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RESEARCH REPORT

Evaluating the effect of temperature and light during cold storage of strawberry transplants and runner tips

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Abstract

The objective of this study was to characterize the effect of temperature and light during cold-storage (CS) of 'Albion' strawberry transplants and runner tips, aiming to identify conditions that would minimize negative effects on quality, growth, and productivity. In the first experiment, transplants with two crown diameters (small≤10 mm or large>10 mm) propagated indoors under either 24 or 16 h·d^{-1} were placed in three CS temperatures under darkness or provided with 5 µmol·m^{-2}·s^{-1}. For transplants propagated under 24 h·d^{-1}, low, medium, or high CS temperature ranges included −2.6 to -0.8 °C, 0.3 to 3.0 °C, or 3.3 to 8.9 °C, respectively, whereas transplants propagated under 16 h·d^{-1} were exposed to -2.2 to 0.0 °C, 0.2 to 3.0 °C, or 3.1 to 6.6 °C, respectively. Overall, transplant quality decreased after 30 d of CS, particularly at low temperatures. Petiole elongation occurred during CS, but this negative response was most pronounced at higher temperatures. In general, there were few growth differences in response to temperature or light during CS, but as expected, transplants with large crowns had higher shoot and root dry mass (DM). Decreases in root DM were measured in transplants propagated under 24 h·d^{-1} following CS exposure. However, those propagated under 16 h·d^{-1} maintained growth comparable to plants that were never exposed to CS. After a carryover finishing phase, growth differences in response to CS temperature, light, and crown diameter were minimal, but transplants with large crowns propagated under 16 h·d^{-1} produced a greater fruit yield than those with small crowns. In the second experiment, unrooted runner tips were placed in CS for 30 d under darkness at -1.5, 2.0, or 4.7 °C. Quality decreased across all temperature treatments, regardless of crown diameter, but was particularly low under −1.5 °C. Despite this, growth of runner tips was generally maintained during CS, as indicated by the absence of temperature response differences in petiole length, leaf area, and shoot DM, and by a lack of differences in these variables with plants that were never exposed to CS. Nonetheless, runner tips showed signs of stress during the finishing phase, suggesting that additional research is needed to optimize propagation strategies following exposure to CS. Overall, our results suggest that although quality was negatively affected immediately after CS, most of the treatments evaluated in this study are suitable for storing strawberry transplants and runner tips for 30 d. Therefore, conditions for CS should be optimized for cost efficiency, which may be achieved by maintaining temperatures near or slightly above the base temperature of strawberry, or by providing darkness. Additionally, our results suggest that using runner tips with larger crowns may provide benefits during post-storage establishment, as they generally produced more growth than those started from small crowns.

Keywords Crown diameter · Dim light · Indoor farming · Indoor propagation · Plant quality

1 Introduction

Open-field strawberry (*Fragaria* × *ananassa*) nurseries enable large-scale production of bare-root plants that are commonly used as propagative material. However, these plants are often susceptible to soil-borne pathogens that greatly reduce yield in the final production environment (Baggio et al. 2021). Controlled-environment (CE) systems can enable year-round production of high-quality and

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disease-free strawberry runner tips, also known as "daughter plants", which are harvested from stock plants grown in specialized systems (Xu and Hernández 2020). Strawberry transplants, sometimes referred to as "plug plants", are propagated from runner tips (Lizalo and Demirsoy 2020). Transplants can also be produced in CEs where various environmental conditions can be adjusted to optimize specific plant processes that help improve yield for field, greenhouse, or indoor production (Durón and Gómez 2025; Hidaka et al. 2014; Samtani et al. 2019). Transplants are gaining popularity among strawberry growers as they provide several production advantages compared to bare-root plants, including earlier harvest dates, higher fruit yield, and a lower risk for soil-borne disease spread (Durner et al. 2002; Duralija et al. 2006; Lieten 2002; Torres-Quezada 2020).

In the United States (US), the typical demand for strawberry propagative material is large and highly seasonal, usually dictated by narrow field-production windows that typically start in late fall to early winter [primarily in California (CA) and Florida (FL)], or in spring to early summer [(in northern regions and the Pacific Northwest)] (Samtani et al. 2019). Open-field nurseries have the capacity to produce the large number of bare-root plants typically required each season. In contrast, CEs are often space-constrained and thus, may be unable to meet the large, seasonal demand required by strawberry growers at time of transplanting. Nonetheless, CEs enable year-round production, so transplants and runner tips could be stored to build up large quantities of propagative material until demand for field planting starts, similar to the approach used for grafted vegetable transplants (Spalholz and Kubota 2017).

Cold storage (CS) is an effective method to preserve quality of propagative plant material while optimizing production scheduling for field or greenhouse planting (Kubota et al. 1997). Storing plants slightly below their base temperature helps delay senescence by slowing down metabolic processes such as photosynthesis, respiration, and ethylene production (Kubota 2003; Rudnicki et al. 1991). Although CS is commonly used for bare-root strawberry plants, few studies have evaluated its effects on transplants (Gamardella et al. 2006; Karhu 2009; Musacchi et al. 2014) and runner tips (Durner et al. 2002; Hokanson et al. 2004). In general, results have shown that strawberry transplants can be stored at lower temperatures (e.g., -2 °C for up to 7 mo) than runner tips (e.g., 1 °C for up to 3 mo), likely due to their greater carbohydrate reserves, which mitigate dehydration and stress during CS (Zencirkiran 2010). Most studies have used temperatures at or below freezing but, to our knowledge, no research has evaluated the potential of storing transplants and runner tips at temperatures slightly above the base temperature of strawberry (~3 °C) (Nestby et al. 2012). This approach could reduce energy costs during CS and allow the use of conventional refrigeration systems rather than specialized low-temperature storage equipment (Brosnan and Sun 2001).

Low-intensity light has also been shown to help preserve plant quality during storage by minimizing chlorophyll degradation and depletion of carbohydrate reserves (Noichinda et al. 2007; Toledo et al. 2003; Woltering et al. 2016). Studies have shown that the optimum light intensity for storing transplants is close to the light compensation point of photosynthesis, which under CS conditions may range from 2 to 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Kozai 2002; Kubota and Kozai 1994; Kubota et al. 1997; Sato and Okada 2014).

The objective of this study was to characterize the effects of temperature and light during CS of strawberry transplants and runner tips, aiming to identify conditions that would minimize negative effects on plant quality and subsequent growth and productivity. Another factor of interest was the effect of crown diameter during CS, as larger crowns are widely known to help increase fruit yield (Bish et al. 2002; Fagherazzi et al. 2021; Takeda and Newell 2007; Torres-Quezada et al. 2015). Evaluating the potential to use runner tips of different sizes could elucidate ways to maximize productivity when propagating strawberry plants in CEs, given that stolons produce runner tips with various crown diameters (Xu and Hernández 2020).

2 Materials and methods

2.1 Experiment 1 — CS of transplants

2.1.1 Plant material and pre-experimental conditions

Two separate experiments were conducted, which differed in the photoperiod used during the propagation phase, prior to exposing transplants to the CS treatments. A photoperiod of 24 $h \cdot d^{-1}$ was used in the first experiment (from here forward referred to as "24 $h \cdot d^{-1}$"), as continuous lighting is commonly used in commercial indoor propagation systems to maximize daily light integral (DLI) while using low photosynthetic photon flux density (PPFD) values that minimize stress (M.Verdel and I. Tchakarov, pers. comm.; Duron and Gómez 2025). A photoperiod of 16 $h \cdot d^{-1}$ was used in the second experiment (from here forward referred to as "16 $h \cdot d^{-1}$") to determine if a shorter daylength and a lower DLI would be suitable for propagating strawberry transplants indoors.

'Albion' runner tips were harvested from stock plants grown in a glass-glazed greenhouse in West Lafayette, IN, USA (lat. 40°N). Runner tips propagated under 24 $h \cdot d^{-1}$ were harvested on 3 August and 27 September 2023,

whereas those propagated under 16 h·d^{-1} were harvested on 13 December 2023 and 20 March 2024. For each experimental run, runner tips pruned to two trifoliate leaves were separated into groups of small (≤10 mm) and large (>10 mm) crown diameters, which were immediately transplanted into industry-standard 42-cell propagation trays (88.7 mL individual cell volume) cut into 2×2 partial trays and filled with horticulture-grade substrate (Berger BM2 Seed Germination; Berger, Saint-Modeste, QC, CA) composed of 70% fine peatmoss, 15% perlite, and 15% vermiculite (v/v). Propagation took place in a multi-shelf unit placed in an air-conditioned growth room set at 22 °C. The unit had three vertical compartments (119.4-cm long × 177.8-cm tall × 60.5-cm wide) with broadband white light-emitting diode (LED) fixtures (RAZRx Modular Array; Fluence Bioengineering, Austin, TX; USA) with peak wavelengths of 450 and 660 nm, which provided a PPFD of 150 µmol·m^{-2}·s^{-1}, resulting in DLIs of 13.0 mol·m^{-2}·d^{-1} for plants propagated under 24 h·d^{-1} and 8.6 mol·m^{-2}·d^{-1} for those propagated under 16 h·d^{-1}. Trays were initially covered with vented humidity domes and hand misted with reverse osmosis (RO) water [0.01±0.01 dS·m^{-1} electrical conductivity (EC)] twice daily to maintain relative humidity (RH) at ~90%. After 10 d, domes were removed to reduce RH and encourage root growth. The propagation phase ended 28 d after transplanting, after which transplants were sprayed with fungicide (Luna® Sensation; Northwest Crop Protection, LLC., Priest River, ID, USA) at a rate of 170 mg·L^{-1} as a preventive measure against botrytis (*Botrytis cinerea*).

2.1.2 Treatments

Before starting each experiment, destructive data were collected from five random trays with transplants of each crown diameter as described subsequently, which were used as non-treated control plants that were never exposed to CS. Each experiment was replicated two times and divided in two phases, a CS phase where temperature and light treatments were imposed to transplants of two crown diameters, followed by a finishing phase in a greenhouse to evaluate carryover treatment effects (Fig. 1). For the CS phase, two compact freezers (42.5 cm depth × 45.3 cm width × 84.5 cm height) (RCA RFR322; Lotus International Co., Canton, MI, USA) and one incubator (78.7 cm depth × 86.4 cm width × 195.6 cm height) (Model 815; Thermo Fisher Scientific Inc., USA) were used as individual CS compartments set at -3.0, 4.0, or 2.0 °C, which also served as experimental blocks, each separated in two sections with a black corrugated cardboard sheet (20 cm width × 84.5 cm height) to provide different light treatments. One section was kept under darkness and the other had a single dimmable broadband white LED fixture (Hapfish LED; Amazon, Inc., USA), which provided a PPFD of 5 µmol·m^{-2}·s^{-1} for 24 h·d^{-1}, delivering a DLI of 0.4 mol·m^{-2}·d^{-1}. Four clear plastic bags with transplants were placed inside each light-treatment section of a CS compartment, two for each crown diameter. Each 1.3-L bag was regarded as an experimental unit, which had a single 2×2 partial tray and a datalogger (Elitech RC-51 H USB; Elitech Technology, Inc., San Jose, CA, USA) that recorded temperature and RH at 60-min intervals. Temperature treatments were categorized into three groups after noting that separating each CS compartment to accommodate the two light treatments created large temperature variability across the different experimental units (bags). For transplants propagated under 24 h·d^{-1}, CS temperature ranges in each group included −2.6 to -0.8 °C (low), 0.3 to 3.0 °C (medium), or 3.3 to 8.9 °C (high), whereas transplants propagated under 16 h·d^{-1} were exposed to CS temperature ranges of -2.2 to 0.0 °C (low), 0.2 to 3.0 °C (medium), or 3.1 to 6.6 °C (high). For each replication over time, there were between six and eight experimental units in each temperature group. The CS phase lasted 30 d and no irrigation was provided during this time.

Immediately after the CS phase, trays were removed from the plastic bags, and two randomly selected transplants per tray were destructively harvested as described subsequently.

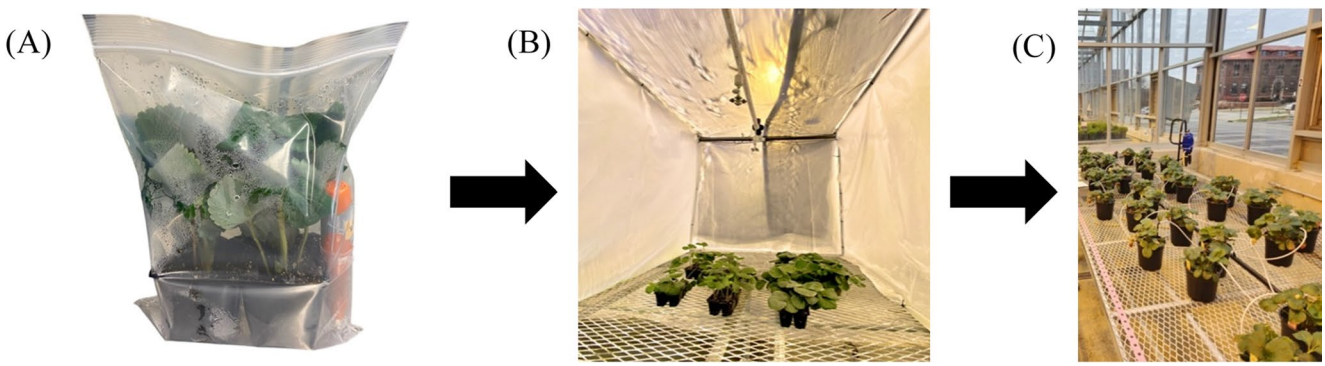

Fig. 1 Phases for Experiment 1. (**A**) Transplants in plastic bags were exposed to low, medium, or high cold-storage (CS) temperatures under darkness or 5 µmol·m^{-2}·s^{-1}. (**B**) Transplants were misted for 48 h to facilitate acclimation to post-CS conditions. (**C**) After transplanting, plants were grown for 8 weeks under greenhouse conditions

The remaining two transplants per tray were transferred to a glass-glazed greenhouse and placed under a mist compartment for 48 h to facilitate acclimation to post-CS conditions before transplanting for the finishing phase. Mist was provided with tap water for 10 s every 30 min during the day (0600 to 2100 h) and every 4 h at night, controlled by a timer (MistTime Controlled; Dramm Corporation, Manitowoc, WI, USA). After 48 h, plants were individually transplanted into 12.7-cm-diameter containers filled with horticulture-grade substrate (Berger BM7 all-purpose mix; Berger, Saint-Modeste, QC, Canada) composed of 50% coarse peatmoss, 35% pine bark, and 15% perlite (v/v). During the finishing phase, plants were randomly kept on a metallic mesh bench (2.4 m wide × 9.8 m long) inside a greenhouse compartment that had retractable shade curtains, pad-and-fan evaporative cooling, and mechanical heating controlled by an environmental control system (Maximizer Precision 10; Priva Computers, Vineland Station, ON, CA). RH was measured with a datalogger (HOBO UX100-023, Onset Computer Corporation, Bourne, MA, USA), and temperature and DLI were measured with probes (107 Temperature Probe; Campbell Scientific, Inc., Logan, UT, USA) and quantum sensors (SQ-500-SS; Apogee Instruments, Inc., Logan, UT, USA), respectively, placed in the center of the bench and interfaced to a datalogger (CR1000; Campbell Scientific) that recorded data at 60 min intervals. Supplemental lighting was delivered by 1000-W high-pressure sodium lamps (P.L. Light Systems Inc., Beamsville, Ontario, CA) used for 16 $h \cdot d^{-1}$ (0500 to 1900 h), providing a PPFD of ~150 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Plants were grown for 8 weeks and irrigated as needed with a two-part water-soluble fertilizer (8 N-4.36P-21.58 K plus 15 N-0P-0 K; Jack's Nutrients, JR Peters Inc., Allentown, PA, USA) that provided 77 $mg \cdot L^{-1}$ nitrogen. Average daily temperature, RH, and DLI (±SD) measured in the greenhouse during the two replications for transplants propagated under 24 $h \cdot d^{-1}$ were 24.8±9.7 °C, 67.2±12%, and 15.3±3.7 $mol \cdot m^{-2} \cdot d^{-1}$, whereas for those propagated under 16 $h \cdot d^{-1}$ were 24.3±4.5 °C, 70.5±8%, and 12.6±3.4 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

2.1.3 Data collected

Before starting each experiment and prior to each final destructive harvest after the CS phase, transplant quality was measured using a subjective visual scale, where 4 = most leaves were dark, green with a healthy appearance; 3 = most leaves had slight chlorosis or discoloration; 2 = most leaves had chlorosis or browning and signs of water-soaked tissues; and 1 = most leaves showed necrosis and severe water-soaked tissues. Chlorophyll concentration was subsequently measured to provide an indication of leaf greenness. Data were measured on a random leaflet of a young, fully expanded leaf from each transplant using a chlorophyll meter (MC-100; Apogee Instruments). Petiole length was measured with a ruler from the substrate surface to the base on the longest leaf. Changes from these three variables were assessed by comparing their means before and after CS, whereas destructive variables were compared against control plants, as previously described.

Shoots of transplants that were destructively harvested at the end of the CS phase were cut at the base of the substrate surface. Leaf number per transplant was then counted and total leaf area was measured with a leaf area meter (LI-3100 C; LI-COR Biosciences). Shoots were separated from roots and, after the substrate was carefully washed off, root tissues were oven-dried for 72 h at 70 °C and shoot and root DM (DM) were subsequently determined.

For each experimental replication, plants in the finishing phase were first harvested approximately 4 weeks after transplanting. Fruit were then harvested twice weekly and the number and fresh mass (FM) of mature fruit were recorded each time. After each final harvest, plants were destructively harvested, and chlorophyll concentration, leaf number, total leaf area, and shoot DM were measured following the procedures previously described. Unlike the CS phase, where control plants were used to compare data with transplants that had been exposed to CS, no control was used in the finishing phase.

2.2 Experiment 2 — CS of runner tips

2.2.1 Plant material and pre-experimental conditions

Stolons of 'Albion' were shipped from a supplier in Raleigh, NC, USA (36° N latitude). Runner tips were cut from stolons, pruned to two trifoliate leaves, and separated into groups of small (≤10 mm) and large (>10 mm) crown diameters. Before starting the experiment, runner tips were hydrated by submerging 1 cm of their base in RO water for 1 h. Runner tips were then dipped in fungicide following the procedures previously described.

2.2.2 Treatments

Before starting the experiment, destructive data were collected on six random runner tips of each crown diameter as described subsequently, which were used as non-treated control plants that were never exposed to CS. The experiment was replicated three times and consisted of two phases, a 30-d CS phase where temperature treatments were imposed to runner tips of two crown diameters, followed by a finishing phase to evaluate carryover treatment effects during propagation (Fig. 2). The same CS compartments as per Experiment 1 were used. However, runner tips were kept in

complete darkness, which eliminated the need to separate compartments and thus, resulted in more uniform temperature treatments. This enabled low, medium, or high temperature treatments to be set and maintained at -1.5±0.1, 2.0±0.3, or 4.7±0.2 °C, respectively. Each CS compartment held four 1.3-L plastic bags with eight individual runner tips, two per crown diameter. Each bag was regarded as an experimental unit and had a datalogger (Elitech RC-51 H USB; Elitech Technology, Inc.) that recorded temperature and RH at 60-min intervals.

Following the CS phase, a sub-group of four runner tips per bag were destructively harvested. The remaining four runner tips were propagated for 28 d under 24 h·d^{-1} following the procedures described for Experiment 1, with the exception that PPFD was set to 75 µmol·m^{-2}·s^{-1} for 24 h to facilitate acclimation to post-CS conditions, and subsequently increased to 150 µmol·m^{-2}·s^{-1} for the rest of the finishing phase.

2.2.3 Data collected

As per Experiment 1, plant quality, chlorophyll concentration, and petiole length were measured on each runner tip before and after CS. Subsequently, leaf area and shoot DM were measured at the end of the CS phase and compared against control plants, as previously described. Chlorophyll concentration, leaf number, leaf area, length of the longest root, and shoot and root DM were measured at the end of the finishing phase.

2.3 Experimental design and statistical analyses

During the CS phase, all experiments used a randomized complete block design where CS compartments were regarded as blocks. In Experiment 1, data from the CS phase were analyzed as a three-way factorial, where light, temperature, and crown diameter were evaluated as factors. No statistical comparisons were made between experiments because they were conducted separately. However, points of discussion comparing trends in the two experiments were made to facilitate discussion. In Experiment 2, data from the CS phase were analyzed as a two-way factorial, where temperature and crown diameter were evaluated as factors. For all experiments, data were pooled among replications over time as the variances among experiments were not different and the statistical interactions among treatments and replications were not significant ($P \geq 0.05$). During the finishing phase, all experiments used a completely randomized design where each individual plant (Experiment 1) or tray with four transplants (Experiment 2) were regarded as an experimental unit. Effects of the categorical independent variables and their interactions on continuous dependent variables were analyzed using a general mixed model analysis of variance (ANOVA). Because interactions were not significant in most cases (Tables 1 and 4), data are only presented for main effect treatment means. When main factors were significant ($P \leq 0.05$), means were compared using Tukey's honestly significant difference (HSD) test ($P \leq 0.05$) or a student's t-test ($P \leq 0.05$). A Dunnett's test was used in both experiments to compare responses to control transplants or runner tips, which were not exposed to CS ($P \leq 0.05$). All data were analyzed using statistical software (RStudio 2023.06.1 524, © 2009–2020; Posit Software PBC, Boston, MA, USA).

3 Results and discussion

3.1 Experiment 1

3.1.1 CS phase with transplants

Only a few differences were measured in response to temperature, light, or crown diameter, regardless of the photoperiod used during propagation (Table 1). Transplant quality generally decreased during CS and was particularly affected by temperature, with the lowest quality measured under low

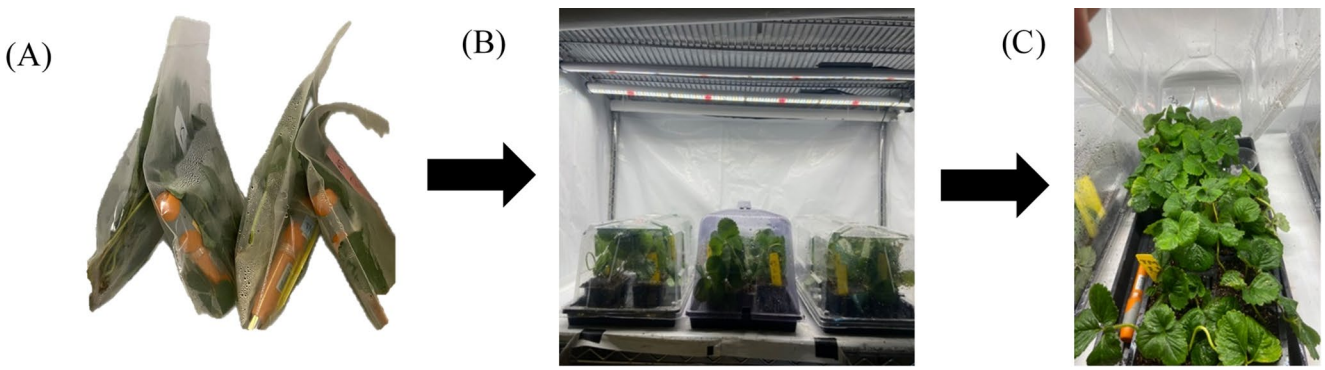

Fig. 2 Phases for Experiment 2. (**A**) Runner tips in plastic bags were exposed to -1.5±0.1, 2.0±0.3, or 4.7±0.2 °C and placed under darkness. (**B**) Runner tips were transplanted intro propagation trays and immediately placed under 75 µmol·m^{-2}·s^{-1} of broadband white light for 24 h to facilitate acclimation to post-CS conditions. (**C**) Transplants were propagated for 28 d under 24 h·d^{-1} at 150 µmol·m^{-2}·s^{-1}

Table 1 Significance level for variables used to measure quality and growth responses of strawberry transplants after 4 weeks of cold storage in Experiment 1

	Quality	Chl. Conc.[i]	Petiole length	Leaf area	Shoot DM[ii]	Root DM
Propagated under 24 h·d^{-1}						
Temperature (T)	*	NS	NS	NS	NS	NS
Light (L)	NS	NS	*	NS	NS	NS
Crown diameter (CD)	NS	NS	NS	NS	*	*
T × L	NS	NS	NS	NS	NS	NS
T × CD	*	NS	*	NS	NS	NS
L × CD	NS	NS	NS	NS	NS	NS
T × L × CD	NS	NS	NS	NS	NS	NS
Propagated under 16 h·d^{-1}						
T	***	**	*	NS	NS	NS
L	NS	*	NS	NS	NS	*
CD	NS	NS	NS	NS	*	*
T × L	NS	NS	NS	NS	NS	NS
T × CD	NS	NS	NS	NS	NS	NS
L × CD	NS	NS	NS	NS	NS	NS
T × L × CD	NS	NS	NS	NS	NS	NS

[i] Chl. Conc. = Chlorophyll concentration; [ii] DM = dry mass

NS, *, **, and *** indicate nonsignificant or significance level at $P \leq 0.05$, 0.01, or 0.001, respectively

temperatures (Table 2). Our results are consistent with those of Gamardella et al. (2006) and Karhu (2009) who reported a decrease in quality of strawberry transplants stored at -2.0 or -1.5 °C, respectively. Their findings were attributed to fungal activity and reductions in starch content, both of which are known to negatively affect plant quality during CS (Lieten et al. 1995). Low CS temperatures have also been shown to increase tissue yellowing and desiccation, negatively affecting quality and subsequent performance of various plants in their final production environment (Heins et al. 1992; Jiang et al. 2012; Kubota and Kozai 1994).

Although there were no treatment effects in chlorophyll concentration in transplants propagated under 24 h·d^{-1} (Table 1), when compared to measurements made before starting the experiment, chlorophyll concentration increased at low temperatures but decreased at high temperatures (Table 2). The increase in chlorophyll concentration at low temperatures was unexpected, as others have reported opposite responses in vegetable transplants after CS, which is often attributed to degradation of chlorophyll molecules (Justus and Kubota 2010; Kwack and Chun 2015). It is plausible that the data collected in our study were affected by the fact that leaves of some transplants, particularly those under ≤ -1.5 °C, had necrotic or water-soaked tissues (Fig. 3), which likely altered readings by our chlorophyll meter. Casa et al. (2015) and Levinsh (2023) explained that structural tissue degradation, such as necrosis or excess water accumulation in intercellular spaces, cause chlorophyll meters to overestimate concentrations due to light disruptions through scattering and refraction.

For transplants propagated under 16 h·d^{-1}, chlorophyll concentration was higher when stored at low compared to high temperatures, and when stored under a PPFD of 5 µmol·m^{-2}·s^{-1} compared to darkness (Table 2). In addition, chlorophyll concentration generally increased after CS compared to measurements made before starting the experiment. Similar findings were reported by Wang et al. (2009), who explained that at low CS temperatures, metabolic processes in transplants slow down, helping preserve or sometimes increase chlorophyll concentration. Kubota and Kozai (1994) also showed that low-intensity light during CS helps maintain activity of metabolic processes, which may explain the slightly higher chlorophyll concentration in transplants stored under a PPFD of 5 µmol·m^{-2}·s^{-1}.

Petioles of transplants stored at low temperatures were shorter than those at high temperatures, regardless of the photoperiod used during propagation (Table 2). This suggests that temperatures below freezing may help minimize unwanted elongation during CS, plausibly attributed to changes in metabolic processes that affect cell expansion and division (Chen et al. 2012). In contrast, higher-than-optimal CS temperatures have been shown to induce elongation of plants due to the accumulation of hexose sugars in stems, which increase osmotic pressure and promote cell elongation (Orzechowski et al. 2021; Sato et al. 1999; Wang and Ruan 2013). However, the biggest change in petiole elongation was generally found after CS, as indicated by differences with measurements made before starting the experiment. In addition, petioles of transplants propagated under 24 h·d^{-1} were longer when stored under a PPFD of 5 µmol·m^{-2}·s^{-1} compared to darkness. This is plausibly explained by a shade-avoidance response that may have been triggered under the low PPFD used in this study, promoting elongation (Kozuka et al. 2010). Our findings are

Table 2 Quality and growth responses of strawberry transplants after 4 weeks of cold storage in Experiment 1

	Quality (1–4) [i]		Chl. Conc. (μmol·m^{-2}) [ii]		Petiole length (cm)		Leaf area (cm^2)	Shoot DM (g) [iii]	Root DM (g)
	Before [iv]	After	Before	After	Before	After			
Propagated under 24 h·d^{-1}									
Temperature categories [v]									
Low	3.9	1.6 b * [viii, ix]	29.6	32.0 *	7.1	7.2 b	106.3	1.22	0.33 ↓
Medium	3.8	3.1 a *	28.7	28.1	6.5	7.3 ab *	108.6	1.16	0.35 ↓
High	3.8	3.3 a *	30.4	28.1 *	6.4	8.4 a *	113.9	1.13	0.37 ↓
Light [vi]									
Darkness	3.8	2.7 *	29.7	30.3	6.4	7.4 b *	106.4	1.13	0.35 ↓
5 μmol·m^{-2}·s^{-1}	3.8	2.7 *	29.9	28.5	6.9	7.9 a *	112.8	1.21	0.36 ↓
Crown diameter [vii]									
Small	3.8	2.8 *	28.6	28.7	6.6	7.7 *	108.0	1.04 b	0.31 b ↓
Large	3.8	2.6 *	30.6	30.1	6.8	7.6 *	111.0	1.30 a	0.40 a ↓
Propagated under 16 h·d^{-1}									
Temperature categories									
Low	3.5	1.9 b *	24.8	33.1 a *	7.6	7.4 b	94.1	1.06	0.54
Medium	3.5	3.1 a *	25.1	28.1 ab *	7.6	8.1 b *	107.2	0.98	0.54
High	3.6	3.3 a *	24.5	25.5 b	8.1	9.4 a *	101.7	0.93 ↓ [x]	0.52
Light-use									
Darkness	3.5	2.8 *	24.7	27.9 b *	7.6	8.4 *	98.3	0.97	0.47 b
5 μmol·m^{-2}·s^{-1}	3.6	2.8 *	24.9	30.0 a *	7.9	8.3	103.7	1.01	0.59 a ↑
Crown diameter									
Small	3.6	2.8 *	25.9	29.2 *	7.8	8.4 *	97.9	0.90 b	0.41 b
Large	3.5	2.8 *	23.7	28.7 *	7.7	8.2 *	104.1	1.08 a	0.65 a

[i] Quality; 4 = most leaves were dark, green with a healthy appearance; 3 = most leaves had slight chlorosis or discoloration; 2 = most leaves had chlorosis or browning and signs of water-soaked tissues; and 1 = most leaves showed necrosis and severe water-soaked tissues

[ii] Chl. Conc. = Chlorophyll concentration; [iii] DM = dry mass. [iv] Before = data collected before starting each experiment; After = data collected at the end of the CS phase

[v] For plants propagated under 24 h·d^{-1}, low = -2.6 to -0.8 °C; medium = 0.3 to 3.0 °C; and high = 3.3 to 8.9 °C. For plants propagated under 16 h·d^{-1}, low = -2.2 to 0.0 °C; medium = 0.2 to 3.0 °C; and high = 3.1 to 6.6 °C

[vi] Light was provided for 24 h·d^{-1}

[vii] Small ≤ 10 mm and large > 10 mm

[viii] For each factor, means within column followed by an asterisk (*) are significantly different from those measured before CS based on pairwise comparisons ($P \leq 0.05$)

[ix] For each factor, treatment means within column followed by different letters are significantly different based on Tukey's Honest Significant Difference test ($P \leq 0.05$) or a student's t-test ($P \leq 0.05$); temperature ($n = 8$), light ($n = 12$), and crown diameter ($n = 12$)

[x] For each factor, means within column followed by an arrow indicate a significant increase (↑) or decrease (↓) compared to transplants that were not exposed to CS (control) based on the Dunnett's test ($P \leq 0.05$)

consistent with those of Sato and Okada (2014) and Sato et al. (1999), who found that vegetable transplants became elongated when placed in CS under low PPFD or darkness. As explained by Yamashita et al. (1999), elongation during CS complicates post-storage handling of plants. Forney et al. (2022) showed that exposure to ethylene effectively suppressed elongation of onion (*Allium cepa*) bulbs by inhibiting cell growth and maintaining dormancy during CS, which may be an alternative strategy to evaluate in future CS studies with strawberry.

Root DM decreased after CS in transplants propagated under 24 h·d^{-1}, regardless of temperature, light, or crown diameter (Table 2). Similar losses in biomass during CS were reported by Kozai et al. (1996) and Kubota et al. (1997) for vegetable transplants. The authors attributed the response to plant respiration that tends to occur during CS, which depletes carbohydrate reserves, especially under darkness. Others have shown that this depletion leads to a negative carbon balance that ultimately reduces plant biomass (Duan et al. 2014; Kubota et al. 1997; Wilson et al. 1998). The fact that the response was significant in roots but not in shoots is likely attributed to the higher rate of dark respiration that occurs in roots (Frantz et al. 2004). For transplants propagated under 16 h·d^{-1}, root DM increased after CS under a PPFD of 5 μmol·m^{-2}·s^{-1}. The different results between transplants propagated under the two photoperiods may be explained by the different mechanisms used by plants to manage and store carbohydrates before the

Fig. 3 Strawberry transplants showing water-soaked and necrotic tissues after 30-d of cold storage. The amplified image illustrates translucent appearance and discoloration of water-soaked tissues

experiments started. For example, transplants propagated under 24 $h \cdot d^{-1}$ likely had lower carbohydrate reserves, as starch breakdown is sometimes suppressed under continuous lighting (Zeeman et al. 2010). In contrast, carbohydrates of transplants propagated under a 16 $h \cdot d^{-1}$ were likely more efficiently stored during the dark period (Rees and Morrell 1990), limiting losses in root DM compared to transplants propagated under 24 $h \cdot d^{-1}$.

The only growth difference in response to light was measured in transplants propagated under 16 $h \cdot d^{-1}$, which had 26% more root DM under a PPFD of 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared to darkness (Table 2). This response is plausibly attributed to the higher respiration rate that transplants under darkness likely experienced, which as previously explained, reduces carbohydrate reserves and negatively affects root DM (Duan et al. 2014; Kubota and Kozai 1994). As expected, shoot and root DM were higher in transplants with large compared to small crowns, regardless of the photoperiod used during propagation. As shown by Fridiaa et al. (2016), large crowns have more carbohydrate reserves, which likely limit respiration-related losses of biomass during CS.

3.1.2 Finishing phase

There were no growth effects in response to CS temperature (Table 3), which is consistent with the findings of Justus and Kubota (2010) and Kwack and Chun (2015), who found no differences in growth of vegetable transplants in a carryover phase following CS treatments. The only response to light was measured in transplants propagated under 24 $h \cdot d^{-1}$, which had 25% larger leaves when stored under darkness compared to a PPFD of 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$. This result differs from the general findings of others, which suggest that low-intensity light during CS helps increase post-storage growth of transplants (Kubota 2003; Kubota and Kozai 1994). Sato and Okada (2014) explained that prolonged exposure to light during CS can negatively affect post-storage growth due to decreases in the concentration of Rubisco. This is supported by the findings of Velez-Ramirez et al. (2011), who showed that continuous lighting inhibits the photosynthetic capacity of several plant species. It is also plausible that the increase in leaf area during the finishing phase is a carryover effect from exposure to darkness during CS, which may have induced a shade-avoidance response that caused leaf enlargement. It is widely known that plants under low-light conditions produce larger and thinner leaves as an adaptive strategy to maximize radiation capture (Evans and Poorter 2001).

The only differences in yield were measured in transplants propagated under 16 $h \cdot d^{-1}$, which indicated that larger crowns produced 40% more fruit and 36% more total fruit FM than smaller crowns (Table 3). Our findings are consistent with those of Khalil (2016), who explained that larger crowns have more buds that can differentiate into flowers and fruit than smaller crowns, resulting in higher yields. Other studies have also reported higher fruit yield when propagating strawberry transplants with larger crowns (Bish et al. 2002; Takeda and Newell 2007; Torres-Quezada et al. 2015). For example, Fagherazzi et al. (2021) reported 18% more fruit and 27% higher fruit FM in plants propagated from crowns > 10 mm than those ≤ 10 mm. The lack of yield differences in transplants propagated under 24 $h \cdot d^{-1}$ was surprising, considering that larger crowns had more biomass during CS, and thus, were expected to produce more fruit. However, transplants under some temperatures below freezing (e.g., -1.4, -1.5, -1.9, -2.6 °C) ultimately died during the finishing phase of that experiment (data not shown), suggesting that prolonged exposure to suboptimal CS temperatures will either result in plant death or can severely affect plant recovery and establishment post-storage, regardless of crown diameter. Similar to our findings, Kwack and Chun (2015) reported that cucumber transplants exposed to 9 °C died after only 2 weeks of CS. Others have shown that unfavorable CS conditions can negatively affect post-transplant growth, sometimes attributed to oxidative stresses that disrupt plant recovery and establishment after CS (Foyer and Noctor 2005; Gill and Tuteja 2010; Justus and Kubota 2010).

Considering the general lack of temperature and light effects on fruit yield, our findings suggest that strawberry transplants can be stored at temperatures that can maintain quality at the lowest possible cost, likely close to or slightly above their base temperature of ~3.0 °C (Nestby et al. 2012). Furthermore, storing transplants under darkness is likely the most feasible option, considering that storage

Table 3 Quality and growth responses of post-storage strawberry transplants grown for 8 weeks during a greenhouse finishing phase in Experiment 1

	Chl. Conc. (µmol·m^{-2}) [i]	Leaf area (cm^2)	Shoot DM (g) [ii]	Fruit (no.)	Fruit FM (g) [iii]
Propagated under 24 h·d^{-1}					
Temperature categories [iv]					
Low	13.6	416.0	3.5	3.6	15.6
Medium	19.3	749.0	6.4	4.7	28.3
High	16.8	806.0	6.1	5.7	35.3
Light [v]					
Darkness	17.0	738.0 a [vii]	5.3	4.7	25.5
5 µmol·m^{-2}·s^{-1}	16.1	576.0 b	5.4	4.8	27.2
Crown diameter [vi]					
Small	16.5	588.0	5.5	4.4	26.0
Large	16.7	725.0	5.1	4.9	26.7
Propagated under 16 h·d^{-1}					
Temperature categories					
Low	14.8	643.0	7.2	4.6	26.8
Medium	13.2	744.0	8.1	3.6	27.7
High	13.9	573.0	5.9	2.5	19.5
Light-use					
Darkness	13.5	672.0	7.3	3.4	23.2
5 µmol·m^{-2}·s^{-1}	14.4	634.0	6.9	3.7	26.1
Crown diameter					
Small	14.2	642.0	6.9	2.7 b	19.2 b
Large	13.7	664.0	7.2	4.4 a	30.1 a

[i] Chl. Conc. = chlorophyll concentration; [ii] DM = dry mass; [iii] FM = fresh mass

[iv] For plants propagated under 24 h·d^{-1}, low = -2.6 to -0.8 °C; medium = 0.3 to 3.0 °C; and high = 3.3 to 8.9 °C. For plants propagated under 16 h·d^{-1}, low = -2.2 to 0.0 °C; medium = 0.2 to 3.0 °C; and high = 3.1 to 6.6 °C

[v] Light was provided for 24 h·d^{-1}

[vi] Small ≤ 10 mm and large > 10 mm

[vii] For each factor, treatment means within column followed by different letters are significantly different based on Tukey's Honest Significant Difference test ($P \leq 0.05$) or a student's t-test ($P \leq 0.05$); temperature ($n = 8$), light ($n = 12$), and crown diameter ($n = 12$)

and shipping practices typically involve the use of boxes that block light and tend to limit light exposure during CS (Kubota 2003).

Our study did not compare freshly-propagated transplants with those exposed to CS treatments, which could help growers make informed decisions about the feasibility of using stored plant material. Although transplants in our study produced a yield that was within range of that reported by Duron and Gómez (2025) under similar conditions, research is still needed to confirm that CS conditions will not cause negative effects that may ultimately affect fruit yield.

3.2 Experiment 2

3.2.1 CS phase with runner tips

The only temperature response during CS was measured for quality (Table 4), which was lowest in runner tips stored at -1.5° C, particularly those with small crowns (Table 5). However, based on measurements made before and after the experiment, quality decreased regardless of temperature or crown diameter. Our findings are consistent with those of Serek et al. (1998) and Arteca et al. (1996), who reported similar changes in quality of ornamental cuttings when comparing CS temperature treatments ranging from 10.0 to 1.0 °C. The authors attributed their findings to ethylene-induced senescence, which can accelerate deterioration of vegetative plant material during CS, usually resulting in leaf yellowing and dehydration (Saltveit 1999). Although ethylene concentration was not measured in our study, the

Table 4 Significance level for variables used to measure quality and growth responses of strawberry runner tips after 4 weeks of cold storage in Experiment 2

	Quality	Chl. Conc.[i]	Petiole length	Leaf area	Shoot DM [ii]
Temperature (T)	*	NS	NS	NS	NS
Crown diameter (CD)	NS	*	NS	*	*
T × CD	***	NS	NS	NS	NS

[i] Chl. Conc. = chlorophyll concentration; [ii] DM = dry mass. NS, *, and *** indicate nonsignificant or significance level at $P \leq 0.05$ or 0.001, respectively

Table 5 Quality and growth responses of strawberry runner tips after 4 weeks of cold storage in Experiment 2

	Quality (1–4) [i]		Chl. Conc. (µmol·m⁻²) [ii]		Petiole length (cm)		Leaf area (cm^2)	Shoot DM (g) [iii]
	Before[iv]	After	Before	After	Before	After		
Temperature (°C)								
-1.5	3.2	1.9 b* [vi]	19.1	18.5	10.9	10.8	88.7	0.92
2.0	3.2	2.8 a*	18.6	18.2	10.7	10.5	104.8	0.87
4.7	3.2	2.8 a*	18.3	18.5	11.4	11.2	98.7	0.84
Crown diameter [v]								
Small	3.2	2.4 *	17.8	17.7 b[vii]	10.4	10.3	79.6 b	0.62 b
Large	3.2	2.6 *	19.5	19.1 a	11.6	11.4	115.2 a	1.02 a

[i] Quality; 4 = most leaves were dark, green with a healthy appearance; 3 = most leaves had slight chlorosis or discoloration; 2 = most leaves had chlorosis or browning and signs of water-soaked tissues; and 1 = most leaves showed necrosis and severe water-soaked tissues

[ii] Chl. Conc. = chlorophyll concentration; [iii] DM = dry mass

[iv] Before = data collected before starting each experiment; After = data collected at the end of the CS phase

[v] Small ≤10 mm and large > 10 mm

[vi] For each factor, means within column followed by an asterisk (*) are significantly different from those measured before CS based on pairwise comparisons ($P \leq 0.05$)

[vii] For each factor, treatment means within column followed by different letters are significantly different based on Tukey's Honest Significant Difference test ($P \leq 0.05$) or a student's t-test ($P \leq 0.05$); temperature ($n = 6$) and crown diameter ($n = 9$)

Table 6 Quality and growth responses of post-storage strawberry runner tips propagated for 4 weeks during a finishing phase in Experiment 2

	Chl. Conc. (µmol·m⁻²) [i]	Leaf no.	Leaf area (cm^2)	Shoot DM (g) [ii]	Root length (cm)	Root DM (g)
Temperature (°C)						
-1.5	22.3	5.0	98.1	1.33	9.0	0.55
2.0	25.6	5.4	177.5	1.41	9.9	0.63
4.7	29.9	5.2	124.2	1.68	10.7	0.73
Crown diameter [iii]						
Small	27.4	5.5	112.0	1.36	9.5	0.52 b [iv]
Large	24.6	5.0	155.0	1.59	10.3	0.76 a

[i] Chl. Conc. = Chlorophyll concentration; [ii] DM = dry mass

[iii] Small ≤10 mm and large > 10 mm

[iv] Treatment means followed by different letters are significantly different based on student's t-test ($P \leq 0.05$); temperature ($n = 6$) and crown diameter ($n = 9$)

decreases in quality may have been partly attributed to ethylene-induced senescence. Nonetheless, the temperature ranges evaluated in our study helped maintain growth of runner tips during CS, as indicated by the lack of treatment differences in petiole length, leaf area, and shoot DM, and by the lack of differences in these variables with control plants (data not shown). Hokanson et al. (2004) also reported that at 1.0 °C, shoot DM of strawberry runner tips was maintained during CS. This maintenance in growth is important for successful post-storage establishment of runner tips, as it can affect energy reserves that are required for early growth and development after transplanting.

As expected, runner tips with large crowns had 31% larger leaves and 40% more shoot DM than those with small crowns, which likely contributed to their higher chlorophyll concentration (Table 5). Our findings are consistent with those of Ullah et al. (2024), who found a positive correlation between chlorophyll concentration and shoot DM in strawberry bare-root plants. As previously mentioned, runner tips with larger crowns tend to perform better in the field, as they are more robust and vigorous after transplanting.

3.2.2 Finishing phase

The only significant effect during the finishing phase was measured for root DM, which was 32% higher in runner tips with large compared to small crowns (Table 6). This result is consistent with our findings for leaf area and shoot DM measured immediately after CS (Table 5), which were expected, as other studies have shown that runner tips with larger crowns have more carbohydrate reserves that support higher biomass production (Cocco et al. 2011; Fridiaa et al. 2016). These reserves likely make larger runner tips better suited for CS than those with small crowns.

Although not measured, runner tips showed visible signs of stress after CS, as indicated by tissue reddening, chlorosis, and necrosis that developed during the finishing phase. This stress was likely induced by the PPFD used during

propagation (150 $\mu mol \cdot m^{-2} \cdot s^{-1}$), which may have been excessive for unrooted runner tips that had just been exposed to CS under darkness, and which as previously described, had declined in quality (Table 5). It is plausible that placing runner tips under lower PPFD (75 $\mu mol \cdot m^{-2} \cdot s^{-1}$), immediately following CS could help minimize stress and improve plant quality during propagation. However, Druege (2019) found that low PPFD limit sugar accumulation after transplanting, hindering root formation of ornamental cuttings after CS. Therefore, future studies should evaluate other light conditions that may help minimize stress of runner tips after exposure to CS.

Although we did not compare responses of stored and non-stored runner tips, it is plausible that the quality and rooting of recently-harvested (non-stored) runner tips would be higher than that of those exposed to CS. For example, Hokanson et al. (2004) reported that 16% of runner tips that were exposed to CS for 2 mo failed to develop roots during propagation, compared to approximately 1% of freshly-harvested runner tips. Similar findings were reported by Serek et al. (1998), who showed that freshly harvested runner tips had higher root DM than those placed in CS for 3 d. Based on these findings, future CS studies should compare responses with freshly-harvested runner tips to better assess the effects of storage on quality and rooting of propagative material. Additionally, more studies are needed to optimize CS conditions that minimize losses in quality while enabling rapid post-storage establishment of strawberry runner tips.

4 Conclusion

Exposure to CS treatments negatively affected quality of strawberry transplants and runner tips, particularly at the lowest temperatures. However, after the carryover finishing phases, plant differences were minimal, indicating that most of the treatments evaluated in this study are suitable for storage. Our findings suggest that conditions for CS should be optimized for cost efficiency, which may be achieved by maintaining temperatures near or slightly above the base temperature of strawberry, or by providing darkness. Additionally, using runner tips with larger crowns may provide benefits during post-storage establishment, as they generally produced more growth than those started from small crowns.

Author contributions Lian Durón: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing original draft, Writing - review & editing, Visualization. Celina Gómez: Conceptualization, Methodology, Validation, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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