water, rinsed in 18 MΩ water, placed in a paper bag, dried in a forced-air oven at 60 °C for at least 3 d, and weighed for dry mass.

At the end of the 16-week trial, mother plant morphology was also assessed. Canopy height was measured from the substrate surface to the top of the plant canopy. Canopy width (cm) was measured at the widest diameter of the canopy and perpendicular to the widest diameter and then divided by two. Total crown number was counted. Crown diameter was measured just above the substrate surface using digital calipers (Fisher Traceable; Fisher Scientific) at the widest point, perpendicular to the widest point, and divided by two. Fresh mass was weighed, mother plants were dipped into 0.1 M HCl-acidified water, rinsed in 18 MΩ water, placed in a paper bag, dried in a forced-air oven at 60 °C for at least 3 d, and weighed for dry mass. Total plant biomass was calculated as the mother plant plus the sum of the stolons and daughter plants at each harvest.

After drying, daughter plants (pooled by pot at each harvest interval) and mother plants (leaf tissue only) were finely ground for elemental analysis. To quantify %N, approximately 2.5 mg of dry tissue was measured into tin capsules (EA Consumables, Marlton, NJ, USA) and analyzed with a CN analyzer (vario MICRO cube; Elementar, Hanau, Germany). For other elements (except N), approximately 0.25 g of dry tissue was weighed, placed in a Teflon vessel, digested using a programmable microwave (MARS6; CEM Corp., Matthews, NC, USA), and analyzed with ICP-OES (iCAP 6300 Duo, Thermo Electron Corp.) using methods described by Boldt and Altland (2021).

Data analysis. In Expt. 1, stolon and daughter plant number were analyzed at each harvest interval (4, 8, 12, and 16 weeks) and cumulatively. Each harvest interval was analyzed separately. Regression analysis was conducted using PROC REG (SAS version 9.4; SAS Institute, Cary, NC, USA) to evaluate linear or quadratic growth responses to %NO_3^-.

The data collected in Expt. 2 were analyzed initially in SAS (version 9.4) as a two-way factorial (cultivar × %NO_3^-) using PROC GLM to conduct an analysis of variance (ANOVA). When cultivar differences existed ($P < 0.05$), they were assessed using Tukey's honestly significant difference post hoc test at $\alpha = 0.05$. Next, regression analysis was conducted using PROC REG to evaluate linear or quadratic responses to %NO_3^-. For variables with a significant ANOVA cultivar × %NO_3^- interaction effect, regression analysis was performed individually by cultivar. For variables without a significant cultivar × %NO_3^- interaction effect, the data for the three cultivars were pooled together for the regression analysis.

Results

Expt. 1

Stolon and daughter plant number. In Expt. 1, %NO_3^-, ranging from 0% to 100%, did not statistically affect 'Fronteras' stolon number or dry mass, daughter plant number, or daughter plant morphology (crown diameter, root number, or dry mass at any of the harvest intervals ($P > 0.05$ for all; Table 3). Cumulative stolon number averaged 22 ± 1 [mean ± standard error (*SE*)], and cumulative daughter plant number averaged 24 ± 2.

Mother plant. 'Fronteras' mother plant growth (canopy height, canopy width, crown diameter, and crown dry mass) was unaffected by %NO_3^- (regression analysis *P* values were > 0.05), and therefore, the overall means are presented in Table 3. Mean canopy height was 20.9 ± 2.5 cm, canopy width was 39.6 ± 3.5 cm, crown diameter was 11.8 ± 1.8 mm, and crown dry mass was 14.5 ± 2.6 g.

Tissue %N. Percent NO_3^- did not affect foliar %N of daughter plants at any of the four harvests or in the mother plant (Table 3). Pooled daughter plant %N at the individual harvests ranged between 2.53% and 2.86% N. Mother plant foliar %N averaged 2.22% ± 0.06%.

Expt. 2

Stolon number. No significant linear or quadratic trends occurred in response to increasing %NO_3^- at 8 weeks (Fig. 1A). After 16 weeks of treatment, stolon number for 'Albion' and 'Fronteras' exhibited quadratic responses to increasing %NO_3^- (Fig. 1B). 'Albion' stolon number increased from 4 to 8 as %NO_3^- increased from 0% to 100% ($P = 0.01$; adjusted $r^2 = 0.19$). 'Fronteras' stolon number increased from 7 at 0% NO_3^- to a calculated maximum of 11 at 56% NO_3^- and

Table 3. Stolon, daughter plant, and mother plant attributes for strawberry (*Fragaria ×ananassa* 'Fronteras') grown in a soilless substrate for 16 weeks.

Plant portion	Variable	Week 4	Week 8	Week 12	Week 16
Stolons	Number	4 ± 0	5 ± 0	5 ± 0	7 ± 1
	Dry mass (g)	0.95 ± 0.05	0.57 ± 0.02	1.12 ± 0.1	1.00 ± 0.12
Daughter plants	Number	5 ± 0	5 ± 0	4 ± 0	7 ± 1
	Crown diam (mm)	7.5 ± 0.2	8.0 ± 0.2	8.5 ± 0.3	5.8 ± 0.4
	Roots (no.)	17 ± 1	10 ± 1	14 ± 1	17 ± 1
	Dry mass (g)	0.51 ± 0.03	0.46 ± 0.03	0.42 ± 0.04	0.79 ± 0.1
	N (% dry mass)	2.59 ± 0.04	2.53 ± 0.03	2.58 ± 0.06	2.86 ± 0.04
Mother plants	Height (cm)	—	—	—	20.9 ± 2.5
	Width (cm)	—	—	—	39.6 ± 3.5
	Crown diam (mm)	—	—	—	11.8 ± 1.8
	Dry mass (g)	—	—	—	14.5 ± 2.6
	Foliar N (% dry mass)	—	—	—	2.22 ± 0.06

The percentage of total N supplied as nitrate (NO_3^-) ranged from 0% to 100%. Daughter plants were harvested every 4 weeks, and mother plants were evaluated at 16 weeks. Regression analysis was not significant ($P > 0.05$) for all variables, and therefore, only the overall means—pooled across treatments—are presented. The values are means ± standard error.

then declined to 8 at 100% NO_3^- ($P = 0.03$; adjusted $r^2 = 0.15$). 'Monterey' stolon number increased linearly as $\%NO_3^-$ increased, from 7 at 0% NO_3^- to 16 at 100% NO_3^- ($P < 0.0001$; $r^2 = 0.49$; Fig. 1B).

Cumulative stolon number represents the sum of the two harvest dates (8 and 16 weeks of treatment). Like the 16-week harvest, stolon number for 'Albion' and 'Fronteras' exhibited quadratic responses to increasing $\%NO_3^-$, whereas 'Monterey' had a linear response to increasing $\%NO_3^-$ (Fig. 1C). 'Albion' stolon number decreased slightly from 0% to 20% NO_3^- and then increased from 8 at 20% NO_3^- to 13 at 100% NO_3^- ($P = 0.04$; adjusted $r^2 = 0.12$). 'Fronteras' stolon number increased from 9 at 0% NO_3^- to a calculated maximum of 14 at 64% NO_3^- and then decreased to 13 at 100% NO_3^- ($P = 0.04$; adjusted $r^2 = 0.13$). 'Monterey' stolon number increased from 14 at 0% NO_3^- to 22 at 100% NO_3^- ($P = 0.0003$; $r^2 = 0.33$).

In addition to stolon number, the percentage of stolons with secondary branching was assessed. No significant linear or quadratic regression responses occurred for 'Albion' or 'Fronteras'. The percentage of stolons with only primary branching ranged between 20% and 39% in 'Fronteras' and between 49% and 74% in 'Albion' (Fig. 2). However, 'Monterey' had a quadratic response. The percentage of stolons with only primary branching increased from 35% of stolons at 0% NO_3^- to a calculated maximum of 79% of stolons at 67% NO_3^- and then decreased to 67% of stolons as $\%NO_3^-$ further increased to 100%.

After 8 weeks of treatment, 'Albion' had the greatest stolon dry mass (2.94 ± 0.19 g), followed by 'Monterey' (2.42 ± 0.11 g), and 'Fronteras' had the least (1.63 ± 0.1 g) ($P < 0.0001$; Table 4). After 16 weeks of treatment, 'Albion' and 'Monterey' had similar stolon dry masses (2.40 ± 0.16 and 2.16 ± 0.14 g, respectively), and 'Fronteras' had a lower dry mass (0.87 ± 0.08 g) ($P < 0.0001$ for cultivar). Additionally, stolon dry mass at 16 weeks increased linearly from 1.26 to 2.11 g as $\%NO_3^-$ increased from 0% to 100% NO_3^- ($P = 0.001$; $r^2 = 0.10$; data not shown).

Daughter plant number. After 8 weeks of treatment, 'Monterey' daughter plant number decreased linearly as $\%NO_3^-$ increased, but no significant linear or quadratic responses occurred for 'Albion' or 'Fronteras' in response to $\%NO_3^-$ (Fig. 1D). After 16 weeks of treatment, 'Fronteras' and 'Monterey' had quadratic responses as $\%NO_3^-$ increased, whereas 'Albion' did not exhibit a trend (Fig. 1E). 'Fronteras' daughter plant number increased to a calculated maximum of 28 at 61% NO_3^- and then declined to 21 at 100% NO_3^- ($P = 0.03$; adjusted $r^2 = 0.15$). 'Monterey' daughter plant number increased from 24 at 0% NO_3^- to a calculated maximum of 69 at 85% NO_3^- and then declined to 67 at 100% NO_3^- ($P < 0.0001$; adjusted $r^2 = 0.44$). At the 16-week harvest, 'Fronteras' had a higher percentage of daughter plants borne on primary (vs. secondary) stolons (81% ± 2%) than 'Albion' (65% ± 3%) or 'Monterey' (55% ± 2%) ($P < 0.0001$ for cultivar; Table 4).

Cumulative daughter plant number exhibited responses similar to the 16-week data. 'Albion' daughter plant number increased

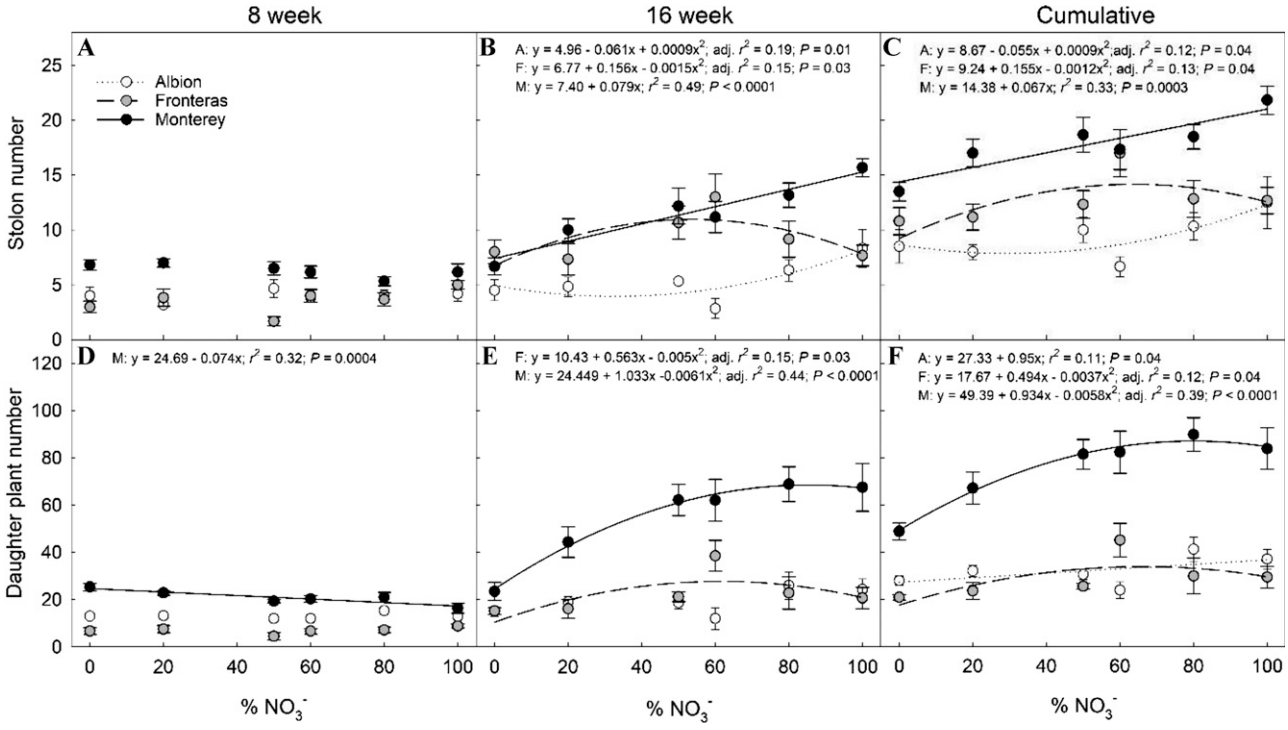

Fig. 1. Stolon number (**A–C**) and daughter plant number (**D–F**) of three strawberry (*Fragaria ×ananassa*) cultivars grown in a soilless substrate for 16 weeks. The percentage of total N supplied as nitrate (NO_3^-) ranged from 0% to 100%. Daughter plants were harvested after 8 (**A, D**) and 16 (**B, E**) weeks of treatment. The values are means ± standard error ($n = 6$). Regression lines (when significant) show 'Albion' (dotted), 'Fronteras' (dashed), and 'Monterey' (solid). The data in **A** did not have a significant linear or quadratic regression response ($P > 0.05$). A = 'Albion', F = 'Fronteras', M = 'Monterey'.

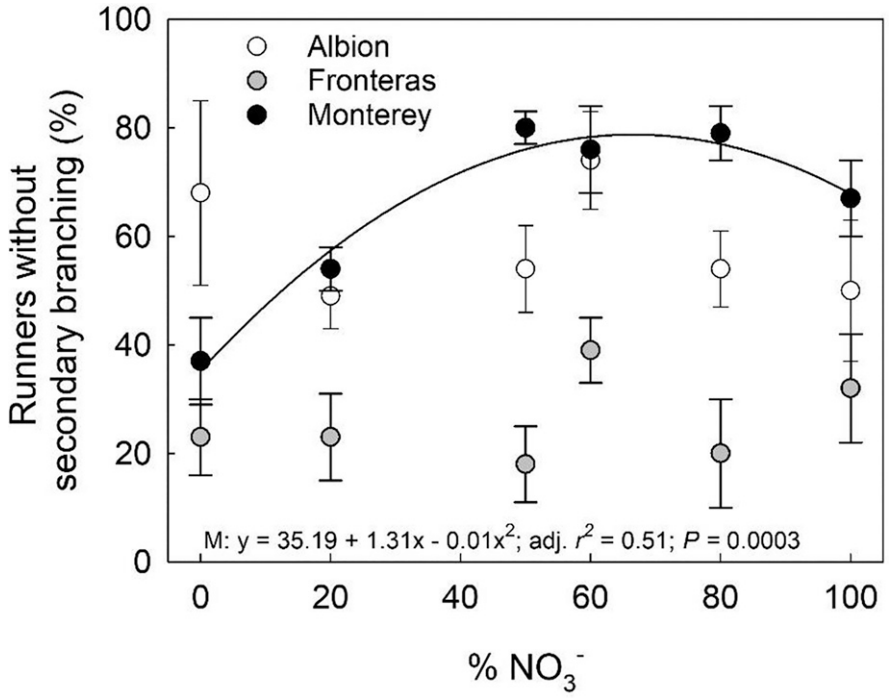

Fig. 2. Percentage of stolons at 16 weeks with only primary branching. Three strawberry (*Fragaria ×ananassa*) cultivars were grown in a soilless substrate for 16 weeks, and the percentage of total N supplied as nitrate (NO_3^-) ranged from 0% to 100%. The values are means ± standard error ($n = 6$). The regression line is for 'Monterey' (M).

linearly, from 27 at 0% NO_3^- to 37 at 100% NO_3^- ($P = 0.04$; $r^2 = 0.11$; Fig. 1F). 'Fronteras' and 'Monterey' exhibited quadratic responses to increasing %NO_3^-. 'Fronteras' daughter plant number increased from 18 at 0% NO_3^- to a calculated maximum of 34 at 66% NO_3^- and then decreased to 30 at 100% NO_3^- ($P = 0.04$; adjusted $r^2 = 0.12$). 'Monterey' daughter plant number increased from 49 at 0% NO_3^- to a calculated maximum of 87 at 81% NO_3^- and then decreased to 85 at 100% NO_3^- ($P < 0.0001$; adjusted $r^2 = 0.39$).

Daughter plant morphology. Daughter plant morphology (e.g., crown diameter, number of root initials, and dry mass) was primarily affected by cultivar (Table 4). After 8 weeks of treatment, 'Fronteras' had the largest daughter plant crown diameter (10.2 ± 0.3 mm), followed by 'Albion' (8.1 ± 0.2 mm), then 'Monterey' (7.1 ± 0.2 mm; $P < 0.0001$ for cultivar). After 16 weeks of treatment, 'Fronteras' and 'Albion' had larger but similar daughter plant crown diameters (7.3 ± 0.2 and 7.2 ± 0.1 mm, respectively), compared with 'Monterey' (6.5 ± 0.1 mm; $P < 0.0001$ for cultivar).

Based on the crown diameter size classifications defined by Xu and Hernández (2020), the percentage of daughter plants distributed into each size category was not affected by %NO_3^- ($P > 0.05$) at 8 or 16 weeks. When pooled across %NO_3^- treatments and harvest date, the size category with the greatest fraction of daughter plants was M for all cultivars (Fig. 3). 'Monterey' had a higher percentage of S- and M-sized daughter plants (71%) than 'Albion' (67%) and 'Fronteras' (49%). 'Fronteras' tended to have a higher amount of L and XL daughter plants (46%) compared with 'Albion' (31%) and 'Monterey' (23%).

After 8 and 16 weeks of treatment, root number per daughter plant was affected by cultivar ($P < 0.0001$ for both; Table 4). 'Fronteras' had the highest root number per daughter plant (16 ± 1 at both harvests). 'Monterey' and 'Albion' had lower but similar root numbers per daughter plant at 8 weeks (10 ± 0 and 8 ± 0, respectively) and at 16 weeks (12 ± 1 and 11 ± 1, respectively). Daughter plant root number at 16 weeks decreased linearly as %NO_3^- increased from 18 at 0% NO_3^- to 10 at 100% NO_3^- ($P < 0.0001$; $r^2 = 0.20$; data not shown).

'Fronteras' daughter plants had a higher dry mass after 8 weeks of treatment (2.93 ± 0.23 g) than 'Albion' and 'Monterey' (1.18 ± 0.04 and 0.83 ± 0.02 g, respectively; $P <$ 0.0001 for cultivar; Table 4). After 16 weeks, 'Fronteras' (1.28 ± 0.11 g) and 'Albion' (1.03 ± 0.08 g) daughter plants had higher dry masses than 'Monterey' (0.66 ± 0.02 g; $P < 0.0001$).

Mother plant morphology. Inflorescence number, crown number, and crown diameter varied with cultivar but not %NO_3^- ($P <$ 0.0001 for all; Table 5). Cumulative inflorescence number was highest in 'Monterey' (28 ± 2), followed by 'Albion' (8 ± 1) and then 'Fronteras' (0 ± 0). 'Monterey' produced the most branch crowns (7 ± 1), followed by 'Albion' (3 ± 0), and then 'Fronteras' (2 ± 0). 'Monterey' had the largest overall crown diameter (53.0 ± 6.5 mm), whereas 'Albion' and 'Fronteras' had smaller but similar crown diameters (39.0 ± 3.6 and 29.6 ± 2.4 mm, respectively).

Table 4. Cultivar differences for daughter plant and stolon morphology of strawberry (*Fragaria ×ananassa*) 'Albion', 'Fronteras', and 'Monterey' grown in a soilless substrate for 16 weeks.

	Daughter plant crown (mm)		Daughter plant root (no.)		Daughter plant dry mass (g)		Stolon dry mass (g)		Daughters on primary stolons (%)	Foliar N (% dry mass)	
	8 wk	16 wk	8 wk	16 wk	8 wk	16 wk	8 wk	16 wk	16 wk	8 wk	16 wk
Cultivar											
Albion	8.1 ± 0.2 b	7.2 ± 0.1 a	8 ± 0 b	11 ± 1 b	1.18 ± 0.04 b	1.03 ± 0.08 a	2.94 ± 0.19 a	2.40 ± 0.16 a	65 ± 3 b	2.88 ± 0.03 a	2.47 ± 0.04 b
Fronteras	10.2 ± 0.3 a	7.3 ± 0.2 a	16 ± 1 a	16 ± 1 a	2.93 ± 0.23 a	1.28 ± 0.11 a	1.63 ± 0.11 c	0.87 ± 0.08 b	81 ± 2 a	2.56 ± 0.06 b	2.61 ± 0.05 a
Monterey	7.1 ± 0.2 c	6.5 ± 0.1 b	10 ± 0 b	12 ± 1 b	0.83 ± 0.02 b	0.66 ± 0.02 b	2.42 ± 0.11 b	2.16 ± 0.14 a	55 ± 2 c	2.64 ± 0.03 b	2.48 ± 0.03 b
HSD	0.7	0.5	3	2	0.46	0.3	0.49	0.39	7	0.15	0.12
Block	0.03	0.25	0.61	0.19	0.85	0.34	0.73	0.19	0.05	0.73	0.005
Cv	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.02
NO_3^-	0.30	0.54	0.45	<0.0001	0.55	0.49	0.15	0.0001	0.07	0.99	0.008
Cv × NO_3^-	0.27	0.24	0.37	0.26	0.51	0.29	0.71	0.49	0.59	0.80	0.45

The percentage of total N supplied as nitrate (NO_3^-) ranged from 0% to 100%. Stolons and daughter plants were harvested at weeks 8 and 16. The percentage of daughter plants borne on primary stolons were recorded at the 16-week harvest. The data were analyzed by a two-way analysis of variance, followed by Tukey's honestly significant difference test at $\alpha = 0.05$ for cultivar ($n = 6$). Within a column, means followed by different letters are statistically different. The values are means ± standard error. Cv = cultivar.

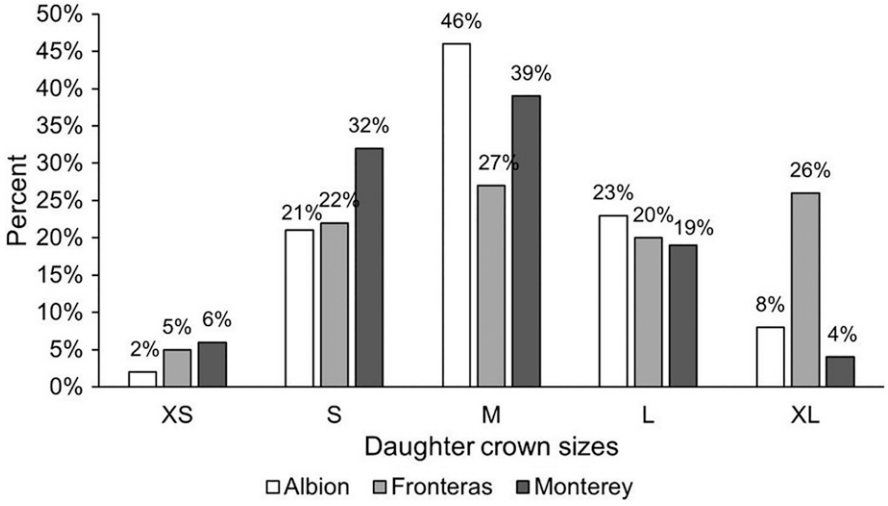

Fig. 3. Distribution of daughter crown diameters for strawberry (*Fragaria ×ananassa*) 'Albion', 'Fronteras', and 'Monterey' grown in a soilless substrate. The effect of increasing the percentage of total N supplied as nitrate (%NO_3^-) was not significant ($P > 0.05$), and the 8- and 16-week harvests were pooled together. The crown diameter categories are defined as extra small (XS, 0 to 3.5 mm), small (S, 3.5 to 6.0 mm), medium (M, 6.0 to 8.5 mm), large (L, 8.5 to 11.0 mm), and extra large (XL, 11 to 20 mm).

Canopy height increased linearly as %NO_3^- increased ($P = 0.006$; $r^2 = 0.07$; Fig. 4A). Canopy width increased linearly in 'Monterey' ($P < 0.0001$; $r^2 = 0.41$) and increased quadratically in 'Albion' ($P = 0.02$; adjusted $r^2 = 0.13$) as %NO_3^- increased from 0% to 100% (Fig. 4B); no significant linear or quadratic trends occurred in 'Fronteras' in response to %NO_3^-. Mother plant dry mass increased linearly in 'Albion' from 21 to 36 g ($P = 0.04$; $r^2 = 0.12$) and in 'Monterey' from 37 to 98 g ($P < 0.0001$; $r^2 = 0.45$) as %NO_3^- increased from 0% to 100% (Fig. 4C); no significant linear or quadratic trends occurred in 'Fronteras' in response to %NO_3^-.

Total cumulative aboveground dry mass (stolons and daughter plants at weeks 8 and 16, plus mother plants at week 16) exhibited linear increases for 'Albion' and 'Fronteras' as %NO_3^- increased (Fig. 4D). 'Albion' increased from 63 to 99 g ($P = 0.003$; $r^2 = 0.23$), and 'Fronteras' increased from 62 to 92 g ($P = 0.03$; $r^2 = 0.14$) as %NO_3^- increased from 0% to 100%. 'Monterey' dry mass increased quadratically, from 96 g at 0% NO_3^- to 210 g at 100% NO_3^- ($P < 0.0001$; adjusted $r^2 = 0.89$).

Cultivar differences occurred for biomass allocation ($P < 0.0001$; Fig. 5). Within a cultivar, Albion and Fronteras allocated the greatest fraction of their biomass to daughter plants (43% and 61%, respectively), whereas 'Monterey' allocated the greatest fraction of its biomass to mother crowns (43%). Across cultivars, Fronteras had the highest percentage of dry mass allocated to daughter plants (61%), followed by 'Albion' (43%) and 'Monterey' (33%). 'Monterey' had the highest allocation to mother crowns (43%), followed by 'Albion' (29%) and 'Fronteras' (21%).

Tissue nutrient composition for daughter and mother plants. The primary focus of tissue nutrient analyses was on whether the N form supplied affected total %N in mother and daughter plants. After 8 weeks of treatment, %NO_3^- did not affect daughter plant foliar N (Fig. 6A), although cultivars differences did occur ($P < 0.0001$). 'Albion' had the highest %N (2.88% ± 0.03%). 'Fronteras' and 'Monterey' had lower but similar %N values (2.56% ± 0.06% and 2.64% ± 0.03%, respectively; Table 4). After 16 weeks of treatment, daughter plant %N had a quadratic response to increasing %NO_3^- ($P = 0.004$; adjusted $r^2 = 0.07$; Fig. 6B). The %N decreased to a calculated minimum at 41% NO_3^- and then increased as %NO_3^- increased to 100%. 'Fronteras' had a higher %N (2.61% ± 0.05%) than 'Albion' and 'Monterey' (2.47% ± 0.04% and 2.48% ± 0.03%, respectively; $P = 0.03$ for cultivar; Table 4). In mother plants, foliar %N in all three cultivars exhibited quadratic responses to increasing %NO_3^- (Fig. 6C; adjusted r^2 values of 0.11 to 0.31). Foliar %N decreased to a calculated minimum at 30% NO_3^- for 'Fronteras', 52% NO_3^- for 'Albion', and 61% NO_3^- for 'Monterey'; then foliar %N increased as the %NO_3^- supplied increased to 100% NO_3^-.

Daughter plant foliar macronutrient concentrations of P, K, Ca, Mg, and S were affected by %NO_3^- at one or both harvests (Supplemental Figs. 1 and 2). Despite these responses, all daughter plants appeared healthy, with no visual deficiency or toxicity symptoms. One response to highlight is that %Ca increased linearly as %NO_3^- increased in daughter plants at 16 weeks of treatment (r^2 values of 0.17 to 0.41) and in mother plants ($r^2 = 0.23$; Supplemental Fig. 2B and 2C). Also, %S decreased linearly as %NO_3^- increased in daughter plants after 8 weeks of treatment ($r^2 = 0.33$), and it generally decreased quadratically in daughter plants at 16 weeks of treatment (r^2 and adjusted r^2 values of 0.47 to 0.85) and in mother plants (adjusted r^2 values of 0.46 to 0.90; Supplemental Fig. 2H and 2I).

Foliar micronutrient concentrations of B, Cu, Fe, Mn, and Zn all decreased linearly or quadratically in response to increasing %NO_3^- in mother (Cu, Fe, Mn, and Zn) or daughter (B, Fe, Mn, and Zn) plants (Supplemental Figs. 3 and 4). Mo increased linearly or quadratically as %NO_3^- increased in mother and daughter plants (Supplemental Fig. 4D–F).

Substrate pH and EC. Leachates collected at 8 and 16 weeks of treatment had quadratic increases in pH in response to increasing %NO_3^- (adjusted r^2 values of 0.86 to 0.97; Fig. 7A and 7B). At 8 weeks, substrate pH increased from 4.01 to 6.53 in 'Albion', from 4.29 to 6.21 in 'Fronteras' and from 3.81 to 6.80 in 'Monterey' as %NO_3^- increased from 0% to 100% (Fig. 7A). At 16 weeks, pH increased from 3.72 to 6.29 in 'Albion', from 3.65 to 6.13 in 'Fronteras', and from 3.77 to 6.25 in 'Monterey as %NO_3^- increased from 0% to 100% (Fig. 7B). Conversely, EC at 8 and 16 weeks had quadratic responses and generally decreased as %NO_3^- increased (adjusted r^2 values of 0.50 to 0.88; Fig. 7C and 7D). At 8 weeks, EC peaked at calculated maximums of 5.31 mS·cm^{-1} at 12% NO_3^- in 'Albion', 5.66 mS·cm^{-1} at 21% NO_3^- in 'Fronteras', and 4.60 mS·cm^{-1} at 29% NO_3^- in 'Monterey' and then decreased to between 1.48 and 2.33 mS·cm^{-1} at 100% NO_3^- (Fig. 7C). At 16 weeks, substrate solution EC peaked at a calculated maximum of 41% NO_3^- and then declined to 2.09 mS·cm^{-1} at 100% NO_3^- (Fig. 7D).

Table 5. Cultivar differences for mother plant growth of strawberry (*Fragaria ×ananassa*) 'Albion', 'Fronteras', and 'Monterey' grown in a soilless substrate for 16 weeks.

Factor	Treatment	Cumulative inflorescence (no.)	Crown (no.)	Crown diam (mm)
Cultivar	Albion	8 ± 1 b	3 ± 0 b	39.0 ± 3.6 b
	Fronteras	0 ± 0 c	2 ± 0 c	29.6 ± 2.4 b
	Monterey	28 ± 2 a	7 ± 1 a	53.0 ± 6.5 a
	HSD	4	1	12.9
ANOVA	Block	0.16	0.01	<0.0001
	Cv	<0.0001	<0.0001	0.0003
	NO_3^-	0.19	0.67	0.66
	Cv × NO_3^-	0.44	0.89	0.61

The percentage of total N supplied as nitrate (NO_3^-) ranged from 0% to 100%. Mother plants were harvested at the end of the 16-week study. Total biomass includes the dry masses of the mother crown plus the 8- and 16-week harvests of stolons and daughter plants. The data were analyzed by a two-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference at $\alpha = 0.05$ for significant sources of variation ($n = 6$). Within a column, means followed by different letters are statistically different. The values are means ± standard error. Cv = cultivar.

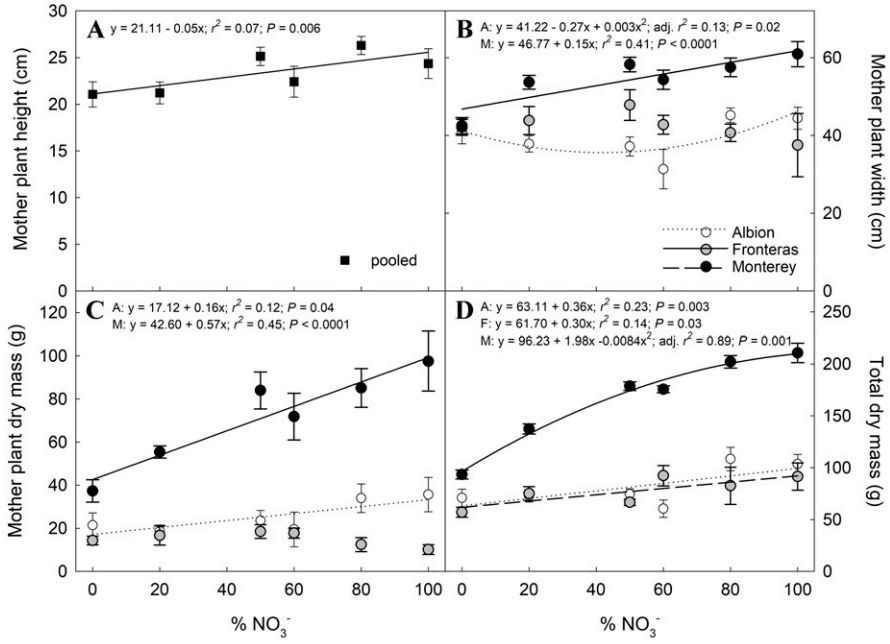

Fig. 4. Mother plant growth and morphology of three strawberry (*Fragaria ×ananassa*) cultivars grown in a soilless substrate for 16 weeks: height (**A**), width (**B**), dry mass (**C**), and total plant dry mass (**D**). The percent of total N supplied as nitrate (NO_3^-) ranged from 0% to 100%. Total plant dry mass includes the dry masses of the mother crown plus the 8- and 16-week harvests of stolons and daughter plants. The values are means ± standard error ($n = 18$ in **A** because cultivar responses to $\%NO_3^-$ were similar, and therefore, the data were pooled; $n = 6$ in **B–D** because cultivar responses to $\%NO_3^-$ differed). Regression lines (when significant) show 'Albion' (dotted), 'Fronteras' (dashed), and 'Monterey' (solid). A = 'Albion', F = 'Fronteras', M = 'Monterey'.

Discussion

This study focused on nutrient management strategies to increase strawberry daughter plant yield in CEA. These CEA-produced daughter plants would support CEA fruit producers looking to source actively growing, well-rooted, "clean" starting plant material year-round, as well as field producers seeking to reduce asymptomatic disease carryover in bare-root strawberries from field nurseries into their fruit production sites. Optimization of the CEA growing environment and crop management practices is crucial to economically produce a high number of high-quality daughter plants.

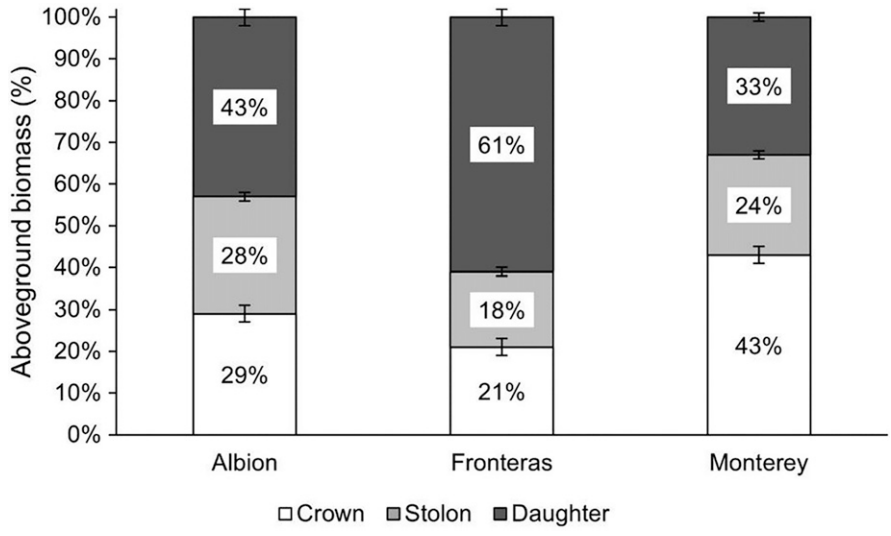

Fig. 5. Distribution of total plant aboveground biomass for three strawberry cultivars (*Fragaria ×ananassa* Albion, Fronteras, and Monterey) grown in a soilless substrate. The effect of increasing the percentage of total N supplied as nitrate ($\%NO_3^-$) was not significant ($P > 0.05$), and the data were pooled together within each cultivar ($n = 36$). Total aboveground biomass includes the mother plant at week 16 plus stolons and daughter plants at the weeks 8 and 16 harvests. The values are means ± standard error. Mean total aboveground biomass was 81.8 g for 'Albion', 75.4 g for 'Fronteras', and 166.3 g for 'Monterey'.

One key yield metric is stolon production. In Expt. 1, stolon number in 'Fronteras' did not differ in response to $\%NO_3^-$ supplied in the nutrient solution. We attributed this to the frequency of harvest (every 4 weeks). Although a harvest interval of 4 weeks has been used in other studies (Shi et al. 2021), it was too frequent 1) to generate high numbers of daughter plants and 2) to delineate treatment effects in our study. Therefore, we extended the harvest interval in Expt. 2 to every 8 weeks. In Expt. 2, cumulative stolon number generally increased as $\%NO_3^-$ increased, and maximum stolon number was calculated to occur at 64% NO_3^- for 'Fronteras' and 100% NO_3^- for 'Albion' and 'Monterey' (Fig. 1C).

'Albion' tended to produce a similar number of stolons at the 8- and 16-week harvests in Expt. 2, whereas stolon production in 'Monterey' and 'Fronteras' increased from week 8 to week 16, especially at the higher $\%NO_3^-$ treatments (Fig. 1A and 1B). Xu and Hernández (2020) observed a higher stolon count in 'Albion' in the last 9 weeks of their study relative to the first 12 weeks of treatment; however, their treatments (light intensity) and harvest durations differed from ours, which may explain why they saw an increase in stolon number over time for 'Albion', but we did not. As mother plants grow over time, plant size and branch crown number tend to increase, which can support higher stolon loads in later harvests.

Strawberry plants can produce either vegetative growth (i.e., a stolon or branch crown) or reproductive growth (i.e., an inflorescence) at each axillary node. Cell differentiation into a stolon or inflorescence depends on photoperiod and temperature (Bradford et al. 2010; Durner et al. 1984; Hytönen et al. 2009; Sønsteby and Heide 2007). Strawberry cultivars can be classified as short-day, long-day, or day-neutral, depending on their photoperiodic flowering response (Darnell et al. 2002; Durner et al. 1984). Albion and Monterey are long-day cultivars, whereas Fronteras is a short-day cultivar (Garcia and Kubota 2017; Larson and Shaw 2015; Park et al. 2023; Shaw and Larson 2006, 2009). To promote vegetative growth and maintain a consistent photoperiod duration throughout the studies (Jul 2022 to Jun 2023), we opted to grow all three cultivars under a 16-h photoperiod and warm temperature (daily mean air temperature of 22.7 °C for Expts. 1 and 2). We recognize that this photoperiod limited flowering in 'Fronteras' but not in 'Albion' and 'Monterey'. As such, stolon number in 'Albion' and 'Monterey' may have been even higher had they been grown under a shorter photoperiod (12 h or less). However, other researchers have noted that photoperiod may affect stolon production less than it affects flower production in 'Albion' (Garcia and Kubota 2017).

Due to the long-day photoperiod provided, Albion and Monterey, the two everbearing cultivars, produced both inflorescences and stolons, while the short-day cultivar Fronteras only produced stolons. Although cumulative inflorescence number varied by cultivar, it did not vary with $\%NO_3^-$ (Table 5). This differs

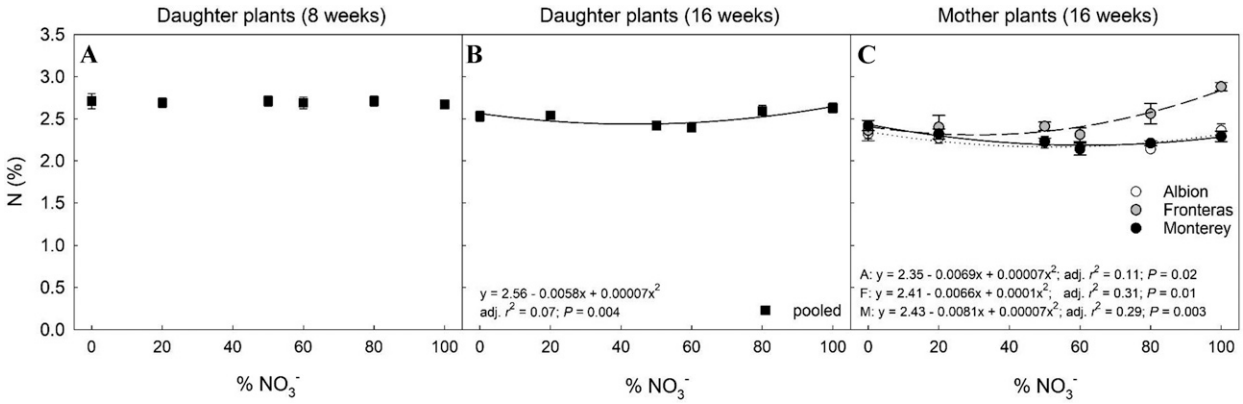

Fig. 6. Foliar percent nitrogen (%N; on a dry mass basis) of three strawberry (*Fragaria ×ananassa*) cultivars grown in a soilless substrate for 16 weeks. The percentage of total N supplied as nitrate (NO_3^-) ranged from 0% to 100%. Daughter plants were harvested after 8 (**A**) and 16 (**B**) weeks of treatment. Mother plants were harvested after 16 weeks of treatment (**C**). The values are means ± standard error (n = 18 for daughter plants pooled across cultivar and n = 6 for mother plants). Regression lines in **C** show 'Albion' (dotted), 'Fronteras' (dashed), and 'Monterey' (solid). The data in **A** did not have a significant linear or quadratic regression response ($P > 0.05$). A = 'Albion', F = 'Fronteras', M = 'Monterey'.

from the results observed by Shi et al. (2021), in which 'Albion' produced more inflorescences when plants were irrigated with 80% to 100% NO_3^-, compared with plants irrigated with ≤60% NO_3^-. It also contradicted our initial hypothesis, which was that decreasing $\%NO_3^-$ would reduce inflorescence development and promote stolon development.

Despite no change in inflorescence number in response to $\%NO_3^-$, cumulative stolon number increased (linearly or quadratically) in all three cultivars in response to increased $\%NO_3^-$ (Fig. 1C). Therefore, other physiological attributes rather than a shift away from inflorescence development in the axillary meristems must have contributed to the increase in stolon number. One possibility could have been a change in crown number, which would have increased the total number of axillary nodes from which an inflorescence or stolon could arise. However, crown number was not affected by $\%NO_3^-$, only cultivar (Table 5). A second possibility is that the change in $\%NO_3^-$ released some axillary buds from dormancy and they developed into stolons (Durner E, personal communication). This may be related to plant biomass. Mother plant size increased in response to an increase in $\%NO_3^-$ (Fig. 4), which would have provided a larger carbohydrate reserve ("source" capacity) to support additional stolon development ("sinks"). In this study, 'Monterey' had the highest crown number, highest stolon number, and highest mother plant biomass, despite also having the highest inflorescence number.

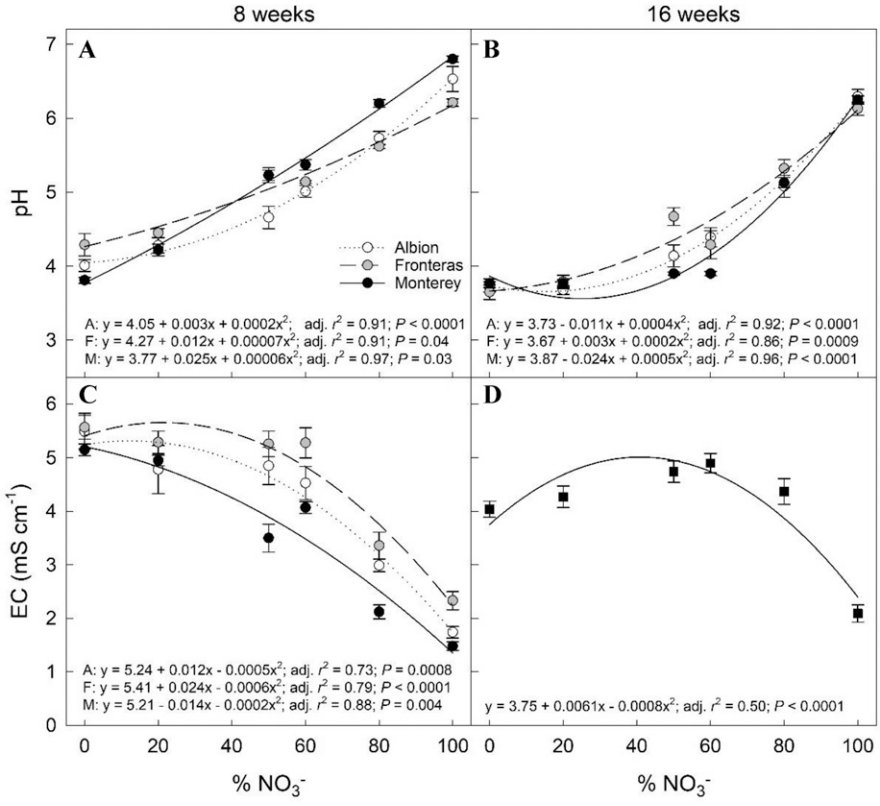

Fig. 7. pH (**A, B**) and electrical conductivity (EC; $mS \cdot cm^{-1}$) (**C, D**) of leachates collected using the pour-through technique at 8 (left) and 16 weeks (right) of treatment. Three strawberry (*Fragaria ×ananassa*) cultivars were grown in a soilless substrate for 16 weeks, and the percentage of total N supplied as nitrate (NO_3^-) varied from 0% to 100%. The values are means ± standard error (n = 6 in **A–C**; n = 18 in **D** and pooled across cultivar). Regression lines in **A–C** show 'Albion' (dotted), 'Fronteras' (dashed), and 'Monterey' (solid). A = 'Albion', F = 'Fronteras', M = 'Monterey'.

In addition to stolon number, other factors such as number, quality, and size of the daughter plants will drive the success of this system in generating new strawberry plants for propagation. Maximum daughter plant number, calculated from the regression equations, occurred at 66% NO_3^- for 'Fronteras', 81% NO_3^- for 'Monterey', and 100% NO_3^- for 'Albion' (Fig. 1F). These results agree with those observed by Cárdenas-Navarro et al. (2006), in which higher daughter plant number occurred in strawberry 'Aromas' after 30 d when irrigated with 50% NO_3^- compared with 0% NO_3^-.

Monterey was the highest yielding cultivar of the three evaluated. This occurred because 'Monterey' had a higher cumulative stolon number, as well as a higher number of daughter plants per stolon (4.3 ± 0.2 for 'Monterey' vs. 3.7 ± 0.2 for 'Albion' and 2.3 ± 0.1 for 'Fronteras'; $P < 0.0001$). A high number of daughter plants per stolon can occur due to a high number of daughter plants developing on the primary stolon (such as a longer interval between successive harvests, like what was observed between Expts. 1 and 2), a high number of daughter plants forming on secondary (or even tertiary) stolon branches, or a combination of the two. Given that the treatment duration was the same for all three cultivars in Expt. 2, the higher daughter plant number per stolon in 'Monterey' occurred because of the prolificness of daughter plant formation on secondary branches. 'Monterey' produced 55% of its daughter plants on primary stolons and 45% of its daughter plants on secondary stolons.

The three cultivars had different stolon architecture patterns. While 'Fronteras' had a high percentage of stolons with secondary branching, it produced 81% of its daughter plants on primary stolons. The first daughter plant that formed on the primary stolon tended to be quite large (based on dry mass and crown diameter), which may have suppressed subsequent daughter plant development on that stolon. 'Albion' produced 65% of its daughter plants on primary stolons and 35% on secondary stolon branches, and as noted above, 'Monterey' had the most-balanced distribution of daughter plants borne on primary (55%) vs. secondary (45%) stolons (Fig. 8).

The maximum cumulative daughter plant yields observed for 'Fronteras' (34), 'Albion' (37), and 'Monterey' (87) after 16 weeks of treatment are similar to those reported for other cultivars produced in soilless substrates and CEA conditions. Greenhouse-grown 'Oso Grande' and 'Sweet Charlie' produced 84 and 80 daughter plants, respectively, after 16 weeks of growth in a vermiculite and perlite (4/1 v/v) substrate (Bish et al. 2001). Xu and Hernández (2020) produced >100 'Albion' daughter plants over a 21-week growing period through optimizing light intensity. Further optimization of the growing environment, substrate, and plant nutrition may provide additional yield increases.

Daughter plant quality (e.g., crown diameter, root count, and dry mass) was primarily affected by cultivar rather than $\%NO_3^-$. This agrees with a study by Xu and Hernández (2020) in which light intensity did not affect crown size distribution of 'Albion' daughter plants after 12 or 21 weeks of treatment. Instead, daughter plant morphology is likely related to its development age and its duration on a stolon before harvest. Crown diameter was correlated with root count ($r = 0.50$; $P < 0.0001$) and dry mass ($r = 0.83$; $P < 0.0001$). In all cultivars, the longer a daughter plant remained on a stolon before harvest, the larger the crown was, with more root initials and a larger overall biomass. However, plant size may be more critical for grading rather than for rooting success. A previous study indicated that despite size differences, daughter plants of all crown diameters readily rooted during propagation (Humphrey et al. 2022).

Crown size distribution would be useful for forecasting propagation logistics, such as what tray cell size to use and propagation duration. Daughter plants are often sorted by size before propagation to place uniformly sized plants in a tray or propagation block. This uniformity would help ensure similar mist requirements, rooting time, and cultural management during rooting, as well as standardize a finish time and plant size at the end of propagation. The largest and smallest daughter plants are often culled and discarded. Therefore, it was important to consider not just the number but also the size distribution of CEA-produced daughter plants. In our study, the highest percentage of daughter plants had M-sized crown diameters (Fig. 3). 'Fronteras' had a higher percentage of XL-sized daughter plants (26%) than 'Albion' (8%) or 'Monterey' (4%). In an unpublished study, XL daughter plants were too large to propagate in a 50-count cell tray but could successfully be rooted directly into 10-cm pots. Additionally, while XS daughter plants did root in 50-count cell trays, they required longer propagation durations than the larger crown sizes (unpublished data).

Some aspects of mother plant quality were affected by $\%NO_3^-$. Plant height and dry mass increased linearly as $\%NO_3^-$ supplied increased (Fig. 4). Total aboveground dry mass (daughter plants and stolons at 8 and 16 weeks, plus mother plants) also increased as $\%NO_3^-$ increased from 0% to 100%. Choi et al. (2011) likewise observed

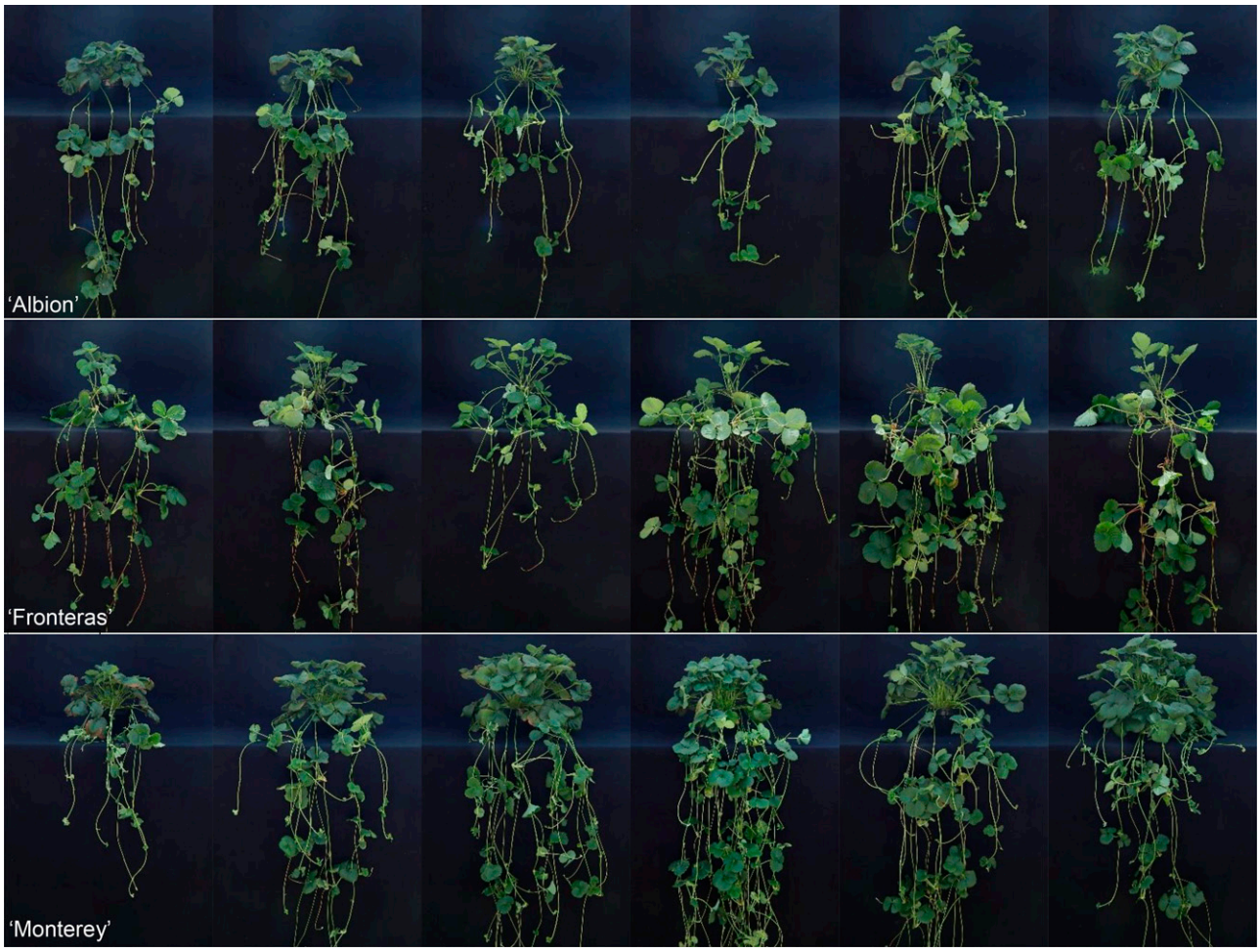

Fig. 8. Strawberry (*Fragaria ×ananassa*) cultivars Albion (top row), Fronteras (middle row), and Monterey (bottom row) grown in a soilless substrate. The percentage of total N supplied as nitrate (NO_3^-) was, from left to right, 0%, 20%, 50%, 60%, 80%, and 100%. The pictures were taken after 16 weeks of treatment.

an increase in biomass of greenhouse-grown 'Seolhyang' as $\%NO_3^-$ increased from 0% to 100% NO_3^- after 120 d of treatment. Shi et al. (2021), however, did not observe any difference in 'Albion' mother plant dry mass (crown, leaf, and roots) after 21 weeks when $\%NO_3^-$ increased from 50% to 100% NO_3^-. The lack of observed differences in their study, compared with ours, may be because their range of $\%NO_3^-$ was narrower than ours and did not include any treatments with $<50\%$ NO_3^-.

Additionally, the $\%NO_3^-$ treatments did not affect biomass allocation in our study. 'Monterey' allocated the greatest fraction of its biomass to the mother crown (43% of total biomass), whereas 'Albion' and 'Fronteras' allocated the greatest fraction of their biomass to daughter plants (43% and 61%, respectively). Biomass allocation may be inherently conserved within cultivars. In a study by Xu and Hernández (2020), biomass allocations for 'Albion' were similar to our study (24% to mother crowns vs. 29% in our study), despite evaluating lighting treatments rather than nutrient recipes.

While the primary focus was to evaluate daughter plant productivity in response to $\%NO_3^-$, it was also important to evaluate whether adjusting the $\%NO_3^-$ affected foliar %N in daughter plants or mother plants. In Expt. 2, the 16-week daughter plants and the mother plants had quadratic responses to an increase in $\%NO_3^-$, in which %N decreased initially and then increased. This response was similar to the response reported by Taghavi et al. (2004), in which foliar %N in 'Selva' was lower when plants were irrigated with 79% to 86% NO_3^- compared with $>93\%$ NO_3^-. While our %N values (2.38% to 2.63% in daughter plants) were lower than the 3.3% to 3.4% N reported by Taghavi et al. (2004), both studies fell within the range of 2.1% to 4.0% N published by Mills and Jones (1996). However, this published range was developed by sampling "healthy" field-grown strawberry plants at the fruiting stage, and no recommended tissue nutrient ranges currently exist for CEA-grown mother plants in soilless substrates or for daughter plants.

The $\%NO_3^-$ supplied in the nutrient solution influenced substrate pH. Despite flowable lime applications when substrate pH declined to $\leq$5.5, plants supplied $\leq$60% NO_3^- had substrate solution pH values of $<$5.2 over the duration of the trial. Micronutrient availability (e.g., Fe, Mn, and Zn) increases and Mo availability decreases in the substrate as pH decreases (Gillespie et al. 2020; Smith et al. 2004a, 2004b). Therefore, the decrease in substrate pH as the $\%NO_3^-$ supplied decreased likely led to the increased foliar concentrations of S, Fe, Mn, and Zn and decreased foliar concentrations of Mo in both the mother and daughter plants (Supplemental Figs. 2–4). Unfortunately, given that substrate solution pH decreased as the $\%NO_3^-$ supplied decreased, this relationship confounds our ability to distinguish whether the negative growth effects observed were due to low substrate pH, high $\%NH_4^+$, or a combination of both. Plants irrigated with 0% NO_3^- (i.e., 100% NH_4^+) appeared stunted, and necrotic margins began to appear on older leaves after 10 weeks of treatment. Of 36 'Fronteras' plants, 2 died, and they were from the 0% to 20% NO_3^- treatments. Other researchers have also observed plant growth suppression or death when strawberry plants were supplied high fractions of NH_4^+, especially in combination with low substrate pH or other environmental stresses. For example, total plant mortality occurred when strawberry 'Aliso' was grown hydroponically in a 100% NH_4^+ nutrient solution maintained at 32 °C (Ganmore-Neumann and Kafkafi 1983). Claussen and Lenz (1999) observed more pronounced effects of NH_4^+ toxicity in strawberry 'Senga Sengana' grown in quartz sand when $CaCO_3$ was not added to increase pH.

Nitrogen is an abundant macronutrient in nutrient solutions, and the ratio of NO_3^- to NH_4^+ will influence substrate pH. Unless the substrate is adequately buffered, root NH_4^+ uptake will cause substrate pH to decline; conversely, root NO_3^- uptake will cause pH to increase (Allen and Raven 1987; Kirkby and Knight 1977; Neumann and Römheld 2012). Therefore, even if strawberry plants can tolerate a high $\%NH_4^+$ in the nutrient solution, it would not be advisable to supply it due to the challenge in maintaining a recommended substrate pH target of 5.5 to 6.2 for optimal nutrient solubility (Argo and Biernbaum 1996; Handreck and Black 1994).

The three cultivars had cultivar-specific responses to $\%NO_3^-$ for stolon number and daughter plant number. In addition to calculating the $\%NO_3^-$ that yielded maximum stolon or daughter plant number, these regression models allow us to see how sensitive a cultivar will be to a small change in $\%NO_3^-$ from the optimum percentage. This can be important for growers who are growing multiple cultivars. One of their considerations will be whether they have the facilities and infrastructure to support custom nutrient solution recipes for each cultivar (i.e., multiple stock tanks or injectors) or whether a "general" recipe, while not optimal for all cultivars, would support good overall growth for most or all cultivars grown. As an example, we identified the range in $\%NO_3^-$ that corresponded to a 5% or 10% decrease from maximum daughter plant number. A 5% yield penalty corresponded to a $\%NO_3^-$ range of 45% to 87% in 'Fronteras', 54% to 100% in 'Monterey', and 81% to 100% in 'Albion'. The overlap in ranges across cultivars was 81% to 87% NO_3^-. A 10% yield penalty corresponded to a $\%NO_3^-$ range of 36% to 96% in 'Fronteras', 43% to 100% in 'Monterey', and 61% to 100% in 'Albion'. The overlap in ranges across cultivars was 61% to 96% NO_3^- if a yield penalty of up to 10% was acceptable for any of the three cultivars evaluated. This information could guide growers 1) in selecting an acceptable $\%NO_3^-$ target for their operation and 2) deciding whether to mix up one nutrient recipe or multiple recipes, with each one optimized to maximize daughter plant production for each cultivar grown.

Conclusions

A harvest interval of 8 weeks, rather than every 4 weeks, improved stolon and daughter plant development. Cultivar-specific responses to increasing $\%NO_3^-$ occurred. Maximum cumulative daughter plant number was calculated to occur at 66% ('Fronteras'), 81% ('Monterey'), or 100% NO_3^- ('Albion'). Total aboveground biomass increased as $\%NO_3^-$ increased in all cultivars evaluated. A calculated range in which all three cultivars overlapped with $\geq$95% of maximum daughter plant yield occurred between 81% to 87% NO_3^-. A strawberry fertilizer recipe in this target range would allow growers the opportunity to use a single recipe and support high daughter plant productivity across multiple cultivars. Our results indicate that optimal strawberry daughter plant production occurs at a lower $\%NO_3^-$ than recommended for inflorescence or fruit production. These results will help improve and refine nutrient management guidelines for CEA production of strawberry daughter plants.

References Cited

Allen S, Raven JA. 1987. Intracellular pH regulation in *Ricinus communis* grown with ammonium or nitrate as N source: The role of long-distance transport. J Exp Bot. 38(4):580–596. https://doi.org/10.1093/jxb/38.4.580.

Andriolo JL, Janisch DI, Dal Picio M, Schmitt OJ, Lerner MA. 2014. Nitrogen accumulation and monitoring by strawberry stock plants for runner tips production. Hortic Bras. 32(3): 273–279. https://doi.org/10.1590/S0102-05362014000300006.

Argo WR, Biernbaum JA. 1996. The effect of lime, irrigation-water source, and water-soluble fertilizer on root-zone pH, electrical conductivity, and macronutrient management of container root media with impatiens. J Am Soc Hortic Sci. 121(3):442–452. https://doi.org/10.21273/JASHS.121.3.453.

Baggio JS, Forcelini BB, Wang N-Y, Ruschel RG, Mertely JC, Peres NA. 2021a. Outbreak of leaf spot and fruit rot in Florida strawberry caused by *Neopestalotiopsis* spp. Plant Dis. 105(2): PDIS06201290RE. https://doi.org/10.1094/PDIS-06-20-1290-RE.

Baggio JS, Marin MV, Peres NA. 2021b. Phytophthora crown rot of Florida strawberry: Inoculum sources and thermotherapy of transplants for disease management. Plant Dis. 105(11):3496–3502. https://doi.org/10.1094/PDIS-11-20-2476-RE.

Bish EB, Cantliffe DJ, Chandler CK. 2001. A system for producing large quantities of greenhouse-grown strawberry plantlets for plug production. HortTechnology. 11(4):636–638. https://doi.org/10.21273/HORTTECH.11.4.636.

Boldt JK, Altland JE. 2021. Petunia (*Petunia ×hybrida*) cultivars vary in silicon accumulation and distribution. HortScience. 56(3):305–312. https://doi.org/10.21273/HORTSCI15486-20.

Bradford E, Hancock JF, Warner RM. 2010. Interactions of temperature and photoperiod determine expression of repeat flowering in strawberry. J Am Soc Hortic Sci. 135(2):102–107. https://doi.org/10.21273/JASHS.135.2.102.

Cantliffe DJ, Castellanos JZ, Paranjpe AV. 2007. Yield and quality of greenhouse-grown strawberries as affected by nitrogen level in coco coir and pine bark media. Proc Florida State Hortic Soc. 120:157–161.

Cárdenas-Navarro R, López-Pérez L, Lobit P, Ruiz-Corro R, Castellanos-Morales VC. 2006. Effects of nitrogen source on growth and development of strawberry plants. J Plant Nutr. 29(9):1699–1707. https://doi.org/10.1080/10739140600853676.

Choi JM, Latigui A, Lee CW. 2011. Growth and nutrient uptake responses of 'Seolhyang' strawberry to various ratios of ammonium to nitrate nitrogen in nutrient solution culture using inert media. Afr J Biotechnol. 10(59):12567–12574.

Claussen W, Lenz F. 1999. Effect of ammonium or nitrate nutrition on net photosynthesis, growth, and activity of the enzymes nitrate reductase and glutamine syntheses in blueberry, raspberry and strawberry. Plant Soil. 208:95–102.

Darnell RL, Cantliffe DJ, Kirschbaum DS, Chandler CK. 2002. The physiology of flowering in strawberry. Hortic Rev. 28:326–335.

Durner EF, Barden JA, Himelrick DG, Poling EB. 1984. Photoperiod and temperature effects on flower and runner development in day-neutral, Junebearing, and everbearing strawberries. J Am Soc Hortic Sci. 109(3):396–400. https://doi.org/10.21273/JASHS.109.3.396.

Ganmore-Neumann R, Kafkafi U. 1983. The effect of root temperature and NO_3^-/NH_4^+ ratio on strawberry plants. I. Growth, flowering and root development. Agron J. 75(6):941–947. https://doi.org/10.2134/agronj1983.00021962007500060020x.

Garcia K, Kubota C. 2017. Flowering responses of North American strawberry cultivars. Acta Hortic. 1156:483–490. https://doi.org/10.17660/ActaHortic.2017.1156.71.

Gillespie DP, Kubota C, Miller SA. 2020. Effects of low pH of hydroponic nutrient solution on plant growth, nutrient uptake, and root rot disease incidence of basil (*Ocimum basilicum* L.). HortScience. 55(8):1251–1258. https://doi.org/10.21273/HORTSCI14986-20.

Handreck K, Black N. 1994. Growing media for ornamental plants and turf. University of New South Wales Press, Sydney, Australia.

Hokanson SC, Takeda F, Enns JM, Black BL. 2004. Influence of plant storage duration on strawberry runner tip viability and field performance. HortScience. 39(7):1596–1600. https://doi.org/10.21273/HORTSCI.39.7.1596.

Humphrey S, Hernández R, Hoffmann M. 2022. Rooting efficacy of different size strawberry tips in a controlled environment propagation system (abstr). HortScience. 56(9S):S103.

Hytönen T, Elomaa P, Moritz T, Junttila O. 2009. Gibberellin mediates daylength-controlled differentiation of vegetative meristems in strawberry (*Fragaria ×ananassa* Duch). BMC Plant Biol. 9:18. https://doi.org/10.1186/1471-2229-9-18.

Kirkby EA, Knight AH. 1977. Influence of the level of nitrate nutrition on ion uptake and assimilation, organic acid accumulation, and cation anion balance in whole tomato plants. Plant Physiol. 60(3):349–353. https://doi.org/10.1104/pp.60.3.349.

Kroggel M, Kubota C. 2017. Controlled environment strategies for tipburn management in greenhouse strawberry production. Acta Hortic. 1156:529–536. https://doi.org/10.17660/ActaHortic.2017.1156.78.

Kubota C. n.d. Controlled environment berry production information: Fertigation. The Ohio State University. https://u.osu.edu/indoorberry/fertigation. [accessed 6 Sep 2024].

Larson KD, Shaw DV (inventors). 2015. Strawberry plant named 'Fronteras'. University of California (assignee). US Plant Patent 26709P3. (Filed 10 Feb 2014, granted 13 Aug 2015).

LeBude AV, Bilderback TE. 2009. The pour-through extraction procedure: A nutrient management tool for nursery crops. North Carolina State Univ. Ext. Bull. AG-717-W. North Carolina State University, Raleigh, NC, USA.

Maas JL. 1998. Opportunities to reduce the potential for disease infection and spread with strawberry plug plants. Acta Hortic. 513:409–416. https://doi.org/10.17660/ActaHortic.1998.513.49.

Mills HA, Jones JB. 1996. Plant analysis handbook II: A practical sampling, preparation, analysis, and interpretation guide (2nd ed). Micro Macro Publishing, Athens, GA, USA.

Neri D, Baruzzi G, Massetani F, Faedi W. 2012. Strawberry production in forced and protected culture in Europe as a response to climate change. Can J Plant Sci. 92(6):1021–1036. https://doi.org/10.4141/cjps2011-276.

Neumann G, Römheld V. 2012. Rhizosphere chemistry in relation to plant nutrition, p 347–368. In: Marschner P (ed). Mineral nutrition of higher plants. Academic Press, San Diego, CA, USA.

Park Y, Sethi R, Temnyk S. 2023. Growth, flowering, and fruit production of strawberry 'Albion' in response to photoperiod and photosynthetic photon flux density of sole-source lighting. Plants. 12(4):731. https://doi.org/10.3390/plants12040731.

Rivera-del Rio R, Pineda-Pineda J, Avitia-Garcia E, Castillo-González AM, Vargas-Hernandez M. 2017. Alteration of physical properties of substrates and accumulation of nutrients in strawberry hydroponic systems (*Fragaria ×ananassa* Duch.). Acta Hortic. 1170:679–686. https://doi.org/10.17660/ActaHortic.2017.1170.85.

Schmitt O, Andriolo E, Schultz MA, Lerner JM, Souza M, Dal Picio JL. 2016. Produção de estolhos de cultivares de morangueiro em função da condutividade elétrica da solução nutritiva. Hortic Bras. 34(2):294–301. https://doi.org/10.1590/S0102-053620160000200022.

Shaw DV, Larson KD (inventors). 2006. Strawberry plant named 'Albion'. University of California (assignee). US Plant Patent 16228P3. (Filed 29 Jan 2004, granted 31 Jan 2006).

Shaw DV, Larson KD (inventors). 2009. Strawberry plant named 'Monterey'. University of California (assignee). US Plant Patent 19767P2. (Filed 25 Jan 2008, granted 24 Feb 2009).

Shi X, Hernández R, Hoffmann M. 2021. Impact of nitrate and ammonium ratios on flowering and asexual reproduction in the everbearing strawberry cultivar *Fragaria ×ananassa* Albion. Horticulturae. 7(12):571. https://doi.org/10.3390/horticulturae7120571.

Smith BR, Fisher PR, Argo WR. 2004a. Nutrient uptake in container-grown impatiens and petunia in response to root substrate pH and applied micronutrient concentration. HortScience. 39(6):1426–1431. https://doi.org/10.21273/HORTSCI.39.6.1426.

Smith BR, Fisher PR, Argo WR. 2004b. Water-soluble fertilizer concentration and pH of a peat-based substrate affect growth, nutrient uptake, and chlorosis of container-grown seed geraniums. J Plant Nutr. 27(3):497–524. https://doi.org/10.1081/PLN-120028875.

Sønsteby A, Heide OM. 2007. Long-day control of flowering in everbearing strawberries. J Hortic Sci Biotechnol. 82(6):875–884. https://doi.org/10.1080/14620316.2007.11512321.

Taghavi TS, Babalar M, Ebadi A, Ebrahimzadeh H, Ali M. 2004. Effects of nitrate to ammonium ratio on yield and nitrogen metabolism of strawberry (*Fragaria ×ananassa* cv. Selva). Int J Agric Biol. 6(6):994–997.

Taghavi T, Fortin J-P, Hughes BR, Zandstra J, Dale A, Wright B. 2017. Developing substrate culture strategies for the production of day-neutral strawberries. Acta Hortic. 1156:277–282. https://doi.org/10.17660/ActaHortic.2017.1156.42.

Takeda F, Newell M. 2007. Effects of runner tip size and plugging date on fall flowering in short-day strawberry (*Fragaria ×ananassa* Duch.) cultivars. Int J Fruit Sci. 6(4):103–117. https://doi.org/10.1300/J492v06n04_10.

Tehranifar A, Poostchi M, Arooei H, Nematti H. 2007. Effects of seven substrates on qualitative and quantitative characteristics of three strawberry cultivars under soilless culture. Acta Hortic. 761:485–488. https://doi.org/10.17660/ActaHortic.2007.761.67.

US Department of Agriculture, National Agricultural Statistics Service. 2023. Noncitrus fruits and nuts 2022 summary. https://downloads.usda.library.cornell.edu/usdaesmis/files/zs25x846c/zk51wx21m/k356bk214/ncit0523.pdf. [accessed 14 May 2024].

Xu X, Hernández R. 2020. The effect of light intensity on vegetative propagation efficacy, growth, and morphology of "Albion" strawberry plants in a precision indoor propagation system. Appl Sci. 10(3):1044. https://doi.org/10.3390/app10031044.

Yamazaki K. 1982. Soilless culture (in Japanese). Hakuyu Press, Tokyo, Japan.